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Surviving off junk: low-energy prey dominates the diet of African penguins *Spheniscus demersus* at Mercury Island, Namibia, between 1996 and 2009

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The diet of African penguins *Spheniscus demersus* in Namibia consisted mainly of sardine *Sardinops sagax* in the 1950s. Since the collapse of pelagic fish stocks in the 1970s, birds fed mainly on bearded (pelagic) goby *Sufflogobius bibarbatus*, a low-energy prey species. We present diet data for African penguins breeding at Mercury Island, the largest colony for this species in Namibia, between 1996 and 2009. Bearded goby was the main prey item throughout the study period, both in terms of frequency of occurrence (67.8%; SD 31.2) and in terms of mass (59.2%; SD 31.5). Diet composition varied throughout the year as well as between years; birds occasionally fed on a variety of fish species other than bearded goby. In Namibia, poor prey abundance is considered as a major factor contributing to the decline of penguin numbers after the collapse of the sardine stocks. However, bearded goby appears to be relatively abundant along Namibia's southern coast and low prey quality rather than low abundance appears to be a key factor influencing population dynamics of African penguins and other marine top predators in southern Namibia.

Keywords: African penguin, bearded (pelagic) goby, Benguela upwelling system, diet, Mercury Island, prey quality, *Spheniscus demersus*, *Sufflogobius bibarbatus*

Introduction

African penguins *Spheniscus demersus* are pelagic feeders, their main prey being sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* when available (Rand 1960, Matthews 1961, Wilson 1985, Randall and Randall 1986, Crawford and Dyer 1995, Petersen et al. 2006). In Namibia, their diet consisted mainly of sardine in the 1950s (Matthews 1961). A combination of overfishing of pelagic fish stocks and environmental changes led to the collapse of the sardine stock and a decline of the anchovy stock off Namibia in the early 1970s, and ecosystem degradation (Armstrong and Thomas 1995, Cury and Shannon 2004, de Young et al. 2004, Roux and Shannon 2004, van der Lingen et al. 2006).

Subsequently, the diet of African penguins in Namibia was found to be dominated by bearded (pelagic) goby *Sufflogobius bibarbatus* (Crawford and Shelton 1981, Crawford et al. 1985, Ludynia 2007, Ministry of Fisheries and Marine Resources [MFMR] unpublished data). The energetic value of bearded goby is 55–61% of that of sardine and anchovy (Balmelli and Wickens 1994, KL unpublished data). Low-energy prey and a decrease in prey's nutritional quality have been shown to lead to reduced breeding success and to influence population trends in seabirds (Wanless et al. 2005, Mavor 2005, 2006, Harris et al. 2007). Indeed, the African penguin population of Namibia has declined by 72% since the 1950s (Kemper et al. 2001) and diet quality has been suggested as a potentially important factor in this decline (Kemper et al. 2007).

Given the downward trend in African penguin numbers and its recent listing as Endangered (IUCN 2010), continued research and monitoring of the population's ecology including trophic relationships is essential. Here, we update information on the diet of African penguins in Namibia by assessing a diet sampling time-series collected between 1996 and 2009 at Mercury Island, the most important African penguin breeding site in Namibia and close to the northern extreme of the species' range. We assess intra- and interannual variation in the composition and energy content of the diet, and discuss implications of the findings for the population dynamics of African penguins and other top predator populations in Namibia.

Material and methods

Mercury Island (25°38′ S, 14°50′ E; Figure 1) is located along the southern Namibian coast in the northern Benguela

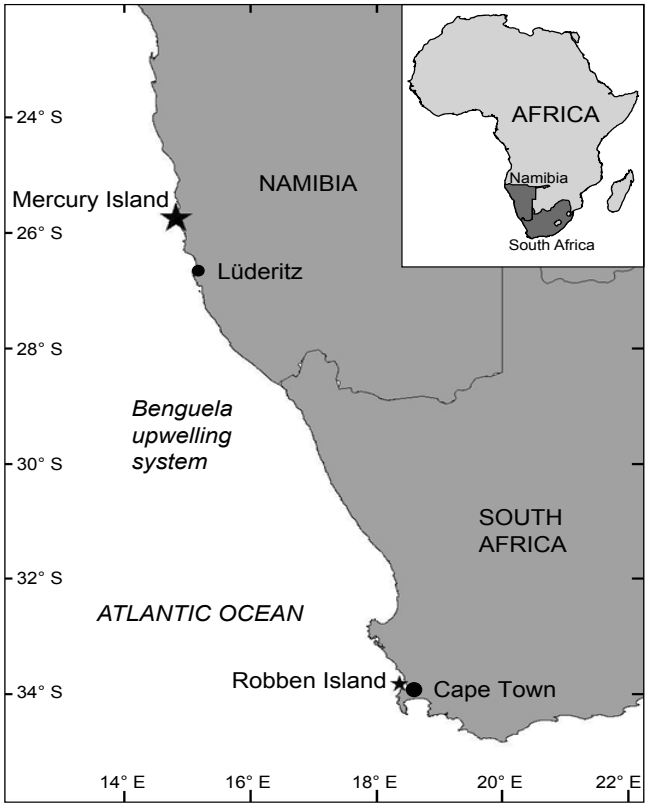

Figure 1: Map of the west coast of Namibia and South Africa showing the locality of Mercury Island

upwelling system, and in 2009 supported the largest African penguin breeding colony in Namibia with 2 565 breeding pairs (measured as numbers of nests containing eggs or chicks at peak breeding; MFMR unpublished data). For the purpose of this study, years were defined as from 1 July of one year to 30 June of the next year to account for the penguin breeding season at Mercury Island, where breeding activities peak roughly between November and February (Kemper 2006).

Diet sampling

Penguins with visibly full stomachs were captured as they arrived at the colony. Diet samples were obtained from them using the stomach-flushing method following Wilson (1984). Regurgitation was induced by filling the birds' stomachs with water. Birds were only flushed once, therefore the entire stomach content was not necessarily obtained. Between one and 10 penguins (median 8) were sampled per sampling session.

