An altered carrying capacity of the Benguela upwelling ecosystem for African penguins (Spheniscus demersus)

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The carrying capacity of an ecosystem for a species is an input parameter that is required for some models that assess population viability. It may be changed by an altered structure or functioning of the ecosystem, e.g. as a consequence of changes brought about by fishing or environmental change. Hence, it cannot necessarily be assumed that the pristine level of abundance of a species reflects the present-day carrying capacity of the ecosystem for that species. Historical and modern information on abundance and density-dependent responses is used to investigate changes in the carrying capacity of the Benguela upwelling ecosystem for African penguins (Spheniscus demersus), a species categorized as vulnerable. The carrying capacity was estimated to decrease from 1.5–3.0 million adult birds in the 1920s to just 10–20% of this value from 1978 to 2006, as a result inter alia of increased competition for food with purse-seine fisheries and fur seals (Arctocephalus pusillus pusillus). From 1988/1989 to 2005/2006, the per capita recruitment of young penguins to a colony where nesting space was not limiting was inversely related to the size of that colony, suggestive of a density-dependent response perhaps related to food availability.

Keywords: African penguin, Arctocephalus pusillus pusillus, Cape fur seal, carrying capacity, density-dependence, fishing, food, recruitment, Spheniscus demersus.

Received 1 November 2006; accepted 12 January 2007; advance access publication 5 March 2007.

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Introduction

The African penguin (Spheniscus demersus) is endemic to the Benguela upwelling ecosystem off southern Africa, which extends from southern Angola in the north to about Nelson Mandela Bay (Algoa Bay) in the east (Crawford et al., 2006b). The species currently breeds at 31 localities between Hollams Bird Island, central Namibia, and Bird Island, Nelson Mandela Bay (Figure 1; Hockey et al., 2005; Underhill et al., 2006). Its usual non-breeding range extends 3200 km around the southern African coast, from 18°S in Namibia to 29°S in KwaZulu-Natal. It occurs as a vagrant north to Sette Cama (2°32′S), Gabon, on the west African coast and to the Limpopo River mouth (25°S), Mozambique, on the east coast (Hockey et al., 2005).

The African penguin is classified as vulnerable, following a large decrease in numbers during the 20th century (BirdLife International, 2004). There were ~570 000 pairs at Dassen Island in 1930 (Shannon and Crawford, 1999). When the first survey of the species at all breeding localities was conducted in 1956, there were ~140 000 breeding pairs in total (Rand, 1963a, b). In 2000, the overall population numbered ~63 000 pairs (Hockey et al., 2005).

In undertaking population viability assessments, individual-based models are frequently used to assess the probability of extinction of species or populations (Miller and Lacy, 2005). Such models often require the carrying capacity to be specified, usually the number of individuals of the species. Determining the carrying capacity is not straightforward. For species with an unfavourable conservation status, there may have been large decreases in the size of populations so that, when the populations are at a low level, density-dependent responses are not readily detected. For example, there may be an abundance of breeding space. Nor, given that there may have been changes to the foodwebs in an ecosystem, can it necessarily be assumed that the size of the pristine population equates to the present-day carrying capacity of the ecosystem.

