

# Changes in prey availability impact the foraging behaviour and fitness of Cape gannets over a decade

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**ABSTRACT:** Seabirds respond to environmental changes by adjusting their breeding and foraging strategies, but this behavioural flexibility has limits. Cape gannets *Morus capensis* breeding in the southern Benguela on Malgas Island off South Africa's west coast have experienced large fluctuations in natural prey availability over the past decade, linked to environmental change and localised overfishing. When small pelagic fish are unavailable, breeding gannets increase their consumption of low-quality fishery discards (primarily hake *Merluccius* spp.). To investigate the limits of foraging flexibility of breeding gannets facing variable prey availability, we monitored foraging behaviour, nest attendance, adult body condition and chick growth between 2002 and 2012, along with diet composition and prey abundance (through annual hydroacoustic assessments) during the birds' breeding season. The combined biomass of sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* within the Malgas gannet colony's foraging range varied tenfold across the study period and was positively correlated with the proportion of these high quality fish in the gannets' diet (17 to 90%). Foraging effort increased and nest attendance decreased with decreasing sardine/anchovy consumption. Adult body condition was negatively impacted by increases in hake in the diet. Chick growth was lowest when low sardine and anchovy composition was coupled with an increase in adult foraging effort, suggesting a limit to behavioural compensation for food shortages. This long-term study demonstrates the consequences of variable prey levels for Cape gannet behaviour and fitness. These results highlight the need for detailed investigations of seabird–fishery interactions, and the necessity to limit fishing within Cape gannet foraging ranges during years of low natural prey abundance.

**KEY WORDS:** Seabirds · Chick growth · Fishery discards · Pelagic fish · Foraging effort

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## INTRODUCTION

Oceanic landscapes are fairly unpredictable at small to medium spatial and temporal scales (Hunt et al. 1999). Faced with irregular food supplies, off-

shore-feeding seabirds have evolved a suite of life history characteristics to cope: e.g. small clutch size, slow chick growth rates, delayed sexual maturity, large body sizes, long life spans (high adult survival) and relatively long foraging trips (Lack 1968). Global

changes (both natural and anthropogenic) may affect the marine environment used by seabirds, leading to changes in the availability of food (Lewison et al. 2012), their foraging strategies (Grémillet et al. 2004), diet composition (Abraham & Sydeman 2006) and survival rates (Distiller et al. 2012). Changing prey distributions may force parents to lower chick provisioning rates or switch to poor-quality food items that may negatively impact their own condition and that of their chicks (Österblom et al. 2008). In many species of seabirds, food availability and quality influence survival, breeding success, nest attendance, adult body condition and chick growth (Österblom et al. 2008). The phenomenon that low-quality food has a negative effect on body condition, breeding success and survival rates of individuals or species that usually consume high-quality food is known as the junk-food hypothesis (Jodice et al. 2006), and has been demonstrated for several seabird species (Batchelor & Ross 1984, Jodice et al. 2006, Kitaysky et al. 2006, Grémillet et al. 2008a, Österblom et al. 2008). 'Junk-food' may be particularly detrimental to juveniles (Batchelor & Ross 1984, Kitaysky et al. 2006, Grémillet et al. 2008a, Österblom et al. 2008, Mullers et al. 2009), while adults usually (but not always) show higher dietary flexibility and maintain their body condition (Moseley et al. 2012). There is also concern that the consumption of fishery discards by seabirds that usually consume high-quality prey may lead to ecological traps, i.e. species become accustomed to habits (such as feeding on discards) that are not beneficial to their survival or reproductive success (Grémillet & Boulinier 2009).

One of southern Africa's 7 endemic seabirds, the Cape gannet *Morus capensis* breeds colonially on 6 small islands off the coasts of Namibia and South Africa and feeds by plunge-diving for small pelagic fish in the productive Benguela upwelling system (Crawford et al. 1983). Monogamous pairs typically return to the same island each year and share parental duties in raising 1 chick during the September to February breeding season (Jarvis 1971). The main threats to Cape gannets are predation of gannet eggs, chicks and fledglings by kelp gulls *Larus dominicanus* (Mullers et al. 2009), great white pelicans *Pelecanus onocrotalus* (de Ponte Machado 2007) and Cape fur seals *Arctocephalus pusillus* (Makhado et al. 2006), and shifting distributions of natural prey (Crawford et al. 2007). Ideally, parents provide chicks with a diet of lipid-rich pelagic fish, dominated by sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* (Batchelor & Ross 1984). These small pelagic fish are also the target of a lucra-

tive commercial purse-seine fishery in South Africa, which developed after World War II (Griffiths et al. 2004). Over-exploitation by the purse-seine fishery in Namibian waters in the 1960s depleted the stocks of sardines, which still have not recovered (Griffiths et al. 2004). Populations of seabirds followed the decreasing fish stock trends and are now a fraction of their past abundance (Crawford 1999). Off the west coast of South Africa, the abundance of pelagic fish has fluctuated substantially over the past decade due to a combination of a south-eastward shift in the distribution of pelagic fish (van der Lingen et al. 2005, Roy et al. 2007) and a lack of spatial management of the purse-seine fishery, with heavy fishing pressure persisting in areas with low fish abundance due to the location of ports and land-based processing plants (Coetzee et al. 2008). This spatial mismatch resulted in local competition between birds and fisheries (Okes et al. 2009, Pichegru et al. 2009). When the preferred sardine and anchovy are unavailable, gannets may consume discards of low-quality hake *Merluccius* spp. (Table 1) from trawler vessels. The distribution and sizes of the catches of the hake fisheries are fairly consistent over years, hence providing a spatially and temporally predictable resource for the gannets (Field et al. 2013).

