Chapter 31

Implications for seabirds of an unfavourable, long-term change in the distribution of prey: a South African experience

Robert JM Crawford[1,2,*], Tracey Fairweather[1], Les G Underhill[2] and Anton C Wolfaardt[2,3]

[1] *Department of Environmental Affairs and Tourism, Marine and Coastal Management, Private Bag X2, Rogge Bay 8012, South Africa*
[2] *Avian Demography Unit, Department of Statistical Sciences, University of Cape Town, Rondebosch 7701, South Africa*
[3] *CapeNature, Private Bag X5014, Stellenbosch 7599, South Africa*
* *Correspondence: e-mail: crawford@deat.gov.za*

From 1997–2005, the distribution of sardine *Sardinops sagax* off South Africa shifted 400 km to the south and east, influencing its availability to breeding seabirds. It became progressively less available to seabirds in the Western Cape Province, where the number of African penguins *Spheniscus demersus* breeding decreased by 45% between 2004 and 2006. The number of penguins in adult plumage that moulted at Robben Island decreased by 62% between 2003/04 and 2006/07, suggesting a maximum annual survival rate in this period of 0.68 compared to 0.82 estimated for the 1990s. Penguins established a new mainland colony in the east of the province in 2003. In the Western Cape Province, the number of Cape gannets *Morus capensis* breeding decreased by 38% between 2001/02 and 2005/06. There was almost complete breeding failure by gannets in 2005/06 and 2006/07. The contribution of sardine to the diet of gannets fell from an average of 40% during 1987–2003 to 5–7% in 2005 and 2006. The proportions of Cape cormorants *Phalacrocorax capensis* and swift terns *Sterna bergii* in the province that bred in the south increased as sardine moved south and east. In the Eastern Cape Province, the number of penguins breeding halved between 2001 and 2003, whereas after 2002 there was an increase in the number of Cape gannets that bred and in the contribution of sardine to their diet. Cape gannets have a greater foraging range than African Penguins when breeding. Management measures that may to some extent mitigate the impacts on seabirds of an unfavourable, long-term change in the distribution of prey include the provision of breeding habitat where prey is abundant, spatial management of fisheries competing for prey and interventions aimed at limiting mortality.

Keywords: African penguin, Cape cormorant, Cape gannet, displacement of food, environmental change, mitigating measures, sardine, seabird, Swift tern

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Introduction

Seabirds when breeding are central-place foragers. They are constrained to return to their colonies to feed young and, if they are successfully to fledge chicks, must source adequate supplies of food within a reasonable distance of their breeding localities. An altered distribution of prey can have a major impact on their breeding success. For example, episodic events such as *El Niños* in the Humboldt ecosystem off Peru and Chile have displaced forage resources away from seabird breeding localities, leading to a greatly reduced reproductive success (Hays 1986, Simeone *et al*. 2002). When oceanographic conditions return to a more normal state, the seabirds again breed successfully (Paredes *et al*. 2002). Seabirds in such unpredictable environments often have a biology that enables the recovery of populations after environmental perturbations. However, if episodic events are of sufficient frequency and severity, long-term population decreases may occur, as with the Galapagos penguin *Spheniscus mendiculus* (Vargas *et al*. in press). In a study of the life-history characteristics of seabirds in two upwelling ecosystems, it was found that those in the Humboldt system, where adverse environmental conditions were frequent, had a biology that enabled them to recover more rapidly than their counterparts in the Benguela system, where such perturbations occur less often (Crawford *et al*. 2006c).

Continuing environmental change, perhaps linked to global climate change, may cause a more permanent displacement of prey, with longer-term, often catastrophic, effects on seabird populations. For example, severe decreases in the populations of rockhopper penguins *Eudyptes chrysocome* at several sub-Antarctic breeding localities have been attributed to an altered distribution of food brought about by a changed environment (Moors 1986, Cunningham and Moors 1994, Guinard *et al*. 1998, Crawford *et al*. 2003). Reproductive output may not only be influenced by a displacement of prey during the breeding season. If seabirds have to travel farther to winter foraging grounds, and consequently return to breeding localities in a poorer condition, the production of fledglings also may be affected. For rockhopper penguins at Marion Island, breeding success was significantly related to the mass of females on arrival for breeding (Crawford *et al*. 2006b). For both rockhopper and macaroni *E. chrysolophus* penguins, over-wintering conditions may influence the proportions of birds breeding (Crawford *et al*. 2006b).

In South Africa, sardine often contributes substantially to the diet of four seabirds: African penguin *S. demersus*, Cape gannet *Morus capensis*, Cape cormorant *Phalacrocorax*

