

Influences of the abundance and distribution of prey on African Penguins *Spheniscus demersus* off western South Africa

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Off South Africa, anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* are the main prey of African penguins *Spheniscus demersus*. The combined spawner biomass of these fish species increased from less than one million t in 1996 to more than nine million t in 2001 and then decreased to four million t in 2005. The combined biomass of young-of-the-year of these species increased from 0.2 million t in 1996 to 3.2 million t in 1991 before falling to 0.4 million t in 2005. There was a large eastward shift in the distribution of sardine between 1999 and 2005. The number of African penguins breeding in the Western Cape Province increased from 18 000 pairs in 1996 to more than 30 000 pairs from 2001–2005 before falling to 21 000 pairs in 2006, as the availability of fish decreased near breeding localities. Numbers of penguins breeding and numbers of birds in adult plumage moulting were significantly correlated with the

young-of-the-year biomass of anchovy and sardine and with the available biomass of older sardine. The increase in the number of penguins breeding was mainly attributable to a greater proportion of mature birds breeding and improved breeding success. The decrease probably resulted from high mortality. Delayed breeding and abstinence from breeding during periods of food shortage may both increase survivorship when food is scarce and enable seabirds rapidly to take advantage of improved feeding conditions. Although long-lived seabirds are buffered against short-term variability in food supplies, environmental change that influences the abundance and availability of prey can have severe consequences for central-place foragers, such as penguins, if prey is displaced to regions where no suitable breeding localities occur.

Keywords: African penguin; breeding proportion; breeding success; food; mortality; *Spheniscus demersus*

Introduction

Seabirds often have life-history characteristics, such as low fecundity, high survivorship and extended longevity, which buffer their populations against inter-annual fluctuations in their food sources (Hunt *et al.*, 1996). However, there are longer-term trends in the supply of food, which pose a much greater challenge. For instance, around the world, the abundance of anchovies *Engraulis* spp. and sardine (pilchard) *Sardinops* spp. has often remained at high or low levels over extended periods (Barange *et al.*, 1999, Schwartzlose *et al.*, 1999). Such long-term fluctuations in fish populations have been termed regimes (Luch-Belda *et al.*, 1989) and it is of interest to consider how seabirds respond to regime changes in the abundance of their prey.

Off South Africa, opportunity to examine such responses arose when there was a large increase in the abundance of anchovy *E. encrasicolus* and sardine *S. sagax* in the late 1990s (Fairweather *et al.*, 2006b), followed by a rapid decrease after 2002. These two fish species dominate the diet of African penguins *Spheniscus demersus* in South Africa (Hockey *et al.*, 2005). There was also an eastward shift in the distribution of sardine-directed fishing (Fairweather *et al.*,

2006b), which implies altered availability to penguins off South Africa's west coast. Fishing effort is often used as an index of relative abundance (King, 1995) and thus it can be argued that the distribution of fishing effort is an index of availability.

African penguins are endemic to southern Africa, where they breed in three regions: southern Namibia, South Africa's Western Cape Province and Nelson Mandela (formerly Algoa) Bay in the Eastern Cape Province (Shelton *et al.*, 1984). Localities where penguins breed in the Western Cape lie about 500 km south of those in Namibia and 600 km west of those in the Eastern Cape. In this paper we consider the responses of penguins in the Western Cape to an altered availability of their prey in this region.

Methods

From 1987–2006, African penguins bred at 13 localities in South Africa's Western Cape Province. The colony at De Hoop was established in 2003 (Underhill *et al.*, 2006; Fig. 1). Annual counts were made of the number of active nest sites of penguins at these localities during the main breeding season, which is February–September (Crawford *et al.*, 1995a;