Cape gannets are currently listed as 'Vulnerable' by the IUCN due to their limited breeding range and competition with fisheries for prey (BirdLife International 2012a). This status may change to 'Endangered' if the global population continues to decline, and if breeding colonies exploiting depleted prey stocks are eventually abandoned (Pichegru et al. 2010).

Changes in natural prey abundance affect many aspects of Cape gannet behaviour and health, such as nest attendance, foraging effort and adult body condition. This highlights the need for long-term studies to identify the effects of changes in prey availability on seabird life history and behavioural characteristics. Recent variability in the Benguela

Table 1. Energy content of the main prey species of Cape gannets (from Batchelor & Ross 1984)

Prey item	Energy content (kJ g <sup>-1</sup> )
Sardine	8.59
Anchovy	6.74
Saury	6.20
Horse mackerel	5.63
Squid	4.55
Fishery discards (i.e. hake)	4.07

system, coupled with the ease of studying gannets, makes the Cape gannet a valuable tool for understanding the effects of global change on seabirds and other organisms. In this study we identified relationships among diet composition, nest attendance, chick growth, adult body condition and foraging effort (time and distance of foraging trips) in contrasting feeding conditions to develop a better understanding of (1) how breeding gannets adjust their foraging strategy in response to changing prey abundances and (2) to what extent this adjustment affects their production and survival. We predicted that gannets should show a high level of foraging flexibility in response to changes in prey abundance. However, it is not clear whether increasing foraging effort is able to buffer reduced provisioning rates and nest attendance which may lead to lower chick growth rates. We also predicted that adult gannets should be less sensitive to changes in diet composition than chicks, which require lipid-rich pelagic fish for adequate growth and survival (Batchelor & Ross 1984, Grémillet et al. 2008a). An understanding of the strategies gannets adopt and the consequences of reproducing in sub-optimal conditions may aid in the conservation of this iconic southern African seabird.

## MATERIALS AND METHODS

Gannet foraging and breeding data were collected on Malgas Island, West Coast National Park, South Africa (Fig. 1; 33° 03' S, 17° 55' E), currently home to about 20 000 to 30 000 pairs of Cape gannets, having decreased from more than 50 000 pairs in the mid-1990s to early 2000s (R. J. M. Crawford unpubl. data). Data were collected every year from 2002 to 2012, during which time the population kept decreasing (Distiller et al. 2012, R. J. M. Crawford unpubl. data). Most data were collected during October and November (see Table 2), facilitating comparisons of variables across years.

### Abundance of sardine and anchovy

The distribution and abundance of sardines and anchovies were determined from hydro-acoustic surveys conducted by Marine and Coastal Management (South African Department of Environment and Tourism) each year from late September to early December. These surveys consist of transects perpendicular to the coast extending from close inshore across the continental shelf to the 200 m isobath. Fish densities along transects were estimated using echo-

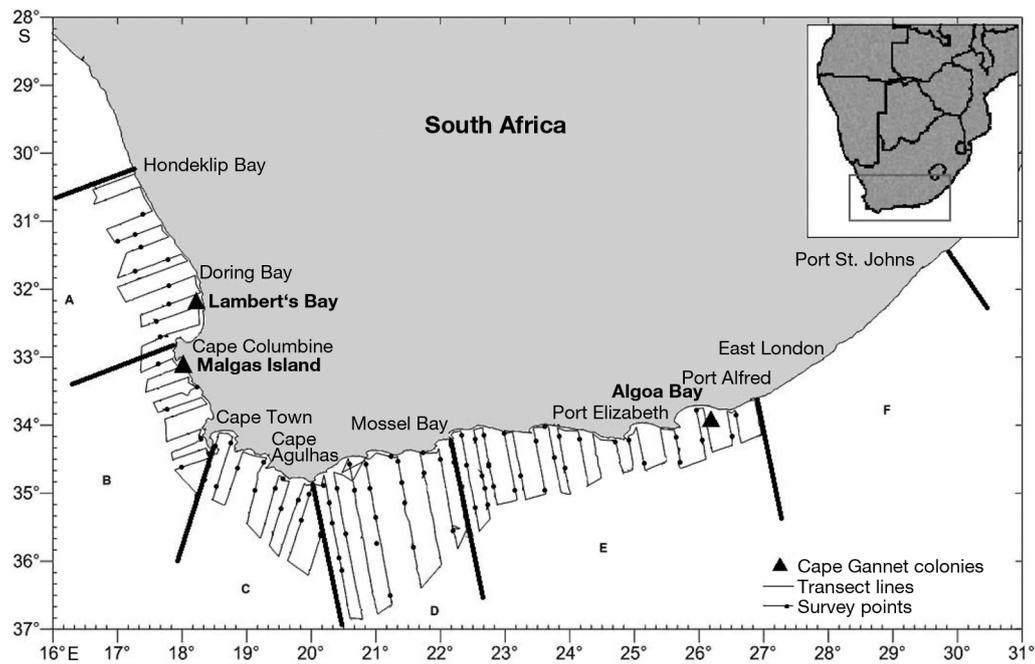


Fig. 1. Zones and transect lines of the annual pelagic fish acoustic surveys conducted by Marine and Coastal Management (MCM). Cape gannets breeding on Malgas Island forage in Zones A, B and C

integration techniques, and species composition and size frequency distributions of pelagic fish were determined from mid-water trawls (see Barange et al. 1999 for details). We only considered fish abundance from Hondeklip Bay to Cape Agulhas (Fig. 1; Zones A–C), as this region includes the entire area in which gannets breeding on Malgas have foraged over the past decade (see Pichegru et al. 2007, Grémillet et al. 2008b, Okes et al. 2009).

