

This article was downloaded by: [41.4.190.59]

On: 11 August 2011, At: 06:12

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



African Journal of Marine Science

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tams20>

Collapse of South Africa's penguins in the early 21st century

RJM Crawford^{a b c}, R Altwegg^{b c d}, BJ Barham^e, PJ Barham^{b c f}, JM Durant^g, BM Dyer^a, D Geldenhuys^h, AB Makhado^a, L Pichegruⁱ, PG Ryanⁱ, LG Underhill^{b c}, L Upfold^a, J Visagie^h, LJ Waller^{b c h} & PA Whittington^{j k}

^a Oceans and Coasts, Department of Environmental Affairs, Private Bag X2, Rogge Bay, 8012, South Africa

^b Animal Demography Unit, University of Cape Town, Rondebosch, 7701, South Africa

^c Marine Research Institute, University of Cape Town, Rondebosch, 7701, South Africa

^d South African National Biodiversity Institute, Private Bag X7, Claremont, 7735, South Africa

^e Penguin Datasystems, 2 Cotham Place, Bristol, BS6 6QS, UK

^f HH Wills Physics Laboratory, University of Bristol, Tyndall Avenue, Bristol, BS8 1TL, UK

^g Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066, Blindern, 0316 Oslo, Norway

^h Cape Nature, Private Bag X29, Rondebosch, 7701, South Africa

ⁱ Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, 7701, South Africa

^j East London Museum, PO Box 11021, Southernwood, 5213, South Africa

^k Department of Zoology, Nelson Mandela Metropolitan University, PO Box 77000, Port Elizabeth, 6031, South Africa

Available online: 10 Jun 2011

To cite this article: RJM Crawford, R Altwegg, BJ Barham, PJ Barham, JM Durant, BM Dyer, D Geldenhuys, AB Makhado, L Pichegru, PG Ryan, LG Underhill, L Upfold, J Visagie, LJ Waller & PA Whittington (2011): Collapse of South Africa's penguins in the early 21st century, *African Journal of Marine Science*, 33:1, 139-156

To link to this article: <http://dx.doi.org/10.2989/1814232X.2011.572377>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.tandfonline.com/page/terms-and-conditions>

This article may be used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan, sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims,

proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Collapse of South Africa's penguins in the early 21st century

RJM Crawford^{1,2,3*}, R Altwegg^{2,3,4}, BJ Barham⁵, PJ Barham^{2,3,6}, JM Durant⁷, BM Dyer¹, D Geldenhuys⁸, AB Makhado¹, L Pichegru⁹, PG Ryan⁹, LG Underhill^{2,3}, L Upfold¹, J Visagie⁸, LJ Waller^{2,3,8} and PA Whittington^{10,11}

¹ Oceans and Coasts, Department of Environmental Affairs, Private Bag X2, Rogge Bay 8012, South Africa

² Animal Demography Unit, University of Cape Town, Rondebosch 7701, South Africa

³ Marine Research Institute, University of Cape Town, Rondebosch 7701, South Africa

⁴ South African National Biodiversity Institute, Private Bag X7, Claremont 7735, South Africa

⁵ Penguin Datasystems, 2 Cotham Place, Bristol, BS6 6QS, UK

⁶ HH Wills Physics Laboratory, University of Bristol, Tyndall Avenue, Bristol BS8 1TL, UK

⁷ Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066, Blindern, 0316 Oslo, Norway

⁸ Cape Nature, Private Bag X29, Rondebosch 7701, South Africa

⁹ Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7701, South Africa

¹⁰ East London Museum, PO Box 11021, Southernwood 5213, South Africa

¹¹ Department of Zoology, Nelson Mandela Metropolitan University, PO Box 77000, Port Elizabeth 6031, South Africa

* Corresponding author, e-mail: crawford@environment.gov.za

Manuscript received August 2010; accepted February 2011

The number of African penguins *Spheniscus demersus* breeding in South Africa collapsed from about 56 000 pairs in 2001 to some 21 000 pairs in 2009, a loss of 35 000 pairs (>60%) in eight years. This reduced the global population to 26 000 pairs, when including Namibian breeders, and led to classification of the species as Endangered. In South Africa, penguins breed in two regions, the Western Cape and Algoa Bay (Eastern Cape), their breeding localities in these regions being separated by c. 600 km. Their main food is anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax*, which are also the target of purse-seine fisheries. In Algoa Bay, numbers of African penguins halved from 21 000 pairs in 2001 to 10 000 pairs in 2003. In the Western Cape, numbers decreased from a mean of 35 000 pairs in 2001–2005 to 11 000 pairs in 2009. At Dassen Island, the annual survival rate of adult penguins decreased from 0.70 in 2002/2003 to 0.46 in 2006/2007; at Robben Island it decreased from 0.77 to 0.55 in the same period. In both the Western and Eastern Cape provinces, long-term trends in numbers of penguins breeding were significantly related to the combined biomass of anchovy and sardine off South Africa. However, recent decreases in the Western Cape were greater than expected given a continuing high abundance of anchovy. In this province, there was a south-east displacement of prey around 2000, which led to a mismatch in the distributions of prey and the western breeding localities of penguins.

Keywords: African penguin, diet, numbers breeding, numbers moulting, *Spheniscus*, survival

Introduction

The African penguin *Spheniscus demersus* is endemic to the greater Benguela upwelling ecosystem off south-western Africa. It breeds from central Namibia (Hollam's Bird Island) to South Africa's Eastern Cape province (Bird Island, Hockey et al. 2005). In South Africa, penguins breed in two groups of localities, one in the Western Cape province and the other in the Eastern Cape province, which are separated by c. 600 km (Figure 1). It is likely that there were 1.5–3.0 million African penguins in the early part of the 20th century (Shannon and Crawford 1999, Crawford et al. 2007a). By 1956, this had reduced to about 0.3 million penguins (Rand 1963a, 1963b).

In 1978/1979, there were 70 000 breeding pairs (Shelton et al. 1984), equivalent to c. 224 000 birds in adult plumage, based on information in Crawford and Boonstra (1994). Numbers decreased to 44 000 breeding pairs in 1993 (Crawford et al. 1995a) and then recovered to 63 000 pairs in 2001 (Kemper et al. 2007), attributable to an increase of penguins in South Africa (Underhill et al. 2006) while numbers stayed low in Namibia. Subsequently, the overall number breeding decreased to 26 000 pairs in 2009, the lowest level recorded, leading to re-classification of the IUCN conservation status of the species from Vulnerable to Endangered (BirdLife International 2010).

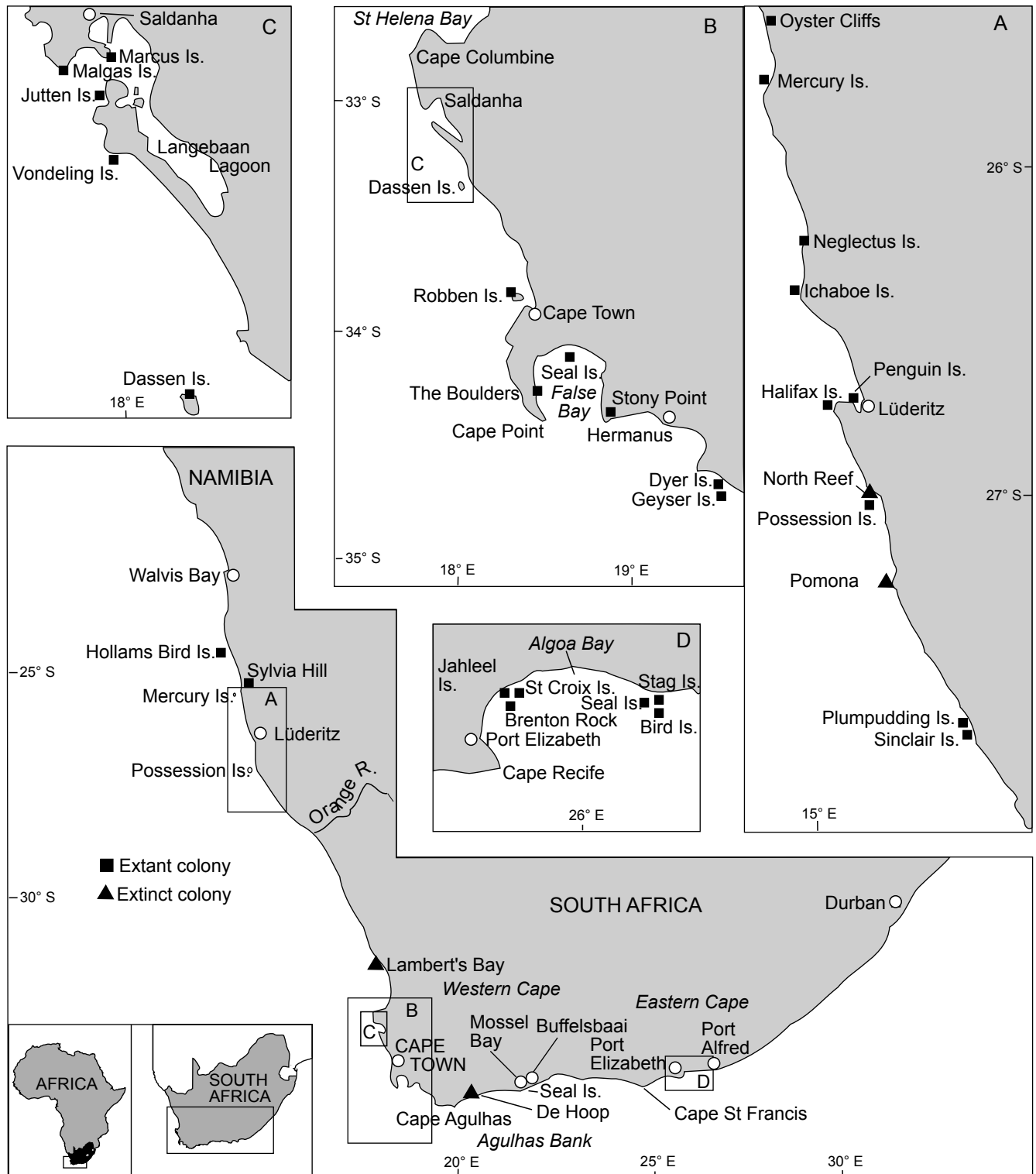


Figure 1: Breeding localities of African penguins, 1990–2010. Different symbols are used for those localities where breeding took place, or was believed to take place, in 2010 and those where breeding ceased after 1990

An altered availability of food can have a major impact on seabird populations. In Namibia, for example, numbers of African penguins and Cape gannets *Morus capensis* decreased by more than 85% after the collapse of the

Namibian stock of sardine *Sardinops sagax* in the late 1960s and early 1970s (Crawford 2007). Sardine *Sardinops sagax* was the main food of both these seabirds in Namibia in the 1950s (93–99% by mass, Matthews 1961). In Peru,

numbers of guanay cormorants *Phalacrocorax bougainvillii* decreased markedly a few years after the introduction of intensive purse-seine fishing for anchovy *Engraulis ringens* and did not subsequently recover; numbers of guanay cormorants were negatively related to the catch of anchovy in the preceding year (Crawford and Janhcke 1999).

In this paper, we document the recent collapse of African penguins in South Africa and trends in survival of adult birds at two western localities in the mid-2000s. We report on the diet of penguins at six localities around the South African coastline since 1989 and consider the long-term relationship between numbers of penguins breeding in the two provinces and the combined abundance off South Africa of anchovy *E. encrasicolus* and sardine, their two main prey species (Hockey et al. 2005). Although African penguins are central-place foragers that feed near to colonies when breeding (Heath and Randall 1989, Petersen et al. 2006, Pichegru et al. 2010), in the non-breeding season they move considerable distances (Randall et al. 1987, Whittington et al. 2005a), so that their pre-breeding condition and their decision whether or not to breed is likely to be influenced by the overall abundance of prey as well as its availability near breeding colonies. There was a recent shift to the east in the distributions of both anchovy and sardine off South Africa (Fairweather et al. 2006, Roy et al. 2007). We expected this might lessen the availability of prey at colonies in the northern Western Cape but increase its availability at colonies in the south of that province. Emigration of first-breeders to localities where feeding conditions are favourable at the time is a mechanism that may help African penguins cope with shifts in the distribution of their prey (Crawford 1998). We anticipated that the shift in the distribution of prey off the Western Cape would lead to decreases in numbers breeding at northern colonies but increases at localities farther south and investigated whether trends at colonies matched this prediction.

