Fishery discards are no alternative for growing Cape gannet chicks

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

Abstract
A recent decline in population numbers of Cape gannets (Morus capensis) breeding at the west coast of South Africa coincided with decreased availability of lipid-rich fish prey anchovies (Engraulis encrasicolus) and sardines (Sardinops sagax). Seabirds can use fishery discards as an alternative, but the quality of this junk-food in the Benguela ecosystem is lower than that of natural prey species. In this paper we consider whether chick growth and survival co-vary with 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 1986-88 and decreased to 16-35% in 2004-06. 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. These patterns are consistent with the idea that a distributional shift of anchovy and sardine decreased their contribution to the diet of Cape gannets and lowered chick growth and survival in the breeding colony. The reduced chick survival may partially explain the decline in numbers of Cape gannets breeding in the southern Benguela.
INTRODUCTION

The Benguela upwelling system off the south-western African coast is one of the most productive oceanic environments in the world (Shannon & O’Toole 2003). Large biomasses of the pelagic fish species anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) exploit these productive waters. Their high energetic value (Batchelor & Ross 1984), high lipid content (FAO 1989) and inshore distribution (Hampton 1987) make anchovy and sardine profitable food sources, providing enough 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 ecosystem. The abundance of anchovies is associated with the numbers of Cape cormorants (*Phalacrocorax capensis*) and swift terns (*Sterna bergii*) attempting to breed and the number of African penguin (*Spheniscus demersus*) chicks that fledge (Crawford & Dyer 1995). Numbers of Cape gannets (*Morus capensis*), breeding in both Namibia and South Africa, are strongly related to the biomass of sardines (Crawford *et al.* 2007a). These pelagic fish are also targeted by human fisheries (Griffiths *et al.* 2005). Besides competing with seabirds and marine mammals for the same fish, the fisheries produce considerable amounts of fishery discards, providing an alternative food source for seals and seabirds (Ryan & 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 have discarded about 7000 tonnes of hake annually off the west coast of South Africa at the end of the 1990s (Walmsley *et al.* 2007).

Since 1997 distributions of both anchovy and sardine have moved eastward along the western and southern 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. Cape gannets from Malgas Island have increased the proportion of fishery discards in their diet, and have since shown an increased foraging effort compared to birds from a colony where sardines were readily available (Pichegru *et al.* 2007). Feeding on fishery waste was considered unsustainable for Cape gannets during the breeding season (Pichegru *et al.* 2007, Grémillet *et al.* 2008) due to the low energy content of the waste (Batchelor & Ross 1984). Cape gannet chicks hand-raised on hake (*Merluccius capensis* and *M. paradoxus*, fishery discards are almost exclusively hakes) have reduced growth rates and lower fledging weights compared to chicks fed anchovy and/or sardine (Batchelor & Ross 1984). However, until now no data have been collected on how the ‘junk-food’ affected chick growth rates on a colony scale.

The Cape gannet is a seabird species endemic to southern Africa, which breeds on only six islands in the Benguela ecosystem. The number of breeding pairs on the west...
coast decreased from 50 000 to 36 000 pairs between 1997 and 2005 (Crawford et al. 2007a), coinciding with the decreased availability of anchovy and sardine. The Cape gannet is listed ‘vulnerable’ by the IUCN. In this study we consider the effects of decreased availability of lipid-rich fish prey on chick growth and survival of Cape gannets and we investigated the suitability of fishery discards as an alternative to natural prey. We use two extensive datasets on chick growth during 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 present a detailed assessment of the impact of natural versus discard diet on chick growth in this seabird species and study these effects between, but also within years. We predict that Cape gannet chicks will show increased growth in periods that coincide with increased proportions of anchovy and sardine in the 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 (33º03’S 17º93’E), Saldanha Bay, South Africa, the largest of the five Cape gannet colonies off the west coast of Namibia and South Africa (Crawford et al. 2007a). The Cape gannet breeding season at Malgas Island lasts eight to nine months. Individual pairs need about five months to incubate the single egg (ca. 43 days, Jarvis 1974) and raise the chick to fledging (ca. 97 days, Jarvis 1974). The onset of egg-laying varies between individuals from August through early November (Staverees et al. 2008). In this paper, we use 2003, for example, to indicate the breeding season from August 2003 until 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 ± 220), which we analysed by weighing the mass of individual fish species in different samples. The percentage contribution (wet mass) of each fish species was calculated for each month. The diet was categorised as anchovy and sardine, saury (Scomberesox saurus), fishery discards (hakes) and other species. Anchovy and sardine were combined for further analyses as in Crawford et al. (2007a).