### Diet composition

Diet samples from up to 50 Cape gannets on Malgas Island were collected monthly over 1 to 3 d by Oceans and Coasts personnel. Gannets returning to the colony were captured haphazardly with a hooked pole and inverted over a bucket to promote regurgitation. Diet samples were analysed to the species level where possible, and prey proportions were calculated by wet mass. Sample sizes were 100 birds sampled over 2 mo (October to November) in each year except for 2005 ( $n = 81$ ), 2011 ( $n = 61$ ) and 2012 ( $n = 35$ , October only). Because breeding and non-breeding gannets have the same diet (Berruti 1991), we consider these diet samples representative of the diet of both the adult gannets and chicks.

### Foraging behaviour

The foraging strategies of adult gannets with small chicks were studied using GPS loggers on approx. 25 to 50 adults  $\text{yr}^{-1}$  from 2002 to 2012. When an adult gannet returned to a nest with a 1 to 5 wk old chick, the partner on the nest was captured with a hooked pole, as it was assumed that this individual would soon leave for a foraging trip. The individual was marked with animal dye and weighed (to the nearest 25 g with a 5 kg spring balance), and GPS loggers were attached to the 3 central rectrices with waterproof Tesa tape. Upon the gannet's return from foraging, the tape and logger were removed, usually approx. 24 h after deployment. The individual was re-weighed, and wing (flattened chord to the nearest 1 mm with a stopped wing rule) and culmen length (to the nearest 0.1 mm with Vernier callipers) were measured. Handling time for GPS logger deployment and removal was  $<10$  min.

Several types of GPS loggers were used over the course of the study, but they were always  $<3\%$  of the body mass of an adult Cape gannet (approx. 2630 g, Grémillet et al. 2008a). GPS loggers used from 2002

to 2008 were from Technosmart, weighed 65 g (see Grémillet et al. 2004 for details) and did not have any negative effects on the behaviour of foraging gannets (Pichegru et al. 2007). Loggers used in 2009 and 2010, also from Technosmart, weighed 45 g and are described by Moseley et al. (2012). Loggers used in 2011 and 2012 weighed 18 g and were designed by Perthold Engineering (Anderson). The loggers recorded the GPS location and speed of the adult at intervals ranging from 1 s to 1 min, depending on year. Information on the total foraging trip duration, the maximum distance from the colony reached and the total path length of the foraging trip was extracted (see Grémillet et al. 2004). To avoid pseudo-replication, each individual was only tracked once per year and second trips made by an individual were not included in analyses.

### Nest attendance patterns

From 2005 to 2012, sets of approx. 25 to 50 nests (different from those used for GPS deployment) with chicks aged 1 to 5 wk were selected in the first 1 to 4 rows of the colony edge (to reduce disturbance). Adults were marked with an animal dye for individual identification. These nests were monitored with binoculars hourly from dawn until dusk from a look-out point. We recorded whether the chick was alone, both parents were present, or only one parent was present to calculate the percentage of time each chick spent alone or was attended by both parents. We also calculated the average attendance bout of each parent and averaged these values to determine the average nest attendance bout for the nest. This parameter represents an average amount of time between chick feedings and is expected to increase as feeding conditions deteriorate. The variability (standard deviation) in the duration of parental attendance bouts was used as a measure of the regularity of food provisioning for the chick (see Schreiber & Burger 2002). Thus it was assumed that nests with a large standard deviation around the attendance bout duration were more likely subjected to sporadic provisioning rates, which could negatively influence chick growth rates, or at least correlate with poor chick body condition.

### Adult body condition and chick growth

All adults of the monitored nests were weighed and measured (wing and culmen) on a morning after they

had spent the night on the nest when possible. A simple index of adult body condition was calculated for these birds as body mass divided by wing chord ( $\text{g mm}^{-1}$ ) following Lewis et al. (2006) and Moseley et al. (2012). The body condition values of the 2 parents of a single nest were averaged to determine an overall index of parent health for that nest. Although there may be limitations in using a mass-to-wing ratio as an index of adult body condition (as it ignores other components of body condition such as parasite levels or physiological condition like nutrient levels), it provided a consistent method to compare conditions among years.

Chick growth rates were determined for the 25 to 50 nests monitored annually from 2005 to 2012. Chicks were measured every 3 to 5 d for approx. 3 to 4 wk each year. Wing chord and culmen length were measured as described above, and mass was recorded with a spring balance to the nearest 10 g with a 2.5 kg balance or to the nearest 25 g with a 5 kg balance (for chicks weighing over 2.5 kg). Growth of a chick's culmen and wing length are largely independent of food quality (Batchelor & Ross 1984), so we considered changes in mass as a useful measure of the chicks' response to varying food availability. In order to standardize chick growth rates for age, we only included measurements of chicks in the linear growth phase, when they weighed 400 to 2500 g (details in Fig. A1 in the Appendix). Daily growth rates ( $\text{g d}^{-1}$ ) were calculated as the difference in a chick's mass between 2 consecutive measurements divided by the number of days between those 2 measurements. An ANOVA performed on the first wing length measurement of chicks (400 to 2500 g) with year as the explanatory variable, revealed that chicks selected for monitoring were not the same size each year (1-way ANOVA,  $F_{7,210} = 11.95$ ,  $p < 0.001$ ). However, there was no correlation between length of first wing measurement and chick growth rates ( $r_s = -0.035$ ,  $p > 0.01$ ), suggesting that growth rates did not vary with chick age for chicks 400 to 2500 g. As a result, growth rates of chicks were calculated for each measurement period and then averaged to estimate average chick growth rates each year.