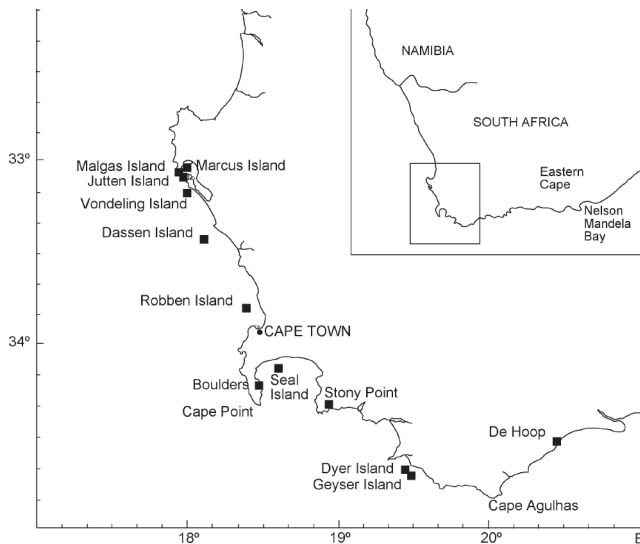


Figure 1: The location of breeding colonies of African penguins in South Africa's Western Cape Province. The inset shows the locations of Namibia, the Eastern Cape Province and Nelson Mandela Bay

1995b). Of the 244 possible counts, 46 were not made, most at smaller localities that are difficult to access. These data gaps were filled by linear interpolation between previous and subsequent counts at the same locality. Numbers that were obtained from interpolation of information contributed 14% of the overall number estimated to be breeding in the 20-year period (Underhill *et al.*, 2006). In 1991 and 2005, all the extant colonies were counted. A nest site was considered active if it contained eggs or chicks, or if it was defended by an adult bird (Crawford *et al.*, 1990). Numbers of chicks in crèches were divided by two to estimate the number of nest sites they represented, with remainders taken to signify an additional site – for example crèches of five and six chicks were both taken to represent three nests (Shelton *et al.*, 1984). Counts from 1987–2005 have been reported by Underhill *et al.* (2006).

At Robben Island, one of the breeding localities in the Western Cape, counts were made along the coast of penguins in adult plumage in the feather-shedding phase of moult at approximately two-weekly intervals, commencing October 1988. At this locality, most penguins moult along the coastline but some, which were not counted, moult inland at breeding sites. It was assumed that the proportion of birds moulting along the coast remained constant during 1988–2006. African penguins moult annually (Randall *et al.*, 1986).

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
African penguin breeders in the Western Cape (pairs)	ar(1) ma(1)
African penguin breeders at Robben Island (pairs)	ar(1) ma(1)
African penguin adults moulting at Robben Island	ar(1) ar(2)
Anchovy recruits (biomass)	ar(1) ma(1)
Anchovy spawners (biomass)	ar(1)
Sardine recruits (biomass)	ar(1) ar(2)
Sardine spawners (biomass)	ar(1) ma(1)
Anchovy and sardine recruits (biomass)	ar(1) ar(2)
Anchovy and sardine spawners (biomass)	ar(1) ma(1)
Sardine availability (biomass)	ar(1) ar(2)

At Robben Island, there is a peak in the numbers moulting between November and early January, with small numbers moulting at other times of the year (Underhill and Crawford, 1999). The feather-shedding phase of moult, from the time the first feathers stand out until the last loose feathers fall away, has a mean duration of 12.7 d (standard deviation 1.4 d, $n = 45$, 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–30 June and divided by 12.7 to estimate the number of birds at Robben Island moulting in each split year: ARI_t , where t = the second of the two years in the split year. An index of the proportion of adults breeding at the island (P_t) was calculated as:

$$P_t = 2NRI_t / ARI_t,$$

where NRI = the number of pairs breeding at Robben Island. P_t is an index and not the actual proportion for two reasons. Firstly, counts of moulting birds were only undertaken around the coast. Secondly, African penguins moult to adult plumage when about 18 months (Randall, 1989) but many breed for the first time when aged four years, although occasional breeding has been reported at two years old (Whittington *et al.*, 2005a).

Hydro-acoustic surveys to estimate the biomass of anchovy and sardine spawning off South Africa were conducted each year in November from 1984–2005. Similar surveys to estimate the abundance of young-of-the-year of these fish species were conducted in May. The surveys covered the known areas of spawning and recruitment. The methods used in the surveys and sampling procedures have been described by Hampton (1987) and Barange *et al.* (1999).