Material and methods

Diet

During the period 1989–2009, the diet of adult African penguins was examined at six breeding localities: two west of Cape Point (Dassen and Robben islands), two between Cape Point and Cape Agulhas (Boulders and Dyer Island) and two in Algoa Bay (St Croix and Bird islands). The six localities were not sampled equally, differences being attributable to the ease and cost of access to localities and numbers of penguins breeding at them. Penguins were caught during the breeding season, as they returned from the sea at dusk. Therefore, samples are likely to reflect the diet fed to chicks, although incubating or non-breeding adults also may have been sampled. A water-offloading technique was used to obtain food from the penguins' stomachs (Randall and Davidson 1981, Wilson 1984), modified by dispensing with the pump and pouring water into the stomach via a funnel and tube. Birds were then checked and released.

For each bird from which food was obtained, prey items were identified — usually to species level — and weighed. The contribution by mass of different species to the diet of penguins was computed for each locality and month.

Annual estimates of the contribution of prey items to the diet at a particular locality were obtained by apportioning equal weight to each month for which samples were collected.

Numbers breeding

From 1991, the numbers of occupied nest sites of African penguins were counted annually at most South African breeding localities. Some of the smaller and more difficult to access localities were not visited every year. An occupied site was considered active if it contained fresh eggs or chicks, or if it was defended by a non-moulting adult bird. An occupied nest was considered potential if it was not active but showed recent signs of use, e.g. through the presence of substantial quantities of fresh guano or nesting material, the recent excavation of sand from a burrow nest, the presence of many penguin footprints in its vicinity, or a combination of these factors. Breeding by African penguins is not always synchronous (e.g. Crawford et al. 1999), so that numbers of active nests may underestimate the number of pairs breeding. This bias may be reduced by incorporating counts of potential nests. For example, potential nests may be occupied by pairs that have recently finished breeding or that are about to breed. However, they may also be used by pairs electing not to breed in a year, or by prospecting adults. Numbers of chicks in crèches were divided by two to estimate the number of nest sites they represented, with remainders taken to represent an additional site, e.g. crèches of five and six chicks would both be taken to represent three nests (Shelton et al. 1984).

Most counts were undertaken during the main breeding season, which in South Africa is February–September (Hockey et al. 2005). At localities that were small and difficult to access, counts made outside the main breeding season were used if no other count was available for that year. Where more than one count was made at a locality in a year, the highest count was taken to represent the number of pairs breeding there in that year. Counts of occupied nests at localities in the Western Cape up until 2005 were reported by Underhill et al. (2006) and in the Eastern Cape up until 2008 by Crawford et al. (2009).

In the late 1990s and the first decade of the 2000s, the largest numbers of African penguins in the Western Cape were at Dassen and Robben islands (Underhill et al. 2006). From 1999 at Dassen Island and 2000 at Robben Island, occupied nests were recorded as active or potential (Wolfaardt et al. 2009a), but this was not the case in earlier years or at other localities. Up until 2006, the proportions of occupied nests that were classified as potential at Dassen Island were reported by Wolfaardt et al. (2009a).

For the period 1989–2009 (except 1990) in the Western Cape and 1999–2009 (except 2002) in the Eastern Cape, numbers of occupied nests of African penguins were counted at all the main colonies in these provinces. Numbers of occupied nests at smaller colonies, for which no count information was available, were estimated from linear interpolation between the nearest counts for those colonies. For each province, estimates of the total numbers of occupied nests were correlated with estimates of the combined spawner biomass of anchovy and sardine off South Africa in the same and previous years, which were obtained from Merkle and Coetzee (2010).

Numbers moulting

At Dassen (commencing mid-1994) and Robben (commencing mid-1988) islands, counts at intervals of about two weeks were made around the coastline of numbers of African penguins in adult and immature plumage that were in the feather-shedding phase of moult. African penguins replace their plumage annually (Wolfaardt et al. 2009b). For individual birds, the feather-shedding phase of moult has a mean duration of 12.7 days (Randall et al. 1986). Therefore, counting birds in the feather-shedding phase of moult every thirteenth day and summing for a year provides an estimate of numbers of birds using a locality (Randall et al. 1986), although some African penguins may moult at localities other than those at which they breed (Crawford et al. 2000a, Whittington et al. 2005a). The counts at Dassen and Robben islands were interpolated linearly to estimate numbers of birds moulting feathers for each day between actual counts. These estimates were summed over a year and divided by 12.7 to calculate the numbers moulting around the coasts of the two islands in any year (Underhill and Crawford 1999). The peak moult of African penguins in South Africa is in the austral summer (Crawford et al. 2006), so that estimates of numbers moulting around the islands were made for the split year July–June. Numbers of adults moulting around the shoreline of Dassen Island up until 2005/2006 have been reported by Wolfaardt et al. (2009a); numbers around Robben Island up until 2006/2007 by Underhill and Crawford (1999) and Crawford et al. (2008a). Counts of moulting birds around the shoreline at Dassen Island, and more recently at Robben Island, underestimate the numbers moulting at the islands, because birds also moult inland (Wolfaardt et al. 2009a).

Adult survival

Substantial numbers of African penguins have been banded with stainless-steel rings. These include many birds that, following the *Treasure* oil spill of 2000, were oiled and rehabilitated; or caught and relocated to prevent their becoming oiled; or orphaned as chicks, captive reared and later released to the wild. The spill affected particularly birds at Dassen and Robben islands (Crawford et al. 2000b). All age classes of penguins were involved. Subsequent to the spill, intensive searches were conducted for banded birds at both these islands. Between 2001 and 2008, data were available for 6 456 banded penguins seen at Robben Island and 5 453 seen at Dassen Island. The years of banding of these penguins are shown in Table App.1 (Appendix). Resighting information was used to estimate survival of adult penguins at each of the two islands from 2002/2003 to 2006/2007.

Non-breeding African penguins range widely (Whittington et al. 2005a, 2005b) and may be oiled and come ashore at localities remote from those where they breed (Underhill et al. 2000). In order to remove from the analysis birds belonging to localities other than Dassen and Robben islands, the first re-encounter of birds at one of these two localities, rather than the banding occasion, was used as the initial encounter. Hence, estimates are based on birds seen at one of the two islands after being released.

Classical capture-mark-recapture (CMR) methods (Lebreton et al. 1992) were used to estimate survival and recapture

probabilities, where recapture refers to the resighting of a live, banded individual. The effects of transients (an excess of birds only encountered once) were accounted for using an age-since-first-encounter model. Birds seen at a locality for the first time consist of a mixture of transients and residents. This leads to survival rates that are biased low during the subsequent time step, but after that, survival estimates are unbiased (Pradel et al. 1996). During the first year of the study, the proportion of transients is not known and therefore a corrected survival estimate could not be calculated for the period 2001/2002. Estimates also were not calculated for 2007/2008 and later split years because estimates of recapture and survival probabilities are strongly correlated and their separate estimates are unreliable for the final years of any survival analysis.

Various survival models were fitted in program MARK 5.1 (White and Burnham 1999), the best four being reported. The most general model allowed for differences among localities and years in survival and recapture rates, and for the proportion of transients to vary among localities and years. Simpler models with a constant proportion of transients and where survival varied over the years in parallel at both localities were also considered.

The CMR methods assume equal survival and recapture among individuals. A further assumption is that the time span during which individuals were recaptured or resighted was short relative to the survival interval. Violation of the latter assumption leads to apparent heterogeneity in survival. Survival estimates are not overly sensitive to violation of these assumptions but, if the violations are strong, survival rates may be biased low (Hargrove and Borland 1994). Heterogeneity in survival and recapture rates leads to overdispersion in the dataset, which was estimated using the median- \hat{c} approach in program MARK (White and Burnham 1999): \hat{c} was 1.6, which indicates moderate overdispersion. This estimate was used to adjust the confidence interval. Model selection was based on QAICc — Akaike's information criterion adjusted for overdispersion and sample sizes (Burnham and Anderson 2002). Further assumptions were that bands were not misread or lost. Misreading of bands would cause heterogeneity in recapture rates and possibly estimates of survival biased towards being large. Loss of bands would result in survival estimates that are biased towards being small.

Results

Diet

Numbers of diet samples collected at localities in each year are shown in Table App.2 (Appendix). Samples were obtained at Dassen Island in all years from 1991 to 2009, at Robben Island in all years from 1989 to 2009, at Boulders in 2003, at Dyer Island from 1991 to 1997 and 2008 to 2009, at St Croix Island in 1996, 1999, 2006 and 2009, and at Bird Island (Algoa Bay) in 1992, 1993, 1999, 2001 and from 2005 to 2009.

At Dassen Island from 1991 to 2009, anchovy dominated the diet of African penguins in most years, contributing an average of 76% by mass of food collected from them (Figure 2). Sardine contributed an average of 6%. Except from 1997 to 1999 and 2005 to 2006, the combined contribution of

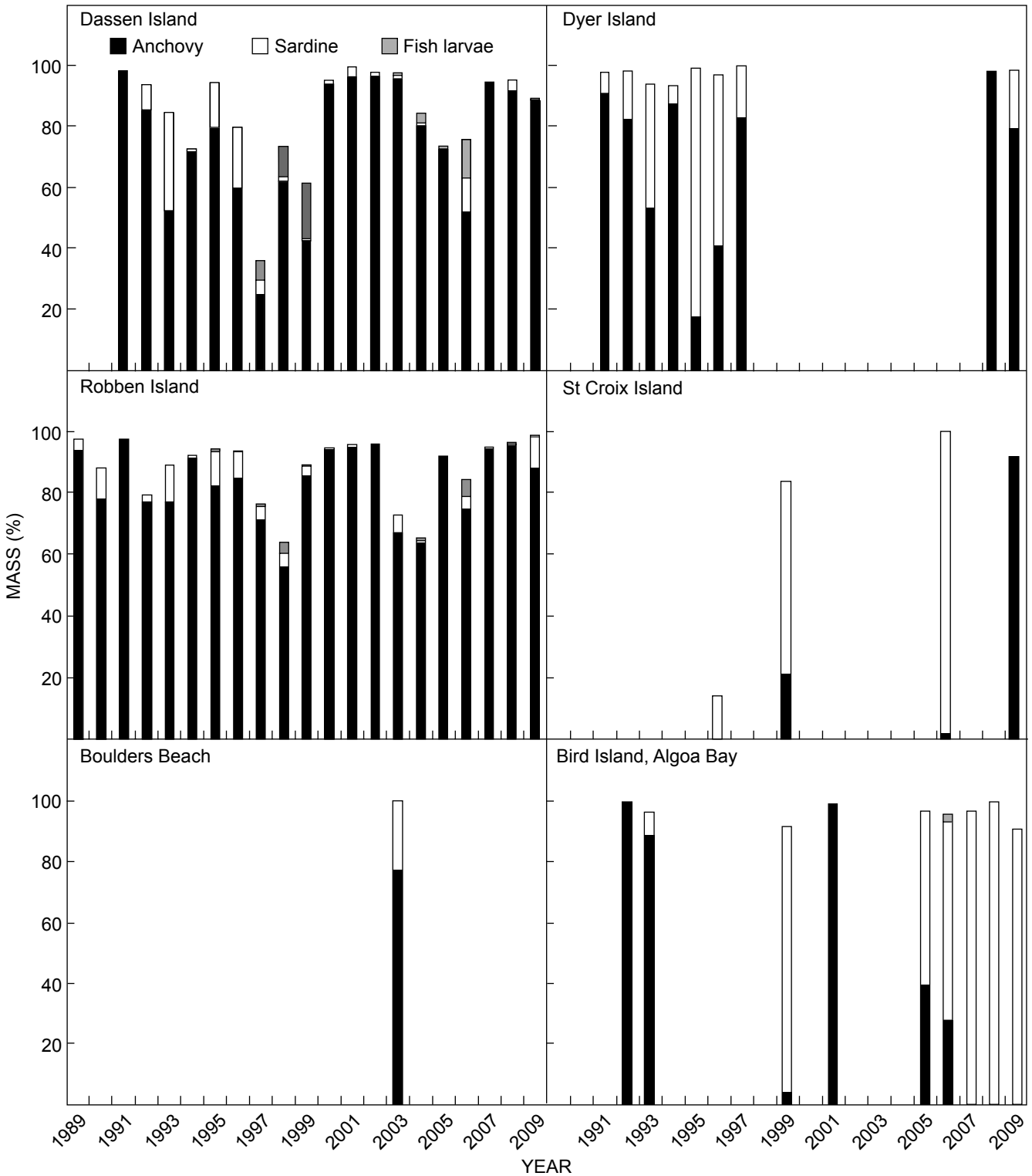


Figure 2: The annual contribution of anchovy, sardine and fish larvae (mostly anchovy and sardine) to the diet of adult African penguins returning to localities during the breeding season, 1989–2009. Robben Island was sampled in all 21 years, Boulders in only one year. For sample sizes see Table App.2 (Appendix)