There were large changes in the structure and functioning of the Benguela ecosystem during the 20th century. Cape fur seals (Arctocephalus pusillus pusillus), which had been exploited to low levels of abundance by the end of the 19th century, increased rapidly in numbers (Butterworth et al., 1995). Commercial fisheries were initiated (Crawford et al., 1987). Between them, seals and the fisheries removed 2 million tonnes more fish and cephalopods from the Benguela ecosystem in the 1980s than they did in the 1930s. In this period, the consumption by seals rose from ~0.1 to 1.0 million tonnes, and the harvest by man from some 0.01 to 1.3 million tonnes (Crawford et al., 1992). The diet of seals and the catch by fisheries overlap considerably with the diet of African penguins (Crawford et al., 1987; David, 1989; Hockey et al., 2005). Here, we explore how the carrying capacity of African penguins by the Benguela upwelling ecosystem may have changed during the 20th century.
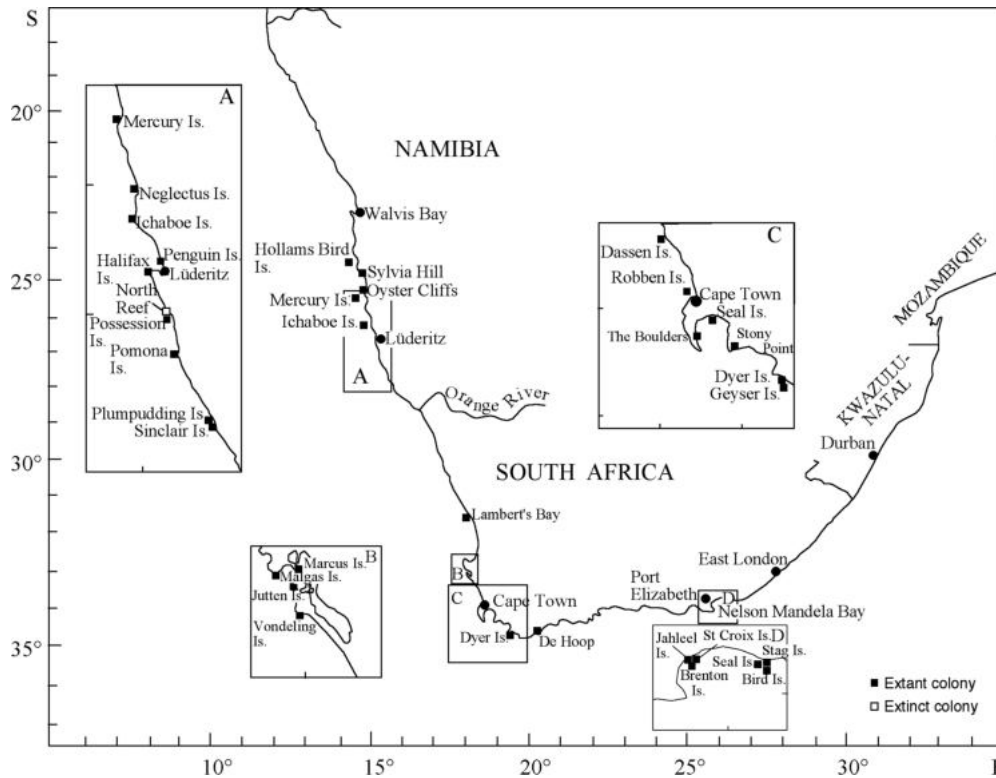
Figure 1. Locations of the 32 breeding colonies of African penguins, which were extant at some stage during the period 1978–2006. The colony at North Reef became extinct about 1988.

Methods

We estimated the number of breeding pairs of African penguins at Dassen Island, off western South Africa, in the period 1921–1931 by multiplying areas occupied by penguins by the densities of nests. We divided the island into three regions, with high and moderate densities of nests or no nests, using information in Kearton (1931) and our own observations of the distribution of penguins at the island made during the years 1988–2006. Kearton (1931, p. 185) first visited Dassen Island in 1921.

Kearton (1931, p. vii) stated "they [penguins] are so numerous that in places one can barely walk between their nesting-burrows, and it is no uncommon thing for two pairs of nesting penguins to find themselves so crowded for space that their burrows run into each other. In the four square miles of the island there are six principal colonies—and each of them contains, at a rough estimate, three-quarters of a million penguins". Kearton (1931, p. 42) provided a sketch of the island showing the approximate locations of the six main colonies at that time. Except for the location of the colony at the centre of the island, they correspond to areas where penguin nests are concentrated today, so we delineated their borders using the current distributions. Subsequent to Kearton's visit, a low wall, completed by about 1942 (unpublished diary of D. B. Price, former inspector of Government Guano Islands, 1942), was built around Dassen Island, ∼100 m from the shoreline, to restrict penguins to the exterior of the island and thereby to facilitate the collection of penguin eggs (Rand, 1963a). The wall remained intact until 1991, when portions of it were removed to permit penguins to move easily to the interior of the island. We gauged the extent of the interior colony, from Kearton's (1931) map and the locations of expanses of flat rock

and areas that are flooded during rains, where penguins could not have nested. Penguins today also nest in high densities in several smaller areas, so we assumed that they also did so between 1921 and 1931.

Kearton (1931, p. 45) stated "Except for the few patches of bare rock, the whole surface of the island is pitted with holes a few feet or less apart—the nesting burrows of penguins; indeed I doubt whether it would be possible, apart from those flat rocks, to find a single patch of thirty square yards that was bare of these nests or burrows. Every spot of earthy ground, every overhanging rock, every spot where tunnelling can be performed, is made use of, and late arrivals who are so unlucky as to find all the best places already occupied have to make what they can of shallow earth where it is possible to make only a slight indentation". We therefore assumed that areas with flat rocks were not used for nesting by penguins, and we delineated such areas using aerial photographs and ground observations. We also assumed that pans that fill with freshwater for a substantial portion of the year were not used. Areas not assigned as high-density or not used were assumed to have moderate densities of nests.

The extents of areas of high and moderate densities of nests were measured on an aerial photograph using an Ibas interactive image-analysis system. The photograph was scaled from ground measurements of straight edges of walls and buildings.