Samples were collected, drained and weighed. Prey items were identified to species level according to Bianchi et al. (1999). Identification was based on complete specimens as well as remains (mainly heads, tails and flesh in the case of fish). Otoliths or cephalopod beaks were not used for species identification. Caudal length was measured for complete fish specimens. The frequency of occurrence was calculated as the percentage of samples collected per month that contained a given species. Samples were pooled per month to determine the percentage mass contribution of each species to the total wet mass of the samples for that month.

Differences in diet composition between years were revealed using a correspondence analysis (Greenacre 1984) in the open source software package R 2.10.1 (http://www.r-project.org, Nenadić and Greenacre 2007). A chi-squared (χ^2) test was used to test for differences in length distributions of bearded goby between years. Energy content of prey species was calculated using bomb calorimetry of homogenised samples of entire fish representative of the various size classes found in the penguin diet (bearded goby 3.68 kJ g^{-1} wet mass, juvenile hake *Merluccius capensis* 3.52 kJ g^{-1}, squid (unidentified species) 3.24 kJ g^{-1}; KL unpublished data), except the species for which energy content were previously estimated by Balmelli and Wickens (1994; anchovy 6.03 kJ g^{-1} wet mass, sardine 6.59 kJ g^{-1}, horse mackerel *Trachurus capensis* 5.65 kJ g^{-1}). For remaining species, the average value for teleosts was used (5.91 kJ g^{-1} wet mass; Balmelli and Wickens 1994).

Results

Diet composition

A total of 620 diet samples was collected during 34 months between July 1996 and January 2009. Between one and 46 samples were collected per month (median 16 samples); some months were not sampled (Tables 1, 2; see also Appendices 1 and 2). Diet composition varied throughout the year as well as between years (Tables 1, 2). Bearded goby was the main prey item throughout the study period, both in terms of frequency of occurrence and in terms of mass and was present in every month sampled. The mean frequency of occurrence per month was 67.8% (SD 31.2) (Table 1) and the mean percentage of mass was 59.2% (SD 31.5) after pooling all samples within months (Table 2).

Other prey species that were present in the diet with relatively high frequencies of occurrence were anchovy, hake, horse mackerel and squid (Table 1). In terms of mass, pelagic species (anchovy, sardine, round herring *Etrumeus whiteheadi* combined), hake and horse mackerel constituted large percentages of mass in single months, but were not found consistently during the entire study period (Table 2). Squid was present in the diet in 32 months and in 38.6% of all individual samples; it constituted 3.1% of the total mass (Table 2). The mean mantle length of 17 intact individuals from 2005 and 2008 was 3.2 cm (SD 1.0). Other species which sporadically made up a substantial percentage of the diet were mullet *Liza* spp. (e.g. 23.4% and 52.4% of total mass in March 2003 and in October 2003 respectively), gurnard *Chelidonichthys* spp. (e.g. 13.2% in October 2001) and unidentified fish (including unidentifiable remains; e.g. large proportions in October and November 1996, February 1999, November and December 2001, November 2003 and January 2004 of between 15.5% and 67.4%).

The correspondence analysis showed that bearded goby was the main factor grouping five out of the 10 years sampled according to the frequency of occurrence of prey species in the diet (Figure 2). Correspondence analysis

Table 1: Frequency of occurrence (percentage of samples containing the species per month) ± SD of the main prey species per year in African penguin diet samples collected at Mercury Island, Namibia, between 1996 and 2009; *n* = number of months sampled per year and number of samples per year

Year	*n* (months, samples)	Frequency of occurrence ± SD (%)							
		Bearded goby	Anchovy	Sardine	Hake	Horse mackerel	Squid	Round herring	Others
1996/1997	4, 45	69.58 ± 36.98	16.67 ± 23.57	0.00	0.00	7.08 ± 12.05	46.25 ± 36.83	0.83 ± 1.67	65.83 ± 44.75
1998/1999	5, 54	89.25 ± 18.95	15.26 ± 23.99	2.67 ± 5.96	4.00 ± 8.94	5.08 ± 8.17	33.35 ± 24.4	0.00	16.36 ± 17.12
2000/2001	1, 46	76.09	50.00	0.00	4.35	4.35	34.78	4.35	23.91
2001/2002	8, 201	57.25 ± 33.40	26.82 ± 21.75	1.84 ± 3.20	10.34 ± 13.12	24.09 ± 16.41	53.61 ± 16.09	12.57 ± 17.17	43.08 ± 28.15
2002/2003	5, 104	72.50 ± 13.15	17.50 ± 18.96	0.00	30.00 ± 9.53	17.50 ± 22.60	15.00 ± 16.89	0.00	24.38 ± 19.06
2003/2004	4, 96	23.96 ± 13.77	37.50 ± 22.31	7.29 ± 9.85	33.33 ± 21.78	33.33 ± 22.82	51.04 ± 7.12	12.50 ± 19.54	67.71 ± 10.96
2004/2005	2, 24	100.00 ± 0	37.50 ± 35.36	6.25 ± 8.84	28.13 ± 13.26	34.38 ± 22.10	15.63 ± 4.42	3.13 ± 4.42	15.63 ± 4.42
2005/2006	1, 16	50.00	62.50	62.50	0.00	18.75	43.75	0.00	12.50
2007/2008	2, 24	68.75 ± 44.19	40.63 ± 48.61	18.75 ± 8.84	25.00 ± 17.68	0.00	21.88 ± 4.42	0.00	6.25 ± 8.84
2008/2009	2, 10	100.00 ± 0	80.00 ± 0	20.00 ± 0	40.00 ± 28.28	60.00 ± 0	50.00 ± 42.43	0.00	30.00 ± 14.14
Overall	34, 620	67.78 ± 31.19	30.11 ± 26.69	6.17 ± 12.47	16.96 ± 18.05	19.97 ± 20.59	38.63 ± 23.92	4.84 ± 11.51	35.96 ± 29.54

Table 2: Mass (percentage mass ± SD of the main prey species per year) of prey species in African penguin diet samples collected at Mercury Island, Namibia, between 1996 and 2009; *n* = number of months sampled per year and number of samples per year

