

The importance of lipid-rich fish prey for Cape gannet chick growth: are fishery discards an alternative?

Ralf H. E. Mullers, René A. Navarro, Robert J. M. Crawford, and Les G. Underhill

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A recent decline in population numbers of Cape gannets (*Morus capensis*) breeding off the west coast of South Africa coincided with decreased availability of lipid-rich fish prey: anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*). Seabirds can use fishery discards as an alternative, but the quality of this food in the Benguela ecosystem is lower than that of their natural prey species. We consider whether chick growth and survival during chick rearing co-vary with the periods of high and low availability of their lipid-rich prey species and whether fishery discards would be an alternative. The proportion of anchovy and sardine in the diet was between 66 and 84% in the years 1986–1988, but just 16–35% from 2004 to 2006. Months with large proportions of anchovy and sardine in the diet were associated with faster chick growth. No association between the proportion of fishery discards in the diet and chick growth was found. The patterns are consistent with the notion that a distributional shift of anchovy and sardine decreased their contribution to the diet of Cape gannets and slowed chick growth along with lessening chick survival at the breeding colony. The reduced survival may partially explain the decline in numbers of Cape gannets breeding in the southern Benguela.

Keywords: Benguela, chick growth, diet quality, food availability, *Morus capensis*.

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R. H. E. Mullers: Behavioural Biology Group, University of Groningen, Kerklaan 30, 9751 NN Haren, The Netherlands. R. H. E. Mullers, R. A. Navarro, and L. G. Underhill: Animal Demography Unit, Department of Zoology, University of Cape Town, Rondebosch 7701, South Africa. R. J. M. Crawford: Department of Environmental Affairs and Tourism, Marine and Coastal Management, Private Bag X2, Rogge Bay 8012, South Africa. Correspondence to R. H. E. Mullers: tel: +31 50 3637847; fax: +31 50 3632148; e-mail: r.h.e.mullers@rug.nl.

Introduction

The Benguela upwelling system off the southwest coast of Africa is one of the most productive oceanic environments in the world (Shannon and O'Toole, 2003). Large biomasses of two pelagic fish species, anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*), exploit the productive waters. The high energetic value (Batchelor and Ross, 1984) and high lipid content (FAO, 1989) of these two fish species and their inshore distribution (Hampton, 1987) make them profitable food sources, providing sufficient energy to sustain large communities of predatory fish, marine mammals, and seabirds (Shannon, 1985). The availability of both main forage fish species is important for several endemic seabird species breeding in the Benguela. The abundance of anchovy is associated with the numbers of Cape cormorants (*Phalacrocorax capensis*) and swift terns (*Sterna bergii*) attempting to breed, as well as with the number of African penguin (*Spheniscus demersus*) chicks that fledge (Crawford and Dyer, 1995; Crawford *et al.*, 2006). The numbers of Cape gannets (*Morus capensis*) breeding in Namibia and South Africa are closely related to the biomass of sardine (Crawford *et al.*, 2007). These pelagic fish are also targeted by fisheries (Griffiths *et al.*, 2005). Besides competing with seabirds and marine mammals for the same fish, commercial fisheries produce considerable quantities of fishery discards, providing an alternative food source for seals and seabirds (Ryan and Moloney, 1988). If the availability of their natural prey decreases, seabirds could compensate by

feeding on discards, which can be beneficial to seabird populations (Tasker *et al.*, 2000; Montevecchi, 2002). The South African hake fisheries discarded some 7000 t of hake annually off the west coast of South Africa at the end of the 1990s (Walmsley *et al.*, 2007).

Since 1997, the distributions of both anchovy and sardine have moved east along the west and south coasts of South Africa (van der Lingen *et al.*, 2005). This shift reduced the availability of these prey species to Cape gannets at the two west coast breeding colonies, Lambert's Bay and Malgas Island. The centre of gravity of sardine catches (a measure for sardine distribution) moved from around Grotto Bay (Western Cape) in 1987 closer to Cape Agulhas in 2005 (van der Lingen *et al.*, 2005; Fairweather *et al.*, 2006), a 440-km return trip. Subsequently, Cape gannets from Malgas Island have shown increased foraging effort compared with birds from a colony where sardine were readily available (Pichegru *et al.*, 2007) and have increased the proportion of fishery discards in their diet. Feeding on hake fishery waste was considered unsustainable for Cape gannets during the breeding season (Pichegru *et al.*, 2007; Grémillet *et al.*, 2008) owing to the low energy content of the discards (Batchelor and Ross, 1984). Cape gannet chicks hand-raised on Cape hake (*Merluccius capensis* and *Merluccius paradoxus*—the fishery discards eaten by Cape gannets are almost exclusively hake) had reduced growth rates and lower fledging weights than chicks fed anchovy and/or sardine (Batchelor and Ross, 1984). However, until now no data

have been collected on how fishery discards affect the growth rates of free-ranging chicks.