### Statistical methods

Statistical analyses were conducted in R (R Development Core Team 2012) and Minitab (Minitab 2000). Significance levels were considered at  $p < 0.01$ , in line with Bonferroni adjustments when multiple tests are carried out. All variables were tested for normality

with Kolmogorov-Smirnov tests, which indicated that most variables were not normally distributed even after various transformations. Therefore, Spearman rank correlations were used to assess relationships between variables across all years, in order to determine which variables change with prey availability, diet composition and foraging effort. Linear regressions were used to determine the effects of diet composition on parental body condition and chick growth.

We ran a multiple linear regression to test how chick growth varied with time chicks spent alone or with both parents at the nest, average parental nest attendance bout, standard deviation in parental nest attendance bouts, proportion of sardine/anchovy and of hake discards in the diet, foraging trip duration, maximum distance and path length, and biomass of sardine and anchovy in the foraging area. Variables with insignificant p-values were then removed (from highest to lowest) and Variance Inflation Factor tests were used to eliminate variables affected by multicollinearity.

## RESULTS

### Sardine and anchovy variability in diet composition

The estimated biomass of sardine and anchovy between Hondeklip Bay and Cape Agulhas (Fig. 1; Zones A–C) fluctuated between 356 000 tonnes (in 2011) and 3 203 000 tonnes (in 2002) (Table 2, Fig. 2). The average proportion of sardine and anchovy in the gannets' diet also fluctuated substantially, ranging from 17% in 2005 to 90% in 2012 (Table 2, Fig. 2) and was positively correlated with the biomass of sardine and anchovy between Hondeklip Bay and Cape Agulhas (Table 3:  $r_s = 0.212$ ,  $p < 0.001$ ). The proportion of hake in the gannets' diet ranged from 2% in 2011 to 53% in 2007 (Table 2, Fig. 2), but was not directly inversely related to the proportion of sardine and anchovy in the diet, because when sardine and anchovy are unavailable, gannets sometimes consume other pelagic fish, such as horse mackerel *Trachurus trachurus* (i.e. in 2005 and 2011, see Fig. A2 in the Appendix), before resorting to eating hake discards.

### Foraging behaviour and nest attendance

The length of the gannets' foraging trips decreased when sardine and anchovy were more abundant in

Table 2. Summary of diet composition, prey biomass, and foraging behaviour recorded for Cape gannets breeding on Malgas Island during 11 breeding seasons from 2002 to 2012. Most data were collected during October and November, except 2002 (December) and 2004 (January 2005). Data are based on nests with chicks aged 1 to 5 wk

	Diet composition		Prey availability Sardine & anchovy biomass ( $\times 10^3$ tonnes)	Foraging behaviour					
	Hake	Sardine & anchovy		Trip duration		Trip path length		Maximum trip distance	
	(%)	(%)		Mean $\pm$ SD (h)	n	Mean $\pm$ SD (km)	n	Mean $\pm$ SD (km)	n
2002	17.8	78.6	3203	23.0 $\pm$ 9.6	25	368.6 $\pm$ 200.3	25	106.0 $\pm$ 59.1	25
2003	19.5	77.4	2524	18.3 $\pm$ 13.2	20	412.7 $\pm$ 323.1	20	114.5 $\pm$ 82.8	20
2004	34.5	24.6	1029	31.3 $\pm$ 14.2	15	476.8 $\pm$ 199.5	15	122.9 $\pm$ 55.9	15
2005	28.6	17.0	746	29.2 $\pm$ 12.7	36	514.4 $\pm$ 234.8	36	132.6 $\pm$ 62.8	36
2006	35.1	50.0	1205	22.8 $\pm$ 11.2	43	397.6 $\pm$ 199.6	43	104.0 $\pm$ 55.7	43
2007	52.5	39.9	947	20.4 $\pm$ 16.2	31	347.7 $\pm$ 190.2	31	93.7 $\pm$ 45.8	31
2008	21.3	74.5	1633	22.2 $\pm$ 8.3	24	314.4 $\pm$ 111.0	23	72.3 $\pm$ 18.8	24
2009	29.5	61.1	2360	14.9 $\pm$ 8.2	13	343.5 $\pm$ 147.0	20	84.3 $\pm$ 40.1	20
2010	3.6	74.4	664	18.5 $\pm$ 9.1	43	371.8 $\pm$ 153.3	43	103.3 $\pm$ 38.2	43
2011	2.1	45.6	356	19.2 $\pm$ 9.4	31	374.3 $\pm$ 162.6	31	110.7 $\pm$ 48.3	31
2012	2.6	90.1	1209	19.2 $\pm$ 10.5	31	298.3 $\pm$ 175.0	31	86.7 $\pm$ 45.7	31
Mean $\pm$ SD	22.5 $\pm$ 15.8	57.6 $\pm$ 23.9	1443 $\pm$ 891	21.8 $\pm$ 11.9		383.5 $\pm$ 200.7		103.2 $\pm$ 53.3	

the gannets' foraging area (Fig. 3; Table 3:  $r_s = -0.147$ ,  $p < 0.01$ ). Likewise, during years when sardine and anchovy were scarce in the birds' diet, they increased their foraging effort (Fig. 4; Table 3) and their nest attendance bouts (Table 4), and they fed their chicks more irregularly (Table 4). However, these parameters were independent of the proportion of hake in the diet (Tables 3 & 4). The time chicks spent alone on their nest increased when parents fed on a larger proportion of hake (Table 4:  $r_s = 0.326$ ,  $p < 0.001$ ) and decreased when parents fed on a larger proportion of sardine and anchovy (Table 4:  $r_s = -0.264$ ,  $p < 0.001$ ).