Year	*n* (months, samples)	Mass ± SD (%)							
		Bearded goby	Anchovy	Sardine	Hake	Horse mackerel	Squid	Round herring	Others
1996/1997	4, 45	67.73 ± 38.61	2.06 ± 2.45	0.00	0.00	0.56 ± 1.12	4.82 ± 5.11	0.07 ± 0.15	24.76 ± 31.09
1998/1999	5, 54	76.00 ± 31.89	1.38 ± 1.94	0.22 ± 0.49	1.19 ± 2.67	0.97 ± 2.16	4.28 ± 8.67	0.00	15.97 ± 29.97
2000/2001	1, 46	77.49	20.21	0.00	0.10	0.35	0.91	0.49	0.45
2001/2002	8, 201	53.18 ± 34.75	3.80 ± 3.86	0.43 ± 0.78	7.18 ± 13.34	6.98 ± 6.92	4.84 ± 3.61	5.87 ± 9.12	17.72 ± 19.38
2002/2003	5, 104	67.60 ± 22.32	4.94 ± 4.83	0.00	8.55 ± 4.55	12.04 ± 24.20	0.65 ± 1.03	0.00	6.22 ± 12.68
2003/2004	4, 96	17.18 ± 13.51	5.38 ± 4.38	1.42 ± 1.66	10.91 ± 9.83	20.52 ± 15.98	2.92 ± 0.55	6.39 ± 11.59	35.29 ± 25.82
2004/2005	2, 24	83.12 ± 4.46	7.76 ± 0.81	0.05 ± 0.06	1.13 ± 0.38	5.62 ± 6.08	0.60 ± 0.57	1.61 ± 2.28	0.13 ± 0.03
2005/2006	1, 16	42.56	34.82	19.11	0.00	1.22	1.63	0.00	0.66
2007/2008	2, 24	63.39 ± 44.87	30.35 ± 42.79	0.70 ± 0.96	5.01 ± 0.87	0.00	0.51 ± 0.33	0.00	0.05 ± 0.07
2008/2009	2, 10	58.46 ± 1.11	11.03 ± 1.21	0.11 ± 0.12	2.39 ± 2.56	16.62 ± 16.32	3.46 ± 2.99	0.00	7.95 ± 10.99
Overall	34, 620	59.21 ± 31.51	7.20 ± 11.76	0.91 ± 3.31	4.91 ± 8.09	7.39 ± 12.71	3.12 ± 4.23	2.25 ± 6.19	15.01 ± 21.86

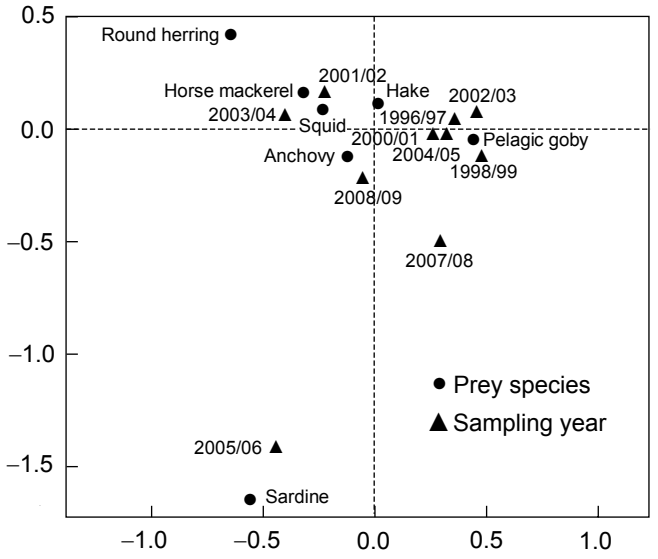

Figure 2: Correspondence analysis of diet composition of African penguins from Mercury Island, Namibia, between 1996 and 2009 using the frequency of occurrence of each prey species per year

separated the year 2005/2006 from all other years sampled due to the higher frequency of occurrence of sardine (Figure 2). Sardine were absent from samples collected in three years: 1996/1997, 2000/2001 and 2002/2003 (see Tables 1, 2). Samples containing round herring, horse mackerel, hake and squid separated years 2001/2002 and 2003/2004 from other years. The diet in 2008/2009 was influenced by a large frequency of occurrence of anchovy and the diet in 2007/2008 by a combination of sardine and anchovy in addition to bearded goby (Table 1).

Goby length in diet

Intact bearded goby individuals found in the diet samples were between 2.0–11.5 cm caudal length (CL), this corresponding to 2.3–14.1 cm total length (TL) (J-PR unpublished data). Mean caudal length was 6.04 cm (SD 2.11 cm, n = 1 656; mean total length was 7.35 cm, SD 2.62 cm). Size frequencies differed between years (χ^2 = 1 477.1, df = 126, p < 0.001). Penguins fed mainly on large gobies in 2000/2001 and 2003/2004 and on small individuals in 2001/2002 and 2005/2006; fish lengths were bimodally distributed in 2004/2005, 2007/2008 and 2008/2009 (Figure 3).

Energy content of diet

The mean energetic content of diet samples calculated from the percentage of mass in each month was 4.11 kJ g^{-1} (SD 0.44) wet mass. The month in which the energy content of the diet was highest was November 2003 (5.19 kJ g^{-1}, Figure 4) when the penguins fed mainly on horse mackerel (31.1% of the diet in terms of mass) and clupeoids (mainly round herring; 23.7%, Table 1). In February 2003, 82.2% of the diet (in terms of total mass) consisted of bearded goby and the energetic content was the lowest measured at 3.66 kJ g^{-1} (Figure 4). Of all years sampled, energetic content of the diet was highest in 2005/2006; the only other years with above average energy values were 2003/2004, 2007/2008 and 2008/2009 (Figure 4). However, sample sizes were relatively small in most of these years (e.g. 24 samples in 2007/2008 and 10 samples in 2008/2009).