The Cape gannet is a seabird that is endemic to southern Africa, breeding on just six islands. The number of pairs breeding on the west coast of South Africa decreased from 60 000 to 36 000 pairs between 1997 and 2005 (Crawford *et al.*, 2007), coinciding with the decreased availability of anchovy and sardine then. The Cape gannet is listed as vulnerable by the IUCN. Here, we consider the effects of decreased availability of lipid-rich fish prey on chick growth and survival during chick-rearing of Cape gannets, and investigate whether fishery discards are a viable alternative to live prey. We use datasets on chick growth during two contrasting periods: 1986–1988, when anchovy and sardine were readily available near the breeding colony of Malgas Island, and 2003–2006 when this availability decreased drastically. We predict that the growth rate of Cape gannet chicks will increase in periods that coincide with increased proportions of anchovy and sardine in their diet.

Methods

Data presented here were collected during the breeding seasons 1986–1988 (by RAN) and 2003–2006 (by RAN and RHEM) at Malgas Island (33°03'S 17°93'E), Saldanha Bay, South Africa, the largest of the five Cape gannet colonies off the west coast of southern Africa (Crawford *et al.*, 2007). The Cape gannet breeding season at Malgas Island lasts 8–9 months, and pairs need ~5 months to incubate the single egg (ca. 43 d; Jarvis, 1974) and raise the chick to fledging (ca. 97 d; Jarvis, 1974). The onset of egg-laying varies between individuals from August through early November (Staveres *et al.*, 2008). Here, we use 2003, for example, to indicate the breeding season from August 2003 to April 2004.

Diet samples

In each study year, diet samples were collected monthly from adult gannets over 1–3 consecutive days. Gannets were captured with a hooked pole upon arrival from a foraging trip and inverted over a bucket in which they regurgitated (Berruti *et al.*, 1993). We collected 2321 diet samples (annual mean 332 samples \pm 220), which we analysed by weighing individual fish species in different samples. The percentage contribution (wet weight) of each fish species was calculated for each month. The diet was categorized as anchovy, sardine, saury (*Scorpaenopsis saurus*), fishery discards (hakes), or other species. The state of digestion of prey items was also determined. All prey could be identified to one of the above five categories, even when they were partly digested. Anchovy and sardine were combined for further analyses, as in Crawford *et al.* (2007), because the numbers of breeding gannets correlate more strongly with the combined biomass of sardine and anchovy than to either prey species alone. Diet samples were not collected from parents of chicks that we measured for growth.

Chick growth

Human access to the interior of the colony involved unacceptable levels of disturbance. Therefore, we selected chicks at different sites near the periphery of the colony to measure growth. Chicks were taken from the nest, measured, and replaced within 3 min. Bill length (to the nearest 0.1 mm with callipers), length of flattened wing chord (to the nearest 1 mm with a wing-ruler), and body weight (<1000 g to the nearest 5 g, >1000 g to the nearest 25 g with a Pesola spring balance) were recorded. Chicks were

measured at approximately the same time of each measuring day and in the same order. One observer (RAN) was involved in both study periods, reducing the risk of inter-observer effects. Chicks were identified either by nest location or by their individually coded colour rings.

To test whether chicks growing at the periphery represented chick growth for the whole colony, we measured chicks in the interior of the colony in the first year (1986). Differences in parental condition (Coulson, 1968; Gibbs *et al.*, 2000) or predation pressure (Tenaza, 1971) within and at the edge of a colony could affect chick growth rates. Nests were at least 3 m from the edge of the colony, surrounded by other nests on all sides, and hence protected against ground predators. The researcher followed the same path to access the nests at each visit and measured the chicks outside the colony.

We combined two datasets on Cape gannet chick growth, and the measuring protocols differed between years. Variation in measuring intervals did not contribute to variation in growth rates (multilevel model: interval $F_{1,3222} = 1.5$, $p = 0.218$). In general, we aimed to measure a sample of chicks of all ages and from different parts of the colony throughout each breeding season. During the 1986 breeding season, chicks were measured at intervals of 3 or 4 d until they died or fledged (see Navarro, 1991, for details). In 1987 and 1988, different samples of chicks were measured over 4 d in each month (mean sample size 53 ± 28 , $n = 635$). Additionally in 1988, another sample of chicks was measured twice per month at a 4-d interval, until they died or fledged. In the years 2003–2006, we selected a sample of chicks at each of four sites and measured the same chicks weekly until they died or fledged. Newly hatched chicks were added into the sample to collect data on the growth of young chicks throughout the breeding season.

Chick age was estimated from the first measurement of each chick, using algorithms derived from data on 103 known-age chicks (Navarro, 1991). When wing length was <40 mm, age was computed from $\text{age} = -\ln((89.78 - b/6.15 \times b)/0.086) + 0.5$, where b is bill length. For chicks with wings of 40 mm or larger, age was computed from $\text{age} = 1.395 - \ln(\ln(588.8/w)/0.0264) + 0.5$, w being wing length. These algorithms were derived during a period when anchovy and sardine were readily available. Batchelor and Ross (1984) showed that the growth rates of wing and culmen did not differ between chicks fed with sardine or with hake, whereas weight increase did, indicating that these growth rates are intrinsic and therefore useful indicators of age.