After 1998 there was a large eastward shift in the distribution of catches of sardine off South Africa (Fairweather *et al.*, 2006b). By 2005 the majority of sardine-directed fishing (and by supposition sardine) was placed to the east of breeding localities of African penguins in the Western Cape, changing their availability to penguins. The longitudinal coordinate for the centre of gravity of the distribution of commercial catches from 1987–2005 (Fairweather *et al.*, 2006b) was standardized to fall between 1 (the most western distribution observed) and 0 (the most eastern distribution) in order to produce an index of W–E distribution. The biomass of spawning sardine in the previous November was multiplied by this standardized index to obtain an estimate of the spawner biomass of sardine (ASS, million t) available to penguins in each year. The foraging range of African penguins while breeding in the Western Cape is about 20–40 km (Hockey *et al.*, 2005; Petersen *et al.*, 2005). After breeding is complete and after moult, penguins at Western Cape breeding localities may travel considerably farther to fatten up, including towards the easternmost distribution observed for sardine catches (Barham *et al.*, 2006). When sardine catches were at their westernmost distribution, they were centred in the vicinity of the main African penguin colonies off the Western Cape. Because anchovy catches maintained their western distribution throughout the study period (Fairweather *et al.*, 2006b), its entire biomass was deemed to be available to penguins in the Western Cape in all years.

The relationships between the numbers of penguins breeding or moulting in the Western Cape and the biomass of spawning and recruiting anchovy and sardine and the availability of sardine were investigated using correlation analysis. Cross correlation was undertaken with “pre-whitened residuals” of time series (Box and Jenkins, 1970), from which autocorrelation was removed using the software programme EViews (Quantitative Micro Software, 2000). The

Table 2: Models use to investigate trends in the number of African penguins breeding in the Western Cape, 1987–2006 (t = year; NWC = number of pairs breeding in the Western Cape; RC = combined recruit biomass of anchovy and sardine; ASS = available spawner biomass of sardine)

Model	Durbin–Watson statistic	Akaike Information Criterion	Adjusted r^2
$NWC_t = 8.21 + 0.39NWC_{t-1} + 2.53RC_{t-1} + 5.31ASS_{t-1}$	2.021	5.106	0.852
$NWC_t = 8.43 + 0.45NWC_{t-1} + 4.66RC_{t-1}$	1.911	5.439	0.785
$NWC_t = 7.09 + 0.45NWC_{t-1} + 7.83ASS_{t-1}$	2.123	5.270	0.818
$NWC_t = 5.31 + 0.77NWC_{t-1}$	1.540	6.088	0.570

models employed to obtain the prewhitened residuals are shown in Table 1. Because most African penguins in the Western Cape commence breeding early in the year, with some pairs establishing territories in January, and stop breeding before November (Crawford *et al.*, 1995a; 1995b), when the surveys to estimate the biomass of spawning fish are undertaken, the numbers of breeders or adults were compared to the biomass or availability of fish in the preceding year.

Based on the results of the correlation analysis, the number (thousand of pairs) of penguins breeding in the Western Cape in year t (NWC_t) was modelled using equations of the form:

$$NWC_t = a + bNWC_{t-1} + cRC_{t-1} + dASS_{t-1},$$

where a , b , c and d are constants and RC is the combined biomass (million t) of young-of-the-year anchovy and sardine. The models used are listed in Table 2. For each model, the Durbin–Watson statistic, the Akaike Information Criterion (AIC) and the adjusted r^2 value were calculated. The Durbin–Watson statistic measures the serial correlation in the residuals. If there is no serial correlation, it will have a value close to two. The smaller values of the AIC are preferred in model selection. The r^2 value indicates the proportion of variation in N_t accounted for by the model.

Results

The number of African penguins estimated to be breeding in South Africa's Western Cape Province decreased from about 23 000 pairs in 1987 and 1988 to 13 000 pairs in 1993. It then increased to 38 000 pairs in 2004 before falling to 21 000 pairs in 2006 (Fig. 2). There were large increases from 18 000 pairs in 1998 to 24 000 pairs in 1999 and from 26 000 pairs in 2000 to 34 000 pairs in 2001.