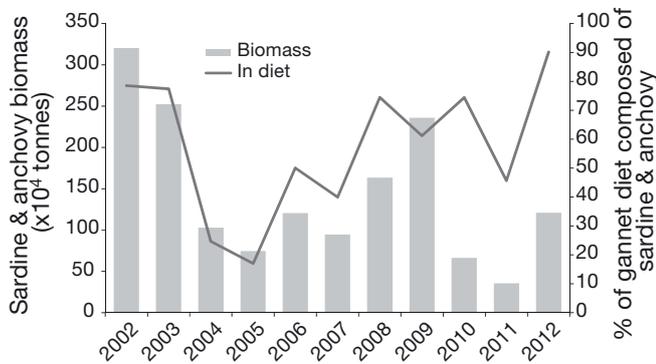


Fig. 2. Trend in biomass of sardine and anchovy from 2002 to 2012 in the southern Benguela (between Hondeklip Bay and Cape Agulhas), and proportion of sardine and anchovy in the diet of Cape gannets breeding on Malgas Island (foraging in the same area). Both variables were sampled in October and November of each year

Trip duration, path length and maximum distance from colony were highly correlated with each other and with the duration and variability of nest attendance bouts (Table 5), validating our decision to use duration of attendance bouts as a proxy for foraging trip duration and chick provisioning rates. The duration of the attendance bouts and the irregularity in the attendance patterns, i.e. in the chick feeding

Table 3. Spearman's rank correlations (with Spearman's rho [ $r_s$ , below diagonal] and p-value [above diagonal]) for comparisons of the diet and foraging behaviour of Cape gannets breeding on Malgas Island from 2002 to 2012. Duration = foraging trip duration; Length = foraging trip path length; Max.dist. = maximum distance from colony foraged; Diet(hake) = % of diet composed of hake; Diet(S/A) = % of diet composed of sardine and anchovy; Biomass = average biomass of sardine and anchovy from acoustic surveys in foraging area. Significant correlations ( $p < 0.01$ ) in **bold**. Foraging trip parameters were analysed at the individual level ( $n = 13$  to  $43$  trips  $\text{yr}^{-1}$ ), while diet composition was based on colony-wide averages ( $n = 35$  to  $100$  ind.  $\text{yr}^{-1}$ ). The biomass of sardine and anchovy between Hondeklip Bay to Cape Agulhas (Zones A–C) was estimated from annual acoustic surveys conducted during October and November

	Duration	Length	Max. dist.	Diet (hake)	Diet (S/A)	Biomass
Duration		<0.001	<0.001	0.047	0.001	0.558
Length	<b>0.804</b>		<0.001	0.149	<0.001	0.009
Max.dist.	<b>0.635</b>	<b>0.875</b>		0.801	<0.001	<0.001
Diet(hake)	0.112	0.081	0.014		<0.001	<0.001
Diet(S/A)	<b>-0.190</b>	<b>-0.242</b>	<b>-0.223</b>	<b>-0.497</b>		<0.001
Biomass	-0.033	<b>-0.147</b>	<b>-0.194</b>	<b>0.212</b>	<b>0.212</b>	

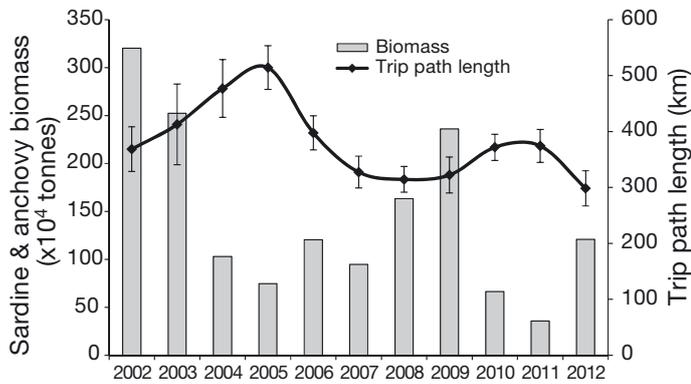


Fig. 3. Biomass estimate of sardine and anchovy between Hondeklip Bay and Cape Agulhas, and average foraging trip path length of Cape gannets breeding on Malgas Island from 2002 to 2012 (bars show  $\pm 1$  SE)

events, increased with increased time spent at sea and distance covered by foraging Cape gannets (Table 5). In general, nest attendance bouts were more regular when the biomass of sardine and anchovy was high (Table 4), and when foraging effort was low (Table 5). Both parents also spent more time together on the nest when sardine and anchovy were abundant (Table 4:  $r_s = 0.334$ ,  $p < 0.001$ ).