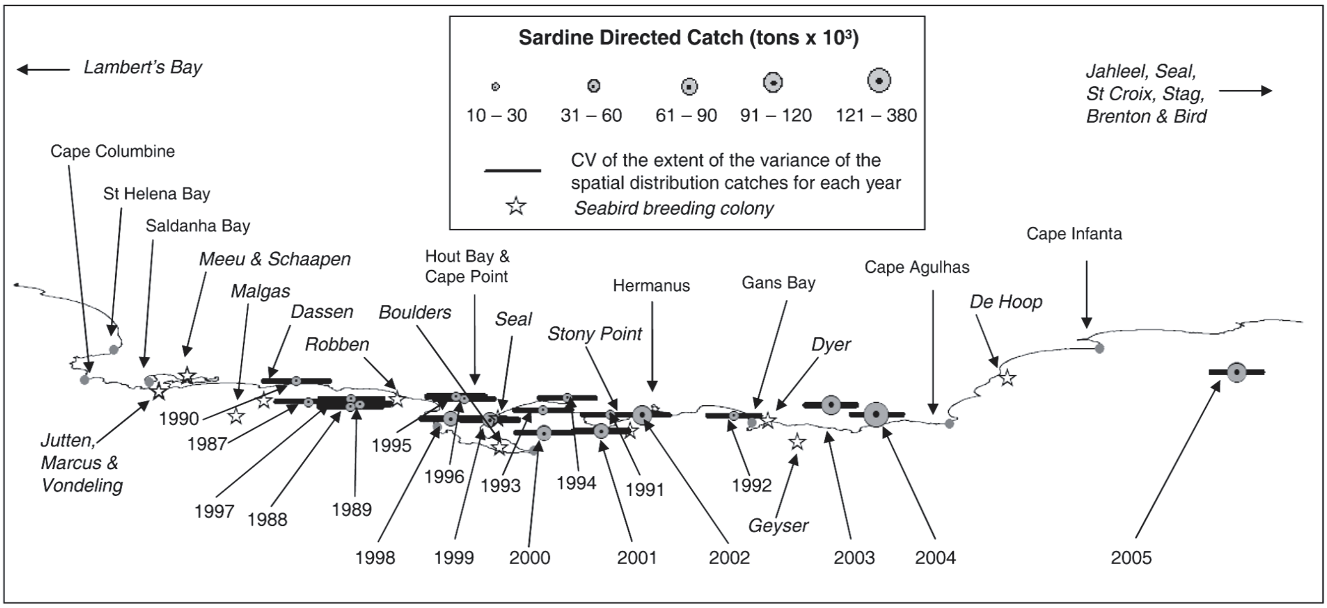


Figure 1: South Africa showing the main breeding localities of seabirds in the Western and Eastern Cape Provinces and the centre of gravity of purse-seine catches of sardine, 1987–2005, from information in Fairweather *et al*. (2006)

capensis and swift (or crested) tern *Sterna bergii* (Hockey *et al*. 2005). Between 1997 and 2005 there was a progressive, large-scale, eastward displacement of catches of sardine *Sardinops sagax* made by the purse-seine fishery off South Africa (Fairweather *et al*. 2006). This has provided the opportunity to examine some consequences for seabirds of an ongoing shift in the distribution of prey, because several parameters of seabirds were monitored over the period of the change. In South Africa, there are two regions where seabird breeding islands are concentrated: the Western Cape Province and Nelson Mandela Bay (formerly Algoa Bay) in the Eastern Cape Province (Fig. 1). These regions are separated by a distance of about 600 km. The centre of gravity of sardine catches coincided with the location of the main seabird breeding colonies in the Western Cape in 1997, but by 2005 had been displaced some 400 km to the south-east placing it between breeding localities in the Western Cape and the Eastern Cape (Figure 1).

The four seabirds also feed on other pelagic shoaling fish, notably anchovy *Engraulis encrasicolus* (Crawford and Dyer 1995), which also affects their population dynamics (e.g. Crawford *et al*. 1992b, 2006a, 2007, Crawford 2003), but we restrict ourselves here to examining the impact of the displacement of sardine for the seabirds. We consider possible means to mitigate the impact for seabirds of an unfavourably altered distribution of prey.

Methods

Longitudinal positions for the centre of gravity of purse-seine catches of sardine off South Africa were available for 1987–2005 (Fairweather *et al*. 2006). These positions were standardized to fall between 1 (the most western point) and 0 (the most eastern point) in order to produce an index of W-E distribution.

Estimates of the number of African penguins, Cape gannets, Cape cormorants (at the six main localities) and swift terns breeding in the Western Cape from 1987/1988 to 2005/2006 were taken from information in Underhill *et al*. (2006, updated by unpublished data held by Marine and Coastal Management), Crawford *et al*. (2007), Crawford and Dyer (1995, updated) and Crawford (2003, updated), respectively. Estimates of the number of African penguins and Cape gannets breeding in the Eastern Cape were taken from Crawford *et al*. (2001, updated) and Crawford (2007), respectively. Most African penguins in South Africa breed from January–September, Cape gannets and Cape cormorants from September–March and swift terns from January–June (Hockey *et al*. 2005). For Cape cormorants and swift terns, the proportion of birds in the Western Cape that bred to the south of Cape Point was calculated. At Robben Island, estimates were also made of the number of African penguins in adult plumage that moulted along the coastline. Counts of penguins in the feather-shedding phase of moult were made at approximately two-week intervals between October 1988 and January 2007. 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). The interpolated counts were summed for the split year 1 July–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).