these two species to the diet was >70%. From 1997 to 1999 and in 2006, considerable quantities of fish larvae, which probably were anchovy or sardine, contributed to the diet.

At Robben Island from 1989 to 2009, anchovy contributed >55% by mass of the diet in all years, the average value being 84% (Figure 2). Sardine contributed an average of

Downloaded by [41.4.190.59] at 06:12 11 August 2011

3%. In all years except 1998 and 2004, the combined contribution of these two species to the diet was >70%.

The diet at Boulders was sampled in 2003, when anchovy (77% by mass) and sardine (23%) contributed almost all the food collected.

At Dyer Island, anchovy dominated the diet in six (1991–1993, 1997, 2008, 2009) of the eight years sampled and sardine in the other two years (1995, 1996; Figure 2). The average contribution by mass to the diet was 70% for anchovy and 27% for sardine. In all years sampled, these two species together contributed >93% of the diet.

At St Croix Island, anchovy dominated the diet in 2009 and sardine in 1999 and 2006 (Figure 2). In 1996, when only six samples were collected, most food identified was squid *Loligo* sp. (86% by mass). Overall in these four years, anchovy contributed 29% of the diet by mass and sardine 44%.

At Bird Island (Algoa Bay), anchovy (1992–1993, 2001, 2007, 2009) or sardine (1999, 2005, 2006, 2008) dominated the diet in the nine years sampled (Figure 2). Overall, anchovy contributed an average of 57% of the diet by mass and sardine 39%.

Numbers breeding

Western Cape

Between 1991 and 2010, African penguins bred at 13 localities in the Western Cape (Underhill et al. 2006). The maximum annual counts of nests at 12 of these localities are shown in Figure 3. The thirteenth locality is De Hoop Nature Reserve, which was colonised by African penguins for the first known time in 2003, held about 15 breeding pairs in 2005 (Underhill et al. 2006), but was extinct by 2008 on account of ready access to the penguins by terrestrial, mammalian predators (LJW unpublished data). Of the other 12 localities, seven occur west of Cape Point and five between Cape Point and Cape Agulhas (Figure 1).

At Lambert's Bay, the northernmost breeding locality in the province, numbers fluctuated around a mean of 22 nests from 1991 to 1998 and then decreased. Breeding ceased at this locality in 2006 (Crawford et al. 2008b).

African penguins breed at three islands in Saldanha Bay, all of which are within the West Coast National Park. At Malgas Island, numbers of nests counted decreased from 99 in 1992 to 17 in 2010. At Marcus Island, numbers of nests decreased from slightly more than 200 in 1991 and 1994 to 21 in 2010. At Jutten Island, numbers of nests fluctuated around a mean of 910 (SD = 216, with counts above 1 300 nests in 1994 and 2001) from 1991 to 2005, but decreased to fewer than 300 in 2010. In the West Coast National Park, numbers of nests fluctuated around a mean of 1 166 (± 227 , maximum above 1 500 in 2001) from 1991 to 2002, but reduced to 333 in 2010.

At Vondeling Island, fewer than 250 nests were counted from 1991 to 1995. Numbers increased to >500 nests (mean 587 ± 48) from 2000 to 2005 before decreasing to 164 in 2010. Vondeling Island was recolonised by Cape fur seals *Arctocephalus pusillus pusillus* in the 1990s (Kirkman 2009). At Dassen Island, counts of nests were <10 000 (mean $8 730 \pm 996$) from 1991 to 1997 but increased to >20 000 (mean $22 440 \pm 1 723$, maximum 24 901 in 2004) from 2001 to 2005. They decreased to <5 000 in 2010. At Robben Island, which was recolonised by African penguins in 1983

(Crawford et al. 1995b), there was an increasing trend in numbers of nests up until a peak of more than 8 500 nests in 2004, and then a decrease to <2 700 nests from 2008 to 2010.

At Boulders, which was colonised by African penguins in 1982 (Crawford et al. 2000a), counts of nests of African penguins increased to a peak of 1 227 in 2005 and then decreased to <1 000 from 2007 to 2010; 933 nests were counted in 2010. At another locality in False Bay, Seal Island, where breeding space is limited by Cape fur seals (Crawford et al. 1994), numbers of breeding African penguins showed stability between 1991 and 2010 (mean count of nests 78 ± 14). At Stony Point, east of False Bay, which was colonised by African penguins in 1985 (Whittington et al. 1996), counts of nests were <100 up until 1998 and increased to 480 and 487 in 2009 and 2010 respectively.

At Dyer Island, where 22 655 pairs of African penguins bred in 1979 (Shelton et al. 1984), counts of nests decreased from 7 579 in 1992 to fewer than 2 000 from 2007 to 2010. At neighbouring Geyser Island, counts of nests decreased from 328 in 1991 to 50 in 1995 and fewer than 10 after 1996. Cape fur seals breed at Geyser Island and limit breeding sites for African penguins.

In the Western Cape, estimates of numbers of nests doubled from an average of 17 753 ($\pm 1 968$) between 1991 and 1998 to an average of 34 749 ($\pm 2 638$) from 2001 to 2005, and then decreased to some 11 000 in 2009 and 2010 (Figure 4). These numbers were significantly correlated with the combined spawner biomass of anchovy and sardine in the same year ($r = 0.647$, $n = 21$, $p < 0.002$), the previous year ($r = 0.709$, $n = 21$, $p < 0.001$) and the year before that ($r = 0.706$, $n = 21$, $p < 0.001$).

At Dassen Island, there was a large increase in the contribution of potential nests, i.e. not active at the time of counting, to the overall count of occupied nests, from 5% in 1999 to 60% in 2006 and 2010 (Figure 5). From 2004 to 2010, potential nests contributed an average of 52% ($\pm 8\%$) of occupied nests. At Robben Island, there also was an increase in the contribution of potential nests to the overall count of occupied nests, from <10% from 2000 to 2003 to an average of 16% ($\pm 8\%$) from 2005 to 2010 (Figure 5).

Eastern Cape

African penguins breed at six islands in Algoa Bay in the Eastern Cape: three are in the St Croix group of islands in the west of the bay, and three in the Bird group of islands in the east (Figure 1). Sporadic counts of penguin nests were made at these islands in the early to mid-1990s, with more consistent coverage from 1998.

Most African penguins in the Eastern Cape are at St Croix Island, where the mean of four counts of nests conducted between 1993 and 2001 was 16 411 ($\pm 2 375$), which halved to 7 194 ($\pm 2 256$, $n = 7$) from 2003 to 2009. Counts of African penguin nests at Jahleel Island decreased from over 500 in 1993 and 2000 to fewer than 200 after 2006 (Figure 6). Counts of nests at Brenton Island averaged 31 (± 5.7 , $n = 6$) from 1993 to 2005, dropping to 6 (± 3.9 , $n = 4$) from 2007 to 2010.

Numbers of penguin nests counted at Seal and Stag islands in the Bird group of islands were stable from 1991

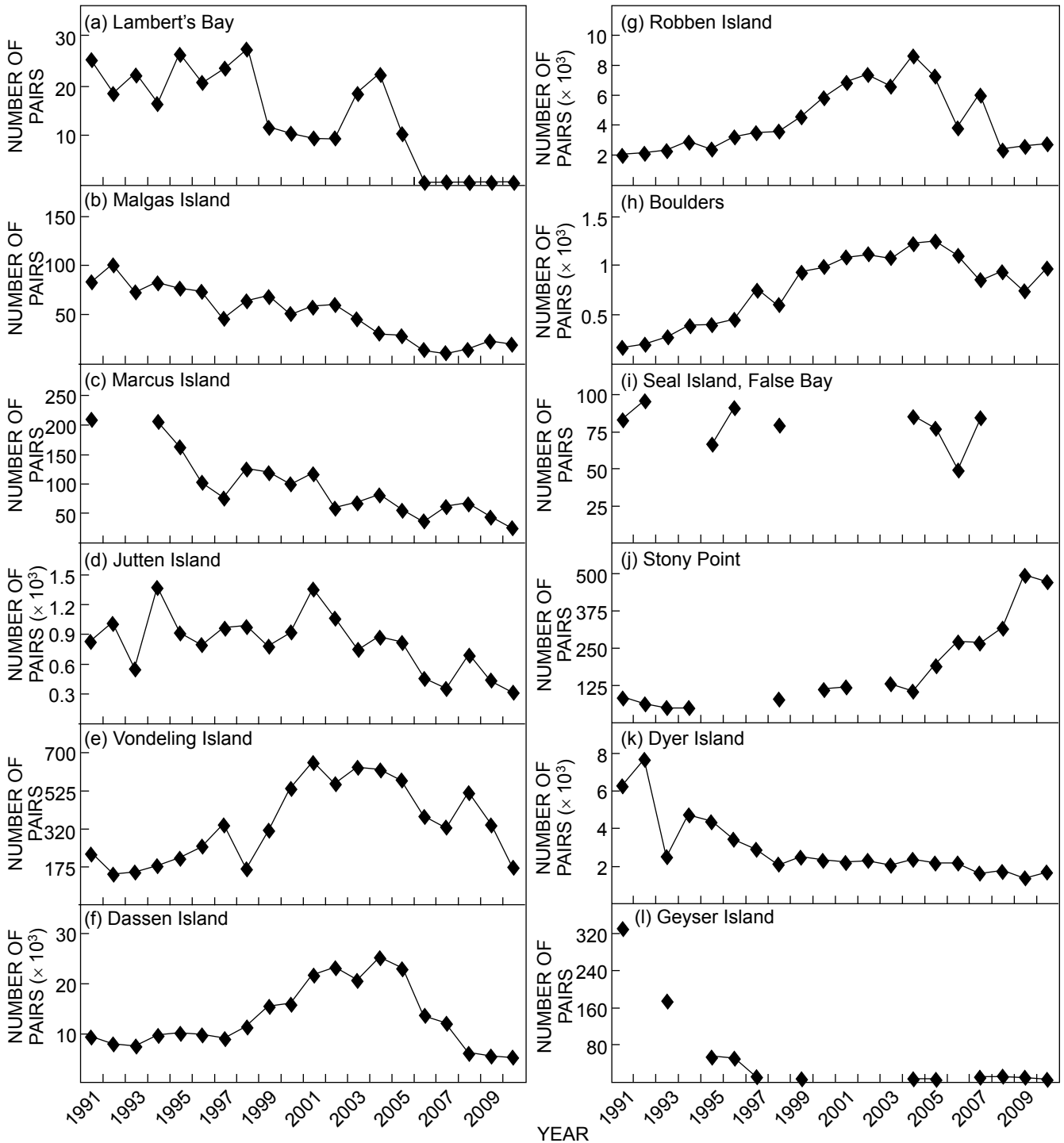


Figure 3: Trends in counts of nests occupied by African penguins at 12 breeding localities in the Western Cape over the 20-year period 1991–2010. Localities are ordered in accordance with their positioning around the South African coastline, from north to south and west to east

to 2005, averaging 351 (± 23 , $n = 7$) and 22 (± 3 , $n = 8$) respectively. They decreased to averages of 106 (± 27 , $n = 3$) and 8 (± 3 , $n = 4$) from 2007 to 2010 respectively. There was substantial fluctuation in numbers of nests counted at Bird Island, which averaged 2 973 ($\pm 1 139$, $n = 15$) from 1991 to 2010, reaching a high of 5 376 in 2000 and a low of 936 in 2003.