At Robben Island, the number of penguins breeding increased from about 500 pairs in 1987 to 8 500 pairs in 2004 and then decreased to 3 700 pairs in 2006 (Fig. 2). The number of birds in adult plumage that moulted along the coast was about 3 500 in 1987, 17 500 in 2004 and 7 800 in 2006. The index of the proportion of adult penguins breeding increased after 1995 (Fig. 2). It averaged 0.68 (standard deviation 0.12) from 1989–1995 and 0.97 (standard deviation 0.11) from 1996–2006. The means of the index in these two periods were significantly different from each other ($t_{16} = 4.54$, $P < 0.01$).

The spawner biomass of anchovy off South Africa fell from 2.5 million t in 1986 to less than one million t in 1989, 1990 and from 1994–1996. It rose rapidly to almost seven million t in 2001 before decreasing to three million t in 2005 (Fig. 2). The spawner biomass of sardine increased from 0.2 million t in 1986 to more than four million t in 2002 and then decreased to one million t in 2005. The biomass of young-of-the-year anchovy and sardine increased from less than one million t during 1986–1999 to three million t in 2001, thereafter falling to 0.4 million t in 2005. The biomass of mature

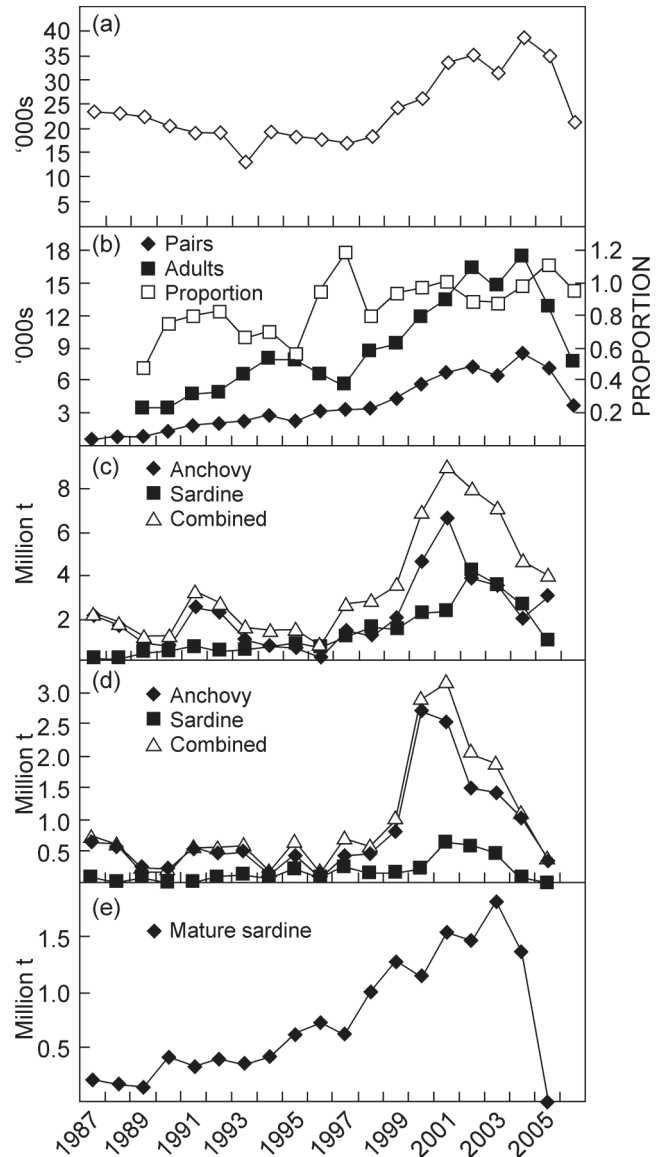


Figure 2: Trends in (a) numbers of African penguins breeding in the Western Cape Province, (b) numbers of penguins breeding, penguins in adult plumage moulting and an index of the proportion of mature penguins breeding, (c) the spawner biomass of anchovy, sardine and these two species combined, (d) the recruit biomass of anchovy, sardine and these two species combined and (e) the biomass of mature sardine available to penguins in the Western Cape

sardine gauged to be available to penguins in the Western Cape increased from 0.2 million t in 1986 to 1–2 million t from 1998–2004, but was negligible in 2005 (Fig. 2).

