

AFRICAN PENGUINS AS PREDATORS AND PREY – COPING (OR NOT) WITH CHANGE

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African penguins *Spheniscus demersus* live in the Benguela and western Agulhas ecosystems off southern Africa. Their numbers decreased throughout the 20th century from at least 1.5 million to about 0.18 million adults, although different regional trends were apparent. They feed to a large extent on shoaling epipelagic fish, notably anchovy *Engraulis capensis* and sardine *Sardinops sagax*, and regional trends in the abundance of penguins are associated with trends in the abundance and distribution of these prey fish. Many first-time breeders emigrate from colonies where feeding or other conditions at the time are unfavourable to more favourable breeding localities. This has led to both the extinction and formation of colonies. Food now may limit colonies at relatively small sizes, a fact attributable to industrial fisheries reducing the densities of forage fish. African penguins share their habitat with several other predators, with which they compete for food and breeding space. One of these, the Cape fur seal *Arctocephalus p. pusillus*, increased through the 20th century to 1.5–2 million animals at its close. Reported observations of predation by fur seals on seabirds have increased in recent decades and threaten the continued existence of small colonies of penguins. Stochastic modelling suggests that colonies of 10 000 pairs have a 9% probability of extinction in 100 years, so smaller populations should be regarded as “Vulnerable”. However, in a period of prolonged food scarcity off southern Namibia, the regional population decreased from more than 40 000 pairs in 1956 to about 1 000 pairs in 2000, and many colonies numbering less than 1 000 pairs became extinct. The minimum viable population for African penguins is currently considered to be >40 000 pairs, likely of the order of 50 000 pairs, a figure equivalent to its level in 2000. The chance of survival of the species through the 21st century is tenuous.

There was a large decrease in numbers of African penguins during the 20th century. At South Africa’s Dassen Island (Fig. 1), the number of birds in adult plumage, i.e. those aged about two years or older, was estimated to be 1.45 million in 1910 (Shannon and Crawford 1999), but just 30 000 in the early 1990s (Crawford *et al.* 1995b). At Namibia’s Possession Island, the number of breeding pairs decreased from 23 245 in 1956 to 895 in 1995 (Cordes *et al.* 1999). At Dyer Island off South Africa’s south coast, there were 22 655 breeding pairs in 1979 (Shelton *et al.* 1984), but fewer than 5 000 in 1994 (Crawford *et al.* 1995b). There were similarly large decreases at a number of other localities (Crawford *et al.* 1990). By 1995, breeding had stopped at seven or more localities (Crawford *et al.* 1995c). Although numbers at some colonies increased, and three new colonies were established in the 1980s (Crawford *et al.* 1995a, Whittington *et al.* 1996, Crawford *et al.* 2000b), the increases were insufficient to offset the downward trend. By the early

1990s the number of birds in adult plumage was about 179 000 (Crawford *et al.* 1995b), some 10% of the number in 1910.

Decreases in the numbers of African penguins have been ascribed to many causes. In the early part of the 20th century, the main reasons were excessive harvests of eggs and disturbance and habitat degradation arising from the scraping of guano (Frost *et al.* 1976). In the latter part of the 20th century, at-sea influences, such as oiling and scarcity of food, were believed to be factors driving the ongoing decreases (Crawford *et al.* 1995b). Off southern Africa, extractions of food from the sea by man and Cape fur seals *Arctocephalus p. pusillus* increased markedly through the 20th century (Crawford *et al.* 1992), and there was a large increase in shipping rounding Africa and an increased incidence of oil spills (Adams 1994).

There has frequently been regional coherence in trends of African penguins with, for example, decreases at all breeding localities between Lüderitz, Namibia,

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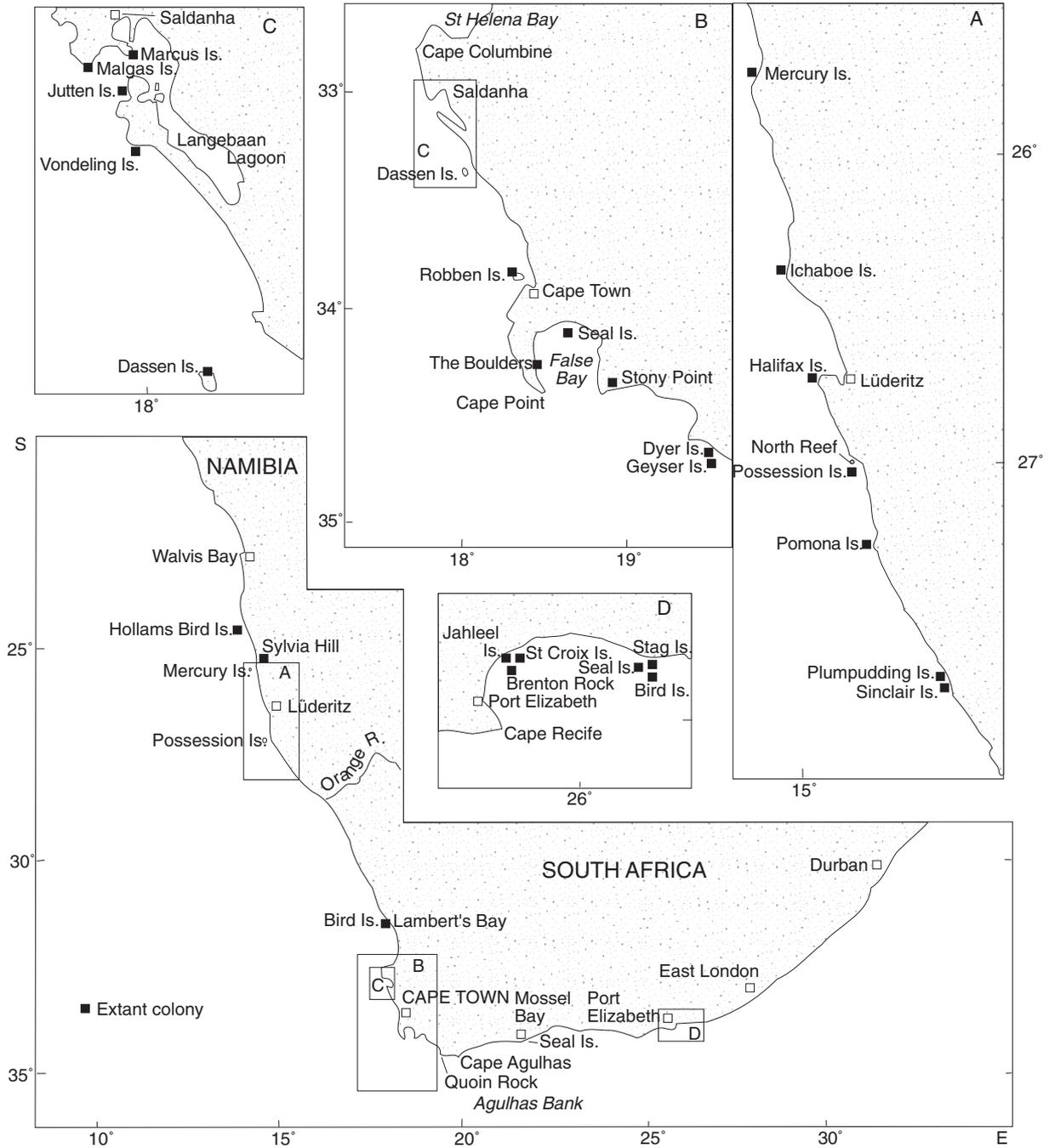