The density of penguin nest sites in November 1988 in areas of high and moderate densities of nests was determined. For each categorization of density, we counted the number of nest sites (both active and inactive) in 15 quadrants measuring 5 m × 5 m. The high-density measurements were made at Boom Point, West Bay, and Whale Bay (Figure 2), each of which was the locality of
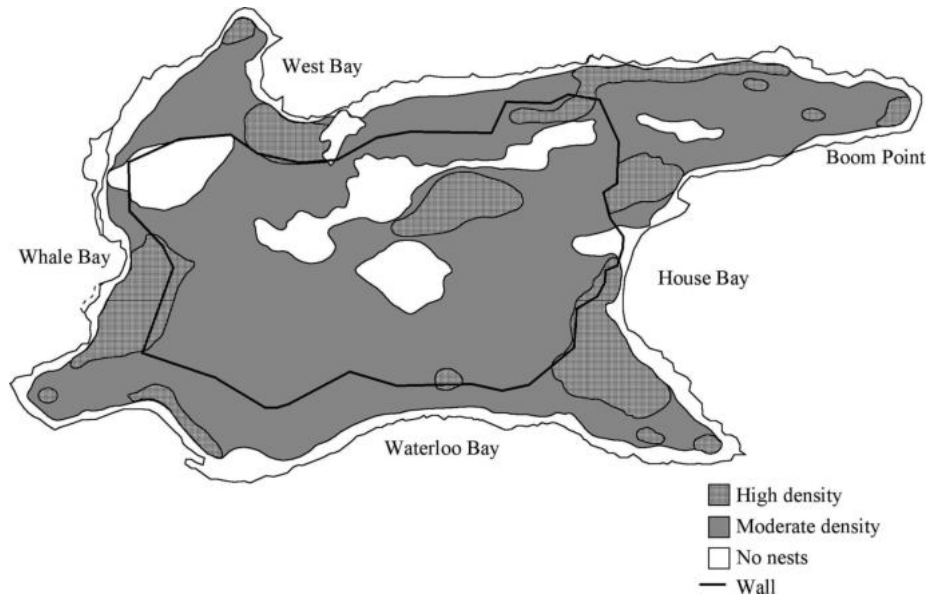
Figure 2. Dassen Island, indicating areas gauged to have high and moderate densities of nests of African penguins during the years 1921–1931, based on observations of Kearton (1931) and of habitat.

one of the main colonies noted by Kearton (1931). We attempted to select those areas having the highest densities of nests. The moderate density measurements were made at Boom Point, House Bay, and Waterloo Bay. We assumed that the mean densities obtained were applicable to the high-density and moderate-density areas of the period 1921–1931.

At Robben Island, off western South Africa, we examined density-dependence in the number of African penguins recruiting to the island. There, we undertook counts of penguins in immature plumage in the feather-shedding phase of moult at approximately two-week intervals between October 1988 and June 2006 (Crawford *et al.*, 2006c). African penguins moult from immature to adult plumage by ∼2 years of age (Randall, 1989). The feather-shedding phase (from the time the first feathers stand out until the last loose feathers fall away) has a mean duration of 12.7 days (s.d. = 1.4 days, $n = 45$; Randall *et al.*, 1986). Counts were interpolated linearly to estimate numbers in moult for each day between actual counts (Underhill and Crawford, 1999). These interpolated counts were summed for the split year 1 July to 30 June, then divided by 12.7 to gauge the number of birds at Robben Island moulting in each split year. At Robben Island, moult is mainly from October to January (Underhill and Crawford, 1999). We took the number of immature birds moulting at the island to be the number of young birds recruiting to the island.

Counts of the number of pairs of penguins breeding at Robben Island were made each year during the main breeding season (February–July) from 1983, when the island was re-colonized (Crawford *et al.*, 1995a), to 2006. The number of immature penguins (I) recruiting to the island in split year $i/(i+1)$ was related to the number of pairs of penguins (P) breeding at the island in year $i-1$, when the immature birds would have fledged, using the model

$$\frac{I}{P} = a \ \log P + b,$$

where a and b are constants.

The overall number of young penguins recruiting to the island, as a function of the number of pairs at the island, was then calculated using the equation

$$I = (a \ \log P + b)P.$$

A colony will decrease when the number of recruits is fewer than the number of breeding adults that die (D), which we estimated as

$$D = 2P(1 - \text{Sa}),$$

where Sa, the annual survival rate of adult birds at Robben Island, was taken to be 0.82 (Crawford *et al.*, 1999; Whittington, 2002). The value of $P > 0$, where $I - D = 0$, was assumed to be the carrying capacity of Robben Island for African penguins during the latter part of the 20th century.