Chick growth

Human access to the interior of the colony involved unacceptable levels of disturbance. For this reason we selected chicks at different sites near the periphery of the
colony to measure growth. Chicks were taken from the nest, measured and put back within three minutes. Bill length (to nearest 0.1 mm), length of flattened wing chord (to nearest 1 mm) and body mass (< 1000 g to nearest 5 g, > 1000 g to nearest 25 g) were measured. 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 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. The researcher followed the same path to access the nests at each visit and measured chicks outside the colony.

We combined two datasets on Cape gannet chick growth and therefore the measuring protocols differed between years. However, all growth increments were analysed in the same way and variation in intervals between measurements did not interfere with our growth results (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 three or four day intervals until they either died or fledged (see Navarro 1991 for details). In 1987 and 1988, different samples of chicks were measured over four days at each month (mean sample size 53 ± 28, n = 635). In addition, in 1988 another sample of chicks was measured twice per month at a four-day interval, but repeated until they died or fledged. In the years 2003 to 2006 we selected a sample of chicks at each of four sites and measured the same chicks at weekly intervals until they died or fledged. Newly hatched chicks were added into the sample in order 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 of 103 known aged chicks (Navarro 1991). When wing length was below 40 mm, age was computed by $\text{age} = -\ln \left( \frac{(89.78 - b) / 6.15 \times b}{0.086} \right) + 0.5$, where $b$ is bill length. For chicks with wings of 40 mm or larger, age was computed by $\text{age} = 1.395 - \ln \left( \ln \left( \frac{588.8}{w} \right) / 0.0264 \right) + 0.5$, $w$ being wing length.

**Growth index**

Growth rates were analysed using a non-parametric approach (see box 2.1 for full description of method), because standard parametric growth models like 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 above or below average growth rate; with this standardization it is appropriately denoted \( z \). For analyses data were pooled across years, growth indices were calculated and then tested for between and within year variation. Only chicks up to the age of 85 days were used for analyses, because the average mass of chick tended to decrease after this age (visual inspection of this dataset).

**Chick survival**

In 2003 and 2004, 10 sites were randomly selected 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 one position which was used by the observer to check the contents of all nests within 2 m. Contents of nests were monitored by lifting 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 approximate age of the chicks (based on plumage) were monitored every two weeks. Survival was analysed for chicks until 12 weeks of age, because after this age 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 of 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 ± standard deviation. Parameters were analysed using multiple regressions in which the potential explanatory effect of predictive variables was tested using a backwards deletion method. The residuals of significant models were tested for normality.

In order 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 like location (periphery or interior), year, month, hatching date and diet. The growth index was independent of chick age and therefore we did not include chick age in the models. Significance levels were calculated with restricted iterative generalized least squares (RIGLS). We only included age in the models testing the relationship between chick growth and diet, to correct for differences in average age between the months. To study effects on survival a multilevel
mixed-modelling procedure was used with plot (site in colony, $n = 10$), plot per year (two 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 September 30), as well as their interactions. Growth indices were calculated using GenStat 8 and statistical analyses were done with the SPSS 13.0 and MLwiN 2.02.

**RESULTS**

**Diet**

The proportion of anchovy and sardine varied from 66 to 84% between 1986 and 1988, and decreased between 2003 and 2005 from 59% to 17% (Fig. 2.1). The contribution of fishery discards was around 5% during the 1980s. This proportion increased to 45% in 2005, after which it decreased again to 20% and concomitantly the proportion of anchovy and sardine increased 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 (Fig. 2.2). The proportion of hake was relatively large from October till December between 2003 and 2006.