#### Chick growth rate and adult body condition

Chick growth rates improved with increased regional biomass of sardine and anchovy, and with increased proportion of sardine and anchovy in the gannets' diet, but decreased with increasing hake consumption (Table 6). Adult body condition, how-

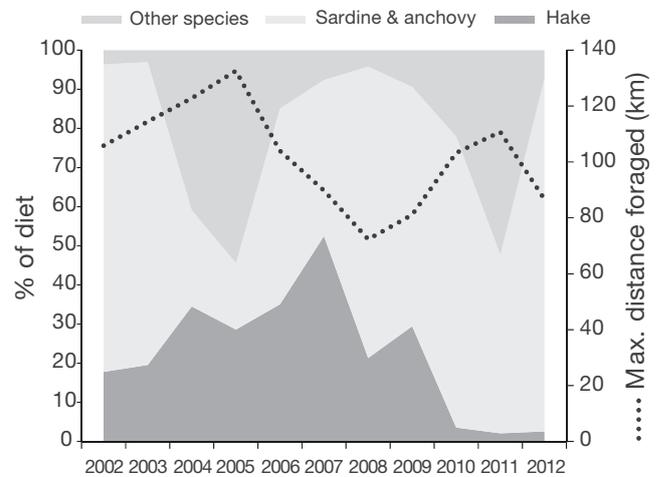


Fig. 4. Diet composition of Cape gannets breeding on Malgas Island and maximum distance travelled from the colony on foraging trips, 2002 to 2012. Diet category 'other species' includes saury, horse mackerel, and other medium-quality prey items (calorific value lower than sardine and anchovy but higher than hake)

ever, did not correlate with the percentage of sardine and anchovy in their diet, but rather was affected only when their diet was rich in hake (Table 6). Linear regressions yielded a negative relationship between adult body condition and hake consumption (Fig. 5: adjusted  $r^2 = 0.14$ ,  $p < 0.001$ ). By comparison, chick growth rates were more strongly related to the proportion of sardine and anchovy in the diet than to the proportion of hake in the diet (Fig. 5: adjusted  $r^2$ -values of 0.25 [ $p < 0.001$ ] and 0.04 [ $p = 0.002$ ], respectively). Chick growth was independent of adult body condition (ANOVA,  $F_{1,206} = 0.48$ ,  $p > 0.01$ ), calculated at the population level.

Table 4. Spearman's rank correlations (Spearman's rho below diagonal and p-value above diagonal) for comparisons of the diet and nest attendance behaviour of Cape gannets breeding on Malgas Island from 2005 to 2012. Alone = % of time chick alone at nest; 2parents = % of time chick attended by both parents; SDattend = average (of both parents) standard deviation in duration of nest attendance bouts; Att.bout = average (of both parents) duration of nest attendance bouts. Significant correlations ( $p < 0.01$ ) in **bold**. Nest attendance parameters were measured at the individual level. See Table 3 for details on diet composition variables

	Alone	2parents	SDattend	Att.bout	Biomass	Diet(S/A)	Diet(hake)
Alone		0.285	0.010	0.235	0.424	<0.001	<0.001
2parents	-0.066		0.027	<0.001	<0.001	<0.001	0.033
SDattend	<b>0.160</b>	-0.138		<0.001	<0.001	<0.001	0.951
Att.bout	-0.074	<b>-0.289</b>	<b>0.354</b>		0.430	<0.001	0.978
Biomass	0.050	<b>0.334</b>	<b>-0.255</b>	0.049		<0.001	<0.001
Diet(S/A)	<b>-0.264</b>	<b>0.380</b>	<b>-0.383</b>	<b>-0.257</b>	<b>0.540</b>		<0.001
Diet(hake)	<b>0.326</b>	-0.132	0.004	0.002	<b>0.265</b>	<b>-0.469</b>	

Table 5. Spearman's rank correlations (Spearman's rho below diagonal and p-value above diagonal) for comparisons of chick growth rates, nest attendance patterns, and foraging behaviour of Cape gannets breeding on Malgas Island from 2005 to 2012. C.growth = chick growth rate; Ad.cond. = average parent body condition. See Tables 3 & 4 for other definitions. Significant correlations ( $p < 0.01$ ) in **bold**. Nest attendance parameters, adult body condition, and chick growth were analysed at the individual level ( $n = 15$  to  $51$  nests  $\text{yr}^{-1}$ ), while foraging trip parameters were based on colony-wide averages ( $n = 13$  to  $43$  ind.  $\text{yr}^{-1}$ )

	C.growth	Ad.cond.	Alone	2parents	SDattend	Att.bout	Duration	Max.dist.	Length
C.growth		0.561	0.038	0.047	<0.001	<0.001	<0.001	<0.001	<0.001
Ad.cond.	-0.041		0.002	0.778	0.399	0.732	<0.001	0.001	0.137
Alone	-0.145	<b>-0.194</b>		0.285	0.010	0.235	0.400	0.508	0.058
2parents	0.139	-0.018	-0.066		0.027	<0.001	0.073	<0.001	<0.001
SDattend	<b>-0.263</b>	-0.053	<b>0.160</b>	-0.138		<0.001	<0.001	<0.001	<0.001
Att.bout	<b>-0.383</b>	-0.021	-0.074	<b>-0.289</b>	<b>0.354</b>		<0.001	<0.001	<0.001
Duration	<b>-0.560</b>	<b>0.250</b>	-0.052	-0.111	<b>0.230</b>	<b>0.493</b>		<0.001	<0.001
Max.dist.	<b>-0.496</b>	<b>0.200</b>	0.041	<b>-0.294</b>	<b>0.394</b>	<b>0.296</b>	<b>0.574</b>		<0.001
Length	<b>-0.529</b>	0.092	0.117	<b>-0.332</b>	<b>0.394</b>	<b>0.359</b>	<b>0.560</b>	<b>0.923</b>	

Table 6. Spearman's rank correlations (Spearman's rho [ $r_s$ ] and p-value) for comparisons of chick growth rates, nest attendance patterns, and diet composition of Cape gannets breeding on Malgas Island from 2005 to 2012. See Table 3 for definitions of variables. Significant correlations ( $p < 0.01$ ) are in **bold**. Chick growth and adult body condition were analysed at the individual level ( $n = 15$  to  $51$  nests  $\text{yr}^{-1}$ ), while diet composition was based on colony-wide averages ( $n = 5$  to  $100$  ind.  $\text{yr}^{-1}$ )