For other colonies of African penguins that were extant between 1978 and 2006, we assumed that the highest count of the number of breeding pairs represented the carrying capacity at that colony during that period. Information was updated from that published by Crawford *et al.* (1995b, 2001), Kemper *et al.* (2001), Hockey *et al.* (2005), and Underhill *et al.* (2006). At each colony that consisted of 1000 pairs or more, a count was conducted in at least 9 years (up to 24) (Table 1). Some small, remote colonies were accessed less often. The overall carrying capacity of the Benguela ecosystem was taken to be the sum of the carrying capacities at the individual colonies.
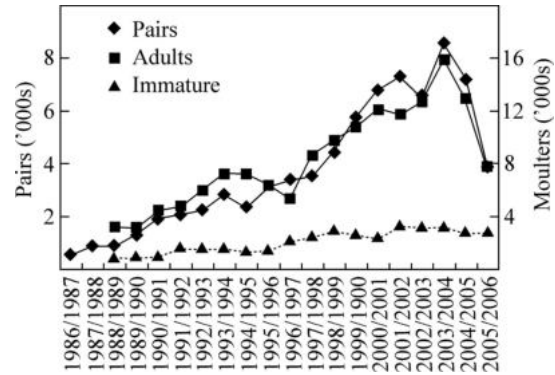
Results

The estimated distribution of breeding African penguins at Dassen Island during the approximate period 1921–1931 is shown in Figure 2. The area occupied by the six main colonies described by Kearton (1931) was estimated to be 31 ha. Elsewhere on the island, it was estimated that penguins bred at high-density in an

Table 1. The maximum counts of breeding pairs of African penguins recorded at the 32 colonies of the species that were extant during the period 1978–2006, indicating the number of years in which counts were made and the year in which the maximum count was recorded. The colony at North Reef became extinct about 1988.

Locality	Number of years in which counts were made	Year of maximum count	Breeding pairs
Hollams Bird Island	1	1988	1
Sylvia Hill	6	2000	45
Oyster Cliffs	1	2002	45
Mercury Island	19	1993	3 666
Neglectus Island	4	2004	11
Ichaboe Island	18	1978	3 598
Penguin Island	1	2006	1
Halifax Island	19	1978	1 750
North Reef	8	1978	151
Possession Island	19	1978	2 568
Pomona Island	10	1978	123
Plumpudding Island	12	1978	438
Sinclair Island	14	1978	246
Lambert's Bay	21	1979	50
Malgas Island	20	1979	1 022
Marcus Island	16	1979	1 243
Jutten Island	17	1979	2 878
Vondeling Island	19	2001	649
Dassen Island	19	2004	24 971
Robben Island	24	2004	8 524
Boulders	21	2005	1 227
Seal Island, False Bay	9	1992	95
Stony Point	18	2006	265
Dyer Island	19	1979	22 655
Geyser Island	10	1991	328
De Hoop	4	2006	18
Jahleel Island	9	1981	578
Brenton Rock	8	1986	38
St Croix Island	9	1993	19 478
Seal Island, Nelson Mandela Bay	9	1990	510
Stag Island	10	1990	50
Bird Island	14	2001	5 376

Figure 3. Trends in the number of African penguins in adult and immature plumage that moulted at Robben Island, 1986/1987–2005/2006, and in the number of breeding pairs in the calendar year that followed the split-year of moult.

densities have been accounted for in calculating the standard deviation.

The number of African penguins breeding at Robben Island increased from nine pairs in 1983 (Crawford *et al.*, 1995a) to 8500 pairs in 2004, before falling to 3700 pairs in 2006 (Figure 3). The numbers of adults moulting at the island peaked at 16000 birds in summer 2003/2004, and the numbers of immature birds peaked at 3000 from 2001/2002 to 2003/2004 (Figure 3).

The number of immature penguins (I) recruiting to Robben Island was related to the number of pairs (P) breeding in the previous season by the expression
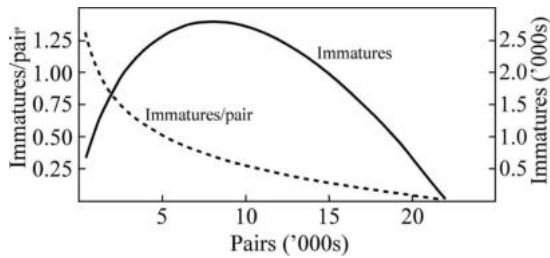
$$\frac{I}{P} = -0.341 \log P + 1.0058.$$

The relationship accounted for 77% of the variation in *per capita* recruitment of immature penguins to the island ($r = 0.877$; $n = 18$; $p < 0.001$; Figure 4). It was estimated that the number of immature birds recruiting to Robben Island would peak when the breeding population was ~8000 pairs (Figure 5). However, once mortality of breeding birds had been accounted for, the estimated carrying capacity for the island was 7700 pairs, ~800 pairs fewer than the maximum number observed to breed at the island.
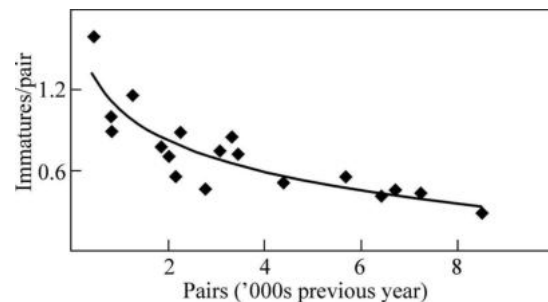
Figure 4. Relationship between *per capita* recruitment of immature African penguins to Robben Island during the seasons 1988/1989–2005/2006 and the number of penguins breeding at the island in the preceding season, when the immature birds would have fledged. Data points and the best-fitting regression line are shown.

additional 5 ha, making a total of 36 ha. It was estimated that penguins bred in moderate densities over 145 ha of island.