**Chick growth**

During seven breeding seasons 1256 gannet chicks were measured (Fig. 2.3A), from which 3375 growth indices could be calculated.

The non-parametric growth curve derived from plotting growth ($g \cdot d^{-1}$) against mass (Fig. 2.3B) showed an initial increase in growth with increasing mass. The point of inflection was at a mass of 839 g (23 days) with a growth rate of 49.5 g $d^{-1}$. From that point onwards the growth rate decreased towards 14.0 g $d^{-1}$ for chicks with a mass of 3250 g (slope = −0.014), but much more gradually than the initial increase (slope = 0.047). The overall mean of the growth indices was −0.015 ($± 0.98$, $n = 3375$) and did not differ from zero (one sample t-test: $t = −0.887$, $df = 3374$, $P = 0.376$).

**Periphery vs. interior**

To check whether growth of chicks at the periphery represented overall growth of the colony we also measured chicks in the interior of the colony. 291 growth increments (14 chicks) were measured in the interior of the colony and compared to 138 (9 chicks) at the periphery (within 1 m from the edge) in 1986. Growth of chicks at the periphery of the colony did not statistically differ from 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 $F_{1,422} = 0.7, P = 0.413$).

Figure 2.1. Contribution (in % wet mass) of four categories of prey species to Cape gannet diet per year. Data are only from months that chick growth was measured and sample sizes are shown at top of graph. Main prey species in the category ‘other’ are snoek, horse mackerel and round herring. Fishery discards consist almost exclusively of hake.

Figure 2.2. Contribution (in % wet mass) of four categories of prey species to the diet of Cape gannets per month during the breeding season. Averages are given per month for two contrasting periods.
Chick growth between and within years

The mean growth indices per year were largest in 1986 and 1987 and smallest in 2003-2006 (Fig. 2.4A). Within each year the growth indices showed considerable fluctuations. Average growth per month combined for all years was generally higher at the beginning of the year (October till December) than at the end (January till March) (Fig. 2.4B). For each month, except February/March, chick growth was faster in 1986-88 than in 2003-06.

The growth indices differed significantly between the seven years (Multilevel model: year $F_{6,3368} = 84.6$, $P < 0.001$) and between months during the seven years (Multilevel model: month $F_{4,3369} = 39.9$, $P < 0.001$). The growth indices were higher in

---

**Figure 2.3.** A) Plot of mass (g) against chick age of Cape gannets in days. The line represents the non-parametric growth curve calculated from plotting growth (g d$^{-1}$) against mass. B) Plot of growth (g d$^{-1}$) against average mass for chicks. The lines represent the non-parametric growth curve and the lower and upper confidence interval. Chick growth from seven breeding seasons, data of 1256 individuals and 3375 measurements.
1986–88 compared to 2003-06 (Multilevel model: period $F_{1,3373} = 59.0, P < 0.001$).
From October until January the growth indices were higher in the 1986-88, but in
February/March growth was faster in 2003-06 (Fig 2.4B). Seasonality was analysed in
a model that tested for the interaction between year and months (GLM: year $F_{6,3346} = 11.1, P < 0.001$; month $F_{4,3346} = 8.2, P < 0.001$; years x 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 only 5.9% of the variation in chick growth.

**Chick growth and diet**

Growth indices were averaged for each calendar month and correlated to the propor-
tion of the different prey species in the diet. Average growth indices were positively
correlated with the contribution of anchovy and sardine to the diet ($r = 0.554, n = 32,
P = 0.001$, Fig. 2.5). For six of the seven years these correlations were also positive
between the months within years, in two 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 to 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) x age $F_{1,28} = 5.4, P = 0.028$). The model
explained 46.9% of the variance in growth.
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 four months. In 2003, chicks hatched at 233 nests; in 2004 at 242 nests. Chick survival until 12 weeks was higher in 2003 (60.9%) compared to 2004 (55.4%) and survival was higher in the interior than the periphery (Table 2.1).