Discussion

There are various methods to determine diet composition in seabirds (see review by Barrett et al. 2007), each with advantages and disadvantages. The stomach flushing method has several limitations, especially when birds are flushed once as was done in this study, because the gastric system is emptied completely only after repeated flushings (e.g. Gales 1987, Neves et al. 2006). Mass calculations and resulting energetic values of penguin diet therefore need to be interpreted with caution because it is likely that the entire stomach contents may not have been obtained. In addition, we estimated only the wet mass of each species in the samples and it is possible that the more readily digestible species in the diet could have been under-represented in samples. Randall and Randall (1986) used reconstituted mass of prey species to overcome this shortcoming, but the often advanced state of digestion of prey items in our study made estimations of fish lengths for entire samples difficult. Squid, which was present in numerous samples in our study — but of minor importance in terms of mass — may have been a case of underestimating easily digestible prey. Randall and Randall (1986) found that squid were an important dietary component of African penguins in the Eastern Cape of South Africa. They, on the other hand, may have overestimated the importance of squid in the diet through reconstituting squid mass from the numbers and sizes of beaks in samples, considering that squid beaks are often retained in the stomach for extended periods of time (Jackson and Ryan 1986, van Heezik and Seddon 1989). The presence and size of squid in the diet samples of African penguins from Mercury Island was not determined from beaks but from complete or semi-digested individuals.

It was possible to identify the fish species in the diet samples from complete or semi-digested individuals; otolith identification was not required for identifying specimens even if they were partially digested. This could have skewed the samples against species encountered farther away from the colony, because these were more likely at a later stage of digestion or possibly fully digested at the time of sampling. However, breeding African penguins at Mercury Island feed relatively close to the colony and return daily to it (Ludynia 2007). Therefore, it is likely that all prey in their stomachs was ingested within a day prior to sampling. Thus, we are confident that the method used here is a reliable estimate of diet composition.

Despite its disadvantages, stomach flushing of penguins seems to be an appropriate method to identify diet composition and changes in diet (Barrett et al. 2007) and is widely used in penguin research (e.g. Wilson 1984, Clausen and Pütz 2002, Takahashi et al. 2003, Herling et al. 2005). Another commonly used method for determining diet composition is stable isotope analysis (Sydeman et al. 1997, Bearhop et al. 1999, Quillfeldt et al. 2005, Weiss et al.

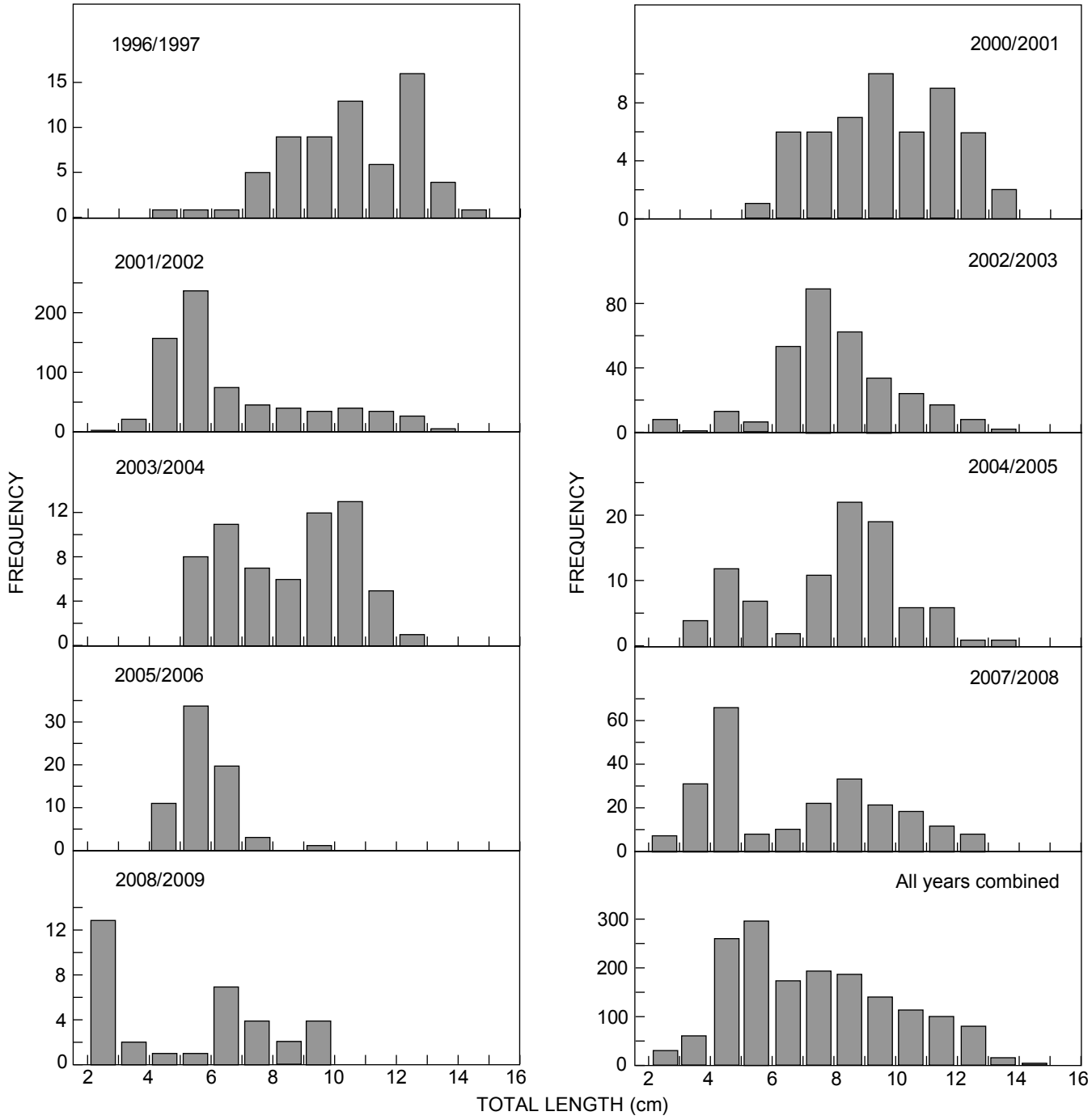

Figure 3: Size frequency distributions of intact bearded goby found in the diet of African penguins at Mercury Island, Namibia, between 1996 and 2009

2009). However, since the diet of African penguins consists of fish species from similar trophic levels, a switch between prey species would not be detectable with this method.