Overall estimates of the numbers of African penguin nests in the Eastern Cape halved from an average of 21 175 ($\pm 2 178$, $n = 4$) between 1993 and 2001 to 10 057 ($\pm 2 505$, $n = 7$) from 1993 to 2010 (Figure 4). The numbers were significantly correlated with the combined spawner biomass of anchovy and sardine in the same year ($r = 0.669$, $n = 10$, $p < 0.05$).

Downloaded by [41.4.190.59] at 06:12 11 August 2011

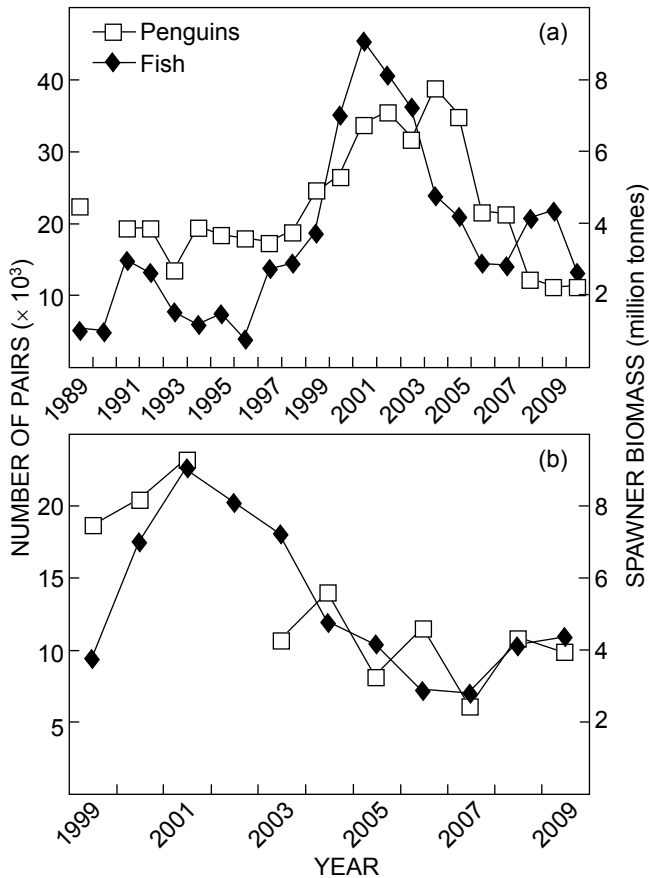


Figure 4: Comparison of trends in estimates of the combined spawner biomass of anchovy and sardine and numbers of nests occupied by African penguins in (a) the Western Cape, 1989–2010 and (b) the Eastern Cape, 1999–2009

Numbers moulting

At Dassen Island, numbers of adults moulting around the coastline increased from some 12 000 in 1994/1995 and 1995/1996 to almost 26 000 in 2001/2002 and then decreased to <500 in 2008/2009 and 2009/2010 (Figure 7). At Robben Island, numbers of adults moulting around the coastline increased from some 3 000 in 1988/1989 and 1989/1990 to almost 16 000 in 2003/2004 and then decreased to <4 000 in 2008/2009 and 2009/2010 (Figure 7).

Adult survival

Model selection favoured a model with different proportions of transients at Dassen and Robben islands, but additive effects of locality and year on survival (Model 1, Table 1). The recapture rate depended on interactive effects of year and locality. The second best model (Model 2, Table 1) was nearly as well supported as the best model and allowed for an interaction between year and locality on survival. Both models yielded similar survival rates (Tables App.3 and App.4, Appendix). At both Dassen and Robben islands, adult survival declined after 2002/2003, markedly so after 2003/2004 (Figure 8). At Dassen Island, Model 1 suggested

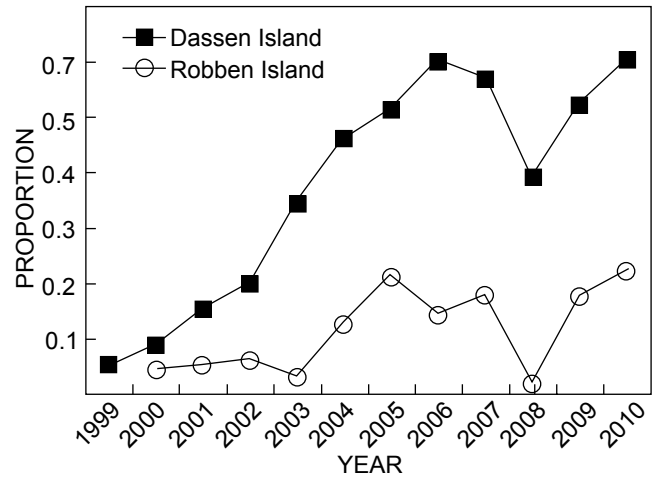


Figure 5: Trends in the proportion of occupied nests at Dassen and Robben islands that were classified as potential nests, 1999–2010. Occupied nests include both active and potential nests

it decreased by 0.24 between 2002/2003 and 2006/2007; at Robben Island by 0.22 in the same period (Table App.3, Appendix).

The recapture rates obtained with Model 1 varied from 0.51 to 0.59 at Dassen Island and from 0.16 to 0.48 at Robben Island (Table App.3, Appendix). The proportion of transients was estimated to be 8% at Dassen Island and 27% at Robben Island.

Discussion

Diet

Anchovy or sardine dominated the diet of African penguins at all localities that were sampled off South Africa during 1989–2009, as they also did in most previous studies (Figure App.1, Appendix). This highlights the dependence of the African penguin for food on small, shoaling pelagic fish, which in Namibia includes pelagic (bearded) goby *Sufflogobius bibarbatus* (Crawford et al. 1985, Ludynia et al. 2010). To date, the single exception to this pattern was in 1980 at Possession Island, southern Namibia, where there was a scarcity of small, shoaling pelagic fish after the collapse of Namibia's sardine stock (Crawford et al. 1987). At this time, numbers of African penguins at Possession Island were decreasing rapidly (Cordes et al. 1999) and they fed mainly on cephalopods (Crawford et al. 1985). From 1979 to 1981, cephalopods, mainly *Loligo reynaudii*, contributed 13% by mass of the diet of African penguins at St Croix Island (Randall and Randall 1986). Food items such as cephalopods and fish larvae, which in the present study were encountered in the diets of penguins at Dassen, Robben, St Croix and Bird (Algoa Bay) islands, are probably fed upon when shoals of larger anchovy, sardine and other forage fish species are less available.

In diet samples collected using the water-offloading technique, it is possible that the contribution of sardine was underestimated because larger organisms may be more difficult to retrieve than smaller prey. Sardine eaten by African

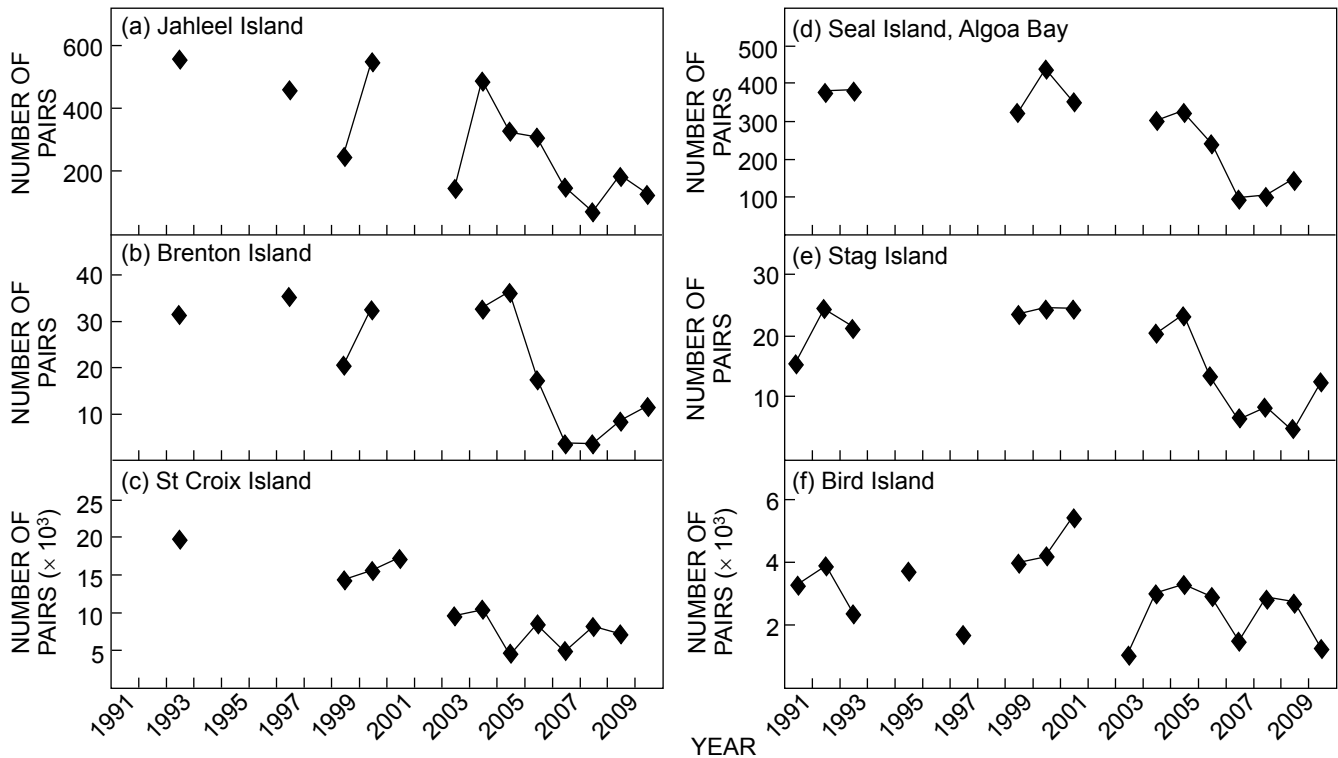


Figure 6: Trends in counts of nests occupied by African penguins at six breeding localities in Algoa Bay over the 20-year period 1991–2010. Localities are ordered in accordance with their positioning around the South African coastline, from west to east

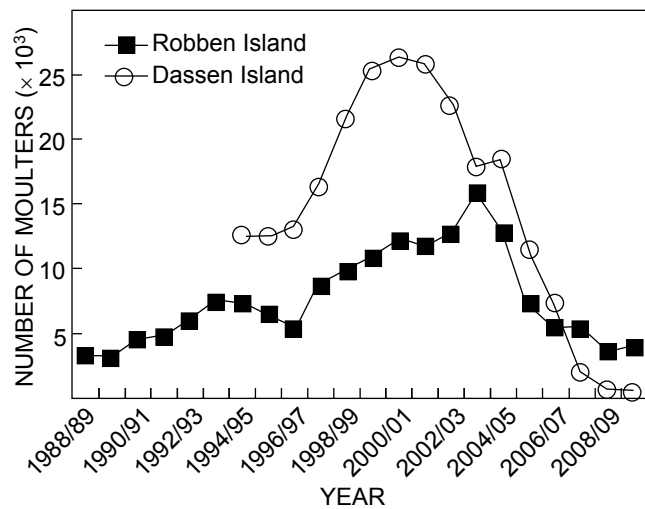


Figure 7: Trends in estimates of adult African penguins moulting around the coastlines of Dassen and Robben islands, 1988/1989–2009/2010

penguins are often larger than are anchovy (Rand 1960). This would not be the case for samples collected in the 1950s by Davies (1955, 1956) and Rand (1960) off the Western Cape and by Matthews (1961) off Namibia, who shot penguins at sea. Sardine dominated the diet of penguins collected in these studies. Those samples also may have been from

penguins away from their breeding localities and need not have reflected food fed to chicks.