Growth index

Growth rates were analysed using a non-parametric approach (see Appendix for a full description of the method) because standard parametric growth models such as Gompertz or logistic growth curves do not fit the data adequately (see also Brown *et al.*, 2007). The growth index measures deviations from average growth and is independent of whether growth is measured at an early age when the absolute growth rates (g d^{-1}) are small, at the maximum growth spurt, or late in development, when growth rates decrease. The growth index is scaled so that it represents the number of standard deviations (s.d.) above or below the average growth rate; with this standardization, it is appropriately denoted z . Data were pooled across years for analyses, and growth indices were calculated then tested for between- and within-year variation. Only chicks up to the age of 85 d were

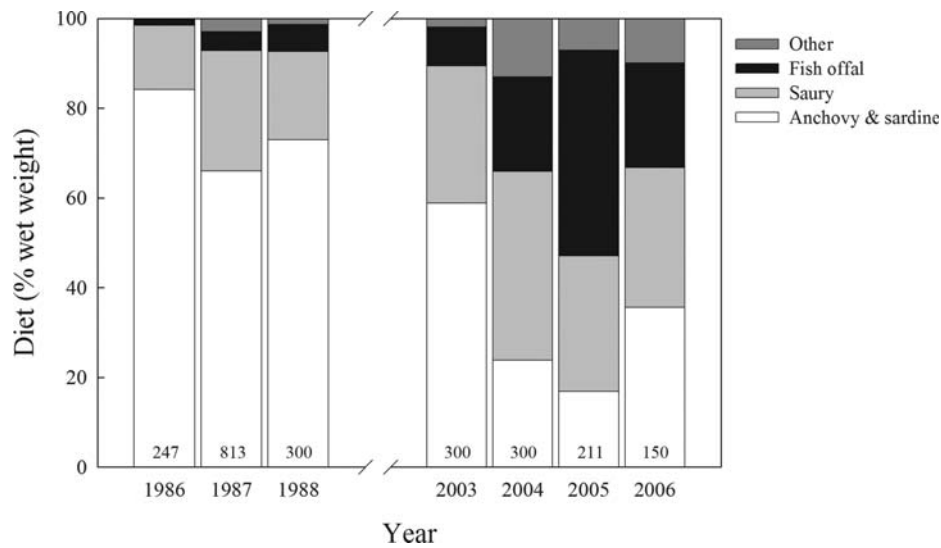


Figure 1. Annual contributions (in % wet weight) of four categories of prey species to Cape gannet diet. Data are only from the months that chick growth was measured, and sample sizes are shown at the bottom. The main prey species in the category “other” are snoek (*Thysites atun*), horse mackerel (*Trachurus t. capensis*), and round herring (*Etrumeus whiteheadi*). Fishery discards consist almost exclusively of hake.

used for analyses because the average weight of chicks tended to decrease thereafter (visual inspection of the dataset) and therefore were not of interest for the aim of this study.

Chick survival

In 2003 and 2004, 10 sites were selected randomly to monitor chick survival: five sites at the periphery and five sites in the interior of the colony (at least 3 m from the edge and surrounded by other nests). At each site, we marked a single position that was used by the observer to check the contents of all nests within 2 m. Contents of nests were monitored by lifting the birds gently when they were sitting on the nest to check for eggs or small chicks. When chicks were visible to the observer, nests were not disturbed. Presence and the approximate age of the chicks (based on plumage) were monitored every 2 weeks. Survival was analysed for chicks until 12 weeks old because thereafter we could not determine whether they had died or fledged when not observed at the nest. Survival of chicks is defined as the proportion of chicks that survived between two nest checks, relative to the number of chicks at the first of the two checks.

All methods used and handling of gannets during this study were approved by the Animal Use and Care Committee of South African National Parks (SANParks), and the research permit was issued by SANParks.

Statistical analyses

Results are presented as mean \pm 1 s.d. Parameters were analysed using multiple regressions in which the potential explanatory effect of predictive variables was tested using a backward-deletion method. The residuals of significant models were tested for normality. To correct for a possible effect of individual on repeated growth measurements, growth indices were tested with multilevel mixed-modelling procedures in MLwiN 2.02, with individual and observation as levels. Further included in the models were parameters such as location (periphery or interior), year, month, hatching date, and diet. The growth index was independent of chick age, so we did not include chick age in the models. Significance levels were calculated with restricted iterative generalized least squares.

We only included age in the models testing the relationship between chick growth and diet to correct for differences in average age between months. To study effects on survival, a multi-level mixed-modelling procedure was used with plot (site in colony, $n = 10$), plot per year (2 years \times 10 plots, $n = 20$), individual identity, and observation (each observation) as levels. The binomial logit-link model included year (2003 and 2004), location of nest (interior or periphery), age of chicks (<4 weeks, 4–8 weeks, and >8 weeks) and date (days after 30 September), as well as their interactions. Growth indices were calculated using GenStat 8, and statistical analyses were carried out with SPSS 14.0 or MLwiN 2.02.

Results

Diet

The combined proportion of anchovy and sardine in the diet varied from 66 to 84% between 1986 and 1988, then dropped between 2003 and 2005 from 59 to 17% (Figure 1). The contribution of fishery discards was \sim 5% during the 1980s, increased to 45% in 2005, then decreased again to 20%, concomitant with the proportion of anchovy and sardine increasing to 35% in 2006. The main seasonal trend was that the proportion of anchovy and sardine decreased as the breeding season progressed, whereas the proportion of saury increased (Figure 2). The proportion of fishery discards was relatively large from October to December between 2003 and 2006.