According to Crawford and Shelton (1981) and Crawford et al. (1985), bearded goby became the main prey species in the diet of African penguins in Namibia following the collapse of the sardine stock in the 1970s. Here, we show that bearded goby remains the main prey of penguins at Mercury Island, Namibia, more than 30 years later. According to Randall and Randall (1986), African penguins show selectivity in their prey choice, which may be related to the prey's food value, shoaling characteristics or abundance and availability. A high energetic food value may explain a preference for sardine and anchovy by African penguins (Randall and Randall 1986). It is unlikely that bearded goby is preferred over other prey species by

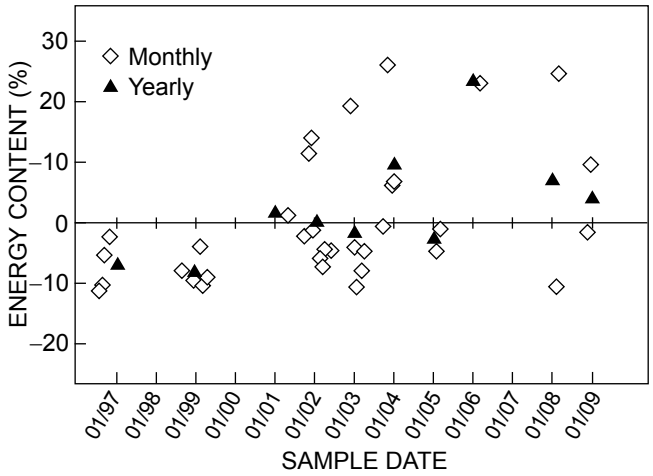

Figure 4: Monthly and yearly energy contents of diet samples of African penguins at Mercury Island, Namibia, between 1996 and 2009. Data are shown as percentage difference from the overall mean (indicated as 0%)

penguins on the basis of its food value, considering that its energy content is about 40% lower than that of sardine or anchovy. Feeding almost entirely on bearded goby, as in February 2003, leads to a reduced energetic value of the diet compared to times when birds feed on energy-richer species. African penguins are adapted to feed pelagically on shoaling fish (Wilson 1985, Wilson and Wilson 1995). Shoals of juvenile goby are found in midwater. Adult bearded goby, however, are generally dispersed on the seabed during the day (Cruickshank et al. 1980, Melo and Le Clus 2005, Utne-Palm et al. 2010). This lack of shoaling behaviour should thus make gobies less unattractive to foraging African penguins, relative to shoaling species such as sardine and anchovy. In several years, birds fed on relatively large bearded gobies, presumably close to the seabed. This could indicate a lack of shoaling fish available to the birds at that time, although in 2000/2001 penguins fed on large bearded goby in addition to (shoaling) anchovy.

Abundance and availability seem to be the main factors influencing the prey choice of African penguins at Mercury Island. The diet in 2003/2004 contained relatively high proportions of round herring and horse mackerel and in 2005/2006, relatively high proportions of sardine. The diet of bank cormorants *Phalacrocorax neglectus*, which feed selectively on bearded goby at Mercury Island (Ludynia et al. 2010), consisted almost exclusively of this species, even in years characterised by relatively large percentages of other species in the penguin diet (MFMR unpublished data). This indicates that, although bearded goby were available to penguins in these years, they selected more energy-rich prey when it was available. Therefore, the diet composition of African penguins at Mercury Island reflected local prey availability, as has been reported for other penguin species (Davis and Renner 2003, Tremblay and Cherel 2003).

Low-energy food, even if abundant or easy to obtain, may negatively affect chick growth, breeding success and thus population trends, a phenomenon that has become known as the junk-food hypothesis (e.g. Grémillet et al. 2008, Österblom et al. 2008). Prey abundance and prey quality are equally important factors influencing top predators in the marine environment (Österblom et al. 2008). For example, a shift from high-energy sandeel *Ammodytes* sp. to low-quality pipefish *Enterulus* sp. has caused breeding failures in common guillemots *Uria aalge* (Mavor et al. 2005, 2006, Harris et al. 2007). Even a change in the energetic value of a particular prey species can lead to reduced breeding success (Wanless et al. 2005). In the Benguela upwelling system, the negative impact of low-energy food on seabird breeding success has been shown for Cape gannets (Lewis et al. 2006, Grémillet et al. 2008, Mullers et al. 2009).

Changes in breeding success and numbers of African penguins in South Africa have been related to the abundance of sardine and anchovy (e.g. Crawford and Shelton 1978, 1981, Crawford et al. 2001, Crawford et al. 2006). Anchovy was the main prey for breeding African penguins at Robben Island, on the south-western coast of South Africa, between 1989 and 1992 (Crawford and Dyer 1995). Recently, an eastward shift of these pelagic fish stocks is believed to have caused a decline in penguin numbers at Robben Island and other breeding colonies in the western part of its South African distribution (Crawford et al. 2008). No detailed published data are available on the diet composition of African penguins in South African waters since this eastward shift of prey. In particular, more information is needed to assess whether the continuous decline in numbers of African penguins in South Africa is related to a switch in diet composition, to decreased abundance and possibly to reduced quality of sardine and anchovy around the breeding sites.

In Namibia, low prey abundance was suggested as a major factor contributing to the decline of penguin numbers after the collapse of sardine stocks (Crawford and Shelton 1981, Crawford et al. 2001). However, considering that bearded goby appears to have been relatively abundant along Namibia's southern coast, based on the diet of top predators including African penguins (this study), Cape fur seals *Arctocephalus pusillus pusillus* (Mecenero et al. 2006) and several cormorant species (MFMR unpublished data), low prey quality rather than low prey abundance *per se* appeared to be a key factor influencing population dynamics of African penguins and other marine top predators in southern Namibia. Numbers of penguins in adult plumage in Namibia declined at an exponential annual rate of 2.5% between 1996/1997 and 2008/2009 and 3.8% per year at Mercury Island during this period (MFMR unpublished data). Between 1996/1997 and 2009/2010, numbers of breeding pairs during peak breeding periods varied between approximately 1 800 and 3 200 at Mercury Island (MFMR unpublished data). These numbers should not necessarily be linked directly to diet composition as other factors, such as heat waves and flooding of nests, may also influence the number of breeding birds. This study supports the belief that food quality is generally low for African penguins at Mercury Island and presumably in the entire northern Benguela upwelling system (Crawford et al. 1985, Kemper et al. 2007). The suggestion that an increase in biomass of bearded

goby (Utne-Palm et al. 2010) is keeping the ecosystem productive and sustains predators (Pennisi 2010) has to be balanced by the fact that the replacement of small pelagic fish by bearded goby has resulted in a drastic decline in the energy content in seabirds' diets. A substantial increase from current population numbers may only be expected if the stock of small pelagics increases so the quality of prey can recover.