Fig. 1: Locations of extant breeding colonies of African penguins

and Table Bay, South Africa (Crawford *et al.* 1990), or the near-simultaneous establishment of three new colonies in the vicinity of Cape Town (Crawford *et al.* 1995a). Trends at localities have also been persistent (Crawford *et al.* 1990), continuing for periods of up to 30 years (Cordes *et al.* 1999). This has led to the suggestion that they are related to long-term changes in the abundance and distribution of sardine *Sardinops sagax* and anchovy *Engraulis capensis*, the most important food items of penguins off southern Africa (Crawford 1998, 1999). This hypothesis is explored further herein.

Persistent decreases in numbers of penguins have led to breeding populations being very small at several localities. The population of Cape fur seals expanded through the 20th century (Best *et al.* 1997). Towards the end of the 20th century, predation by fur seals on seabirds was regularly observed off southern Africa (Cooper 1974, Rebelo 1984, Crawford and Robinson 1990, Crawford and Cooper 1996, Marks *et al.* 1997).

The aims of this paper are to summarize trends, investigate the consequences of predation for the future viability of small populations of African penguins, and explore the likelihood of populations of African penguins surviving the 21st century. This is done through stochastic modelling to assess probabilities of extinction for colonies of different sizes. Information is presented on the extinction of colonies at Halifax and Possession islands off southern Namibia during the latter part of the 20th century, and the minimum viable population size for African penguins is considered.

MATERIAL AND METHODS

Published data (Rand 1963a, b, Shelton *et al.* 1984, Crawford *et al.* 1995b, Kemper *et al.* 2001) on numbers of pairs of African penguins breeding at different localities were used to ascertain trends, provided counts were undertaken during the main breeding seasons for different regions (Randall and Randall 1981, Crawford *et al.* 1995a, b, Crawford and Whittington 1997). Additionally, counts of penguins on aerial photographs of some Namibian colonies in 1956, 1967 and 1969 (Rand 1963b) were converted to estimate sizes of the breeding populations. For calibration, ratios of counts of penguins from aerial photographs taken in December 1978 to counts of active nests at the respective colonies undertaken in November or December 1978 (Shelton *et al.* 1984) were used. At St Croix Island, there were an estimated 44 781 adult birds during the period

1979–1981 (Randall *et al.* 1986). At Robben Island, the ratio of birds in adult plumage to the number of active nests averaged 3.2 (± 0.52) between 1988 and 1993 (Crawford and Boonstra 1994). This average was used to convert the count of Randall *et al.* (1986) to an estimate of the number of breeding pairs.

Relationships between penguin populations and prey resources were assessed by comparing trends in the breeding populations at localities off Namibia and western South Africa with trends in the biomass of sardine and anchovy in the same regions. The latter are summarized in Schwartzlose *et al.* (1999).

The effect of predation was ascertained by conducting studies at Lambert's Bay. Numbers of fledged chicks, birds in immature plumage and birds in adult plumage that were killed by Cape fur seals between November 1997 and January 2000 were obtained from daily collection and examination of carcasses that had washed ashore at the island. The production of chicks in this period was estimated from counts of the numbers of breeding pairs at Lambert's Bay and the mean number of chicks fledged per breeding pair at Robben Island (0.47 – Crawford *et al.* 1999a). The number of birds produced at Lambert's Bay that attained an age of about one year, i.e. that survived their first eight months at sea, was estimated by assuming that 50% of fledged chicks survived this period (Shannon and Crawford 1999). The number of birds in adult plumage was estimated by multiplying the number of breeding pairs by a factor of 3.2 (Crawford and Boonstra 1994). Losses to fur seals were converted to mortality rates for each of these maturity categories.