Results from the model are presented in Table 2.2. Until day 80 (19 December) chick survival was lower in 2004 than 2003. Survival decreased in both years as the breeding season progressed (Fig. 2.6A). This decrease was less steep in 2004 than in 2003. Survival increased with the age of chicks. This effect appeared to be stronger in 2004 than in 2003 (Fig. 2.6B). Chicks at the interior of the colony had higher survival compared to chicks reared at the periphery, but the difference decreased as the season progressed (Table 2.2).

**Figure 2.5.** 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 ($n = 32$).

**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 four months. In 2003, chicks hatched at 233 nests; in 2004 at 242 nests. Chick survival until 12 weeks was higher in 2003 (60.9%) compared to 2004 (55.4%) and survival was higher in the interior than the periphery (Table 2.1).

Results from the model are presented in Table 2.2. Until day 80 (19 December) chick survival was lower in 2004 than 2003. Survival decreased in both years as the breeding season progressed (Fig. 2.6A). This decrease was less steep in 2004 than in 2003. Survival increased with the age of chicks. This effect appeared to be stronger in 2004 than in 2003 (Fig. 2.6B). Chicks at the interior of the colony had higher survival compared to chicks reared at the periphery, but the difference decreased as the season progressed (Table 2.2).

**Table 2.1.** Summary statistics of Cape gannet chick survival until 12 weeks of age. Chick survival is defined as percentage of chicks that survived between consecutive nest checks. Chicks nested at least 3 m from the periphery are defined as reared in the interior.

<table>
<thead>
<tr>
<th>Location</th>
<th>Survival</th>
<th>2003</th>
<th>2004</th>
</tr>
</thead>
<tbody>
<tr>
<td>Periphery</td>
<td>Success</td>
<td>47 (43.5%)</td>
<td>47 (45.2%)</td>
</tr>
<tr>
<td></td>
<td>Failure</td>
<td>61 (56.5%)</td>
<td>57 (54.8%)</td>
</tr>
<tr>
<td>Interior</td>
<td>Success</td>
<td>95 (76.0%)</td>
<td>87 (63.0%)</td>
</tr>
<tr>
<td></td>
<td>Failure</td>
<td>30 (24.0%)</td>
<td>51 (37.0%)</td>
</tr>
</tbody>
</table>
Figure 2.6. A) Survival of Cape gannet chicks throughout the breeding season for two years (2003 and 2004). Survival rates are estimates from the multi-level model (see results) and predictions are made from the model including year, date and their interaction. B) Fraction of chicks that survived between consecutive nest check for three age-classes. Survival rates are estimates from the multi-level model and corrected for year, date and location in the colony (periphery or interior) effects.

Table 2.2. Results for the multi-level binomial logit-link model of survival of Cape gannet chicks. The model corrected for the levels of plot, year-plot, individual and observation. Year, location, and age were included as categories and date included as covariate. For further model details see results.

<table>
<thead>
<tr>
<th></th>
<th>B (SE)</th>
<th>d.f.</th>
<th>$\chi^2$</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>6.1 (0.85)</td>
<td>1</td>
<td>19.7</td>
<td>&lt; 0.001 **</td>
</tr>
<tr>
<td>Year$^a$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2004</td>
<td>-4.3 (0.98)</td>
<td>1</td>
<td>19.7</td>
<td>&lt; 0.001 **</td>
</tr>
<tr>
<td>Age$^b$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&lt; 4 weeks</td>
<td>-1.6 (0.29)</td>
<td>2</td>
<td>84.3</td>
<td>&lt; 0.001 **</td>
</tr>
<tr>
<td>&gt; 8 weeks</td>
<td>2.9 (0.43)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Location$^c$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>interior</td>
<td>3.4 (0.78)</td>
<td>1</td>
<td>19.0</td>
<td>&lt; 0.001 **</td>
</tr>
<tr>
<td>Date</td>
<td>-0.06 (0.01)</td>
<td>1</td>
<td>53.5</td>
<td>&lt; 0.001 **</td>
</tr>
<tr>
<td>Year x date</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2004 x date</td>
<td>0.05 (0.01)</td>
<td>1</td>
<td>29.3</td>
<td>&lt; 0.001 **</td>
</tr>
<tr>
<td>Year x age</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2004 x &lt; 4 weeks</td>
<td>0.3 (0.38)</td>
<td>2</td>
<td>11.0</td>
<td>0.004 **</td>
</tr>
<tr>
<td>2004 x &gt; 8 weeks</td>
<td>-1.6 (0.53)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Location x date</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>interior x date</td>
<td>-0.03 (0.01)</td>
<td>1</td>
<td>12.1</td>
<td>&lt; 0.001 **</td>
</tr>
</tbody>
</table>