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References

Armstrong MJ, Thomas RM. 1995. Clupeoids. In: Payne AIL, Crawford RJM (eds), *Oceans of life off southern Africa* (2nd edn). Cape Town: Vlaeberg. pp 105–121.

Balmelli W, Wickens PA. 1994. Estimates of daily ration for the South African (Cape) fur seal. *South African Journal of Marine Science* 14: 151–157.

Barrett R, Camphuysen CJ, Anker-Nilssen T, Chardine JW, Furness RW, Garthe S, Huppop O, Leopold MF, Montevecchi WA, Veit RR. 2007. Diet studies of seabirds: a review and recommendations. *ICES Journal of Marine Science* 64: 1675–1691.

Bearhop S, Thompson DR, Waldron S, Russell IC, Alexander G, Furness RW. 1999. Stable isotopes indicate the extend of freshwater feeding by cormorants *Phalacrocorax carbo* shot at inland fisheries in England. *Journal of Applied Ecology* 36: 75–84.

Bianchi G, Carpenter KE, Roux JP, Molloy FJ, Boyer D, Boyer HJ. 1999. *FAO species identification guide for fishery purposes. Field guide to the living marine resources of Namibia*. Rome: Food and Agricultural Organization.

Clausen AP, Pütz K. 2002. Recent trends in diet composition and productivity of gentoo, Magellanic and rockhopper penguins in the Falkland Islands. *Aquatic Conservation: Marine and Freshwater Ecosystems* 12: 51–62.

Crawford RJM, Barham PJ, Underhill LG, Shannon LJ, Coetzee JC, Dyer BM, Leshoro TM, Upfold L. 2006. The influence of food availability on breeding success of African penguins *Spheniscus demersus* at Robben Island, South Africa. *Biological Conservation* 132: 119–125.

Crawford RJM, Cruickshank RA, Shelton PA, Kruger I. 1985. Partitioning of a goby resource amongst four avian predators and evidence of 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, 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, Shelton PA. 1978. Pelagic fish and seabird interrelationships off the coast of South West and South Africa. *Biological Conservation* 14: 85–109.

Crawford RJM, Shelton PA. 1981. Population trends for some southern African seabirds related to fish availability. In: Cooper J (ed.), *Proceedings of the symposium on birds of the sea and shore.* Cape Town: African Seabird Group. pp 15–41.

Crawford RJM, Underhill LG, Coetzee JC, Fairweather T, Shannon LJ, Wolfaardt AC. 2008. 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.

Cruickshank RA, Cooper J, Hampton I. 1980. Extension to the geographical distribution of pelagic goby *Sufflogobius bibarbatus* off South West Africa and some mensural and energetic information. *Fisheries Bulletin of South Africa* 13: 77–82.

Cury P, Shannon L. 2004. Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. *Progress in Oceanography* 60: 223–243.

Davis LS, Renner M. 2003. *Penguins*. London: T&AD Poyer.

de Young B, Harries R, Alheit J, Beaugrand G, Mantua N, Shannon L. 2004. Detecting regime shifts in the ocean: data considerations. *Progress in Oceanography* 60: 143–164.

Gales RP. 1987. Validation of the stomach-flushing technique for obtaining stomach contents of penguins. *Ibis* 129: 335–342.

Greenacre MJ. 1984. *Theory and applications of correspondence analysis*. London: Academic Press.

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 Royal Society B* 275: 1149–1156.

Harris MP, Beare D, Toresen R, Nottestad L, Kloppmann M, Dörner H, Peach K, Rushton DRA, Foster-Smith J, Wanless S. 2007. A major increase in snake pipefish (*Entelurus aequoreus*) in northern European seas since 2003: potential implications for seabird breeding success. *Marine Biology* 151: 973–983.

Herling C, Culik BM, Hennicke JC. 2005. Diet of the Humboldt penguin (*Spheniscus humboldti*) in northern and southern Chile. *Marine Biology* 147: 13–25.

IUCN. 2010. *IUCN Red List of threatened species. Version 2010.3*. Available at www.iucnredlist.org [accessed 22 October 2010].

Jackson S, Ryan PG. 1986. Differential digestion rates of prey by white-chinned petrels (*Procellaria aequinoctialis*). *Auk* 103: 617–619.

Kemper J. 2006. Heading towards extinction? Demography of the African penguin in Namibia. PhD thesis, University of Cape Town, South Africa.

Kemper J, Roux J-P, Bartlett PA, Chesselet YJ, James JAC, Jones R, Wepener S, Molloy FJ. 2001. Recent population trends of African penguins *Spheniscus demersus* in Namibia. *South African Journal of Marine Science* 23: 429–434.

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 325–342.

Lewis S, Grémillet D, Daunt F, Ryan PG, Crawford RJM, Wanless S. 2006. Using behavioural and state variables to identify proximate causes of population change in a seabird. *Oecologia* 147: 606–614.

Ludynia K. 2007. Identification and characterisation of foraging areas of seabirds in upwelling systems. Biological and hydrographic implications for foraging at sea. PhD thesis, University of Kiel, Germany.

Ludynia K, Jones R, Kemper J, Garthe S, Underhill LG. 2010. Foraging behaviour of bank cormorants in Namibia: implications for conservation. *Endangered Species Research* 12: 31–40.

Matthews JP. 1961. The pilchard of South West Africa (*Sardinops ocellata*) and the maasbanker (*Trachurus trachurus*) – bird predators, 1957–1958. *Investigational Report, Marine Research Laboratory, South West Africa* 3: 1–35.

Mavor RA, Parsons M, Heubeck M, Schmitt S. 2005. *Seabird numbers and breeding success in Britain and Ireland, 2004*. UK Nature Conservation No. 28. Peterborough: Joint Nature Conservation Committee.

Mavor RA, Parsons M, Heubeck M, Schmitt S. 2006. *Seabird numbers and breeding success in Britain and Ireland, 2005*. UK Nature Conservation No. 30. Peterborough: Joint Nature Conservation Committee.