A population model for African penguins (Shannon and Crawford 1999) was used to investigate the probability of extinction of colonies of African penguins of different sizes. Parameters were based on measurements made at Robben Island (Crawford *et al.* 1999a), except for survival of birds from fledging until the end of the year in which they were hatched (s_I), which was not estimated. Parameters were assumed to be normally distributed about their mean and were allowed to vary within three standard deviations of the mean, the range that includes 99.6% of the values of a normally distributed parameter. Where the standard deviation was not known, the estimated range for the parameter was assumed to include 99.6% of the values. Parameters were sampled from within these distributions and s_I was estimated such that it would maintain the population in equilibrium. This was repeated to obtain 2 000 sets of parameters that would maintain the population in equilibrium. More details are given in Shannon and Crawford (1999). In each year of the

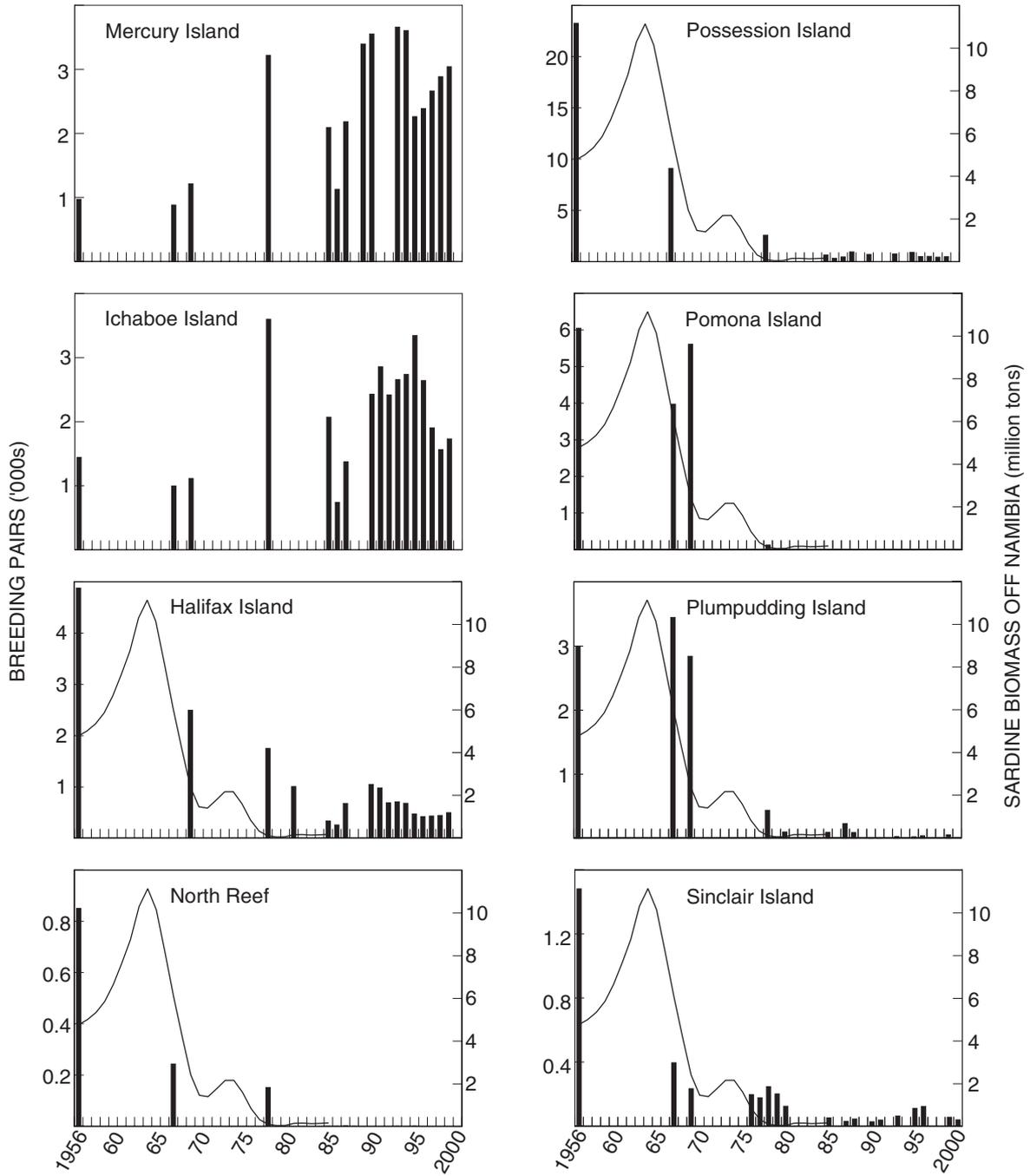


Fig. 2: Trends in breeding populations of African penguins at eight Namibian localities, 1956–2000 (histograms), illustrating how decreases at the six southernmost localities were related to the collapse of sardine off Namibia. Biomass estimates for the Namibian population of sardine (lines) are as summarized in Schwartzlose *et al.* (1999)