The results of cross correlation of residuals of prewhitened time series are shown in Table 3. The number of

penguins breeding at Robben Island was significantly correlated with the number breeding in the Western Cape and with the number of adults moulting at Robben Island immediately before the breeding season. In all 21 comparisons made, the number of penguins breeding in the Western Cape or at Robben Island, or the number of adults moulting at Robben Island, was positively related to the biomass of fish in the previous year. In only one of nine comparisons was the relationship between penguins and biomass of spawning fish significant. However, in seven of nine comparisons the relationship between penguins and biomass of recruiting fish was significant. All three comparisons between numbers of penguins and the available biomass of mature sardine were significant.

The number of penguins breeding in the Western Cape was best modelled by an equation that incorporated estimates for the previous year of the number of penguins breeding, the combined abundance of young-of-the-year anchovy and sardine and the biomass of mature sardine available to penguins (Table 2). This model accounted for 85% of the observed variation in the number of penguins breeding. The Durbin–Watson statistic was close to two and the value of the AIC was less than for any other model investigated.

Discussion

Responses to an altered availability of food

From 1996–2001, an increase in the biomass of anchovy and sardine off South Africa from less than one million t to nine million t was followed by a large increase in the numbers of

African penguins breeding in the Western Cape. The increase could have been achieved by a decrease in the age at first breeding, reduced absenteeism of breeders from colonies, strong recruitment of first-time breeders to colonies (e.g. as a result of increased breeding productivity), increased survival, immigration of birds from elsewhere, or a combination of these factors, which are considered below.

At Robben Island, from 1989–1995, 26% of all known-age birds bred before they were four years old, most (36%) made their first breeding attempt when aged four years, and 80% were breeding before the age of six years (Crawford *et al.*, 1999). From 1995–1999, more than 30% of birds at both Robben and Dassen islands initiated breeding before they were four years old. At Robben Island, the mean age at breeding of chicks that were banded in 1992, 1993 and 1994 was 4.8, 4.9 and 3.8 years, respectively (Whittington *et al.*, 2005a). Hence, most of the 1994 cohort was breeding by 1998. At Dassen Island, the mean age at first breeding of chicks banded in 1992, 1993 and 1994 was 4.6, 4.7 and 4.4 years, respectively (Whittington *et al.*, 2005a). These results suggest that a reduced age at first breeding may have contributed to an increase in the number of penguins breeding in the Western Cape from 1998 onwards.

African penguins may not breed each year. At Robben Island from 1988–1995, the proportion of adults which bred is estimated to have varied from 0.7–1.0 and was related to the spawner biomass of both anchovy and sardine (Crawford *et al.*, 1999). At Stony Point from 1982–1986 and 1989–1996, 20% of the possible number of breeding attempts was skipped (Whittington *et al.*, 1996). At Robben Island, the mean of the index of the proportion of mature birds breeding increased by 40% between 1989–1995 and 1996–2006 (Fig. 2). Hence, a decreased absenteeism of breeders is also likely to have contributed to the increase in the number of penguins breeding in the Western Cape in the late 1990s.

From 1989–1995 at Robben Island, African penguin pairs fledged an average of 0.47 chicks annually, with a maximum of 0.59 chicks per pair in both 1991 and 1992 (Crawford *et al.*, 1999). During 1987–1999, annual survival of penguins in their first year averaged 38% at Dassen Island and 31% at Robben Island. From 1990–1999, annual survival of adults was estimated to be 80% at Dassen Island and 82% at Robben Island (Whittington, 2002). Most African penguins breed for the first time when 3–5 years old (Whittington *et al.*, 2005a). Therefore, breeding productivity at Robben Island up until 1995 would have been insufficient to result in a large increase in the numbers of penguins breeding there before 2000, by which time most birds from the 1995 cohort would have recruited to the colonies. It is unlikely that the large increase in the number of penguins breeding in 1999 resulted from good recruitment of first breeders to colonies. From 1997–2004, African penguins at Robben Island fledged an annual average of 0.76 chicks per pair, with a peak of 0.97 in 1997 (Crawford *et al.*, 2006). These birds are likely to have recruited to the breeding colonies from about 2001 onwards, contributing to the large increase in the number of breeders at that time. From 1987–1994, survival of African penguins in their first year was usually higher in years of high abundance of anchovy than in years of scarcity of this fish species (Whittington, 2002). Improved first-year survival in the late 1990s and early 2000s, as the anchovy population increased would have further strengthened recruitment to the breeding population.