Mecenero S, Roux JP, Underhill LG, Kirkman SP. 2006. Diet of Cape fur seals *Arctocephalus pusillus pusillus* at three mainland breeding colonies in Namibia. 2. Temporal variation. *African Journal of Marine Science* 28: 73–88.

Melo YC, Le Clus F. 2005. Growth and reproduction of the pelagic goby *Sufflogobius bibarbatus* off the Orange River, southern Africa. *African Journal of Marine Science* 27: 265–273.

Mullers REH, Navarro RA, Crawford RJM, Underhill LG. 2009. The importance of lipid-rich fish prey for Cape gannet chick growth: are fishery discards an alternative? *ICES Journal of Marine Science* 66: 2244–2252.

Nenadić O, Greenacre M. 2007. Correspondence analysis in R, with two-and three-dimensional graphics: the ca package. *Journal of Statistical Software* 20: 1–13.

Neves VC, Bolton M, Monteiro LR. 2006. Validation of the water offloading technique for diet assessment: an experimental study with Cory's shearwaters (*Calonectris diomedea*). *Journal of Ornithology* 147: 474–478.

Österblom H, Olsson O, Blenckner T, Furness RW. 2008. Junk-food in marine ecosystems. *Oikos* 117: 1075–1085.

Pennisi E. 2010. How a little fish keeps overfished ecosystem productive. *Science* 329: 268.

Petersen SL, Ryan PG, Grémillet D. 2006. Is food availability limiting African penguins *Spheniscus demersus* at Boulders? A comparison of foraging effort at mainland and island colonies. *Ibis* 148: 14–26.

Quillfeldt P, McGill RAR, Furness RW. 2005. Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson`s storm petrel. *Marine Ecology Progress Series* 295: 295–304.

Rand RW. 1960. The biology of guano-producing seabirds. The distribution, abundance and feeding habitats of the Cape penguin, *Spheniscus demersus*, off the south-western coast of the Cape Province. *Investigational Report, Division of Sea Fisheries, South Africa* 41: 1–28.

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.

Roux JP, Shannon L. 2004. Ecosystem approach to fisheries management in the northern Benguela: the Namibian experience. *African Journal of Marine Science* 26: 79–93.

Sydeman WJ, Hobson KA, Pyle P, McLaren EB. 1997. Trophic relationships among seabirds in central California: combined stable isotope and conventional dietary approach. *Condor* 99: 327–336.

Takahashi A, Dunn MJ, Trathan PN, Sato K, Naito Y, Croxall JP. 2003. Foraging strategies of chinstrap penguins at Signy Island, Antarctica: importance of benthic feeding on Antarctic krill. *Marine Ecology Progress Series* 250: 279–289.

Tremblay Y, Cherel Y. 2003. Geographic variation in the foraging behaviour, diet and chick growth of rockhopper penguins. *Marine Ecology Progress Series* 251: 279–297.

Utne-Palm AC, Salvanes AGV, Currie B, Kaartvedt S, Nilsson GE, Braithwaite VA, Stecyk JAW, Hundt M, van der Bank M, Flynn B, Sandvik GK, Klevjer TA, Sweetman AK, Brüchert V, Pittman K, Peard KR, Lunde IG, Strandabø RAU, Gibbons MJ. 2010. Trophic structure and community stability in an overfished ecosystem. *Science* 329: 333–336.

van der Lingen C, Shannon LJ, Cury P, Kreiner A, Moloney CL, Roux JP, Vaz-Velho F. 2006. Resource and ecosystem variability, including regime shifts, in the Benguela Current system. In: Shannon V, Hempel G, Malanotte-Rizzoli P, Moloney C, Woods J (eds), *Benguela: predicting a large marine ecosystem. Large marine ecosystems*, Vol. 14. Amsterdam: Elsevier. pp 147–185.

van Heezik YM, Seddon P. 1989. Stomach sampling in the yellow-eyed penguin: erosion of otoliths and squid beaks. *Journal of Field Ornithology* 60: 451–458.

Wanless S, Harris MP, Redman P, Speakman JR. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Marine Ecology Progress Series* 294: 1–8.

Weiss F, Furness RW, McGill RAR, Strange IJ, Masello JF, Quillfeldt P. 2009. Trophic segregation of Falkland Islands seabirds: insights from stable isotope analysis. *Polar Biology* 32: 1753–1763.

Wilson RP. 1984. An improved stomach pump for penguins and other seabirds. *Journal of Field Ornithology* 55: 109–112.

Wilson RP. 1985. Seasonality in diet and breeding success of the jackass penguin *Spheniscus demersus*. *Journal of Ornithology* 126: 53–62.

Wilson RP, Wilson MP. 1995. The foraging behaviour of the African penguin *Spheniscus demersus*. In: Dann P, Norman I, Reilly P (eds), *The penguins: ecology and management*. Chipping Norton: Surrey Beatty & Sons Pty. pp 244–265.

Appendix 1: Monthly frequency of occurrence (percentage of samples containing the species per month) of prey species in African penguin diet samples collected at Mercury Island, Namibia, between 1996 and 2009