Chick growth

During seven breeding seasons, 1256 gannet chicks were measured (Figure 3a), from which 3375 growth indices could be calculated.

The non-parametric growth curve derived from plotting growth (g d^{-1}) against weight (Figure 3b) showed an initial increase in growth with increasing weight. The point of inflection was at a weight of 839 g (23 d) with a growth rate of 49.5 g d^{-1} . From that point on, the growth rate decreased towards 14.0 g d^{-1} for chicks with a weight of 3250 g (slope = -0.014), but much more gradually than the initial increase (slope = 0.047).

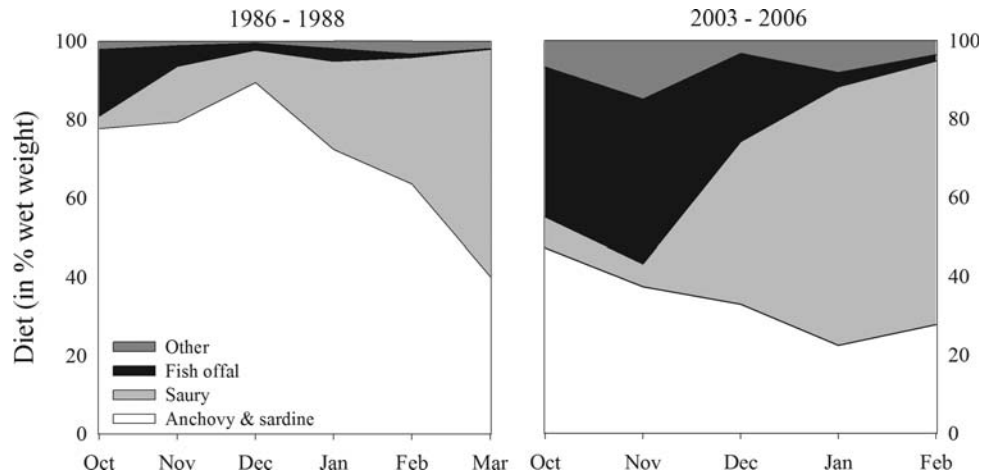


Figure 2. Monthly contributions (in % wet weight) of four categories of prey species to the diet of Cape gannets during the breeding season. Averages are given per month for two contrasting periods.

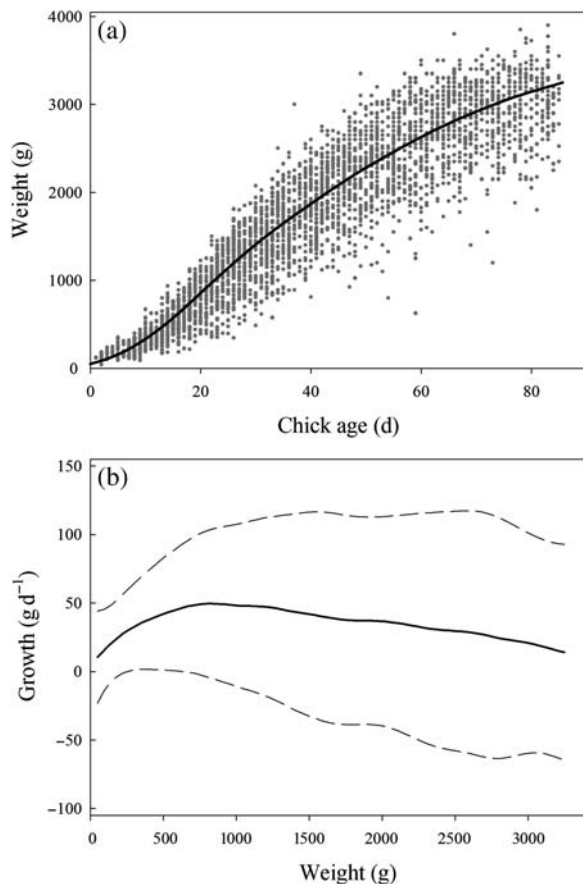


Figure 3. (a) Plot of weight (g) against chick age (d) of Cape gannets. The line represents the non-parametric growth curve calculated from plotting growth (g d^{-1}) against weight. (b) Plot of growth (g d^{-1}) against average weight for chicks. The lines represent the non-parametric growth curve and the lower and upper confidence intervals. Chick growth was from seven breeding seasons, the data from 1256 individuals and 3375 measurements.

The overall mean of the growth indices was $-0.015 (\pm 0.98, n = 3375)$ and did not differ from zero (one-sample t -test: $t = -0.887$, d.f. = 3374, $p = 0.376$).

Growth rates at the periphery and in the interior

To check whether the growth of chicks at the periphery represented overall growth of the colony, 291 growth increments of 14 chicks were measured in the interior of the colony and compared with 138 growth increments of nine chicks at the periphery (within 1 m of the edge) in 1986. Growth of the chicks at the periphery of the colony did not differ statistically from the growth of chicks in the interior (multilevel model: location $F_{1,427} = 2.2$, $p = 0.140$). All measured chicks hatched between 2 and 6 November 1986. If we include hatching date and survival of chicks in the model, the location was still not associated with chick growth (multilevel model: hatch date $F_{4,422} = 1.0$, $p = 0.306$; survival $F_{1,422} = 3.8$, $p = 0.052$; location $F_{1,422} = 0.7$, $p = 0.413$).