For the period 2003/04–2006/07, an estimate of the annual mortality rate of penguins in adult plumage was made from the equation:

$$S = (N_{2006/07}/N_{2003/04})^{1/3},$$

where S is the annual survival rate and $N_{t/t+1}$ is the number of adults moulting in split year t/t+1. The estimate is based on two assumptions. The first is that no birds in adult plumage that were at Robben Island in 2003/04 moved to other localities to moult in 2006/07. This is thought to be correct because there were also large decreases in the numbers of birds moulting at Dassen and Dyer islands, the other main breeding localities in the Western Cape (ACW and L. Waller, CapeNature, pers. comm.). Other localities were not checked as often, but none had obviously more moulting birds than usual. The second assumption is that no young adult-plumaged birds recruited to Robben Island between 2003/04 and 2006/07. It is likely that some did, in which case the survival rate will have been overestimated.

The breeding success of Cape gannets was measured at Lambert's Bay from 1991/92–2005/06, except 2001/02, and at Malgas Island from 1987/88–2006/07, using methods described by Staverees *et al*. (in press). The value for Lambert's Bay in 2001/02 was taken to be the mean of those in 2000/01 and 2002/03.

From 1987–2005 at Lambert's Bay and 1987–2006 at Malgas Island, the diet of the Cape gannet was monitored by collecting about 50 regurgitations at each locality in each month, using methods described by Berruti *et al*. (1993). These are the only localities where gannets breed in the Western Cape. For each locality, the percentage contribution by mass of sardine to the diet was calculated for each year, weighting months equally. The mean of the annual contributions at the two localities was used as an index of the contribution of sardine to the diet of Cape gannets in the Western Cape. Cape gannets also breed at Bird Island in the Eastern Cape. From 1987–2006, the diet was monitored at this locality by collecting up to 400 regurgitations annually over several visits (Klages *et al*. 1992, updated).

The relationships between the index of distribution of sardine and continuous time series of seabird parameters were investigated using correlation analysis. Cross correlation was undertaken with "prewhitened residuals" of time series (Box and Jenkins 1970), from which autocorrelation was removed using the software programme EViews (Quantitative Micro Software 2000). The models employed to obtain the prewhitened residuals are shown in Table 1. Cross correlations were made between indices in the same year, except for the number of penguins breeding in the Western Cape and the proportion of swift terns breeding south of Cape Point, which were related to the index of distribution of sardine in the previous year because African penguins and swift terns commence breeding at the start of each calendar year.

Results

The index of the distribution of sardine was more than 0.9 from 1987–1990 and in 1997, indicating a western distribution in these periods. Thereafter, the index decreased rapidly as sardine moved to the east (Fig. 2).

The number of pairs of African penguins breeding in the Western Cape decreased from about 23 000 in 1987 and 1988 to 13 000 in 1993. It then increased to 38 000 in 2004 before falling to 21 000 in 2006 (Fig. 2). The number breeding in the Eastern Cape fluctuated around 20 000 pairs from 1987–2001 and half this value from 2003–2006. The number of penguins in adult plumage that moulted at Robben Island increased from 3 500 in 1988/89 to 17 400 in 2003/04 and then fell to 6 600 in 2006/07. The annual survival rate between 2003/04 and 2006/07 was estimated to be 0.724.

About 60 000 pairs of Cape gannets bred in the Western Cape from 1994/95–2001/02. The number fell to less than 40 000 pairs in 2005/06 (Fig. 2). The number breeding in the Eastern Cape increased from about 60 000 pairs from 1993/95–2001/02 to 90 000 pairs in 2005/06. At Lambert's Bay, from 1991/92–2004/05 Cape gannets fledged on average 0.58 chicks per pair during a breeding season (range 0.15–0.98, s.d. 0.19). In 2005/06, the entire colony abandoned the island and no chicks were fledged (Wolfaardt and Williams 2005). At Malgas Island, from 1991/92–2004/05 Cape gannets fledged on average 0.44 chicks per pair during a breeding season (range 0.19–0.82, s.d. 0.13). This fell to 0.01–0.02 chicks per pair in the 2005/06 and 2006/07 breeding seasons. Sardine contributed 26–61% by mass of the diet of Cape gannets off the Western Cape between 1987 and 2003 (mean 40%, s.d. 12%), but just 18% in 2004 and 5–7% in 2005 and 2006. In the Eastern Cape, sardine contributed 15–58% of the diet from 1989–2002 (mean 46%, s.d. 11%) and 78–97% from 2003–2005 (mean 85%, s.d. 10%).

There were 96 000 pairs of Cape cormorants breeding in the Western Cape in 1988/89 and 90 000 pairs in 1991/92. The number decreased to 15 000–46 000 (mean 30 000, s.d. 8 000) pairs from 1993/94–2006/07. The proportion of birds in the Western Cape that bred at Dyer Island increased from 0.24 in 1988/89 to 0.80 in 2006/07 (Fig. 2).

The number of swift terns breeding in the Western Cape fluctuated from 1 400 to 5 700 pairs between 1987 and 2001. It then increased to 10 000 pairs in 2006. The proportion breeding south of Cape Point was 0.00–0.04 from 1987–1997, but increased to 0.66 in 2006 (Fig. 2).

The results of cross correlation of residuals of pre-whitened time series of the index of sardine distribution and seabird parameters are shown in Table 2. The contribution of sardine to the diet of Cape gannets off the Western Cape was significantly positively related to the index of sardine distribution, and the proportion of swift terns breeding south of Cape Point was significantly negatively related to this index. No other relationship was significant at the 5% level. However, relationships between the index of sardine distribution and numbers of African penguins in adult plumage moulting at Robben Island, and the breeding success of Cape gannets at both Lambert's Bay and Malgas Island, were positively related to the distribution of sardine ($P < 0.1$). Numbers of African penguins breeding in the Western Cape, the contribution of sardine to the diet of Cape gannets in the Eastern Cape and the proportion of Cape cormorants breeding south of Cape Point were negatively, but not significantly, related to the index.