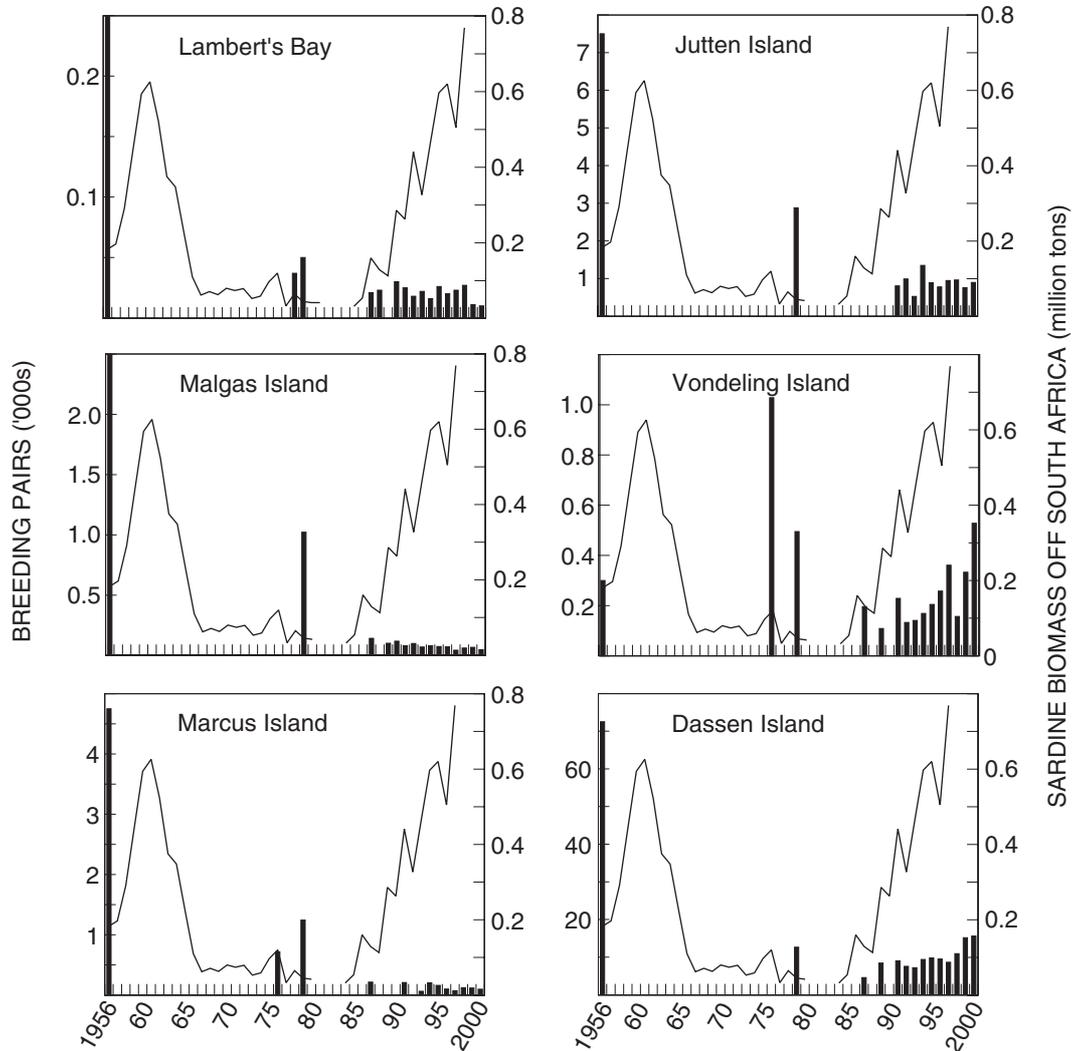


Fig. 3: Trends in breeding populations of African penguins at six South African localities north of Table Bay, 1956–2000 (histograms), illustrating how decreases were related to the collapse of sardine off South Africa. Recoveries at the two southernmost localities appear to have been initiated in response to a recent increase in sardine. Biomass estimates for the South African population of sardine (lines) are as summarized in Schwartzlose *et al.* (1999)

model runs, each parameter was selected at random from values occurring in the 2 000 derived sets of parameters that would maintain the population in equilibrium. For each of 10 different starting populations (10, 50, 100, 250, 500, 1 000, 5 000, 10 000, 50 000 and 100 000 breeding pairs), the model was run 100 times to determine the probability of the population becoming

extinct over timeframes of 50 and 100 years. For one starting population more runs were undertaken, but results indicated that 100 runs were sufficient to estimate the likelihood of extinction.

In 1956, there were several discrete colonies of African penguins at North Reef and Halifax and Possession islands off southern Namibia (Rand 1963b).

Many of these colonies are now extinct (Berry *et al.* 1974, Cordes *et al.* 1999). Information on the fate of those colonies that were in existence in 1956 was used to determine the probability of extinction of colonies of different sizes. Sizes of colonies at North Reef and Possession Island in 1956 are given in Cordes *et al.* (1999). Sizes of colonies at Halifax Island in 1956 were estimated by allocating Rand's (1963b) estimate of the breeding population at the island *pro rata* to the surface area of each colony, which was obtained from planimeter measurements on aerial photographs. At Possession Island, the number of breeding pairs in a colony was significantly related to its surface area (Cordes *et al.* 1999).

RESULTS

Trends at breeding localities

Large decreases in the breeding populations of African penguins at North Reef, Halifax, Possession, Pomona, Plumpudding and Sinclair islands off Namibia between 1956 and 1980 conform with the massive decrease in biomass of Namibian sardine during the same period (Fig. 2). Decreases at North Reef, Halifax, Possession and Sinclair islands were well underway by 1967, whereas at Pomona and Plumpudding islands, most of the decrease came after 1967. The penguin populations at Mercury and Ichaboe islands increased markedly between 1956 and 1978. Both populations decreased in the 1980s and then recovered. In the latter part of the 1990s, the population at Ichaboe Island decreased again.

Similarly, there were large decreases in penguin populations at most localities off western South Africa, to the north of Table Bay, between 1956 and 1980 (Fig. 3). Again these appear related to the decrease of sardine off South Africa. The exception is Vondeling Island, where an increase between 1956 and 1976 was followed by a large subsequent decrease. Since 1990, breeding populations at Dassen and Vondeling islands have increased. This accords with a recent increase in the biomass of sardine off South Africa (Fig. 3).

Trends in penguin populations from Table Bay to Cape Agulhas were substantially different from those at localities farther north. The population at Seal Island, in False Bay, decreased after 1956, but not to the same extent (Fig. 4). The populations at Dyer and Geyser islands both increased markedly between 1956 and 1980, and then decreased rapidly. The decreases correspond with a fluctuating decrease in the biomass of anchovy off South Africa. Three new colonies of

African penguins were established near Cape Town between 1982 and 1985. These populations have all since increased, corresponding with the recent increase in biomass of sardine off South Africa (Fig. 4).

In Algoa Bay, records of population sizes are sporadic, but numbers at St Croix Island appear to have increased considerably since 1956 (Fig. 5). There has also been a large increase in the population at Bird Island since 1980.