Chick growth between and within years

The growth indices differed significantly between the 7 years (multilevel model: year $\chi^2 = 84.6$, $p < 0.001$) and between months during the 7 years (multilevel model: month $\chi^2 = 39.9$, $p < 0.001$). The growth indices were higher in the period 1986–1988 than in 2003–2006 (multilevel model: period $\chi^2 = 59.0$, $p < 0.001$; Figure 4a). From October to January, the growth indices were higher in 1986–1988, but in February/March growth was faster in 2003–2006 (Figure 4b). Seasonality was analysed in a model that tested for the interaction between years and months (GLM: year $F_{6,3346} = 11.1$, $p < 0.001$; month $F_{4,3346} = 8.2$, $p < 0.001$; year \times month $F_{18,3346} = 3.8$, $p < 0.001$). The model showed that growth did not follow the same seasonal pattern in different years. The model explained just 5.9% of the variation in chick growth.

To assess the biological difference in growth between the two periods, we also tested the absolute growth rates (g d^{-1}) between years. When growth was averaged per chick and corrected for age differences, the chicks grew 6.0 g d^{-1} faster in 1986–1988 than in 2003–2006 (37.2 vs. 31.2 g d^{-1} , respectively; one-way ANOVA: periods $F_{1,1252} = 9.1$, $p = 0.003$; age $F_{1,1252} = 14.4$, $p < 0.001$).

Chick growth and diet

Growth indices were averaged for each calendar month and correlated with the proportion of the different prey species in the diet.

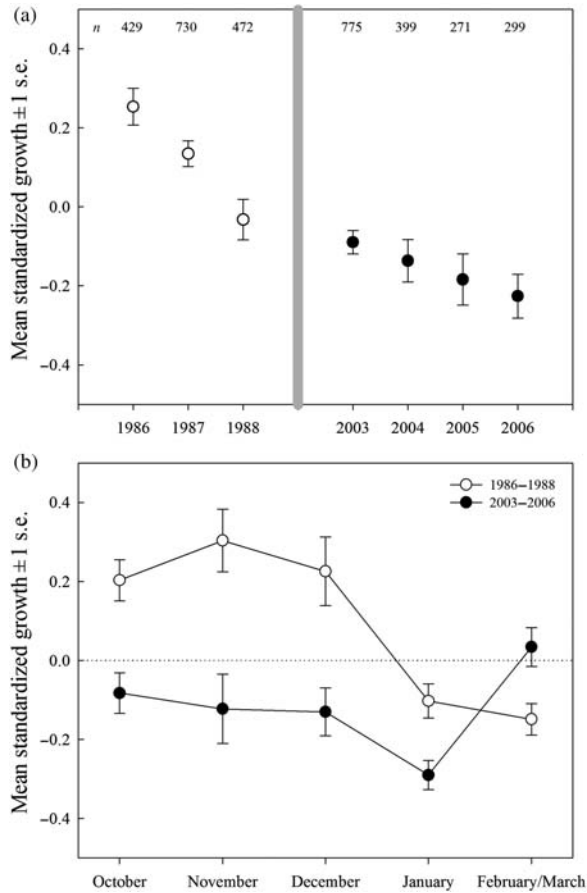


Figure 4. (a) Mean growth index for all Cape gannet chicks in each of seven breeding seasons. Sample sizes are indicated. (b) Average monthly growth index within the breeding season for the years 1986–1988 (open circles) and 2003–2006 (dots). The error bars represent 1 s.e.

Average growth indices were positively correlated with the contribution of anchovy and sardine to the diet ($r = 0.554$, $n = 32$, $p = 0.001$; Figure 5). For 6 of the 7 years, these correlations were also positive between the months within years, in 2 years significantly (1989: $r = 0.850$, $n = 6$, $p = 0.032$; 2006: $r = 0.998$, $n = 3$, $p = 0.042$). The proportion of fishery discards in the diet was not correlated with growth ($r = 0.011$, $p = 0.952$).

The combined proportion of anchovy and sardine in the diet had a positive effect on chick growth. In periods when chicks were older, growth was marginally faster with a larger proportion of anchovy and sardine in the diet than in periods when chicks were younger [GLM: anchovy and sardine $B = 0.013$, $F_{1,28} = 9.8$, $p = 0.004$; age $F_{1,28} = 1.9$, $p = 0.182$; (anchovy and sardine) \times age $F_{1,28} = 5.4$, $p = 0.028$]. The model explained 46.9% of the variance in growth.

Chick survival

During the 2003 and 2004 breeding seasons, 303 and 396 nests, respectively, were monitored for chick survival at both the interior and the periphery of the colony. Nests were monitored for at least 4 months. In 2003, chicks hatched at 233 nests; in 2004 at 242 nests. Chick survival until 12 weeks was better in 2003 (60.9%) than in 2004 (55.4%), and survival was greater in the interior than at the periphery (Table 1).