$^a$ reference category is 2003
$^b$ reference category is 4 – 8 weeks
$^c$ reference category is periphery
DISCUSSION

Although Cape gannets are opportunistic feeders with large 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 have a considerable influence on their reproductive performance. At Malgas Island, a decreased availability of anchovies and sardines (van der Lingen et al. 2005) was associated with an increase in foraging effort (Pichegru et al. 2007) and a decrease in numbers of gannets breeding (Crawford et al. 2007a). Our results demonstrate that the growth of Cape gannet chicks is also associated with the proportion of these lipid-rich prey species in the diet and that fishery discards are an inadequate substitute for natural prey. This confirms earlier observations on captive birds that chicks fed anchovy and sardine exhibit better growth than those fed hake (Batchelor & 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). At the periphery, predation pressure is also thought to be larger (Tenaza 1971). This might result in differences of chick growth rates or survival. In this study we found that chick survival was lower at the periphery compared to the interior. This was most likely due to higher predation pressure at the periphery by kelp gulls (Larus dominicanus) (RAN and RHEM pers. obs.). Growth rates did not differ between chicks from the interior and periphery, so the growth of chicks at the periphery of the colony was representative for the whole colony. Although we combined two datasets collected at 20 years intervals, one researcher (RAN) was present during both study periods, which is seldom the case and minimises measurement errors.

The impact of natural versus discards diet on chick growth

Fishery discards can be a potential alternative food source for seabirds (Montevecchi 2002) and increases of 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 & Ross 1984), the Cape gannet’s natural prey. Hake is also poor in lipid content (average fat content: Cape hake 2.5%, southern African anchovy 4.2%, southern African sardine 7.9%, FAO 1989). The hake diet samples regurgitated by Cape gannets mainly consisted of bony heads or body portions with large bones. Nevertheless, the proportion of fishery discards (almost exclusively hake) increased from about 5% in the 1980s to 45% in 2005 in the diet of breeding Cape gannets.
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 were growing faster than in the years with reduced availability of these species (2003-2006). The importance of lipid-rich species for chick growth was also evident within years. Chicks had faster growth rates in months with 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 the chick 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 prey to anchovy and sardine and had to feed on this junk-food, at least during parts of the breeding season.

There is growing evidence that 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 & Schew 1994). Feeding on fishery discards 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 an indicator of local food availability (Ricklefs et al. 1984, Shea & 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 onwards might affect chick growth in different ways. In 1986-1988 the lower energy content per gram wet mass of saury (6.20 kJ g⁻¹, Batchelor & Ross 1984) may have affected growth negatively at the end of the breeding season. From 2003 to 2006, with higher proportions of lipid-poor fishery discards, the occurrence of better quality saury from January onwards may have increased the growth performance of the chicks at the end of the year (February-March, Figure 2.3B). 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 to months with larger proportions of fishery discards.
Reproductive output
In pigeon guillemots (*Cepphus columba*) chicks reared on lipid-rich diets showed faster growth and higher fledging success (Litzow et al. 2002, Golet et al. 2000), which may drive population dynamics in this species. Cape gannet chicks with a high fledging mass have higher survival chances than chicks that fledge later or with a lower mass (Jarvis 1974). Chick survival was slightly lower in 2004 than in 2003, coinciding with the reduced availability of anchovy and sardine in 2004. Increased predation of chicks and fledglings by Cape fur seals (Makhado et al. 2006) and great white pelicans (*Pelecanus onocrotalus*) (De Ponte Machado 2007) is contributing to the decrease of the Cape gannet colony at Malgas Island. However, the decreased availability of lipid-rich prey species is likely to have been the main cause of large population decreases of Cape gannets in Namibia (Crawford et al. 2007a). Demographic data are essential for ongoing discussions about population declines of many different vulnerable species. 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. This study illustrates the dramatic effects that a decreased availability of lipid rich prey can have on a population scale and that fishery discards do not provide an alternative food source during the breeding season (Wanless et al. 2005).