In 1988, based on samples of size 15, the mean density of nest sites at Dassen Island was 0.72 nests m^{-2} (s.d. 0.07; range 0.64–0.88) in high-density areas, and 0.46 nests m^{-2} (s.d. 0.11; range 0.20–0.64) in moderate density areas. Using these values, it is estimated that ~259 000 (s.d. 6500) pairs of penguins bred in the high-density areas and some 667 000 (s.d. 41 000) pairs elsewhere on the island. Hence, the estimated overall population at the island was ~926 000 (s.d. 42 000) pairs, where only variations in nesting

Figure 5. Estimated relationships between the number/pair and the overall number of immature African penguins recruiting to Robben Island and the number of pairs breeding at the island. The number of pairs relates to the number breeding in the season of fledging. The greatest number breeding at the island was 8500 pairs. Above this value, recruitment was estimated from the relationship between immatures/pair and breeding pairs.

The maximum counts of breeding penguins recorded at the 32 colonies of the species that were extant during the period 1978–2006 are shown in Table 1—the colony at North Reef is now extinct (Crawford *et al.*, 2001). The largest colonies were about 25 000 pairs at Dassen Island, 23 000 pairs at Dyer Island, and 19 000 pairs at St Croix Island. At no other locality were there 10 000 pairs or more during this period. The sum of the maximum counts amounted to slightly more than 100 000 pairs.

Discussion

At Robben Island during the period 1988–1993, based on counts of active nest sites and moulting birds, on average only 60% of African penguins in adult plumage (termed adults) bred in a given year (Crawford and Boonstra, 1994). Although African penguins moult to adult plumage by an age of some 2 years, they often only commence breeding when ∼4 years old (Randall, 1989; Crawford *et al.*, 1995a, Whittington *et al.*, 2005a). If it is assumed that at Dassen Island only 60% of adult penguins bred, the estimate of 926 000 (s.d. 42 000) pairs for the 1920s suggests a population then of ∼3 million (s.d. 140 000) adults. If space limitation caused a smaller proportion of adults to breed, the population would have been greater than this value. It is possible that nests were at higher densities from 1921 to 1931 than at the close of the 20th century, in which case the population then would also have been underestimated.

Shannon and Crawford (1999) estimated, on the basis of egg harvests at Dassen Island and the exploitation rate that would have resulted in the observed decrease in these harvests, that there were 570 000 pairs and 1.45 million birds aged 2 years or more at the island in 1910. Westphal and Rowan (1971), also based on egg harvests, considered that there were 1.5 million penguins at the island from 1900 to 1930. The estimate derived here is somewhat higher than this, but substantially less than the estimates of 4.5–5 million penguins of Kearton (1931) and nine million penguins by a lighthouse-keeper (Shannon and Crawford, 1999).

Our estimate of the number of penguins at Dassen Island during the period 1921–1931 is particularly dependent on the extent of the area at Dassen Island where penguins were assumed to breed in moderate densities. Kearton (1931) roughly gauged that, outside the six main colonies, there were ∼500 000 penguins. If we add this value to our estimate for the numbers of penguins in high-density areas (863 000 adults), our overall estimate for the island reduces to about 1.4 million adults. If the other

breeding localities of African penguins are also taken into consideration, it seems likely that the Benguela ecosystem in the early part of the 20th century supported some 1.5–3.0 million African penguins in total.

The method used to estimate the carrying capacity for Robben Island assumes that immature birds moulting at the island later breed there. First-breeding kittiwakes *Rissa tridactyla* tend to recruit to the previous year's most productive colonies and emigrate from the least-productive ones (Danchin *et al.*, 1998). For guillemots *Uria aalge*, visiting birds form a substantial proportion of the immature population at a colony (Halley and Harris, 1993). Because most African penguins breed for the first time when aged ∼4 years (Whittington *et al.*, 2005a), immature moulters will have another 2 years to select the locality where they will breed. Of more than 20 000 African penguins banded as chicks between 1978 and 1999, 14% settled to breed at non-natal colonies (Whittington *et al.*, 2005b). However, of those banded off western South Africa and later re-sighted alive, there was no significant directional trend in their movements (Whittington *et al.*, 2005c). This suggests that the number of immature birds moulting at Robben Island was a reasonable index of those recruiting there during the period under consideration.