There is no information on trends in the mortality of adult African penguins. It is noteworthy that there was a large increase in the number of African penguins breeding in the Western Cape after 2000 in spite of the deaths in 2000 of about 2 000 birds that were oiled in the *Treasure* spill (Crawford *et al.*, 2000). This suggests that the large increase

Table 3: Results of cross correlation between pairs of residuals from pre-whitened time series ($t = \text{year}$; $NWC = \text{number of pairs breeding in the Western Cape}$; $NRI = \text{number of pairs breeding at Robben Island}$; $ARI = \text{number of adults moulting at Robben Island}$; $SA = \text{spawner biomass of anchovy}$; $SS = \text{spawner biomass of sardine}$; $SC = \text{combined spawner biomass of anchovy and sardine}$; $RA = \text{recruit biomass of anchovy}$; $RS = \text{recruit biomass of sardine}$; $RC = \text{combined recruit biomass of anchovy and sardine}$; $ASS = \text{available spawner biomass of sardine}$; $Ns = \text{not significant}$)

Series 1	Series 2	n	r	P
NWC_t	NRI_t	19	0.804	<0.001
NRI_t	ARI_t	16	0.810	<0.001
NWC_t	SA_{t-1}	19	0.262	Ns
NWC_t	SS_{t-1}	19	0.362	Ns
NWC_t	SC_{t-1}	19	0.382	Ns
NWC_t	RA_{t-1}	19	0.590	<0.01
NWC_t	RS_{t-1}	19	0.274	Ns
NWC_t	RC_{t-1}	19	0.646	<0.005
NWC_t	ASS_{t-1}	17	0.620	<0.01
NRI_t	SA_{t-1}	19	0.261	Ns
NRI_t	SS_{t-1}	19	0.239	Ns
NRI_t	SC_{t-1}	19	0.345	Ns
NRI_t	RA_{t-1}	19	0.504	<0.01
NRI_t	RS_{t-1}	19	0.482	<0.05
NRI_t	RC_{t-1}	19	0.600	<0.01
NRI_t	ASS_{t-1}	17	0.796	<0.002
ARI_t	SA_{t-1}	16	0.473	Ns
ARI_t	SS_{t-1}	16	0.189	Ns
ARI_t	SC_{t-1}	16	0.519	<0.05
ARI_t	RA_{t-1}	16	0.476	Ns
ARI_t	RS_{t-1}	16	0.673	<0.005
ARI_t	RC_{t-1}	16	0.567	<0.05
ARI_t	ASS_{t-1}	16	0.712	<0.002

in pelagic fish prey available to African penguins more than counteracted the increased mortality caused by the oil spill (Wolfaardt *et al.*, 2001).

Up until 1999 there was only low-level emigration of penguins from Namibia and the Eastern Cape to the Western Cape (Whittington *et al.*, 2005b). However, there has been a recent large decrease in numbers of African penguins breeding in the Eastern Cape (Crawford and Kemper, in press), so it is possible that emigration of young adults from that region occurred.

The number breeders in the Western Cape began to decrease after 2004, 2–3 years after a downturn in the abundance of young-of-the-year and spawning anchovy and sardine. The reduced number of breeders became especially evident in 2006. In 2003 and 2004, prey abundance, although decreasing, remained high and it is probable that sufficient fish were available in the vicinity of penguin breeding localities. After 2004, the reduced recruitment of fish and the eastward displacement of mature sardine brought a large decrease in the number of penguins breeding. Co-incident with the decrease in numbers of penguins breeding, there was a large decrease in numbers of birds in adult plumage moulting at Robben Island (Fig. 2) and at other islands (ACW, pers. obs). This suggests substantial mortality, unless large numbers of birds moved to other breeding localities, for which there is no evidence.