Table 1: Models used to obtain prewhitened residuals of time series that were cross correlated – ar(x) and ma(x) indicate autoregressive and moving average models of order x

Time series	Model
Index of centre of gravity of purse-seine catches	ma(1)
African penguin breeders in the Western Cape (pairs)	ar(1) ma(1)
African penguin adults moulting at Robben Island	ar(1) ma(1)
Cape gannet breeding success at Lambert's Bay (chicks/pair)	ar(1)
Cape gannet breeding success at Malgas Island (chicks/pair)	ar(1)
Contribution of sardine to Cape gannet diet in Western Cape (% mass)	ar(1) ma(1)
Contribution of sardine to Cape gannet diet in Eastern Cape (% mass)	ar(1) ma(1)
Proportion of Cape cormorants in Western Cape breeding south of Cape Point	ar(1) ar(2)
Proportion of swift terns in Western Cape breeding south of Cape Point	ar(1) ar(2)

Figure 2: A comparison of the index of the distribution of sardine off South Africa with:

a) the number of African penguins breeding in the Western Cape ('000 pairs) and the number of penguins in adult plumage moulting at Robben Island ('000s),

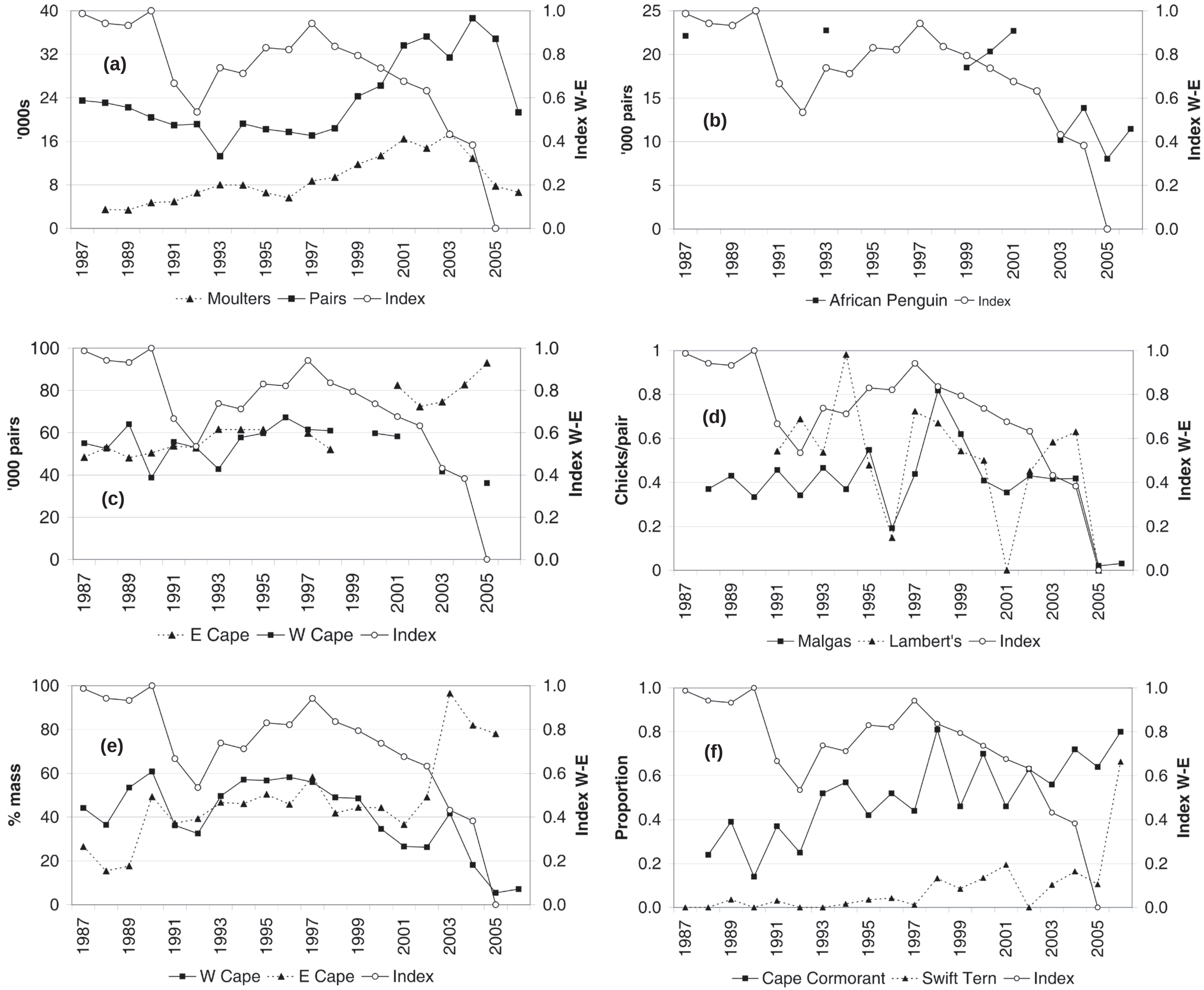
b) the number of African penguins breeding in the Eastern Cape ('000 pairs),

c) the number of Cape gannets breeding in the Western Cape and the Eastern Cape,

d) the breeding success of Cape gannets at Lambert's Bay and Malgas Island (chicks fledged per pair),

e) the contribution of sardine to the diet of Cape gannets in the Western Cape and the Eastern Cape (% mass), and

f) the proportion of Cape cormorants and swift terns in the Western Cape that bred in the south of this province