A regional concordance in trends at African penguin colonies has been observed, colonies increasing in some regions, but decreasing in others (Crawford *et al.*, 2001; Underhill *et al.*, 2006). The emigration of first breeders is a mechanism whereby African penguins cope with an altered distribution of prey (Crawford, 1998). Hence, the summation of maximum counts obtained over the 29-year period 1978–2006 may overestimate the carrying capacity of the Benguela ecosystem. The carrying capacity estimated for Robben Island was about 90% of the maximum number of birds observed breeding there. However, when counts are made there may also be absenteeism of breeders (Randall *et al.*, 1986). Therefore, it is thought likely that the carrying capacity of the Benguela ecosystem is currently of the order of 100 000 pairs or 300 000 birds aged 2 years or more, i.e. some 10–20% of the population in the 1920s. For Dassen Island, the present carrying capacity for penguins may be as low as 5% of that in the 1920s.

In theory, where the maximum sizes of fish are not available to seabirds, exploitation of such fish species may, by increasing production, increase the abundance of smaller fish and hence the availability of prey to seabirds (Furness, 2006). However, in the Benguela ecosystem, penguins are able to eat sardine (*Sardinops sagax*) and the smaller anchovy (*Engraulis encrasicolus*) at their maximum sizes. Sardine of length 21–25 cm were commonly eaten in the 1950s, with one fish of 29 cm being taken (Rand, 1960). These two fish are the main prey of African penguins (Hockey *et al.*, 2005). The introduction of commercial purse-seine fisheries after World War II decreased the overall abundance of sardine and anchovy in the Benguela ecosystem (Crawford *et al.*, 1987). The density of prey around penguin breeding localities will have decreased, lowering the carrying capacity of the ecosystem for penguins. Conversely, in the North Sea, the carrying capacity of the ecosystem for seabirds may have increased. A decreased abundance of predatory fish brought about by fishing may have led to an increase in the abundance of forage fish (Furness, 2002).

The increased population of fur seals will also have reduced the food available to African penguins. At present, other factors, such as oiling of birds and predation by Cape fur seals, through

reducing survival (Crawford *et al.*, 2001; Underhill *et al.*, 2006), are also likely to be influencing the carrying capacity. Although space, and particularly competition with Cape fur seals for space (Shaughnessy, 1980, 1984; Crawford *et al.*, 1989), limits the numbers of African penguins at some smaller colonies, this was not the case at any of the larger colonies during the period 1978–2006. However, it appears that space for nesting may have limited the penguin colony at Dassen Island in the early part of the 20th century (Kearton, 1931).

Cairns (1989) proposed that seabirds from neighbouring colonies typically occupy non-overlapping feeding zones, and that birds recruiting as first breeders choose the colony at which feeding conditions are most favourable. Investigation of isotopes in the blood of Magellanic penguins (*S. magellanicus*) has suggested that high densities of penguins at breeding colonies led to a depletion around colonies of high-quality prey items (Forero *et al.*, 2002). A low density of food may recently have slowed the recruitment of first-breeding African penguins to the colony at Boulders (Petersen *et al.*, 2005). The density-dependent response shown in this paper is further evidence that food in the vicinity of colonies may limit the recruitment of young African penguins.

Adults of several long-lived seabirds, including African penguins (Hockey *et al.*, 2005), once breeding, show strong fidelity to partners and consequently return to the same breeding colonies, even though conditions at those colonies may have changed. For species displaying such life history characteristics, trends in the recruitment of first breeders to colonies present an opportunity to detect density-dependent responses. At colonies of northern gannets (*Morus bassanus*), *per capita* population growth rates decreased with increasing colony size, whereas mean foraging trip duration of breeding gannets was positively correlated with colony size (Lewis *et al.*, 2001). There seemed to be net movement of young birds from big colonies to small ones (Moss *et al.*, 2002). However, for Cape gannets (*M. capensis*) in the Benguela ecosystem, population growth rates are positively related to colony size, suggesting that environmental modulation of food supply is more important than density-dependent effects (Lewis *et al.*, 2006). Trends in colonies of Cape gannets are related to long-term shifts in the distribution of prey species, indicating the potential of environmental change, as well as fishing, to modify the carrying capacity of ecosystems (Crawford *et al.*, 2007). This will especially be the case if it places prey beyond the range of central-place foragers during their breeding season, but will also apply if the distribution of prey is altered such that it influences the condition of a predator at the onset of breeding (Crawford *et al.*, 2006a). An altered distribution of prey, probably influenced by both environmental variability and fishing, led to severe decreases of African penguins in Namibia (Crawford *et al.*, 2001).

Acknowledgements

References

BirdLife International. 2004. Threatened Birds of the World 2004. CD Rom version. BirdLife International, Cambridge, UK.