Predation by fur seals

At Lambert's Bay in 1999, there were 11 breeding pairs representing some 35 adults. Assuming that pairs fledged 0.47 chicks each, about five chicks would have been fledged, of which half might be expected to survive to the end of their first year (Crawford *et al.* 1999a). Between November 1997 and January 2000, fur seals killed at least two fledglings, nine immature birds and three adults. Observations were conducted during 24 months in this period, so these numbers can be halved to obtain the annual losses. Therefore, fur seals are killing about 20% of chicks fledged at Lambert's Bay, more than the local production of immature birds (some are likely to be birds fledged at other breeding colonies), and 4% of adults annually. In addition to reducing the adult population, recruitment to the breeding population is severely impaired.

Colony extinctions

The stochastic model indicates that isolated colonies of 10 breeding pairs have a 25% likelihood of becoming extinct within 50 years. The probability of extinction decreases as colony size increases, such that the probability of colonies of 1 000 pairs becoming extinct within this time period is just 2% (Fig. 6). Over a period of 100 years, the probabilities of extinction are considerably higher: 37% for a colony of 10 pairs, 25% for a colony of 100 pairs, 17% for a colony of 1 000 pairs and as much as 9% for a colony of 10 000 pairs.

Of 41 discrete colonies at North Reef (1), Halifax (10) and Possession (30) islands in 1956, only eight were extant in 1996. In 1956, sizes of those colonies that survived were 297, 659 and 1 879 pairs at Halifax Island, and 47, 688, 3 138, 5 641 and 7 401 pairs at Possession Island. Only one of 28 colonies that in 1956 had fewer than 250 pairs was extant in 1996. Half of the colonies that in 1956 had between 500 and 1 000 pairs survived, as did 67% of those having between 1 000 and 5 000 pairs and all larger colonies (Fig. 6).

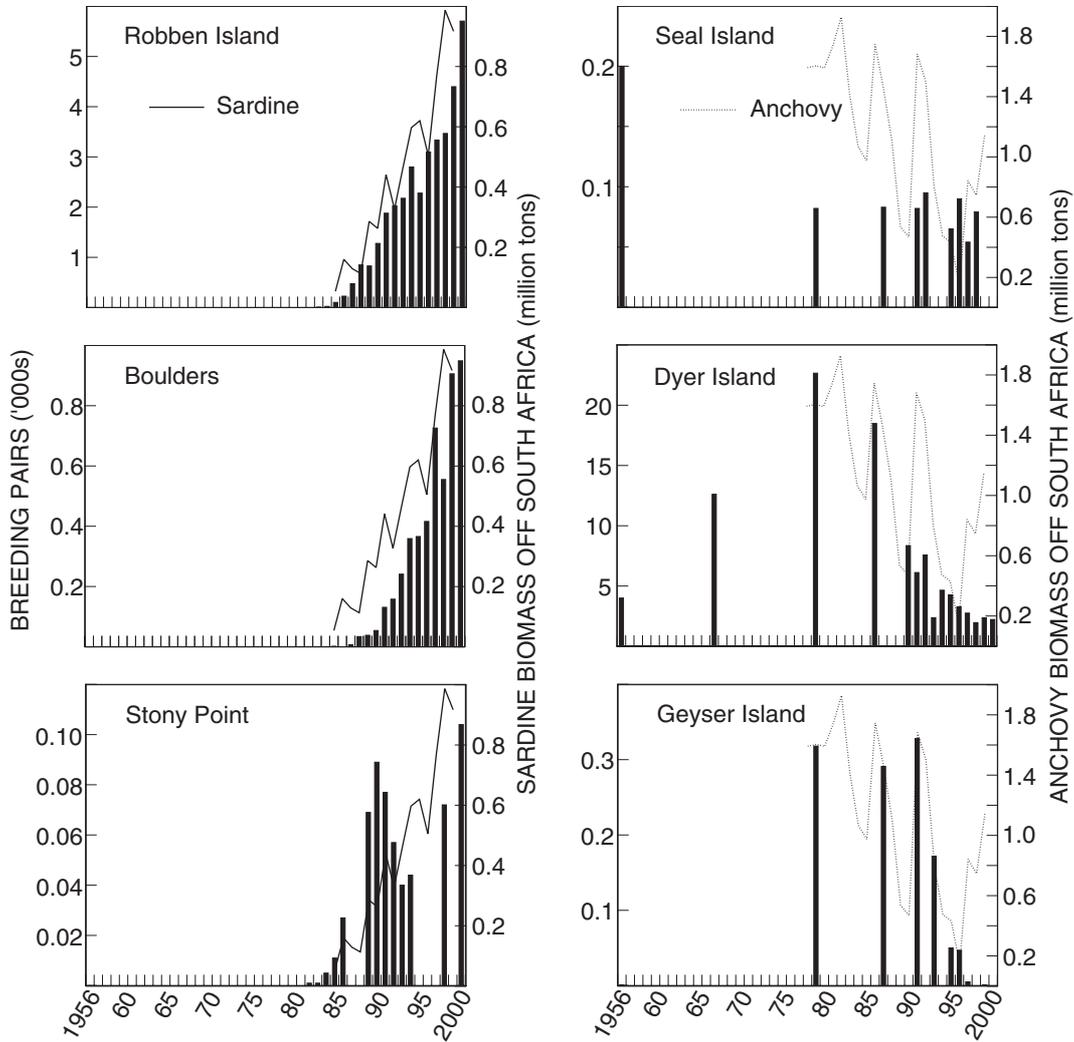


Fig. 4: Trends in breeding populations of African penguins at six South African localities between Table Bay and Cape Agulhas, 1956–2000, illustrating (left) how growth of three newly established populations corresponded with the recent increase of sardine off South Africa and (right) how populations at Dyer and Geysers islands decreased as anchovy decreased. Biomass estimates for the South African populations of sardine and anchovy are as summarized in Schwartzlose *et al.* (1999)