Discussion

Influence on seabirds of an unfavourably altered distribution of sardine

The availability of a prey resource to seabirds is affected by its distribution and its abundance. In this paper we investigated only the influence of the distribution of sardine for seabirds in South Africa. Over the same period, there were also large changes in the abundance of sardine and anchovy (van der Lingen *et al.* 2005, Fairweather *et al*. 2006), which altered the total amount of food available to the seabirds (Crawford *et al*. 2006a, 2007), but our aim here was to examine the consequences of a long-term change in the distribution of prey.

Our index of the distribution of sardine will not necessarily reflect that portion of the sardine biomass that was available to all seabirds, because seabirds breed at several localities within a region (Fig. 1) and the four species examined have widely different foraging ranges while breeding (Hockey *et al*. 2005). However, one would expect that as sardine shifted to the south and east, this food resource became less available to seabirds breeding in the northern portion of the Western Cape but more available to those breeding in the southern portion of this province (Fig. 1). As the displacement of sardine continued, its availability to seabirds breeding at southern localities in the Western Cape may have decreased, and it may have become increasingly available to seabirds breeding in the Eastern Cape, especially those having longer foraging ranges.

The results of cross-correlation analysis tend to confirm these outcomes. In seven of the eight comparisons, the sign of the correlation coefficient was that which would have been expected, the exception being the weak negative relationship between the number of penguins breeding in the Western Cape and the index of distribution for sardine. In the Western Cape, through much of the period considered there was a high availability of anchovy (Fairweather *et al*. 2006), an important contributor to the diet of African Penguins (Hockey *et al*. 2005). This probably influenced the number of penguins breeding. Although only two of the eight correlations were significant at the 5% level, a further three had a probability of occurrence of less than 10%. The number of African penguins breeding in the Western Cape decreased by 45% between 2004 and 2006, when sardine attained its most eastern distribution for the period for which information is available. A substantial proportion of African penguins may not breed in years of food scarcity (Crawford *et al*. 1999). However, there was also a large decrease in the number of penguins in adult plumage that moulted at Robben Island. The survival rate estimated for the period 2003/04–2006/07 was 0.68, compared with two independent estimates of 0.82 for Robben Island during the 1990s (Crawford *et al*. 1999, Whittington 2002), suggesting an increased mortality rate as the availability of sardine decreased. The number of penguins breeding decreased first at the northernmost colonies in the Western Cape, then at the central colonies, while the southern colony of Dyer Island remained stable from 1998–2006 (Underhill *et al*. 2006, updated). In 2003, a new colony was initiated at De Hoop on the mainland, to the east of all other colonies in the Western Cape (Underhill *et al*. 2006). When not breeding, African penguins often undertake extensive trips that last several weeks (Randall 1989). In 2000, an African penguin tracked from Dassen Island moved east of Cape Agulhas on a feeding trip (Barham *et al*. 2006). It appears that the penguins which established a colony at De Hoop sought to mitigate the effect of the eastward displacement of sardine.

The significant relationship between the index of sardine distribution and its contribution to the diet of gannets suggests that sardine became progressively less available to gannets in the Western Cape. By 2005, it was contributing minimally to the diet of gannets in this province, the number of gannets breeding in the province was decreasing, and the poor breeding success of gannets at both colonies in the province was without known precedent. At Lambert's Bay, in the 2005/06 breeding season Cape fur seals *Arctocephalus pusillus pusillus* initiated a new behaviour of attacking large numbers of gannets at nests. About 200 adult gannets were killed and the entire gannet colony abandoned the island (Wolfaardt and Williams 2005). In the same season, seals also killed about 20 gannets at Malgas Island (Crawford *et al*. 2007). Both the abnormal behaviour of the seals and rapid abandonment of breeding by gannets at Lambert's Bay may have been influenced by a scarcity of food. By contrast, from 2002/03–2005/06 the colony of gannets in the Eastern Cape increased as sardine dominated their diet, suggesting an enhanced availability of sardine to gannets in this province (Crawford *et al*. 2007).

The number of Cape cormorants breeding in the Western Cape decreased in the early 1990s (Crawford and Dyer 1995) following an outbreak of avian cholera *Pasteurella multocida* (Crawford *et al*. 1992a). There were further outbreaks of cholera in the late 1990s and early 2000s (Williams and Ward 2002, Waller and Underhill in press) when the population in the Western Cape fluctuated around a level of about 30 000 pairs. In this period, the proportion of birds that bred in the southern portion of the province increased, despite the loss of some 29 000 birds to cholera during 2002/02–2005/06 (Waller and Underhill in press), possibly reflecting enhanced feeding opportunities in the south as sardine moved south and east.