In the present study, diet samples were collected during the breeding period and, although some samples may have been taken from non-breeding birds, it is likely that the samples reflect food fed to chicks. In the non-breeding period, on fattening trips undertaken before and after moult, penguins may forage considerably farther from colonies and their diet may be different. For example, birds may travel from West Coast colonies to the South Coast where both anchovy and sardine spawn (Barange et al. 1999, Barham et al. 2008). Feeding conditions before breeding may influence both the decision to participate in breeding and breeding success (e.g. Crawford et al. 2008c). Therefore, although Figure 2 indicates that from 1989 to 2009 anchovy dominated the diet of penguins during the breeding period at Dassen and Robben islands, sardine may have played an important role in determining the pre-breeding condition of birds. During the 1980s and 1990s, growth of the colonies at Robben Island, Boulders and Stony Point, which were all formed between 1982 and 1985, was strongly related to the recovery of South Africa’s sardine stock (Cury et al. 2000, Crawford et al. 2001).

Food and trends in numbers

The significant correlations between the combined biomass of anchovy and sardine in South Africa and the numbers of penguin nests counted in both the Western Cape and the Eastern Cape suggest that the overall abundance of food

Table 1: Summary of model selection for capture-mark-recapture analysis of African penguins at Dassen and Robben islands. The models consisted of two components describing survival (ϕ) and recapture (P) rates. The models included the following factors: year, locality (loc), and effect of transients (trans), either in a fully interactive way (*) or as additive effects (+). If only a two-way interaction was included, this is indicated by (-) between the two factors involved. The table shows Akaike's information criterion (AICc) adjusted for overdispersion and sample size (QAICc), and the difference in QAICc between each model and the best model (Δ QAICc). AICc weights give the relative support of a particular model compared to the other models in the set, K is the number of estimated parameters, and QDeviance is the deviance adjusted for overdispersion

Model	QAICc	Δ QAICc	AICc weights	K	QDeviance
1 $\phi(\text{trans:loc+year})P(\text{loc*year})$	22 111.195	0.000	0.443	24	518.736
2 $\phi(\text{trans:loc:year})P(\text{loc*year})$	22 111.805	0.610	0.327	30	507.309
3 $\phi(\text{trans+loc+year})P(\text{loc*year})$	22 113.379	2.184	0.149	23	522.926
4 $\phi(\text{trans*loc*year})P(\text{loc*year})$	22 114.596	3.401	0.081	38	494.040

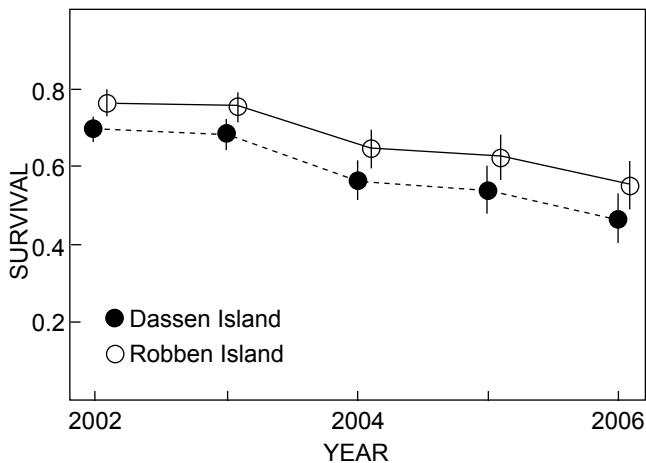


Figure 8: Survival estimates for African penguins on Dassen and Robben islands, obtained from Model 1 (see Table 1). The x-axis indicates the starting year of the relevant survival interval. For example, the first estimate corresponds to the interval 2002/2003. The vertical lines represent 95% confidence intervals

influences the numbers of birds that breed. In Namibia, numbers of penguins breeding also were significantly related to prey abundance (Crawford 2007). Similarly to the collapse of penguins off Namibia, the recent decrease of penguins off South Africa was coincidental with a large reduction in abundance and an altered distribution of sardine (Fairweather et al. 2006, de Moor et al. 2008). However, unlike the situation in Namibia, there was a high abundance of anchovy during the recent demise of South Africa's penguins (de Moor et al. 2008). This suggests that the regional or local availability of prey also may be important in influencing penguin numbers.

In the Western Cape, the number of occupied nests of African penguins increased rapidly between 1998 and 2004, when anchovy and sardine were particularly plentiful (Underhill et al. 2006). Numbers in this province then decreased sharply, from nearly 38 000 pairs in 2004 to 11 000–12 000 pairs from 2008 to 2010, the lowest level yet recorded. This was in spite of the combined biomass of anchovy and sardine being greater in 2008 and 2009 than it was from 1989 to 1998 (Figure 4), and was probably a consequence of recent eastward displacements of both anchovy and sardine. During breeding, African penguins need to source food for chicks within about 40 km of breeding

localities (Heath and Randall 1989, Petersen et al. 2006, Pichegru et al. 2010).

Abstinence from breeding (e.g. Crawford et al. 1999, 2008a) may mean that in some years counts of occupied nests underestimate the numbers of African penguins at localities. The increased proportions of potential nests in the overall counts of active and potential nests at Dassen and Robben islands in the mid- and late-2000s (Figure 5) suggest that fewer birds may have participated in breeding in this period. Nevertheless, counts around the coastline of Dassen Island of adults in the feather-shedding phase of moult decreased by 98% between 2004/2005 and 2009/2010, an even more severe decrease than the 80% observed for occupied nests at this locality. Around Robben Island, estimates of adults moulting feathers decreased by 70% in the same period, which was equivalent to the decrease of 69% in the number of occupied nests. African penguins may moult at localities other than those at which they breed (Whittington et al. 2005a), so it is likely that some penguins from Dassen Island moulted at localities farther east, especially after stocks of prey fish shifted south and east (Wolfaardt et al. 2009a). However, at eastern colonies, only at Stony Point was the number of moulting adults (about 5 000 in 2009/2010, LJW unpublished data) greater than expected from the number breeding at the locality: about 500 pairs bred at Stony Point in 2009 and 2010. The large and sustained decreases in both numbers breeding and numbers of adults moulting at localities north-west of Cape Town indicate a substantial reduction in the penguin population of that region.

Between 1997 and 2005, the centre of gravity of purse-seine catches of sardine moved 400 km south-east (Fairweather et al. 2006), placing sardine increasingly distant from localities in the north of the Western Cape. At the northernmost locality, Lambert's Bay, breeding stopped in 2006 (Crawford et al. 2008b). Colonies to the east of Cape Point should have been less disadvantaged or favoured by the eastward displacement of prey species. In agreement with this expectation, numbers of nests at Boulders peaked in 2005 and then did not decrease as severely as for colonies farther north, numbers at Seal Island in False Bay were stable and, after 2004, numbers at Stony Point increased markedly. In 2003, African penguins initiated breeding at a new locality, De Hoop, to the east of all other extant breeding localities in the Western Cape (Underhill et al. 2006). The only exception to the anticipated response of penguins in the Western Cape to an eastward displacement

of prey was at the Dyer Island archipelago (Dyer and Geyser islands), located between Stony Point and De Hoop, where numbers decreased. A possible reason for this may be that the exploitation rate of sardine by the purse-seine fishery in the region between Cape Point and Cape Agulhas increased in the 2000s, especially after 2004 (Coetzee et al 2008). Regional coherence in trends of African penguins at breeding localities has been noted previously and is thought to be attributable to a similar food environment existing around localities in the same vicinity (Crawford et al. 1990, 1995a, 2001, Crawford 1998, Underhill et al. 2006).

That food became scarce during the mid-2000s in the north and central portions of the Western Cape, for seabirds that feed preferentially on anchovy and sardine, is suggested by several other observations. Numbers of Cape gannets breeding in the Western Cape decreased (Crawford et al. 2007b). There was a marked decrease in survival of adult Cape gannets at both Lambert's Bay and Malgas Island after 2003 (Altwegg et al. 2008). At Malgas Island, measured breeding success for Cape gannets in the 2005/2006 season was low — 0.02 chicks per pair (Grémillet et al. 2008). In the same season, all gannets at Lambert's Bay abandoned breeding at an early stage (Crawford et al. 2007b). In 2005, Cape gannets in the Western Cape fed primarily on low-energy fishery discards, had a higher foraging effort and exploited a greater surface area of the ocean than did those in the Eastern Cape, which ate mainly anchovy and sardine (Pichegru et al. 2007). The proportions of populations of Cape cormorant *Phalacrocorax capensis* and swift tern *Thalasseus bergii* in the Western Cape that bred in the south of that province increased (Crawford et al. 2008d, Crawford 2009). In 2005 and 2006, the combined biomass of young-of-the-year anchovy and sardine, which recruit off South Africa's west coast from the austral autumn to spring (Crawford 1980), and form an important part of the diet of seabirds in the region in this period (Berruti et al. 1993), was lower than at any stage since 1996 (Merkle and Coetzee 2010).

Local factors, such as oiling (Crawford et al. 2000b, Underhill et al. 2000) and predation (Crawford et al. 2001, Underhill et al. 2006), also may influence trends at localities. For example, almost 20 000 African penguins were oiled in 2000 (Crawford et al. 2000b). Predation of penguins by Cape fur seals was thought unsustainable at Lambert's Bay, where seals killed 4% of adults annually (Crawford et al. 2001) and at Dyer Island, where 872 penguins were killed by seals over 12 months in 1995 and 1996 (Marks et al. 1997). Such predation may increase when fish species that form a large component of the diet of Cape fur seals, such as anchovy, sardine, horse mackerel *Trachurus* spp. and hake *Merluccius* spp., become scarce (David 1987, Makhado et al. 2006). Ongoing efforts are made to manage adverse local influences on penguins, e.g. to remove seals that prey on seabirds around their breeding localities (Makhado et al. 2009), to minimise the impact of oil spills on African penguins (Barham et al. 2006, 2008) and to mitigate outbreaks of disease (Waller and Underhill 2007).

In the Eastern Cape, numbers of breeding African penguins halved from 21 000 pairs in 2001 to about 10 000 pairs in 2003 (Crawford et al. 2009). Counts have since fluctuated around 10 000 occupied nests. The decrease in

numbers breeding coincided with a large increase in the purse-seine catch of sardine taken to the east of Cape St Francis. This catch was minimal before 1990 and remained below 10 000 t until 2002. It then increased sharply, reaching 23 000 t in 2003, and may have reduced the availability of sardine to penguins (Crawford et al. 2009). The decrease of penguins also coincided with construction of a harbour at Coega (Port of Ngqura), which is 7.5 km west of St Croix Island, the main penguin breeding locality in the Eastern Cape. Construction of the harbour commenced in 2002, was completed in 2005, and included considerable dredging (Crawford et al. 2009). Turbidity in the vicinity of the harbour was elevated in 2004 and early 2005, but returned to pre-construction levels by September 2005 (Klages and Bornman 2005). The increased turbidity may have hampered feeding by penguins. However, the big decreases in the region's main penguin colonies at St Croix and Bird islands occurred between 2001 and 2003 and Bird Island is some 60 km east of Coega. Furthermore, the large decreases after 2005 in numbers of penguins breeding at each of the four smaller localities in Algoa Bay, Jahleel, Brenton, Seal and Stag islands, followed a period of three years (2003–2005) in which the average annual catch of sardine in the region was 20 000 t and were coincidental with the largest catch yet of sardine in the region, 30 000 t in 2006 (Crawford et al. 2009). In that year, the overall biomass of sardine between Mossel Bay and Port Alfred was estimated to be 298 000 t (Merkle and Coetzee 2010), but finer-scale estimates will be required to estimate the impact of catches on local availability of prey.