DISCUSSION

Influence of food

The large decreases of penguin populations at all Namibian localities south of Lüderitz have been at-

tributed to a scarcity of food resulting from the collapse of sardine off Namibia (Crawford and Shelton 1981, Crawford *et al.* 1990). As the sardine collapsed, its range contracted northwards. Populations at Mercury and Ichaboe islands, north of Lüderitz, appear not to have been affected by the collapse of the sardine, and may have benefited through immigration of birds

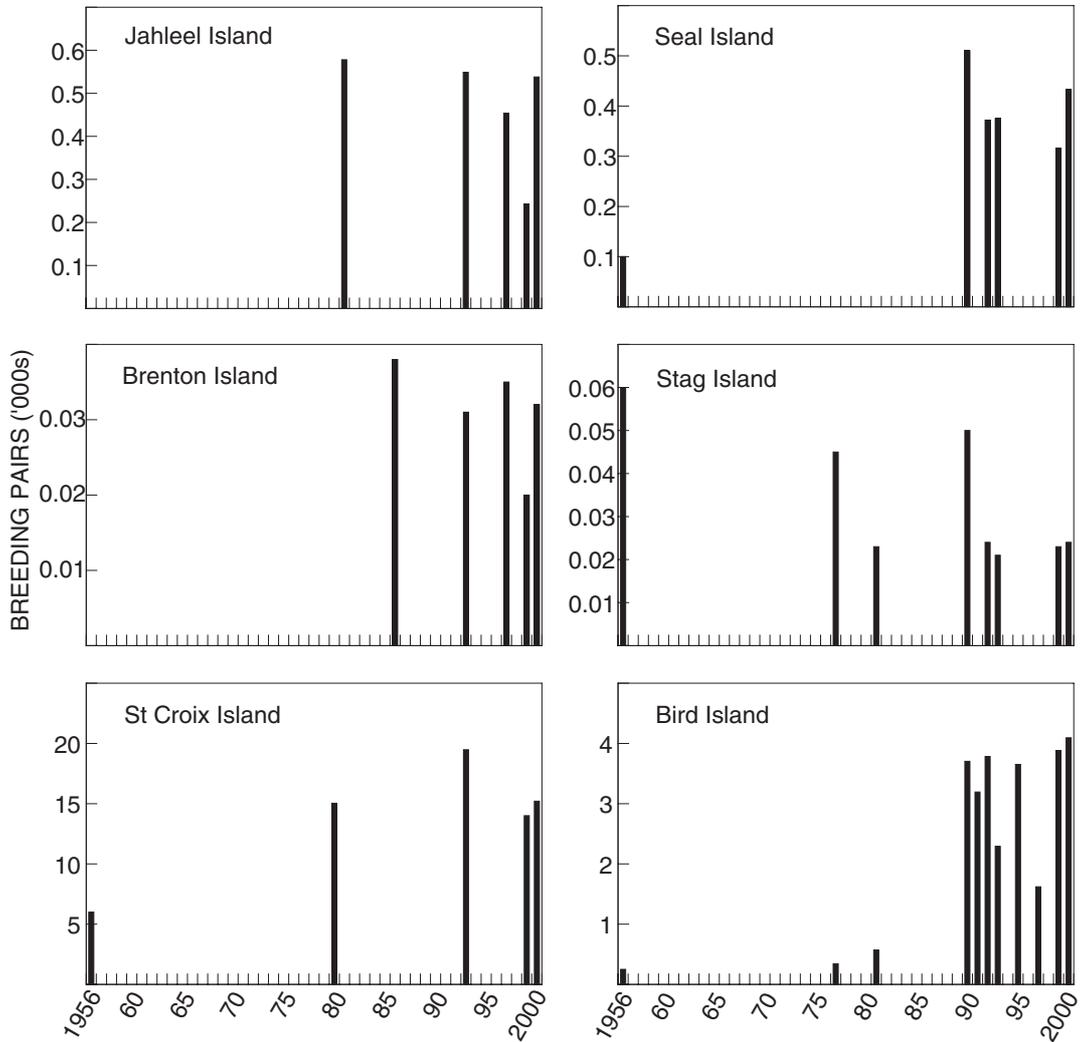


Fig. 5: Trends in breeding populations of African penguins at six South African localities in Algoa Bay, 1956–2000

hatched at colonies farther south. Pelagic goby *Sufflogobius bibarbatus* provided an alternative food for the penguins at these two localities (Crawford *et al.* 1985). Disconcertingly, however, the population at Ichaboe Island has decreased since 1995. In 1994 and 1995, all fish stocks in the region, including pelagic goby, were severely depleted (Sea Fisheries Research Institute 1995, Kemper *et al.* 2001). Subsequently there has also been a substantial decrease in the population of bank cormorants *Phalacrocorax neglectus* at Ichaboe Island, where pelagic goby is their main food (Crawford

et al. 1999b).