In the late 1990s and early 2000s, the proportion of swift terns in the Western Cape that bred in the southern portion of the province also increased. It was significantly negatively

Table 2: Results of cross correlation between the index of sardine availability and time series of seabird parameters; Ns indicates not significant. Correlations were for prewhitened residuals of the same year, except for the number of pairs of African penguins breeding in the Western Cape and the proportion of swift terns in the Western Cape breeding south of Cape Point when the residuals for sardine availability in the previous year were used

Seabird parameter	N	R	P
Number of pairs of African penguins breeding in the Western Cape	18	–0.252	Ns
Number of African penguins in adult plumage moulting at Robben Island	17	0.440	< 0.1
Breeding success of Cape gannets at Lambert's Bay	18	0.475	< 0.1
Breeding success of Cape gannets at Malgas Island	17	0.439	< 0.1
Contribution of sardine to the diet of Cape gannets in the Western Cape	14	0.496	< 0.05
Contribution of sardine to the diet of Cape gannets in the Eastern Cape	17	–0.097	Ns
Proportion of Cape cormorants in the Western Cape breeding south of Cape Point	16	–0.347	Ns
Proportion of swift terns in the Western Cape breeding south of Cape Point	18	–0.581	< 0.05

related to the index of sardine distribution, i.e. highest when sardine had an easterly distribution. After breeding, swift terns from the Western Cape disperse eastwards as far as KwaZulu-Natal. Between breeding seasons, many occur over, or to the east of, the Agulhas Bank (Underhill *et al*. 1999). Hence, although sardines were displaced to the east, they remained readily available to swift terns prior to their returning to the Western Cape to breed. Following a large eastward displacement of sardine to the east between 2004 and 2005 (Fig. 1), there was a large increase in the proportion of swift terns breeding in the south of the Western Cape. The foregoing suggests that the eastward shift of sardine had substantial impacts for seabirds breeding in South Africa. Of particular concern, was that the centre of gravity of purse-seine catches of sardine moved to a location between the main seabird breeding islands in the Western and Eastern Cape Provinces. The usual foraging range of African penguins when breeding is less than about 40 km (Heath and Randall 1989, Hockey *et al*. 2005, Petersen *et al*. 2005), which meant that by 2004 and 2005 much of the sardine was unavailable to penguins breeding in both provinces. Although Cape gannets forage up to 250 km from colonies (Grémillet *et al*. 2004) and gannets from Malgas Island are able to feed as far east as Cape Agulhas (Lewis *et al*. 2006), by 2004 and 2005 much of the sardine was beyond the foraging range of gannets from the Western Cape. However, unlike the situation for African penguins, there were signs that it was becoming increasingly available to birds in the Eastern Cape.

Mitigating the effects of an unfavourably altered distribution of prey

The possibility that climate change may alter the distribution of prey of seabirds in the long term, placing it beyond the foraging ranges of breeders with severe consequences for populations, poses the question of what mitigating measures might be implemented to reduce the impacts of such change. For central-place foragers, it is desirable to have the breeding localities situated within the range of the prey species, so that food is available to breeders. Some seabirds, such as swift terns, have shown considerable flexibility in the selection of breeding sites at the commencement of a breeding season (Crawford *et al*. 2002). Cape cormorants also have demonstrated their ability to occupy new breeding habitats, such as the guano platforms that were erected off central Namibia in the 20th century (Cooper *et al*. 1982). Other species of cormorant have shown similar adaptability (Carter *et al*. 1992). Hence the provision of artificial nesting habitat within the new distribution of the prey may benefit some species. However, other seabirds, such as Cape gannets and, once breeding, African penguins show strong attachment to breeding localities (Crawford *et al*. 1994) and the formation of new colonies is a rare event (Crawford *et al*. 1983, 1995). The emigration of first breeders from natal colonies to localities where feeding conditions are favourable at the time of first breeding is a strategy whereby African penguins attempt to cope with an altered distribution of prey (Crawford 1998). Penguins are unable to access platforms that stand above the sea surface, so along stretches of coastline that have no islands they must use mainland localities for breeding, which renders them susceptible to mainland predators (Whittington *et al*. 1996). At De Hoop, substantial numbers of penguins were killed by such predators in 2006. Attempts have since been made to exclude predators from the area used by penguins (CapeNature, unpublished information). It may be possible to boost such new colonies of seabirds through the release of chicks that have been orphaned and reared in captivity or hatched in zoos (Underhill *et al*. 2006).

When prey is becoming scarce around seabird breeding localities, it is desirable to prevent any further depletion of that prey. Most of South Africa's factories that process the catch of purse-seine boats are located near seabird breeding localities in the Western Cape. As sardine moved to the east, it became less available to boats operating from these factories. Fishers sought to make catches as close to factories as possible, further reducing the abundance of prey in the west. This preference of fishers means that the extent of the displacement of sardine to the east was probably underestimated. Because existing fish factories are often sited near the historical distributions of target species, it is likely that some form of spatial management of the catch of fisheries will be important in ensuring adequate availability of prey for predators in the event of a future displacement of prey.