Survival

Capture-mark-recapture analysis points to a large decrease in survival of adult penguins at both Dassen and Robben islands after 2003/2004. Although extreme heterogeneity in recapture rates can cause apparent time trends in survival (Devineau et al. 2006), this seems only to happen if the recapture rates are very low, and it would not lead to such steep trends as observed in Figure 8. Further, the estimate of \hat{c} did not indicate extreme heterogeneity and the recapture rates were reasonably high, thereby providing a degree of confidence in the results. Based on measurements of breeding success and assuming an age at first breeding of four years and a first-year survival rate of 0.51 per annum, survival of adult African penguins would need to be of the order of 0.85 per annum to maintain a population in equilibrium (Crawford et al. 2006). The recent estimates of adult survival at Dassen and Robben islands were considerably less than this, in accord with decreased counts of nests and adults at the two localities.

Life-history theory predicts that seabirds will respond to a reduction in food abundance by changes in behaviour and breeding effort, thereby buffering adult survival (Cairns 1987), but some studies indicate a trade-off in which survival of breeding seabirds may be reduced by food shortage (Harris et al. 1998, Furness 2007). A penguin will expend more energy the further it travels to forage, which will reduce the effective resources delivered to chicks and increase adult maintenance costs (Boersma et al. 2009). Adult penguins in poor condition at the conclusion of breeding may find it difficult to accumulate sufficient energy reserves to moult

successfully, especially if prey is located far from colonies, as may have been the case for colonies in the northern Western Cape following the eastward displacement of prey. If moult is deferred, worn plumage may lead to reduced insulation, thereby increasing maintenance costs.

Because large numbers of dead African penguins were not seen ashore, it is assumed that most died at sea. One report was received on 13 July 2009 of 'hundreds of dead penguins' off Buffelsbaai (Figure 1; DM Harebottle, Animal Demography Unit, University of Cape Town, *in litt.*).

Concluding remarks

The recent decrease in the numbers of penguins breeding in South Africa reduced the global population to 26 000 pairs in 2009, the smallest level yet recorded (BirdLife International 2010). The degree of threat now facing the African penguin may be gauged by comparing the present population with losses of 40 000 pairs off southern Namibia between 1956 and 2000 (44 years, Crawford et al. 2001), of 10 000 pairs in Algoa Bay between 2001 and 2003 (two years, Crawford et al. 2009) and of 24 000 pairs in the Western Cape between 2004 and 2009 (five years), each of which may have been influenced by a reduced availability of food.

In the late 1990s and early 2000s, the biomass of both anchovy and sardine off South Africa was high (de Moor et al. 2008). As a consequence, large catches of both species were sanctioned. However, although there were substantial shifts in the distributions of the two species, no spatial management of catches was applied. It is necessary further to investigate the possible influence of fishing on the availability of food to African penguins and, if it is found to be important, how it may be managed. Research in this regard is being pursued *inter alia* under the auspices of the Pelagic Scientific Working Group of South Africa's Department of Agriculture, Forestry and Fisheries. For example, the feasibility of assessing the usefulness of closing areas around African penguin colonies to purse-seine fishing in order to enhance food densities around colonies is being investigated (Anon. 2010). Surveys to assess the density of prey in the vicinity of penguin breeding colonies have been initiated (Merkle et al. 2009). Several hypotheses that relate specific measures of sardine and anchovy abundance or density, at various temporal and spatial scales, to population processes of African penguins have been proposed (Moseley et al. 2011) and it is hoped to collect data that will enable these hypotheses to be tested.

Three pivotal breeding localities for African penguins in South Africa are at Dassen, Dyer and St Croix islands, each of which since 1979 has supported of the order of 20 000 breeding pairs or more (Crawford et al. 1995a, 2009, Underhill et al. 2006). Recruitment of first breeders can be expected at Dyer Island if the distribution of forage fish off the Western Cape shifts to the south-east (cf. Shelton et al. 1984), or at western localities, of which Dassen Island has the largest penguin colony, if it reverts to the north-west (cf. Crawford et al. 2001, Underhill et al. 2006). There are no suitable breeding localities between Dyer Island and Algoa Bay, a distance of some 600 km, which makes it particularly desirable to ensure healthy numbers of breeding birds at Dyer and St Croix islands. The cessation of breeding at Lambert's Bay in 2006 increased separation of breeding localities in Namibia and the Western Cape to 600 km

(Crawford et al. 2008b). Further fragmentation of the African penguin population should be avoided because it removes loci for future population growth should the distribution of forage prey change (Underhill et al. 2006). Fragmentation also may alter population sex ratios, either through demographic stochasticity in small populations or through increased mortality associated with dispersal (Banks et al. 2007). In monogamous species, biased sex ratios may reduce rates of pair formation and reproductive output (Nel et al. 2003). The example of the African penguin emphasises the need for fisheries management, in accounting for the food requirements of dependent species, to consider not only the overall abundance of prey, but also its local availability.

Acknowledgements — We thank all who assisted with the collection of diet samples, with the counts of nests and moulting birds and with the banding and resighting of African penguins, including many volunteers on teams of Earthwatch Institute that visited Robben Island. We are especially grateful to TM Leshoro (Robben Island Museum) for his assistance at Robben Island and to CapeNature, who through DC Nel, AJ Williams and AC Wolfaardt pioneered much of the monitoring at Dassen Island. We are grateful to JC Coetzee and JJ van der Westhuizen (Department of Agriculture, Forestry and Fisheries), who provided information on the distribution, biomass and catch of anchovy and sardine. We thank CapeNature, Department of Environmental Affairs, Dyer Island Conservation Trust, Earthwatch Institute, the National Research Foundation, through its SEACHANGE programme, and the Norway South Africa Fisheries Agreement for funding this research. We are grateful to SAFRING for developing and maintaining the database on banded birds. We thank CapeNature, Department of Agriculture, Forestry and Fisheries, Department of Environmental Affairs, SANParks and the South African Navy for facilitating transport to island breeding localities. We are grateful to JC Coetzee and three anonymous reviewers who made valuable comments on the initial manuscript.

References

- Altwegg R, Crawford RJM, Underhill LG, Williams AJ. 2008. Long-term survival of de-oiled Cape gannets after the *Castillo de Bellver* oil spill of 1983. *Biological Conservation* 141: 1924–1929.
- Anon. 2010. Island Closure Task Team report. Unpublished report, No. MCM/2010/SWG-PEL/51. Cape Town: Branch Fisheries, Department of Agriculture, Forestry and Fisheries.
- Barange M, Hampton I, Roel BA. 1999. Trends in the abundance and distribution of anchovy and sardine on the South African continental shelf in the 1990s, deduced from acoustic surveys. In: Pillar SC, Moloney CL, Payne AIL, Shillington FA (eds), *Benguela dynamics: impacts of variability on shelf-sea environments and their living resources*. *South African Journal of Marine Science* 19: 367–391.
- Barham PJ, Crawford RJM, Underhill LG, Wolfaardt AC, Barham BJ, Dyer BM, Leshoro TM, Meyer MA, Navarro RA, Oschadleus D, Upfold L, Whittington PA, Williams AJ. 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.
- Barham PJ, Underhill LG, Crawford RJM, Altwegg R, Leshoro TM, Bolton D, Dyer BM, Upfold L. 2008. Hand-reared African Penguin chicks orphaned in the *Treasure* oil spill in 2000: survival, age at first breeding and breeding productivity. *Bird Conservation International* 18: 1–9.
- Banks SC, Piggott MP, Stow AJ, Taylor AC. 2007. Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions. *Canadian Journal of Zoology* 85: 1065–1079.