	Chick growth		Adult condition	
	$r_s$	p	$r_s$	p
Adult condition	-0.041	0.561		
Diet(S/A)	<b>0.460</b>	<0.001	-0.013	0.839
Diet(hake)	<b>-0.207</b>	0.002	<b>-0.470</b>	<0.001
Biomass	<b>0.194</b>	0.004	<b>-0.347</b>	<0.001

Across all years (2005 to 2012), chick growth rates decreased when foraging effort increased, most notably as foraging trip duration increased (Table 5:  $r_s = -0.560$ ,  $p < 0.001$ ). A multiple linear regression indicated that chick growth increased as hake consumption, foraging trip duration and irregularity of parental attendance bouts all decreased simultaneously: chick growth =  $118 - 0.25 \times (\% \text{ of diet composed of hake discards}) - 2.30 \times (\text{foraging trip duration}) - 20.90 \times (\text{standard deviation in parental nest attendance bouts})$ , with an adjusted  $r^2 = 0.32$  ( $p < 0.001$ ;  $F_{3,202} = 33.30$ ).

Of all nests monitored from 2002 to 2012, 70.4% were never observed with a lone chick at the nest. Chick growth rates decreased slightly with increasing time spent alone (Table 5). Irregular provisioning was associated with lower chick growth rates and chicks being left alone more often (Table 5).

## DISCUSSION

### Gannet behavioural flexibility in response to changing prey availability

Cape gannets consume a variety of prey species, but breeding gannets depend on high quality natural prey to rear chicks. Exploiting alternative prey items, especially low-quality fishery discards, may lead to reduced breeding success (Grémillet et al. 2008a). Pichegru et al. (2010) found that Cape gannets increase their foraging effort to compensate for reduced availability of natural prey, but reach a point when they are forced to supplement their diet with fishery discards (mostly hake). We found that during years when gannets fed largely on hake, chicks spent more time unattended at the nest (thus increasing the risk of predation) and had slower growth rates (increasing starvation risks), and adults were in poorer condition. Thus poor diet may affect colony recruitment and ultimately drive local and global population declines should the availability of natural prey remain low. Demographic data on the survival rates and breeding success of gannets would be needed to confirm these effects.

Most seabirds show flexibility in foraging behaviour linked to varying environmental conditions (Cairns 1987, Grémillet & Charmantier 2010), and our results clearly show such inter-annual variability in the foraging strategy of breeding Cape gannets from the same colony over the past decade (Table 2). The variation in gannet foraging trip durations and distances appears to be closely linked to changing food availability—a circumstance that likely shaped the evolution of seabird foraging strategies. Because

the proportion of sardine and anchovy in gannet diet is positively correlated with the biomass of these fishes in the gannets' foraging area (Table 3), the increase in gannet foraging effort presumably resulted from the reduced availability of their prey. This supports the idea of using gannet foraging effort to estimate prey abundance and overall ecosystem health (Lewis et al. 2006, Grémillet & Charmantier 2010). Because the colony size has decreased in conjunction with an increase in foraging effort and a decrease in prey availability, we can assume that intraspecific competition for food is not an issue for the remaining individuals breeding at the colony. The lack of correlation between foraging effort and the percentage of hake in the diet, however, indicates that hake-related foraging trips could be associated with both long and short foraging trips or, perhaps, that hake was consumed only after a certain amount of time was spent searching for natural prey.

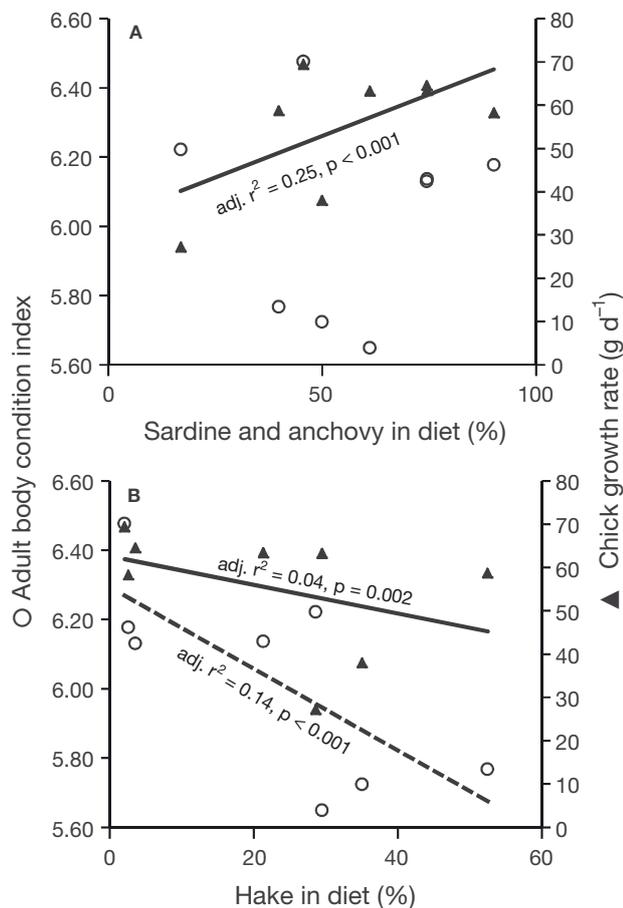


Fig. 5. Relationship of Cape gannet adult body condition (O; dashed line) and chick growth rate (▲; solid lines) with (A) % of sardine and anchovy in the diet and (B) % of hake in the diet

### Regular nest attendance patterns and provisioning rates are necessary for better chick growth

Predation is a serious threat to gannet chicks on Malgas Island (Makhado et al. 2006, de Ponte Machado 2007, Mullers et al. 2009). Poor nest attendance generally occurs when environmental conditions are unfavourable, because if the foraging parent has been gone for an extended period of time, the attending parent may leave for his/her own foraging trip, leaving the chick unattended. This likely occurs because young chicks can only survive for a few days without food (Navarro 1992). Intraspecific aggression by neighbouring adult gannets on young unattended chicks significantly reduces the latter's survival compared to attended chicks (Jarvis 1971). While chicks might benefit from an increase in feeding rate when both parents forage at the same time, the costs of non-attendance and lower food availability are likely to be higher, as is shown by our chick growth data (Table 7).