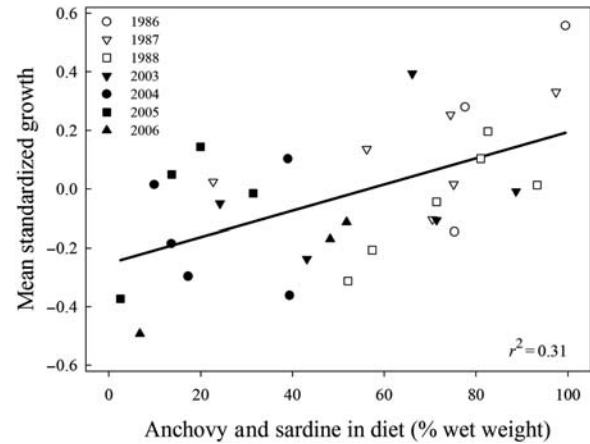


Figure 5. The correlation between the combined proportion of anchovy and sardine in Cape gannet diet and the mean chick growth index per month. Data are for seven breeding seasons ($n = 32$).

Results from the model are presented in Table 2. Until day 80 (19 December), chick survival was lower in 2004 than in 2003. Survival decreased in both years as the breeding season progressed (Figure 6a). This decrease was less steep in 2004 than in 2003. Survival increased with the age of the chicks, an effect that appeared to be stronger in 2004 than in 2003 (Figure 6b). Chicks at the interior of the colony survived better than chicks reared at the periphery, but the difference decreased as the season progressed (Table 2).

Discussion

Although Cape gannets are opportunistic feeders with great variability in their diet (Berruti *et al.*, 1993) and foraging behaviour (Lewis *et al.*, 2006; Pichegru *et al.*, 2007), the availability of anchovy and sardine appears to influence their reproductive performance. At Malgas Island, a decreased availability of anchovy and sardine (van der Lingen *et al.*, 2005) was associated with an increase in foraging effort (Pichegru *et al.*, 2007) and a decrease in the numbers of gannets breeding (Crawford *et al.*, 2007). Our results have revealed a positive correlation between the growth of Cape gannet chicks and the proportion of these lipid-rich prey species in their diet. The lack of a similar correlation between fishery discards and the growth of Cape gannet chicks lends support to the assumption that fishery discards are an inadequate substitute for natural prey in the Benguela. This finding is consistent with earlier observations on captive birds that chicks fed anchovy and sardine exhibited better growth than those fed discards (Batchelor and Ross, 1984).

Growth measurements

Birds breeding in the interior of a colony are expected to be more experienced or in a better condition than birds at the periphery (Coulson, 1968; Gibbs *et al.*, 2000). The interior nests in our study were ~ 3 m from the periphery, and all were surrounded by other nests. Owing to the population decrease at Malgas (Crawford *et al.*, 2007), many gaps developed in the colony, increasing the number of nests at the edge and decreasing the average distance of interior nests to the edge of the colony. We believe that 3 m was far enough inside the colony to answer the questions in which we were interested. At the periphery, predation pressure is thought to be greater (Tenaza, 1971). This might result

Table 1. Summary statistics of Cape gannet chick survival until 12 weeks old.

Location	Survival	2003	2004
Periphery	Success	47 (43.5%)	47 (45.2%)
	Failure	61 (56.5%)	57 (54.8%)
Interior	Success	95 (76.0%)	87 (63.0%)
	Failure	30 (24.0%)	51 (37.0%)

Chick survival is defined as percentage of chicks that survived between consecutive nest checks. Chicks at nests at least 3 m from the periphery are defined as reared in the interior of the colony.

Table 2. Results for the multilevel binomial logit-link model of the survival of Cape gannet chicks.

Parameter	B	s.e.	d.f.	χ^2	p-value
Intercept	6.1	0.85	1		
Year ^a			1	19.7	<0.001
2004	-4.3	0.98			
Age (weeks) ^b			2	84.3	<0.001
<4	-1.6	0.29			
>8	2.9	0.43			
Location ^c			1	19.0	<0.001
Interior	3.4	0.78			
Date	-0.06	0.01	1	53.5	<0.001
Year × date			1	29.3	<0.001
2004 × date	0.05	0.01			
Year × age			2	11.0	0.004
2004 × <4 weeks	0.3	0.38			
2004 × >8 weeks	-1.6	0.53			
Location × date			1	12.1	<0.001
Interior × date	-0.03	0.01			

^aReference category is 2003.

^bReference category is 4–8 weeks.

^cReference category is periphery.

in differences in growth rates or survival of chicks. We found that chick survival was less at the periphery than in the interior, most likely because of the greater predation pressure at the periphery exerted by kelp gulls (*Larus dominicanus*; RAN and RHEM, pers. obs.). Growth rates did not differ between chicks from the interior

and the periphery, so the growth of chicks at the periphery of the colony was representative of the whole colony. However, the measurements were carried out in a year when both anchovy and sardine were available. We cannot exclude the possibility, therefore, that in a poor year, some differential effect on growth rate and survival might have been apparent.