Season	Month	No. of samples	Frequency of occurrence (%)							
			Bearded goby	Anchovy	Sardine	Hake	Horse mackerel	Squid	Round herring	Others
1996/1997	July 1996	1	100.00	0.00	0.00	0.00	0.00	100.00	0.00	0.00
	September 1996	10	100.00	0.00	0.00	0.00	0.00	20.00	0.00	80.00
	October 1996	30	53.33	16.67	0.00	0.00	3.33	40.00	3.33	83.33
	November 1996	4	25.00	50.00	0.00	0.00	25.00	25.00	0.00	100.00
1998/1999	September 1998	7	100.00	57.14	0.00	0.00	0.00	57.14	0.00	14.29
	December 1998	16	56.25	12.50	0.00	0.00	18.75	56.25	0.00	37.50
	February 1999	10	90.00	0.00	0.00	20.00	0.00	0.00	0.00	30.00
	March 1999	6	100.00	0.00	0.00	0.00	0.00	33.33	0.00	0.00
	April 1999	15	100.00	6.67	13.33	0.00	6.67	20.00	0.00	0.00
2000/2001	May 2001	46	76.09	50.00	0.00	4.35	4.35	34.78	4.35	23.91
2001/2002	October 2001	32	43.75	62.50	0.00	25.00	15.63	53.13	0.00	84.38
	November 2001	32	6.25	50.00	3.13	0.00	25.00	68.75	34.38	65.63
	December 2001	33	21.21	21.21	9.09	6.06	51.52	42.42	42.42	57.58
	January 2002	40	50.00	22.50	2.50	35.00	32.50	50.00	17.50	35.00
	February 2002	16	68.75	37.50	0.00	12.50	0.00	56.25	6.25	56.25
	March 2002	24	95.83	4.17	0.00	4.17	12.50	41.67	0.00	12.50
	April 2002	18	72.22	0.00	0.00	0.00	38.89	33.33	0.00	0.00
	June 2002	6	100.00	16.67	0.00	0.00	16.67	83.33	0.00	33.33
2002/2003	December 2002	16	50.00	37.50	0.00	18.75	56.25	43.75	0.00	50.00
	January 2003	32	78.13	37.50	0.00	21.88	15.63	12.50	0.00	3.13
	February 2003	32	84.38	0.00	0.00	40.63	3.13	0.00	0.00	18.75
	March 2003	16	75.00	0.00	0.00	31.25	0.00	6.25	0.00	37.50
	April 2003	8	75.00	12.50	0.00	37.50	12.50	12.50	0.00	12.50
2003/2004	October 2003	24	25.00	37.50	0.00	54.17	0.00	50.00	4.17	79.17
	November 2003	24	8.33	62.50	8.33	16.67	45.83	41.67	41.67	58.33
	December 2003	24	41.67	8.33	0.00	50.00	50.00	54.17	0.00	58.33
	January 2004	24	20.83	41.67	20.83	12.50	37.50	58.33	4.17	75.00
2004/2005	February 2005	16	100.00	12.50	0.00	18.75	18.75	18.75	6.25	18.75
	March 2005	8	100.00	62.50	12.50	37.50	50.00	12.50	0.00	12.50
2005/2006	March 2006	16	50.00	62.50	62.50	0.00	18.75	43.75	0.00	12.50
2007/2008	February 2008	16	100.00	6.25	12.50	37.50	0.00	18.75	0.00	12.50
	March 2008	8	37.50	75.00	25.00	12.50	0.00	25.00	0.00	0.00
2008/2009	December 2008	5	100.00	80.00	20.00	60.00	60.00	80.00	0.00	40.00
	January 2009	5	100.00	80.00	20.00	20.00	60.00	20.00	0.00	20.00

Appendix 2: Monthly percentage of mass of prey species in African penguin diet samples collected at Mercury Island, Namibia, between 1996 and 2009

Season	Month	No. of samples	Mass (%)							
			Bearded goby	Anchovy	Sardine	Hake	Horse mackerel	Squid	Round herring	Others
1996/1997	July 1996	1	96.97	0.00	0.00	0.00	0.00	3.03	0.00	0.00
	September 1996	10	95.58	0.00	0.00	0.00	0.00	0.88	0.00	3.54
	October 1996	30	63.81	4.86	0.00	0.00	0.01	3.04	0.29	27.99
	November 1996	4	14.57	3.36	0.00	0.00	2.24	12.33	0.00	67.50
1998/1999	September 1998	7	94.54	4.67	0.00	0.00	0.00	0.55	0.00	0.24
	December 1998	16	64.06	0.69	0.00	0.00	4.83	19.77	0.00	10.65
	February 1999	10	25.07	0.00	0.00	5.97	0.00	0.00	0.00	68.96
	March 1999	6	99.79	0.00	0.00	0.00	0.00	0.21	0.00	0.00
	April 1999	15	96.52	1.52	1.09	0.00	0.004	0.87	0.00	0.00
2000/2001	May 2001	46	77.49	20.21	0.00	0.1	0.35	0.91	0.49	0.45
2001/2002	October 2001	32	22.86	11.92	0.00	35.36	2.18	3.09	0.00	24.59
	November 2001	32	5.92	2.81	0.54	0.00	7.62	8.94	22.89	51.28
	December 2001	33	15.42	2.55	0.69	1.51	20.56	2.96	17.39	38.92
	January 2002	40	49.83	1.53	2.22	20.14	7.71	4.33	5.47	8.77
	February 2002	16	67.96	5.64	0.00	0.41	0.00	6.99	1.23	17.77
	March 2002	24	93.27	5.35	0.00	0.03	0.46	0.82	0.00	0.07
	April 2002	18	86.42	0.00	0.00	0.00	12.52	1.06	0.00	0.00
	June 2002	6	83.72	0.57	0.00	0.00	4.79	10.54	0.00	0.38
2002/2003	December 2002	16	29.45	5.45	0.00	6.59	55.27	2.48	0.00	0.76
	January 2003	32	79.9	9.23	0.00	7.19	3.27	0.38	0.00	0.03
	February 2003	32	82.19	0.00	0.00	16.55	0.13	0.00	0.00	1.13
	March 2003	16	65.82	0.00	0.00	5.19	0.00	0.11	0.00	28.88
	April 2003	8	80.65	10.01	0.00	7.22	1.54	0.29	0.00	0.29
2003/2004	October 2003	24	7.86	7.86	0.00	19.32	0.00	2.13	0.1	62.73
	November 2003	24	5.03	10.06	2.56	4.52	31.14	2.98	23.74	19.97
	December 2003	24	34.34	0.41	0.00	19.29	35.04	3.35	0.00	7.57
	January 2004	24	21.48	3.17	3.12	0.5	15.89	3.22	1.73	50.89
2004/2005	February 2005	16	86.27	7.18	0.00	0.86	1.32	1	3.22	0.15
	March 2005	8	79.96	8.33	0.09	1.4	9.92	0.19	0.00	0.11
2005/2006	March 2006	16	42.56	34.82	19.11	0.00	1.22	1.63	0.00	0.66
2007/2008	February 2008	16	95.12	0.09	0.02	4.39	0.00	0.28	0.00	0.10
	March 2008	8	31.66	60.61	1.38	5.62	0.00	0.74	0.00	0.00
2008/2009	December 2008	5	59.24	10.17	0.02	4.2	5.08	5.57	0.00	15.72
	January 2009	5	57.67	11.88	0.19	0.58	28.16	1.34	0.00	0.18