The later decreases of the populations at Pomona and Plumpudding islands, compared to those at other localities, are of interest. There may have been migration of birds from Sinclair Island to nearby Plumpudding Island, as a result of displacement of birds from breeding sites at Sinclair Island by fur seals (Shaughnessy 1980, Shelton *et al.* 1984). It is possible that the population at Pomona Island was also maintained for some time by immigration of birds from other localities. Fur seals displaced penguins at Mercury Island in the

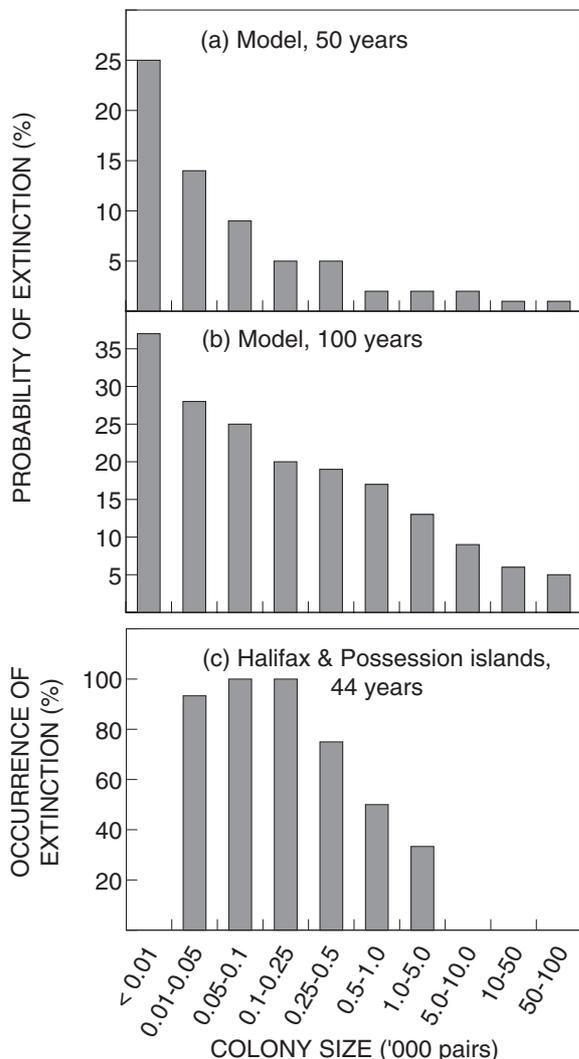


Fig. 6: Model predictions of the probability of extinction of different sizes of colonies of African penguins over time-frames of (a) 50 and (b) 100 years compared with (c) the occurrence of extinctions of colonies at islands off southern Namibia between 1956 and 2000

1980s (Crawford *et al.* 1989), but when fur seals were evicted, the penguin population at the island recovered (Crawford *et al.* 1994).

Off South Africa, to the north of Table Bay, the trend between 1956 and 1980 was similar to that off southern Namibia, with generally large decreases in penguin populations (Fig. 3). These decreases appear to have

been caused by the collapse of the South African sardine stock (Crawford and Shelton 1981, Crawford 1998). Only at Vondeling Island was there an apparent increase between 1956 and 1976, and then a large decrease. This is probably attributable to the 1956 count being an underestimate. Rand (1963a) only counted penguins outside the wall on this island, but substantial numbers of penguins also nest within the wall. In 1956, Vondeling Island had the smallest penguin population of South African breeding localities north of Table Bay (Rand 1963a). Therefore, it is possible that this population was not initially impacted by food scarcity to the same extent as the other localities. Growth of the mainland population at Boulders slowed or reversed in years of reduced abundance of food when it was larger than 366 pairs, but not when it was 54 pairs or less (Crawford *et al.* 2000b). A reduced density of food within the foraging range of colonies can be expected first to limit large populations.

The populations at Dyer and Geysers islands increased while those at localities between Lüderitz and Dassen Island were decreasing (Crawford *et al.* 1990). The increase at Dyer Island was too rapid to have resulted from production at the island (Shelton *et al.* 1984), and it is thought that there was considerable immigration of first-time breeders from colonies to the north. The increase in colony size at Dyer Island coincided with an increased abundance of anchovy off South Africa (Crawford 1998), but after 1980, the colony decreased rapidly in size, as the anchovy stock decreased. As at Possession Island during the 1950s and 1960s (Cordes *et al.* 1999), the rate of decrease was similar to that expected from adult mortality in the absence of recruitment of young breeders to the population (Crawford 1998). The population at Seal Island in False Bay is small. Breeding space is limited by the fur seal population that occupies most of the island (Crawford *et al.* 1989, 1994).

Coincident with the rapid decrease of the Dyer Island colony, from more than 22 500 pairs in 1979 to fewer than 3 000 pairs in 2000, was the formation and rapid expansion of the populations at Stony Point, Robben Island and Boulders, which appear related to the recovery of the South African sardine stock (Fig. 4). Increase of the population at Stony Point was temporarily reversed by the losses of a large number of penguins to leopards *Panthera pardus* in 1986, 1987 and 2000. Other predators continued to restrict growth of that population until 1995 (Crawford *et al.* 1995b, Whittington *et al.* 1996). Growth of the populations at Stony Point, Robben Island and Boulders is largely attributable to immigration of first-time breeders, most of which are from Dyer Island (Whittington *et al.* 1996, Crawford *et al.* 1999a, 2000b).

More recently, the breeding populations at Dassen and Vondeling islands also have increased, despite the loss of several thousand birds at Dassen Island during the *Apollo Sea* oil spill in 1994 (Crawford *et al.* 1997, Underhill *et al.* 1999). It appears that the increases are spreading northwards as the sardine stock recovers.

The influence of fish populations on penguin populations in Algoa Bay is less clear. The population at St Croix Island increased as anchovy increased off South Africa but, unlike at Dyer Island, it has been relatively stable since 1980 (Fig. 5). The population at Bird Island increased as sardine increased off South Africa, but it may also have benefited from the cessation of guano scraping at the island and a resultant substantial decrease in disturbance to the colony.

Predation by fur seals

The mortality inflicted by fur seals on penguins at Lambert's Bay is unsustainable because it prevents recruitment to the breeding population. If the entire adult mortality is attributable to fur seals, the penguin population will cease to exist in 23 years. However, because other factors are likely to contribute to mortality, extinction will probably occur much earlier. If fur seals kill 1.5 adults on average each year, and this is added to "normal" natural mortality of 10% p.a. (Crawford *et al.* 1999a), the population at Lambert's Bay would cease to exist within 11 years, i.e. by 2011.