- Berruti A, Underhill LG, Shelton PA, Moloney C, Crawford RJM. 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.
- BirdLife International. 2010. Species factsheet: *Spheniscus demersus*. Available at <http://www.birdlife.org> [accessed 27 May 2010].
- Boersma PD, Rebstock GA, Frere E, Moore SE. 2009. Following the fish: penguins and prey productivity in the South Atlantic. *Ecological Monographs* 79: 59–76.
- Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: a practical information-theoretic approach* (2nd edn). New York: Springer.
- Cairns DK. 1987. Seabirds as indicators of marine food supplies. *Biological Oceanography* 5: 261–287.
- Coetzee JC, van der Lingen CD, Hutchings L, Fairweather TP. 2008. Has the fishery contributed to a major shift in the distribution of South African sardine? *ICES Journal of Marine Science* 65: 1676–1688.
- Cooper J. 1984. Changes in resource division among four breeding seabirds in the Benguela upwelling system, 1953–1978. In: Ledger JA (ed.), *Proceedings 5th Pan-African Ornithological Congress. Southern African Ornithological Society: Johannesburg*. pp 217–230.
- Cordes I, Crawford RJM, Williams AJ, Dyer BM. 1999. Decrease of African Penguins at the Possession Island group, 1956–1995: contrasting trends for colonial and solitary breeders. *Marine Ornithology* 27: 129–138.
- Crawford RJM. 1980. Seasonal patterns in South Africa's Western Cape purse-seine fishery. *Journal of Fish Biology* 16: 649–664.
- Crawford RJM. 1998. Responses of African penguins to regime changes of sardine and anchovy in the Benguela system. In: Pillar SC, Moloney CL, Payne AIL, Shillington FA (eds), *Benguela dynamics: impacts of variability on shelf-sea environments and their living resources*. *South African Journal of Marine Science* 19: 355–364.
- Crawford RJM. 2007. Food, fishing and seabirds in the Benguela upwelling system. *Journal of Ornithology* 148 (Suppl 2): S253–S260.
- Crawford RJM. 2009. A recent increase of swift terns *Thalasseus bergii* off South Africa – the possible influence of an altered abundance and distribution of prey. *Progress in Oceanography* 83: 398–403.
- Crawford RJM, Boonstra HGvD. 1994. Counts of moulting and breeding jackass penguins – a comparison at Robben Island, 1988–1993. *Marine Ornithology* 22: 213–219.
- Crawford RJM, Boonstra HGvD, Dyer BM, Upfold L. 1995b. Recolonization of Robben Island by African penguins, 1983–1992. In: Dann P, Norman I, Reilly P (eds), *The penguins: ecology and management*. Chipping Norton, Australia: Surrey Beatty. pp 333–363.
- Crawford RJM, Cruickshank RA, Shelton PA, Kruger I. 1985. Partitioning of a goby resource amongst four avian predators and evidence for altered trophic flow in the pelagic community of an intense, perennial upwelling system. *South African Journal of Marine Science* 3: 215–228.
- Crawford RJM, David JHM, Shannon LJ, Kemper J, Klages NTW, Roux J-P, Underhill LG, Ward VL, Williams AJ, Wolfaardt AC. 2001. African penguins as predators and prey – coping (or not) with change. *South African Journal of Marine Science* 23: 435–447.
- Crawford RJM, Davis SA, Harding R, Jackson LF, Leshoro TM, Meyer MA, Randall RM, Underhill LG, Upfold L, van Dalsen AP, van der Merwe E, Whittington PA, Williams AJ, Wolfaardt AC. 2000b. Initial impact of the *Treasure* oil spill on seabirds off western South Africa. *South African Journal of Marine Science* 22: 157–176.
- Crawford RJM, Dundee BL, Dyer BM, Klages NTW, Meyer MA, Upfold L. 2007b. 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 RJM, Dyer BM. 1995. Responses by four seabird species to a fluctuating availability of Cape anchovy *Engraulis capensis* off South Africa. *Ibis* 137: 329–339.
- Crawford RJM, Dyer BM, Brooke RK. 1994. Breeding nomadism in southern African seabirds – constraints, causes and conservation. *Ostrich* 65: 231–246.
- Crawford RJM, Hemming M, Kemper J, Klages NTW, Randall RM, Underhill LG, Venter AD, Ward VL, Wolfaardt AC. 2006. Molt of the African Penguin, *Spheniscus demersus*, in relation to its breeding season and food availability. *Acta Zoologica Sinica* 52 (Supplement): 444–447.
- Crawford RJM, Jahncke J. 1999. Comparison of trends in abundance of guano-producing seabirds in Peru and southern Africa. *South African Journal of Marine Science* 21: 145–156.
- Crawford RJM, Makhado AB, Upfold L, Dyer BM. 2008c. Mass on arrival of rockhopper penguins at Marion Island correlated with breeding success. *African Journal of Marine Science* 30: 185–188.
- Crawford RJM, Ryan PG, Williams AJ. 1991. Seabird consumption and production in the Benguela and western Agulhas ecosystems. *South African Journal of Marine Science* 11: 357–375.
- Crawford RJM, Sabarros PS, Fairweather T, Underhill LG, Wolfaardt AC. 2008d. Implications for seabirds off South Africa of a long-term change in the distribution of sardine. *African Journal of Marine Science* 30: 177–184.
- Crawford RJM, Shannon LJ, Whittington PA. 1999. Population dynamics of the African Penguin *Spheniscus demersus* at Robben Island, South Africa. *Marine Ornithology* 27: 139–147.
- Crawford RJM, Shannon LJ, Whittington PA, Murison G. 2000a. Factors influencing growth of the African penguin colony at Boulders, South Africa, 1985–1999. *South African Journal of Marine Science* 22: 111–119.
- Crawford RJM, Shannon LV, Pollock DE. 1987. The Benguela ecosystem. Part IV. The major fish and invertebrate resources. *Oceanography and Marine Biology Annual Review* 25: 353–505.
- Crawford RJM, Tree AJ, Whittington PA, Visagie J, Upfold L, Roxburg KJ, Martin AP, Dyer BM. 2008b. Recent distributional changes of seabirds in South Africa: is climate having an impact? *African Journal of Marine Science* 30: 189–193.
- Crawford RJM, Underhill LG, Coetzee JC, Fairweather T, Shannon LJ, Wolfaardt AC. 2008a. Influences of the abundance and distribution of prey on African penguins *Spheniscus demersus* off western South Africa. *African Journal of Marine Science* 30: 167–175.
- Crawford RJM, Underhill LG, Upfold L, Dyer BM. 2007a. An altered carrying capacity of the Benguela upwelling ecosystem for African penguins (*Spheniscus demersus*). *ICES Journal of Marine Science* 64: 570–576.
- Crawford RJM, Whittington PA, Martin AP, Tree AJ, Makhado AB. 2009. Population trends of seabirds breeding in South Africa's Eastern Cape, and the possible influence of anthropogenic and environmental change. *Marine Ornithology* 37: 159–174.
- Crawford RJM, Williams AJ, Hofmeyr JH, Klages NTW, Randall RM, Cooper J, Dyer BM, Chesselet Y. 1995a. Trends of African penguin *Spheniscus demersus* populations in the 20th century. *South African Journal of Marine Science* 16: 101–118.
- Crawford RJM, Williams AJ, Randall RM, Randall BM, Berruti A, Ross GJB. 1990. Recent population trends of jackass penguins *Spheniscus demersus* off southern Africa. *Biological Conservation* 52: 229–243.
- Cury P, Bakun A, Crawford RJM, Jarre A, Quiñones RA, Shannon LJ, Verheye HM. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist”

- ecosystems. *ICES Journal of Marine Science* Symposium Edition 57: 603–618.
- David JHM. 1987. Diet of the South African fur seal (1974–1985) and an assessment of competition with fisheries in southern Africa. *South African Journal of Marine Science* 5: 693–713.
- Davies DH. 1955. The South African pilchard (*Sardinops ocellata*) – bird predators, 1953–54. *Investigational Report of the Sea Fisheries Research Institute, South Africa* 18: 1–32.
- Davies DH. 1956. The South African pilchard (*Sardinops ocellata*) and maasbanker (*Trachurus trachurus*) – bird predators, 1954–55. *Investigational Report of the Sea Fisheries Research Institute, South Africa* 23: 1–40.
- de Moor CL, Butterworth DS, Coetzee JC. 2008. Revised estimates of abundance of South African sardine and anchovy from acoustic surveys adjusting for echosounder saturation in earlier surveys and attenuation effects for sardine. *African Journal of Marine Science* 30: 219–232.
- Devineau O, Choquet R, Lebreton JD. 2006. Planning capture-recapture studies: straightforward precision, bias, and power calculations. *Wildlife Society Bulletin* 34: 1028–1035.
- Duffy DC, Wilson RP, Ricklefs RE, Broni SC, Veldhuis H. 1987. Penguins and purse seiners: competition or coexistence? *National Geographic Research* 3: 480–488.
- Fairweather TP, van der Lingen CD, Booth AJ, Drapeau L, van der Westhuizen JJ. 2006. Indicators of sustainable fishing for South African sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*. *African Journal of Marine Science* 28: 661–680.
- Furness RW. 2007. Responses of seabirds to depletion of food stocks. *Journal of Ornithology* 148 (Suppl 2): S247–S252.
- Grémillet D, Pichegru L, Kuntz G, Woakes AG, Wilkinson S, Crawford RJM, Ryan PG. 2008. A junk-food hypothesis for gannets feeding on fishery waste. *Proceedings of the Royal Society, London Biological Series* 18: 1–8.
- Hargrove JW, Borland CH. 1994. Pooled population parameter estimates from mark-recapture data. *Biometrics* 50: 1129–1141.
- Harris MP, Wanless S, Elston DA. 1998. Age-related effects of a nonbreeding event and a winter wreck on the survival of shags *Phalacrocorax aristotelis*. *Ibis* 140: 310–314.
- Heath RGM, Randall RM. 1989. Foraging ranges and movements of jackass penguins (*Spheniscus demersus*) established through radio telemetry. *Journal of Zoology* 217: 367–379.
- Hockey PAR, Dean WRJ, Ryan PG. 2005. *Roberts birds of southern Africa* (7th edn). Cape Town: John Voelcker Bird Book Fund.
- Kemper J, Underhill LG, Crawford RJM, Kirkman SP. 2007. Revision of the conservation status of seabirds and seals breeding in the Benguela ecosystem. In: Kirkman SP (ed.), *Final report of the BCLME (Benguela Current Large Marine Ecosystem) project on top predators as biological indicators of ecosystem change in the BCLME*. Cape Town: Avian Demography Unit. pp 697–704.
- Kirkman SP. 2009. Evaluating seal-seabird interactions in southern Africa: a critical review. *African Journal of Marine Science* 31: 1–18.
- Klages, NTW, Bormann, TG. 2005. Port of Ngqura marine biomonitoring programme. Winter 2005. IECM Report No. C128. Port Elizabeth: Institute for Environmental and Coastal Management, Nelson Mandela Metropolitan University.
- Lebreton JD, Burnham KP, Clobert J, Anderson DR. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67–118.
- Ludynia K, Roux J-P, Jones R, Kemper J, Underhill LG. 2010. Surviving off junk: low-energy prey dominates the diet of African penguins *Spheniscus demersus* at Mercury Island, Namibia, between 1996 and 2009. *African Journal of Marine Science* 32: 563–572.
- Makhado AB, Crawford RJM, Underhill LG. 2006. Impact of predation by Cape fur seals *Arctocephalus pusillus pusillus* on Cape gannets *Morus capensis* at Malgas Island, Western Cape, South Africa. *African Journal of Marine Science* 28: 681–687.
- Makhado AB, Meyer MA, Crawford RJM, Underhill LG, Wilkie C. 2009. The efficacy of culling seals seen preying on seabirds as a means of reducing seabird mortality. *African Journal of Ecology* 47: 335–340.
- Marks MA, Brooke RK, Gildenhuys AM. 1997. Cape fur seal (*Arctocephalus pusillus pusillus*) predation on Cape Cormorants (*Phalacrocorax capensis*) and other birds at Dyer Island, South Africa. *Marine Ornithology* 25: 9–12.
- Matthews JP. 1961. The pilchard of South West Africa (*Sardinops ocellata*) and the maasbanker (*Trachurus trachurus*) – bird predators, 1957–1958. *Investigational Report South West African Marine Research Laboratory* 3: 1–35.
- Merkle D, Coetzee JC. 2010. Acoustic biomass time series data for island closure task team. Island Closure Task Team Report. Unpublished report, No. MCM/2010/SWG-PEL/16. Cape Town: Branch Fisheries, Department of Agriculture, Forestry and Fisheries.
- Merkle D, Coetzee JC, Rademan J. 2009. Hydro-acoustic monitoring of the biomass of pelagic fish available to penguins in a 20 km radius around Robben Island. Unpublished report, No. MCM/2009/SWG-PEL/36. Cape Town: Branch Marine and Coastal Management, Department of Environmental Affairs and Tourism.
- Moseley C, Wanless R, Altwegg R, Crawford R[JM], Badenhorst A, Coetzee J[C]. 2011. Hypotheses for relating anchovy and sardine abundance with African Penguin population processes. Unpublished report, No. 2011/SWG-PEL/03. Cape Town: Branch Fisheries, Department of Agriculture, Forestry and Fisheries.
- Nel DC, Taylor F, Ryan PG, Cooper J. 2003. Population dynamics of the wandering albatross *Diomedea exulans* at Marion Island: longline fishing and environmental influence. *African Journal of Marine Science* 25: 503–517.
- Petersen SL, Ryan PG, Grémillet D. 2006. Is food availability limiting African Penguins at Boulders? A comparison of foraging effort at mainland and island colonies. *Ibis* 148: 14–26.
- Pichegru L, Grémillet D, Crawford RJM, Ryan PG. 2010. Marine no-take zone rapidly benefits endangered penguin. *Biology Letters* 6: 498–501.
- Pichegru L, Ryan PG, van der Lingen CD, Coetzee J, Ropert-Coudert Y, Grémillet D. 2007. Foraging behaviour and energetics of Cape gannets *Morus capensis* feeding on live prey and fishery discards in the Benguela upwelling system. *Marine Ecology Progress Series* 350: 127–136.
- Pradel R, Hines JE, Lebreton J-D, Nichols JD. 1996. Capture-recapture survival models taking into account of transients. Report No. 96-03. Montpellier: Unite de biometrie, Université Montpellier II.
- Rand RW. 1960. The biology of guano-producing seabirds. 2. The distribution, abundance and feeding habits of the Cape penguin, *Spheniscus demersus*, off the south-western coast of the Cape Province. *Investigational Report of the Sea Fisheries Research Institute, South Africa* 41: 1–28.
- Rand RW. 1963a. The biology of guano-producing seabirds. 4. Composition of colonies on the Cape islands. *Investigational Report of the Sea Fisheries Research Institute, South Africa* 43: 1–32.
- Rand RW. 1963b. The biology of guano-producing seabirds. 5. Composition of colonies on the South West African islands. *Investigational Report of the Sea Fisheries Research Institute, South Africa* 46: 1–26.
- Randall RM, Davidson IS. 1981. Device for obtaining food samples from the stomachs of jackass penguins. *South African Journal of Wildlife Research* 11: 121–125.
- Randall RM, Randall BM. 1986. The diet of jackass penguins *Spheniscus demersus* in Algoa Bay, South Africa, and its bearing on population declines elsewhere. *Biological Conservation* 37: 119–134.
- Randall RM, Randall BM, Cooper J, Frost PGH. 1986. A new census