In the Humboldt upwelling system off Peru, where similarly to southern Africa the main prey of seabirds are anchovy and sardine (Crawford and Jahncke, 1999), *El Niños* cause reproductive failure, delayed breeding, absenteeism from breeding and mortality for several seabirds (e.g. Hays, 1986; Schreiber, 2002; Simeone *et al.*, 2002). Similarly to the situation off South Africa, subsequent population recoveries are boosted by increased reproductive success and a greater proportion of mature birds breeding (e.g. Paredes *et al.*, 2002).

In Australia, reproductive success of little penguins *Eudyptula minor* was much reduced after a widespread mortality of sardine, one of their main food sources (Dann and Cullen, 1990; Dann *et al.*, 2000). At South Georgia, a four-fold decrease in biomass of krill *Euphausia superba* led to a 90% decrease in breeding success of gentoo penguins *Pygoscelis papua* (Croxall *et al.*, 1999). There was extensive non-breeding by gentoo and macaroni *Eudyptes chrysolophus* penguins following a severe and prolonged winter (Williams and Rodwell, 1992). In California, breeding success of elegant terns *S. elegans* was correlated to estimates of food abundance (Schaffner, 1986). In Scotland, in years of poor availability of food Arctic terns *S. paradisaea* refrained from breeding or abandoned breeding at an early stage (Monaghan *et al.*, 1992). At Kerguelen Island, poor body condition of blue petrels *Halobaena caerulea* early in the breeding season resulted in a high proportion of non breeders and massive egg desertion (Chastel *et al.*, 1995).

Availability of food

The relationships between numbers of African penguins breeding or moulting and food sources were strongest for young-of-the-year fish and mature sardine. Most young-of-the-year anchovy and sardine recruit along South Africa's west coast in the austral autumn and winter (Crawford, 1980), which is where and when the penguins breed in the Western Cape (Crawford *et al.*, 1995b; Underhill *et al.*, 2006; Fig. 1). At this time they are fed upon extensively by African penguins (Crawford and Dyer, 1995). After breeding, African penguins leave breeding localities to fatten up prior to moult. The moult of African penguins lasts about three weeks, when birds do not feed. Subsequently, adults again leave their

colonies to fatten up. The pre- and post-moult fattening trips may last several weeks (Randall, 1989). On these fattening trips, penguins often move considerable distances from their breeding colonies (Randall *et al.*, 1987; Whittington *et al.*, 2005c). Birds from the Western Cape may move to the Agulhas Bank to feed (Barham *et al.*, 2006). This is where most mature anchovy and sardine congregate to spawn from September to February (Shelton, 1986; Hampton 1987). Good recruitment of anchovy and sardine along the west coast will result in good feeding conditions during the breeding season. A western location of spawning fish after breeding will result in a greater availability of fish before and after moult. Hence, the number of penguins breeding in any year is related to feeding conditions in the previous breeding season and the availability of food in the period before and after moult.

The recent eastward displacement of sardine has reduced its availability to penguins on the west coast. Similarly the contribution of sardine to the diet of Cape gannets *Morus capensis* in the Western Cape has decreased in recent years. There has been an eastward displacement of Cape gannets in South Africa (Crawford *et al.*, 2007). There were also large eastward expansions in the breeding ranges of Hartlaub's gull *L. hartlaubii* from 1995–2001 (Hockey *et al.*, 2005) and crowned cormorant *Phalacrocorax coronatus* at some time between 1981 and 2003 (Whittington, 2004).

Seabirds are central-place foragers when breeding. If the distribution of their prey changes and there are no suitable breeding localities that will enable them to utilize the prey in its new location, large decreases in the affected seabird populations can be expected. The gap of about 600 km in the location of islands at which penguins breed in the Western Cape and in Nelson Mandela Bay has led to a substantial decrease in the overall population of African penguins, as sardine have shifted to the east. In an apparent attempt to adapt to the displacement of prey, African penguins initiated a new colony on the mainland at De Hoop in 2003 (Underhill *et al.*, 2006). This colony is the most eastern of those in the Western Cape (Fig. 1). However, terrestrial predators have recently reduced the number of penguins there (CapeNature, unpublished information). At several localities in the Southern Hemisphere severe decreases in numbers of rockhopper penguins *Eudyptes chrysocome* are thought to have resulted from climate change affecting the distribution of their prey (Crawford *et al.*, 2003). The impact of environmental change on seabird populations may require considerable care in the management of fisheries on prey populations (e.g. Frederiksen *et al.*, 2004). In South Africa, most of the fish factories are located along the west coast. After displacement of fish to the east, boats from these factories have continued to seek fish in the west (Fairweather *et al.*, 2006a; 2006b), further reducing the availability of prey to penguins.