Acknowledgements
We are grateful to Prof. Dr. G.H. Visser, whose enthusiasm led to this project and it’s funding by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO), but whose untimely death precluded his participation in the manuscript. Several anonymous referees, L. Pichegru, S. Verhulst, J.M. Tinbergen and S. Daan commented on earlier drafts of this manuscript. The South African National Parks gave us permission to work on Malgas Island and helped with transport to and from the island. R.H.E.M. was funded by WOTRO. L.G.U., R.J.M.C. and R.A.N. acknowledge support from the National Research Foundation, Pretoria, including through its SeaChange programme. We are grateful to our organizations, listed under addresses, for supporting this research. This paper is a contribution to the project LMR/EAF/03/02 on top predators of the Benguela Current Large Marine Ecosystem (BCLME) Programme.

Box 2.1: Growth indices
Several studies have previously explored growth of Cape gannet chicks and give indications that standard parametric growth models, like Gompertz or logistic growth curves, do not describe chick growth adequately (Cooper 1978, Navarro 1991). The assumption for these parametric models is that the growth rates before and after the point of inflection have the same slope, but in opposite directions. In Cape gannets the rate of decrease after the point of inflection is about three times slower than the rate of increase before the inflection-point. Therefore growth rates were analysed using a non-parametric approach (compare Brown et al. 2007).
Growth rates were calculated between each pair of successive mass measurements, so if successive masses at times $t$ and $u$ were $m_t$ and $m_u$, the growth rate over this time period is $g = (\text{change in size})/(\text{time period}) = (m_u - m_t)/(u - t)$ and the mean of the pair of measurements is $a = (m_t + m_u)/2$.

For a set of observed masses (target mass) the average growth rate was estimated using weighted regression. Weights for all pairs of observations were calculated $(a, g)$ in such way that values close to the target mass had large weights and values farther away had increasingly smaller weights. If the target mass was $m^*$, then the weight $w$ attached to observation $(a, g)$ was $w = \exp(-((a - m^*)/\sigma)^2)$ where $\sigma$ was chosen to be 200, which is about 8% of the adult mass. The weight attached to observations 200 g distant from the target mass is substantial (0.37), at 300 g small (0.105), and at 400 g tiny (0.018). A weighted linear regression was fitted by GenStat8 (GenStat Committee 2005) to predict the growth rate $g^*$ at the target mass. By varying $\sigma$, the extent of the influential neighbourhood can be modified. The value for $\sigma$ 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 nearly 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 mass was calculated as $CV^* = 100 \times (s_m^*/m^*)$.

The estimated growth rates and the lower and upper confidence limits at each target mass were plotted, and the points were linked by interpolation. A normal distribution was assumed, so that the lower and upper confidence limits were $g^* - 1.96 \times s_m^*$ and $g^* + 1.96 \times s_m^*$ respectively. Using hatching mass as the starting value on day 0, the growth rate curve was integrated to produce a plot of mass against time. The non-parametric growth curve (table with predicted value of growth curve can be obtained from the first author) describes the pattern of growth as determined by the data rather than 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 expected growth rate. The observed growth rate was computed as the average of the two measurements, and its approximate standard deviation calculated as described above. The standardised 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.