- method for penguins tested on jackass penguins *Spheniscus demersus*. *Ostrich* 57: 211–215.
- Randall RM, Randall BM, Cooper J, la Cock GD, Ross GJB. 1987. Jackass penguin *Spheniscus demersus* movements, inter-island visits, and settlement. *Journal of Field Ornithology* 58: 445–455.
- Roy C, van der Lingen CD, Coetzee JC, Lutjeharms JRE. 2007. Abrupt environmental shift associated with changes in the distribution of Cape anchovy *Engraulis encrasicolus* spawners in the southern Benguela. *African Journal of Marine Science* 29: 309–319.
- Shannon LJ, Crawford RJM. 1999. Management of the African Penguin *Spheniscus demersus* – insights from modelling. *Marine Ornithology* 27: 119–128.
- Shelton PA, Crawford RJM, Cooper J, Brooke RK. 1984. Distribution, population size and conservation of the jackass penguin *Spheniscus demersus*. *South African Journal of Marine Science* 2: 217–257.
- Underhill LG, Crawford RJM. 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 LG, Crawford RJM, Wolfaardt AC, Whittington PA, Dyer BM, Leshoro TM, Ruthenberg M, Upfold L, 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 LG, Whittington PA, Crawford RJM, Wolfaardt AC. 2000. Five years of monitoring African penguins *Spheniscus demersus* after the *Apollo Sea* oil spill: a success story made possible by ringing. *Vogelwarte* 40: 315–318.
- Waller LJ, Underhill LG. 2007. Management of avian cholera *Pasteurella multocida* outbreaks on Dyer Island, South Africa, 2002–2005. *African Journal of Marine Science* 29: 105–111.
- White GC, Burnham KP. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46: S120–139.
- Whittington PA, Hofmeyr JH, 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.
- Whittington PA, Randall RM, Crawford RJM, Wolfaardt AC, Klages NTW, Randall BM, Bartlett PA, Chesselet YJ, Jones R. 2005b. Patterns of immigration to and emigration from breeding colonies by African penguins. *African Journal of Marine Science* 27: 205–213.
- Whittington PA, Randall RM, Randall BM, Wolfaardt AC, Crawford RJM, Klages NTW, Bartlett PA, Chesselet YJ, Jones R. 2005a. Patterns of movement of the African penguin in South Africa and Namibia. *African Journal of Marine Science* 27: 215–229.
- Wilson RP. 1984. An improved stomach pump for penguins and other seabirds. *Journal of Field Ornithology* 55: 9–12.
- Wilson RP. 1985. The jackass penguin (*Spheniscus demersus*) as a pelagic predator. *Marine Ecology Progress Series* 25: 219–227.
- Wolfaardt AC, Underhill LG, Crawford RJM. 2009a. Comparison of moult phenology of African penguins *Spheniscus demersus* at Robben and Dassen islands. *African Journal of Marine Science* 31: 19–29.
- Wolfaardt AC, Underhill LG, Visagie J. 2009b. Breeding and moult phenology of African penguins *Spheniscus demersus* at Dassen Island. *African Journal of Marine Science* 31: 119–132.

Appendix: Supplementary material

Table App.1: Numbers of African penguins banded in different years, the resightings of which at Dassen and Robben islands were used to estimate survival of adult birds at these two localities

Year	Number banded		
	Dassen Island	Robben Island	Total
1972		3	3
1978		1	1
1980	1		1
1981		2	2
1983	1	1	2
1985	5	8	13
1986	1		1
1987	5	6	11
1988	4	3	7
1989	20	11	31
1990	18	19	37
1991	47	32	79
1992	53	44	97
1993	32	42	74
1994	499	100	599
1995	15	7	22
1996	23	14	37
1997	50	44	94
1998	204	219	423
1999	480	110	590
2000	3 309	4 480	7 789
2001	129	383	512
2002	143	340	483
2003	140	375	515
2004	39	110	149
2005		40	40
2006		35	35
2007		27	27
2008	235		235
1972–2008	5 453	6 456	11 909

Table App.2: Numbers of food samples obtained from adult African penguins returning to six localities during the breeding season, 1989–2009

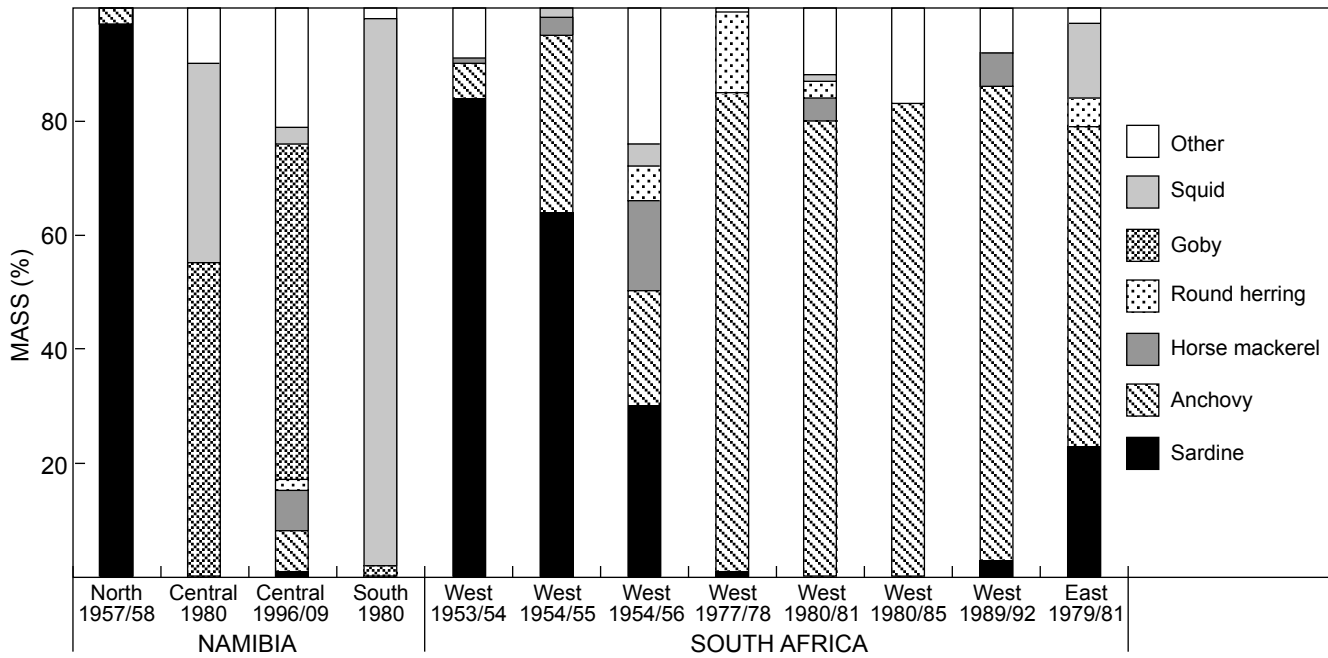
Year	Number of food samples					
	Dassen	Robben	Boulders	Dyer	St Croix	Bird
1989		21				
1990		104				
1991	50	114		112		
1992	66	112		92		5
1993	109	109		51		11
1994	73	75		12		
1995	82	112		19		
1996	145	127		19	6	
1997	72	131		8		
1998	22	135				
1999	121	121			5	10
2000	31	99				
2001	62	107				10
2002	50	117				
2003	98	107	12			
2004	51	94				
2005	24	95				18
2006	35	75			5	25
2007	20	84				10
2008	60	51		19		5
2009	57	68		21	28	43
Total	1 228	2 058	12	353	44	137
Mean	65	98	12	39	11	15

Table App.3: Survival and recapture estimates from Model 1 (Table 1). In addition to the estimates, the table shows standard errors (SE) and lower (LCI) and upper (UCI) bounds of the confidence interval

Year	Estimate	SE	LCI	UCI
<i>Survival, Dassen Island</i>				
2002/2003	0.697	0.017	0.662	0.729
2003/2004	0.682	0.021	0.640	0.721
2004/2005	0.561	0.025	0.511	0.610
2005/2006	0.535	0.032	0.473	0.597
2006/2007	0.462	0.033	0.399	0.526
<i>Survival, Robben Island</i>				
2002/2003	0.765	0.016	0.731	0.795
2003/2004	0.752	0.019	0.714	0.787
2004/2005	0.644	0.025	0.593	0.691
2005/2006	0.620	0.029	0.562	0.675
2006/2007	0.548	0.031	0.487	0.608
<i>Recapture rate, Dassen Island</i>				
2002	0.584	0.019	0.547	0.621
2003	0.517	0.019	0.479	0.554
2004	0.532	0.022	0.489	0.574
2005	0.511	0.028	0.456	0.565
2006	0.591	0.038	0.514	0.663
2007	0.521	0.051	0.422	0.619
<i>Recapture rate, Robben Island</i>				
2002	0.179	0.031	0.126	0.247
2003	0.280	0.017	0.247	0.315
2004	0.277	0.016	0.246	0.310
2005	0.165	0.013	0.141	0.193
2006	0.398	0.025	0.350	0.447
2007	0.477	0.033	0.412	0.543

Table App.4: Survival and recapture estimates from Model 2 (Table 1). In addition to the estimates, the table shows standard errors (SE) and lower (LCI) and upper (UCI) bounds of the confidence interval

Year	Estimate	SE	LCI	UCI
<i>Survival, Dassen Island</i>				
2002/2003	0.673	0.021	0.630	0.712
2003/2004	0.696	0.026	0.642	0.745
2004/2005	0.552	0.030	0.492	0.611
2005/2006	0.528	0.038	0.453	0.602
2006/2007	0.533	0.066	0.404	0.657
<i>Survival, Robben Island</i>				
2002/2003	0.795	0.020	0.752	0.831
2003/2004	0.747	0.027	0.691	0.796
2004/2005	0.663	0.039	0.582	0.735
2005/2006	0.618	0.045	0.528	0.702
2006/2007	0.522	0.036	0.451	0.592
<i>Recapture rate, Dassen Island</i>				
2002	0.574	0.019	0.536	0.612
2003	0.527	0.020	0.488	0.566
2004	0.530	0.023	0.484	0.575
2005	0.517	0.030	0.459	0.574
2006	0.606	0.041	0.523	0.684
2007	0.473	0.062	0.356	0.593
<i>Recapture rate, Robben Island</i>				
2002	0.215	0.039	0.149	0.301
2003	0.274	0.018	0.240	0.312
2004	0.278	0.018	0.244	0.314
2005	0.162	0.015	0.134	0.193
2006	0.391	0.027	0.340	0.445
2007	0.493	0.035	0.425	0.560



Matthews 1961 (19); Crawford et al. 1985 (93); Ludynia et al. 2010 (620); Crawford et al. 1985 (66); Davies 1955 (16);
 Davies 1956 (112); Rand 1960 (247); Cooper 1984 (30); Wilson 1985 (556); Duffy et al. 1987 (667);
 Crawford and Dyer 1995 (341); Randall and Randall 1986 (240)

Figure App.1: Published estimates of the contribution (% by mass, except for Cooper 1984 and Duffy et al. 1987, which were % by number; % by number was also presented in Crawford et al. 1985 but was converted to % mass using information in Crawford et al. 1991) of different prey items to the diet of African penguins. Studies are listed by region, anticlockwise around the southern African coast from Namibia to the Eastern Cape, and within region chronologically. Sources and sample sizes are indicated in the same sequence. Taxa that contributed 10% or more of the diet in any study are indicated; less important prey items are grouped as 'Other'. Duffy et al. (1987) noted that sardine and horse mackerel were also present in their samples but did not indicate the extent of their contributions to the numbers of prey items sampled

Downloaded by [41.4.190.59] at 06:12 11 August 2011