The impact on chick growth of natural prey vs. discards

Fishery discards can be a potential alternative food source for seabirds (Montevicchi, 2002), and increases in several seabird populations have been attributed to opportunities to scavenge fishery waste (Mitchell *et al.*, 2004; Oro *et al.*, 2004). Seabirds seem to select discards from fishing vessels that are of good digestibility and high caloric content (Furness *et al.*, 2007). However, the energy content of hake (4.07 kJ g⁻¹), the main fishery waste in the Benguela ecosystem, is half that of anchovy or sardine (6.74 and 8.59 kJ g⁻¹, respectively; Batchelor and Ross, 1984), the Cape gannet's natural prey. Cape hake are also poor in lipid content (average fat content: hake 2.5%, anchovy 4.2%, sardine 7.9%; FAO, 1989). The hake diet samples regurgitated by Cape gannets consisted mainly of bony heads or body portions with large bones. Nevertheless, the proportion of fishery discards in the diet of breeding Cape gannets (almost exclusively hake) increased from ~5% in the 1980s to 45% in 2005.

Average growth of Cape gannet chicks reared at Malgas Island was positively associated with the proportion of lipid-rich prey species in the diet. In years with good availability of anchovy and sardine (1986–1988), chicks grew faster than in years with reduced availability of these species (2003–2006). The importance of lipid-rich species for chick growth was also evident within years. Chicks grew faster in months when there was more anchovy and sardine in their diet. Moreover, there was no relationship between chick growth and the proportion of fishery discards in the diet, suggesting partial compensation by adult gannets returning more discards to chicks, as found by Pichegru *et al.* (2007). Although the fishery discards were of poor quality, both in terms of caloric content and digestibility, Cape gannets seemed to have no other suitable alternatives for decreased availability of anchovy and sardine and had to feed on this “junk-food”, at least during parts of the breeding season.

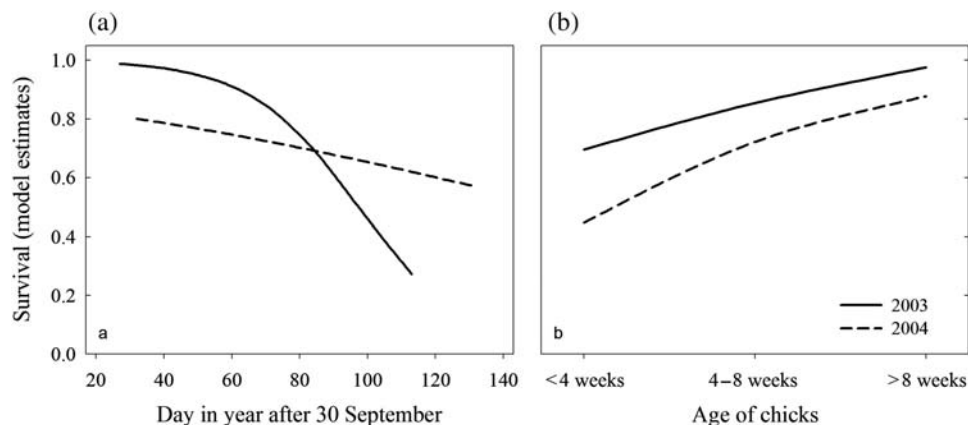


Figure 6. (a) Survival of Cape gannet chicks throughout the breeding season for 2 years (2003 and 2004). Survival rates are estimates from the multilevel model (see Results), and predictions are made from the model including year, date, and their interaction. (b) The proportion of chicks that survived between consecutive nest checks for three age classes. Survival rates are estimates from the multilevel model and are corrected for year, date, and location in the colony (periphery or interior) effects.

There is growing evidence that the quality of the diet, in particular the lipid content of fish prey, is crucial for growing seabird chicks (Golet *et al.*, 2000; Litzow *et al.*, 2002; Wanless *et al.*, 2005; Kitaysky *et al.*, 2006). Chicks reared on lipid-rich diets can probably increase energy reserves by storing more body fat (Kennedy *et al.*, 2007), enhancing the chances of successful fledging of individuals by buffering periods of fluctuating food availability (Ricklefs and Schew, 1994). Feeding on fishery discards in this situation proved to be an unsuitable alternative for breeding Cape gannets to sustain their own energy requirements and those of their chick (Pichegru *et al.*, 2007), but can be an alternative to ensure survival outside the breeding season (Grémillet *et al.*, 2008).

Fluctuations in food availability

In colonial seabirds, chick growth is considered to be an indicator of local food availability (Ricklefs *et al.*, 1984; Shea and Ricklefs, 1996; le Corre *et al.*, 2003). The diet of Cape gannets breeding at Malgas Island showed a consistent occurrence of saury at the end of the breeding season when anchovy and sardine were less available (Berruti *et al.*, 1993; this study). It seems that at the beginning of the breeding season, breeding birds do not have this option and can only turn to scavenging behind hake trawlers. The prevalence of saury from December on might affect chick growth in different ways. In the years 1986–1988, the lesser energy content per gramme wet weight of saury (6.20 kJ g^{-1} ; Batchelor and Ross, 1984) may have affected growth negatively at the end of the breeding season. From 2003 to 2006, with greater proportions of lipid-poor fishery discards, the occurrence of better quality saury from January on may have increased the growth performance of the chicks at the end of the year (February/March; Figure 3b). Indeed, Grémillet *et al.* (2008) showed an increase in the caloric value of the diet in 2005, when the proportion of saury increased in the diet, compared with months with larger proportions of fishery discards.