Over a period of 12 months during 1995/96, fur seals killed 842 African penguins at Dyer Island, i.e. 8.7% of the total population there (Marks *et al.* 1997). As at Lambert's Bay, this is likely to be an unsustainable additional mortality for the population, which numbers fewer than 2 500 pairs (8 000 adults).

In 2000, African penguins were believed to breed at 28 localities (some remote populations may now be extinct), but five of these had ten or fewer pairs and an additional eight had fewer than 100 pairs. Increased predation by fur seals on those populations would drive them rapidly to extinction, and may even jeopardize the long-term survival of populations numbering several thousand pairs.

Colony extinctions and viability

Based on demographic parameters measured at Robben Island, there is a 0.09 (c. 10%) probability of colonies numbering 100 pairs becoming extinct within 50 years. This statement should be weighed against the fact that, at 13 of the 28 localities where African penguins

were breeding in 2000, the populations were smaller than 100 pairs. Over 100 years, a colony of 10 000 pairs had an equivalent probability of extinction. In 2000, only two of the breeding localities had populations larger than this. Therefore, most of the extant African penguin colonies have a reasonable likelihood (10% or more) of becoming extinct in the 21st century. However, given the large-scale emigration of first-time breeders, it may be best to consider regional populations, rather than island colonies, as the population entities.

This situation worsens dramatically if observed extinctions of colonies off southern Namibia are considered. There, almost all colonies of fewer than 250 pairs were extinct within 40 years. In 2000, half the extant breeding localities had smaller populations. Off southern Namibia, six of 11 colonies having between 250 and 5 000 breeding pairs were extinct within 40 years. In 2000, nine (39%) breeding localities had populations within this range. In 2000, only three of the 28 localities had populations in excess of 5 000 pairs.

The Namibian experience is largely attributable to a massive decrease in food available to penguins, following collapse of the Namibian sardine (Crawford and Shelton 1981). At the time sardine was decreasing off Namibia, anchovy was viewed as a competitor and was fished intensively to prevent it from increasing. The result was that sardine was depleted and not replaced by anchovy (Crawford 1999). The remnants of the sardine and anchovy stocks retreated well north of the penguin colonies.

Off South Africa, sardine and anchovy have alternated in relative abundance (Schwartzlose *et al.* 1999). Although this has had major impacts on the regional distribution of penguins, the overall South African population has not decreased to the same extent as that off Namibia (Crawford *et al.* 1995b). Some colonies that decreased dramatically when sardine collapsed off South Africa are now starting to recover as sardine stocks recover and presumably expand again into areas where the species formerly was abundant.

Clearly, if the African penguin is to have a realistic chance of survival through the 21st century, it is necessary to manage forage fish resources so as to avoid extended periods of food shortage. Sporadic years of food scarcity slowed or reversed growth of the penguin population at Boulders when it numbered fewer than 650 breeding pairs, but when food attained adequate levels the population again expanded (Crawford *et al.* 2000b). Conversely, where larger populations competed with commercial fisheries for food in the 1950s and 1960s, severe reductions in penguin populations were recorded within 10 years (Figs 2, 3). It was another 30 years before populations at Dassen and Vondeling

islands began to recover. At localities between Vondeling Island and Lüderitz, there is as yet no sign of recovery in commercial epipelagic fish stocks or penguin populations.

Although small populations of African penguins may not be limited by food, their survival is threatened through predation by fur seals. Such populations contribute only a small fraction of the overall population of African penguins, but it is desirable to maintain as many of them as possible as foci for future growth. The distribution and abundance of food in the Benguela and western Agulhas ecosystems is subject to long-term change (Crawford 1998, Schwartzlose *et al.* 1999). Observations of predation by fur seals on other seabirds, mainly Cape gannets *Morus capensis*, at Malgas Island indicates that most of it is attributable to bulls (Marine & Coastal Management, unpublished records). More research on how such predation can be limited is needed.

Minimum viable population

Determination of a minimum viable population (MVP) for African penguins depends on the risk of extinction one is prepared to accept within a specified timeframe. In terms of IUCN criteria, a species is regarded as Vulnerable if its probability of extinction is $\geq 10\%$ within 100 years (Ellis *et al.* 1988). On the presumption that a status of Vulnerable is not desired, the risk of extinction should be less than this. In terms of the model based on parameters measured at Robben Island, this would require the African penguin population to be maintained above 10 000 breeding pairs. However, off southern Namibia the population decreased from some 40 000 pairs in 1956 to about 1 000 pairs in 2000. In this period, many colonies of $< 1 000$ pairs, and some of $> 1 000$ pairs, became extinct in that region. In such unfavourable conditions, it would be necessary for the population to be more than 40 000 pairs, say 50 000 pairs, to survive for 100 years.

Parameters at Robben Island were estimated during a period of growth of that colony, when conditions were sufficiently favourable to be attracting immigrants (Crawford *et al.* 1999a). However, if the principle of precautionary management were to be applied, a worst-case scenario should be catered for. Therefore, the MVP for African penguins should be regarded as 50 000 pairs. The overall population in 2000 (54 000 pairs) was only marginally higher than this.

The structures of the ecosystems in which African penguins live changed markedly in the 20th century. Adverse interactions between penguins and fur seals,

such as displacement from breeding sites (Crawford *et al.* 1989) and predation, will need to be managed. Additionally, catastrophic events such as large mortalities of birds from oil spills will need to be countered (Underhill *et al.* 1999, Crawford *et al.* 2000a). Given this, and the conservative management of prey resources, the African penguin may survive the 21st century. On the other hand, if there are prolonged periods of food scarcity, as off southern Namibia in the latter part of the 20th century, it may not. In either event, we wish the species well. To conclude with the words of King George VI of Great Britain "The wild life of today is not ours to dispose of as we please. We must account for it to those who come after."

ACKNOWLEDGEMENTS

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