Mortality of seabirds may be expected to increase when prey becomes exceptionally scarce (Cairns 1987). Hence, it will be desirable to reduce other causes of mortality, such as losses to predators, disease and pollution, to the extent that this is possible. In South Africa, management interventions to limit the extent of mortality of seabirds have included culling individual seals that inflict high mortality on seabirds (David *et al*. 2003), removing terrestrial predators from islands, burning carcases of seabirds that have died from disease to prevent further spread of the disease (Waller and Underhill in press), rescuing and rehabilitating oiled birds, relocating birds to prevent their becoming oiled, and rearing orphaned chicks (Barham *et al*. 2006).

Acknowledgements – We thank our research institutes (listed under addresses), the Darwin Initiative, the Earthwatch Institute and the National Research Foundation for supporting this research. We are grateful to all who assisted with surveys of breeding seabirds. CapeNature, Department of Environmental Affairs and Tourism, Robben Island Museum, South African National Parks and South African Navy provided logistical support for the surveys. This paper is a contribution to the project LMR/EAF/03/02 on top predators in the Benguela Current of the Benguela Current Large Marine Ecosystem (BCLME) Programme.

References

Barham, P.J., Crawford, R.J.M., Underhill, L.G., Wolfaardt, A.C., Barham, B.J., Dyer, B.M., Leshoro, T.M., Meÿer, M.A., Navarro, R.A., Oschadleus, H.D., Upfold, L., Whittington, P.A. and Williams, A.J. (2006) Return to Robben Island of African penguins that were rehabilitated, relocated or reared in captivity following the *Treasure* oil spill of 2000. *Ostrich* **77:**202–209.

Berruti, A., Underhill, L.G., Shelton, P.A., Moloney, C. and Crawford, R.J.M. (1993) Seasonal and interannual variation in the diet of two colonies of the Cape gannet *Morus capensis* between 1977/1978 and 1989. *Colonial Waterbirds* **16:**158–175.

Box, G.E.P. and Jenkins, G.M. (1970) *Time Series Analysis, Forecasting and Control*. San Francisco: Holden-Day.

Cairns, D.K. (1987) Seabirds as indicators of marine food supplies. *Biological Oceanography* **5:**261–271.

Carter, H.R., Sowls, A.L., Rodway, M.S., Wilson, U.W., Lowe, R.W., McChesney, G.J., Gress, F. and Anderson, D.W. (1992) Population size, trends, and conservation problems of the double-crested cormorant on the Pacific coast of North America. *Colonial Waterbirds* **18:**189–215.

Cooper, J., Brooke, R.K., Shelton, P.A. and Crawford, R.J.M. (1982) Distribution, population size and conservation of the Cape cormorant, *Phalacrocorax capensis*. *Fisheries Bulletin South Africa* **16:**121–143.

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. (2003) Influence of food on numbers breeding, colony size and fidelity to localities of Swift Terns in South Africa's Western Cape, 1987–2000. *Waterbirds* **26:**44–53.

Crawford, R.J.M., Allwright, D.M. and Heÿl, C.W. (1992a) High mortality of Cape cormorants (*Phalacrocorax capensis*) off western South Africa in 1991 caused by *Pasteurella multocida*. *Co-*