Reproductive output

Pigeon guillemot (*Cephus columba*) chicks reared on lipid-rich diets grew faster and fledged more successfully (Golet *et al.*, 2000; Litzow *et al.*, 2002), which may drive the population dynamics in that species. Cape gannet chicks with a greater fledging weight have better chances of survival than chicks that fledge later or with a lower weight (Jarvis, 1974). Although increased predation of chicks and fledglings by Cape fur seals (*Arctocephalus pusillus pusillus*; Makhado *et al.*, 2006) and great white pelicans (*Pelicanus onocrotalus*; de Ponte Machado, 2007) does contribute to the decrease in size of the Cape gannet colony at Malgas Island, it is our opinion that the decreased availability of lipid-rich prey species is likely to be the driving force on the current population decrease at Malgas Island, as has been suggested for the Namibian population by Crawford *et al.* (2007). Survival for the period 1986–1988 was 70% (Navarro, 1991). The sample sizes were small and survival was calculated differently from our estimates in 2003 and 2004, but it seems that faster growth in the period 1986–1988 was associated with better survival of the chicks. We agree with Grémillet *et al.* (2008) that marine management policies should be careful in assuming that fishery waste is beneficial for seabirds scavenging behind trawlers. Indeed, the results of this study illustrate some of the effects that a decreased availability of lipid-rich prey can have at a population scale and particularly that fishery discards

do not provide an alternative food source for the birds during their breeding season.

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Appendix

Several studies have previously explored the growth of gannet chicks to give indications that standard parametric growth models, such as the Gompertz or logistic growth curves, do not describe chick growth adequately (Cooper, 1978; Navarro, 1991). Even the Richards growth curve family is not sufficiently flexible to describe gannet chick growth, largely because there is a long period in which the decrease in growth rate is near linear (Figure 3b), and none of the parametric models capture this. The non-parametric approach to growth rates (cf. Brown *et al.*, 2007) developed here can be applied in all growth contexts. It generates a growth curve that is explicitly driven by the data alone, rather than having artefacts that are attributable to the chosen model; the philosophical underpinning of this approach to data analysis is given, for example, by Greenacre (1984, pp. 1–11). The disadvantage of this non-parametric approach is that it requires substantial quantities of data, because the general shape of the growth curve is not predetermined by the choice of parametric model.

Growth rates were calculated between each pair of successive weight measurements, so if successive weights at times t and u were m_t and m_u , the growth rate over this period is $g = (\text{change}$

in size)/(period) = $(m_u - m_t)/(u - t)$ and the mean of the pair of measurements is $a = (m_t + m_u)/2$.

For a set of observed weights (target weight), the average growth rate was estimated using weighted regression. Weights for all pairs of observations were calculated (a, g) in such a way that values close to the target weight had large weights, and values farther away had increasingly smaller weights. If the target weight was m^* , then the weight w attached to observation (a, g) was $w = \exp(-((a - m^*)/\sigma)^2)$, where σ was chosen to be 200, some 8% of the adult weight. The weight attached to observations 200 g distant from the target weight is substantial (0.37), at 300 g small (0.105), and at 400 g tiny (0.018). A weighted linear regression was fitted by GenStat 8 (GenStat Committee, 2005) to predict the growth rate g^* at the target weight. By varying σ , the extent of the influential neighbourhood can be modified. The value for σ was selected by visual inspection, but the results do not depend critically on this value. Data exploration showed that if a chosen value was twice as large or half as small, the results would have been almost identical.

The same weights used for the regression were used to estimate a weighted standard deviation s_m^* ; where $s_m^* = (1/\sum w)((w(g - g^*)^2))$. An approximate coefficient of variation for each target weight was calculated as $CV^* = (s_m^*/m^*)$.

The estimated growth rates and the lower and upper confidence limits at each target weight were plotted, and the points were

linked by interpolation. A normal distribution was assumed, so the lower and upper confidence limits were $g^* - 1.96 s_m^*$ and $g^* + 1.96 s_m^*$, respectively. Using hatching weight as the starting value on day 0, the growth-rate curve was integrated to produce a plot of weight against time. The non-parametric growth curve (a table with the predicted values of the growth curve can be obtained from the first author) describes the pattern of growth as determined by the data rather than by forcing the data into a pattern as a consequence of the parametric model chosen by the analyst. The growth indices are age-independent.

For the interval between two measurements of a chick, a comparison was made between the observed and the expected growth rates. The observed growth rate was computed as the average of the two measurements, and its approximate standard deviation was calculated as described above. The standardized growth rate (z) was then computed by dividing the difference between the observed and expected growth rate by the standard deviation, so $z = (g - g^*)/s^*$. The z -scores are assumed to be approximately normally distributed, so the magnitudes of z -values can be expected to stay within the standard normal distribution. For large samples, the overall mean of all z -values is asymptotically zero; negative values indicate below-average growth rates, and positive values indicate above-average growth rates.

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