Prey regime considerations

Seabirds have not always been able to maintain their populations on the descending and trough phases of prey regimes (Crawford, 1999; Crawford and Jahncke, 1999). For example, during and after the collapse of the Namibian stock of sardine in the 1960s and 1970s, the numbers of African penguins breeding in southern Namibia fell from 40 000 pairs in 1956 to about 1 000 pairs in 2000 (Crawford *et al.*, 2001a). In Peru, following intensive fishing on anchoveta *E. ringens*, there was a large and sustained decrease in numbers of guanay cormorants *P. bougainvillii*, from usually more than 10 million birds between 1953 and 1964 to fewer than five million thereafter (Crawford and Jahncke 1999).

Delayed breeding (e.g. Crawford *et al.*, 2001b) and abstinence from breeding during periods of food scarcity (e.g.

Crawford, 2003) are factors improving survival and longevity (Hamer *et al.*, 2002; Weimerskirch, 2002). During a period of high winter mortality, middle-aged shags *Phalacrocorax aristotelis* that had not bred in the previous summer had much better survival than those that had bred (Harris *et al.*, 1998). For California gulls *Larus californicus*, reduced reproductive effort with age was associated with increased survivorship (Pugesek, 1987). The significant relationships obtained, between the abundance of food immediately prior to the breeding season and the numbers of birds that later breed, suggest African penguins may decide to skip breeding before the breeding season commences.

Various factors may enhance the survivorship of a bird that takes this decision in a period of food scarcity. Firstly, the bird will not be constrained to be a central-place forager for a period of several months, having to find food within a fixed distance of the breeding colony. It will be able to travel to where food is more plentiful at the time. Secondly, the bird will not need to expend energy on breeding activities, such as breeding displays, building and defence of nests, guarding of mate and chicks and feeding of chicks. Thirdly, it does not have to spend time at or near colonies, where risks of death through factors such as predation (e.g. Marks *et al.*, 1997) or contagious diseases (e.g. Crawford *et al.*, 1992) may be increased. Some predators lurk near colonies waiting for birds to return from or depart to sea (e.g. David *et al.*, 2003). Attendance of least auklets *Aethia pusilla* at breeding colonies was low when the proportion of adults breeding was low (Jones, 1992). A decision not to breed may be particularly important for longer-lived seabirds (Chastel *et al.*, 1995). African penguins have been shown to live for periods of more than 27 years (Hockey *et al.*, 2005).

Other strategies that seabirds have used to mitigate the influence of extended periods of scarcity of a particular prey species have included prey-switching (Crawford, 1999; Crawford and Jahncke, 1999) and emigration of first breeders from their natal colonies to localities where feeding conditions are more favourable at the time of first breeding (Crawford, 1998). Thereafter, the tactic may be to breed with the same partner and, in order to locate the partner, to return to the same locality to breed. Emigration of first breeders, but not of established breeders, has resulted in colonies of African penguins decreasing at about the rate that would be expected from estimates of adult mortality, if there were no recruitment of young breeders to the colonies (Crawford, 1998).

Delayed breeding and abstinence from breeding by seabirds during periods of food shortage may not only boost their survival but, by doing so, also provide a mechanism whereby seabird populations are able, by decreasing the proportions of birds not breeding, rapidly to respond to an enhanced availability of food. Where seabird populations are decreased by prolonged periods of food scarcity, as during troughs in prey regimes, their long-term survival will be enhanced by a rapid response to favourable feeding conditions. In periods of abundant food, increases in numbers of birds breeding may be sustained by improved breeding success and recruitment to colonies, subject to other considerations, such as the availability of breeding sites (e.g. Cairns, 1992). This appears to have been the case with African penguins in the Western Cape.

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