Butterworth, D. S., Punt, A. E., Oosthuizen, W. H., and Wickens, P. A. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 3. Modelling the dynamics of the Cape fur seal, *Arctocephalus pusillus pusillus*. South African Journal of Marine Science, 16: 161–183.

Cairns, D. K. 1989. The regulation of seabird colony size: a hinterland model. American Naturalist, 134: 141–146.

Crawford, R. J. M. 1998. Responses of African penguins to regime changes of sardine and anchovy in the Benguela system. South African Journal of Marine Science, 19: 355–364.

Crawford, R. J. M., and Boonstra, H. G. V. D. 1994. Counts of moulting and breeding jackass penguins — a comparison at Robben Island, 1988–1993. Marine Ornithology, 22: 213–219.

Crawford, R. J. M., Boonstra, H. G. V. D., Dyer, B. M., and Upfold, L. 1995a. Recolonization of Robben Island by African penguins, 1983–1992. *In* The Penguins: Ecology and Management, 333–363. Ed. P. Dann, I. Norman, and P. Reilly. Surrey Beatty, Chipping Norton, Australia.

Crawford, R. J. M., David, J. H. M., Shannon, L. J., Kemper, J., Klages, N. T. W., Roux, J-P., Underhill, L. G. *et al.* 2001. African penguins as predators and prey — coping (or not) with change. South African Journal of Marine Science, 23: 435–447.

Crawford, R. J. M., David, J. H. M., Williams, A. J., and Dyer, B. M. 1989. Competition for space: recolonising seals displace endangered, endemic seabirds off Namibia. Biological Conservation, 48: 59–72.

Crawford, R. J. M., Dundee, B. L., Dyer, B. M., Klages, N. T. W., Meÿer, M. A., and Upfold, L. 2007. Trends in numbers of Cape gannets (*Morus capensis*), 1956/57–2005/06, with a consideration of the influence of food and other factors. ICES Journal of Marine Science, 64: 169–177.

Crawford, R. J. M., Dyer, B. M., Cooper, J., and Underhill, L. G. 2006a. Breeding numbers and success of *Eudyptes* penguins at Marion Island, and the influence of mass and time of arrival of adults. CCAMLR Science, 13: 175–190.

Crawford, R. J. M., Goya, E., Roux, J-P., and Zavalaga, C. B. 2006b. Comparison of assemblages and some life-history traits of seabirds in the Humboldt and Benguela systems. African Journal of Marine Science, 28: 553–560.

Crawford, R. J. M., Hemming, M., Kemper, J., Klages, N. T. W., Randall, R. M., Underhill, L. G., Venter, A. D. *et al.* 2006c. Molt of the African penguin, *Spheniscus demersus*, in relation to its breeding season and food availability. Acta Zoologica Sinica, 52 (Supplement): 444–447.

Crawford, R. J. M., Shannon, L. J., and Whittington, P. A. 1999. Population dynamics of the African penguin *Spheniscus demersus* at Robben Island, South Africa. Marine Ornithology, 27: 139–147.

Crawford, R. J. M., Shannon, L. V., and Pollock, D. E. 1987. The Benguela ecosystem. 4. The major fish and invertebrate resources. Oceanography and Marine Biology: An Annual Review, 25: 353–505.

Crawford, R. J. M., Underhill, L. G., Raubenheimer, C. M., Dyer, B. M., and Martin, J. 1992. Top predators in the Benguela ecosystem—implications of their trophic position. South African Journal of Marine Science, 12: 675–687.

Crawford, R. J. M., Williams, A. J., Hofmeyr, J. H., Klages, N. T. W., Randall, R. M., Cooper, J., Dyer, B. M. *et al.* 1995b. Trends of African penguin *Spheniscus demersus* populations in the 20th century. South African Journal of Marine Science, 16: 101–118.

Danchin, E., Boulinier, T., and Massot, M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology, 79: 2415–2428.

David, J. H. M. 1989. Seals. *In* Oceans of Life off Southern Africa, 288–302. Ed. by A. I. L. Payne and R. J. M. Crawford. Vlaeberg Publishers, Cape Town. 380 pp.

Forero, M. G., Tella, J. L., Hobson, K. A., Bertellotti, M., and Blanco, G. 2002. Conspecific food competition explains variability in colony size: a test in Magellanic penguins. Ecology, 83: 3466–3475.

Furness, R. W. 2002. Management implications of interactions between fisheries and sandeel-dependent seabirds and seals in the North Sea. ICES Journal of Marine Science, 59: 261–269.

Furness, R. W. 2006. Responses of seabirds to prey depletion. Journal of Ornithology, 147 (Suppl. 1): 14.

Halley, D. J., and Harris, M. P. 1993. Intercolony movement and behaviour of immature guillemots *Uria aalge*. Ibis, 135: 264–270.

Hockey, P. A. R., Dean, W. R. J., and Ryan, P. G. (Eds). 2005. Roberts Birds of Southern Africa, 7th edn. John Voelcker Bird Book Fund, Cape Town.