lonial Waterbirds **15:**236–238.
Crawford, R.J.M., Barham, P.J., Underhill, L.G., Shannon, L.J., Coetzee, J.C., Dyer, B.M., Leshoro, T.M. and Upfold, L. (2006a) The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. *Biological Conservation* **132:**119–125.
Crawford, R.J.M., Boonstra, H.G.v.D., Dyer, B.M. and Upfold, L. (1995) Recolonization of Robben Island by African penguins, 1983–1992. In *The Penguins: Ecology and Management*. P. Dann, I., Norman, I. and P. Reilly (eds), pp. 333–363. Chipping Norton, NSW: Surrey Beatty & Sons.
Crawford, R.J.M., Cooper, J., Dyer, B.M., Greyling, M.D., Klages, N.T.W., Nel, D.C., Nel, J.L., Petersen, S.L. and Wolfaardt, A.C. (2003) Decrease in numbers of the eastern rockhopper penguin *Eudyptes chrysocome filholi* at Marion Island, 1994/95–2002/03. *African Journal of Marine Science* **25:**487–498.
Crawford, R.J.M., Cooper, J., Dyer, B.M., Upfold, L., Venter, A.D., Whittington, P.A., Williams, A.J. and Wolfaardt, A.C. (2002) Longevity, inter-colony movements and breeding of crested terns in South Africa. *Emu* **102:**1–9.
Crawford, R.J.M., David, J.H.M., Shannon, L.J., Kemper, J., Klages, N.T.W., Roux, J-P., Underhill, L.G., Ward, V.L., Williams, A.J. and Wolfaardt, A.C. (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., 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. and Dyer, B.M. (1995) Responses by four seabirds to a fluctuating availability of Cape anchovy *Engraulis capensis* off South Africa. *Ibis* **137:**329–339.
Crawford, R.J.M., Dyer, B.M. and Brooke, R.K. (1994) Breeding nomadism in southern African seabirds – constraints, causes and conservation. *Ostrich* **65:**231–246.
Crawford, R.J.M., Dyer, B.M., Cooper, J. and Underhill, L.G. (2006b) 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. (2006c) 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., 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., Shelton, P.A., Cooper, J. and Brooke, R.K. (1983) Distribution, population size and conservation of the Cape gannet *Morus capensis*. *South African Journal of Marine Science* **1:**153–174.
Crawford, R.J.M., Underhill, L.G., Raubenheimer, C.M., Dyer, B.M. and Martin, J. (1992b) Top predators in the Benguela ecosystem – implications of their trophic position. *South African Journal of Marine Science* **12:**675–687.
Cunningham, D.M. and P.J. Moors (1994) The decline of rockhopper penguins *Eudyptes chrysocome* at Campbell Island, Southern Ocean and the influence of rising sea temperatures. *Emu* **94**:27–36.
David, J.H.M., Cury, P., Crawford, R.J.M., Randall, R.M., Underhill, L.G. and Meÿer, M.A. (2003) Assessing conservation priorities in the Benguela ecosystem: analysing predation by seals on threatened seabirds. *Biological Conservation* **114:**289–292.
Fairweather, T.P., van der Lingen, C.D., Booth, A.J., Drapeau, L. and van der Westhuizen, J.J. (2006) Indicators of sustainable fishing for South African sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*). *African Journal of Marine Science* **28:**661–680.
Grémilet, D., Dell'Omo, G., Ryan, P.G., Peters, G., Ropert-Coudert, Y. and Weeks, S. J. (2004) Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. *Marine Ecology Progress Series* **268:**265–279.
Guinard, E., Weimerskirch, H. and P. Jouventin (1998) Population changes and demography of the northern rockhopper penguin on Amsterdam and Saint Paul Islands. *Colonial Waterbirds* **21**:222–228.
Hays, C. (1986) Effects of the 1982–83 *El Niño* on Humboldt penguin colonies in Peru. *Biological Conservation* **36:**169–180.
Heath, R.G.M. and Randall, R.M. (1989) Foraging ranges and movements of jackass penguins (*Spheniscus demersus*) established through radio telemetry. *Journal of Zoology* **217:**367–379.
Hockey, P.A.R., Dean, W.R.J. and Ryan, P.G. (eds) (2005) *Roberts Birds of Southern Africa, 7th edn*. Cape Town: John Voelcker Bird Book Fund.
Klages, N.T.W., Willis, A.B. and Ross, G.J.B. (1992) Variability in the diet of the Cape gannet at Bird Island, Algoa Bay, South Africa. *South African Journal of Marine Science* **12:**761–771.
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.
Moors, P.J. (1986) Decline in numbers of rockhopper penguins at Campbell Island. *Polar Record* **23:** 69–73.
Paredes, R., Zavalaga, C.B. and Boness, D.J. (2002) Patterns of egg laying and breeding success in Humboldt penguins (*Spheniscus humboldti*) at Punta San Juan, Peru. *Auk* **119:**244–250.
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.
Quantitative Micro Software 2004. *EViews User's Guide*. Irvine, California: Quantitative Micro Software 692 pp.
Randall, R.M. (1989) Jackass penguins. In *Oceans of Life off Southern Africa*. A.I.L. Payne and R.J.M. Crawford (eds), pp. 244–256. Cape Town: Vlaeberg Publishers.
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.
Simeone, A., Araya, B., Bernal, M., Diebold, N., Grzybowski, K., Michaels, M., Teare, J.A., Wallace, R.S. and Willis, M.J. (2002) Oceanographic and climatic factors influencing breeding and colony attendance patterns of Humboldt penguins *Spheniscus humboldti* in central Chile. *Marine Ecology Progress Series* **227:**43–50.
Staverees, L., Crawford, R.J.M. and Underhill, L.G. (in press) Factors influencing the breeding success of Cape gannets *Morus capensis* at Malgas Island, 2002/03. *Ostrich*.
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., Upfold, L. and Visagie, J. (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.
Underhill, L.G., Tree, A.J., Oschadleus, H.D. and Parker, V. **(**1999) *Review of Ring Recoveries of Waterbirds in Southern Africa*. Cape Town: Avian Demography Unit, University of Cape Town.
van der Lingen, C.D., Coetzee, J.C., Demarcq, H., Drapeau, L., Fairweather, T.P., Hutchings, L. (2005) An eastward shift in the distribution of southern Benguela sardine. *GLOBEC International Newsletter* 11 (2): 17–22.
Vargas, F.H., Lacy, R.C., Johnson, P.J., Steinfurth, A., Crawford, R.J.M., Boersma, P.D. and Macdonald, D.W. (in press) Modeling the effect of *El Niño* on the persistence of small populations: The Galápagos Penguin as a case study. *Biological Conservation*.
Waller, L.J. and Underhill, L.G. (in press) The management of avian cholera *Pasteurella multocida* outbreaks on Dyer Island, South Africa, 2002–2005. *African Journal of Marine Science*.
Whittington, P.A. (2002) Survival and movements of African penguins, especially after oiling. PhD thesis, University of Cape Town.
Whittington, P.A., Hofmeyr, J.H. and Cooper, J. (1996) Establishment, growth and conservation of a mainland colony of jackass penguins *Spheniscus demersus* at Stony Point, Betty's Bay, South Africa. *Ostrich* **67:**144–150.
Williams, A.J. and Ward, V.L. (2002) Catastrophic cholera: coverage, causes, context, conservation and concern. *Bird Numbers* **11(2):**2–6.
Wolfaardt, A.[C.] and Williams, A.[J.] (2006) Sealed off – predation threatens seabirds and tourism. *Africa – Birds and Birding* **11(2):**60–67.