Kearton, C. 1931. The Island of Penguins. Longmans, Green and Co., London.

Kemper, J., Roux, J-P., Bartlett, P. A., Chesselet, Y. J., James, J. A. C., Jones, R., Wepener, S. *et al.* 2001. Recent population trends of African penguins *Spheniscus demersus* in Namibia. South African Journal of Marine Science, 23: 429–434.

Lewis, S., Grémilet, D., Daunt, F., Ryan, P. G., Crawford, R. J. M., and Wanless, S. 2006. Using behavioural and state variables to identify proximate causes of population change in a seabird. Oecologia, 147: 606–614.

Lewis, S., Sherratt, T. N., Hamer, K. C., and Wanless, S. 2001. Evidence of intra-specific competition for food in a pelagic seabird. Nature, 412: 816–819.

Miller, P. S., and Lacy, R. C. 2005. VORTEX: a Stochastic Simulation of the Extinction Process, Version 9.50. User's Manual. Conservation Breeding Specialist Group (SSC/IUCN), Apple Valley, MN.

Moss, R., Wanless, S., and Harris, M. P. 2002. How small northern gannet colonies grow faster than big ones. Waterbirds, 25: 442–448.

Petersen, S. L., Ryan, P. G., and Gremillet, D. 2005. Is food availability limiting African penguins at Boulders?: a comparison of foraging effort at mainland and island colonies. Ibis, 147: 14–26.

Rand, R. W. 1960. The biology of guano-producing seabirds. The distribution, abundance and feeding habits of the Cape penguin, *Spheniscus demersus*, off the south-western coast of the Cape Province. Investigational Report Division of Fisheries, South Africa, 41. 28 pp.

Rand, R. W. 1963a. The biology of guano-producing seabirds. 4. Composition of colonies on the Cape Islands. Investigational Report Division of Sea Fisheries, South Africa, 43. 32 pp.

Rand, R. W. 1963b. The biology of guano-producing seabirds. 5. Composition of colonies on the South West African islands. Investigational Report Division of Sea Fisheries, South Africa, 46. 26 pp.

Randall, R. M. 1989. Jackass penguins. *In* Oceans of Life off Southern Africa, pp. 244–256. Ed. by A. I. L. Payne and R. J. M. Crawford. Vlaeberg Publishers, Cape Town. 380 pp.

Randall, R. M., Randall, B. M., Cooper, J., and Frost, P. G. H. 1986. A new census method for penguins tested on jackass penguins *Spheniscus demersus*. Ostrich, 57: 211–215.

Shannon, L. J., and Crawford, R. J. M. 1999. Management of the African penguin *Spheniscus demersus*—insights from modelling. Marine Ornithology, 27: 119–128.

Shaughnessy, P. D. 1980. Influence of Cape fur seals on jackass penguin numbers at Sinclair Island. South African Journal of Wildlife Research, 10: 18–21.

Shaughnessy, P. D. 1984. Historical population levels of seals and seabirds on islands off southern Africa, with special reference to Seal Island, False Bay. Investigational Report Sea Fisheries Research Institute, South Africa, 127. 61 pp.

Underhill, L. G., and Crawford, R. J. M. 1999. Season of moult of African penguins at Robben Island, South Africa, and its variation, 1988–1998. South African Journal of Marine Science, 21: 437–441.

Underhill, L. G., Crawford, R. J. M., Wolfaardt, A. C., Whittington, P. A., Dyer, B. M., Leshoro, T. M., Ruthenberg, M. *et al.* 2006. Regionally coherent trends in colonies of African penguins *Spheniscus demersus* in the Western Cape, South Africa, 1987–2005. African Journal of Marine Science, 28: 697–704.

Westphal, A., and Rowan, M. K. 1971. Some observations on the effects of oil pollution on the jackass penguin. Ostrich (Suppl.), 8: 521–526.

Whittington, P. A. 2002. Survival and movements of African penguins, especially after oiling. PhD thesis, University of Cape Town.

Whittington, P. A., Klages, N. T. W., Crawford, R. J. M., Wolfaardt, A. C., and Kemper, J. 2005a. Age at first breeding of the African penguin. Ostrich, 76: 14–20.

Whittington, P. A., Randall, R. M., Crawford, R. J. M., Wolfaardt, A. C., Klages, N. T. W., Randall, B. M., Bartlett, P. A. *et al.* 2005b. Patterns of immigration to and emigration from breeding colonies by African penguins. African Journal of Marine Science, 27: 205–213.

Whittington, P. A., Randall, R. M., Randall, B. M., Wolfaardt, A. C., Crawford, R. J. M., Klages, N. T. W., Bartlett, P. A. *et al.* 2005c. Patterns of movement of the African penguin in South Africa and Namibia. African Journal of Marine Science, 27: 215–229.