The significant positive correlation between the proportion of time parents spend at the nest together and prey abundance (Table 4) suggests that when parents can spend more time at the nest together they are not struggling to find food and have more resting time. Thus there is a potential for nest attendance parameters to be used as indices of environmental conditions. In addition, good feeding conditions are usually coupled with regularity in the duration of nest attendance bouts, and therefore provisioning rates.

### Adults and chicks are affected differently by diet composition

Although previous studies showed that adult Cape gannets can survive on poor-quality prey (Grémillet et al. 2008a, Moseley et al. 2012), we found that breeding adults tend to have poor body condition in years when hake comprises a large proportion of their diets. There was a stronger relationship between adult body condition and the proportion of hake in the diet than with the proportion of sardine and anchovy in the diet (Fig. 5). This suggests that, although sardine and anchovy have the highest nutritional value amongst the pelagic fish upon which Cape gannets feed (our Table 1; Batchelor & Ross 1984), adults can still maintain their health on alternate fish species of slightly lower energetic quality, such as horse mackerel and Atlantic saury *Scomberesox saurus*.

Table 7. Summary of mean ( $\pm$ SD) chick growth rates, nest attendance patterns, and adult body condition for Cape gannets breeding on Malgas Island during 8 breeding seasons from 2005 to 2012. All data were collected in October and November. Data are based on nests with chicks aged 1 to 5 wk

	Chick growth rate		Time chick was left alone at nest		Time both parents at nest		Parent nest attendance bout		SD of parent nest attendance bout		Adult body condition, nest avg.	
	(g d <sup>-1</sup> )	n	(%)	n	(%)	n	(d)	n	(d)	n	(g mm <sup>-1</sup> )	n
2005	27.2 $\pm$ 28.5	51	3.6 $\pm$ 7.0	50	2.1 $\pm$ 3.6	50	1.0 $\pm$ 0.3	50	0.6 $\pm$ 0.2	50	6.2 $\pm$ 0.5	51
2006	38.0 $\pm$ 15.2	28	1.1 $\pm$ 4.0	31	3.6 $\pm$ 3.5	31	0.8 $\pm$ 0.2	31	0.4 $\pm$ 0.1	30	5.7 $\pm$ 0.3	31
2007	58.8 $\pm$ 10.4	30	1.9 $\pm$ 2.6	33	0.8 $\pm$ 1.0	33	0.5 $\pm$ 0.1	33	0.4 $\pm$ 0.0	33	5.8 $\pm$ 0.5	33
2008	63.3 $\pm$ 21.9	28	1.7 $\pm$ 5.7	39	4.5 $\pm$ 4.5	39	0.7 $\pm$ 0.1	37	0.3 $\pm$ 0.1	37	6.1 $\pm$ 0.4	39
2009	63.3 $\pm$ 11.5	22	2.3 $\pm$ 4.0	39	4.0 $\pm$ 3.0	39	0.8 $\pm$ 0.5	39	0.5 $\pm$ 0.7	39	5.6 $\pm$ 0.3	39
2010	64.6 $\pm$ 16.8	23	0.4 $\pm$ 1.3	25	2.0 $\pm$ 2.5	25	0.5 $\pm$ 0.2	25	0.4 $\pm$ 0.2	25	6.1 $\pm$ 0.3	25
2011	67.3 $\pm$ 27.3	12	0.0 $\pm$ 0.0	19	4.6 $\pm$ 7.8	19	0.7 $\pm$ 0.2	19	0.5 $\pm$ 0.2	19	6.5 $\pm$ 0.3	19
2012	62.7 $\pm$ 15.8	20	0.1 $\pm$ 0.4	26	8.1 $\pm$ 5.6	26	0.6 $\pm$ 0.1	25	0.4 $\pm$ 0.1	25	6.2 $\pm$ 0.5	26
Mean $\pm$ SD	51.1 $\pm$ 25.5		1.7 $\pm$ 4.5		3.5 $\pm$ 4.5		0.7 $\pm$ 0.3		0.4 $\pm$ 0.3		6.0 $\pm$ 0.5	

The abundance of sardine and anchovy in the gannets' foraging area was extremely low in 2005 and 2011 (Table 2), when gannets consumed high levels of an alternate prey species, horse mackerel. In both 2005 and 2011, the proportion of sardine and anchovy in the diet was <50%, suggesting that chick growth rates should have been low. Consuming horse mackerel helped parents compensate for the lack of sardine and anchovy in 2011, but not in 2005, as energy expended in foraging was very high that year. Indeed, in 2005, gannets had very long foraging trips in terms of both duration (29.2 h) and distance (514 km), the most variable attendance bout durations (i.e. provisioning patterns), and they left their chicks alone for the greatest amount of time (Table 7). As a result, chick growth rates averaged only 27.2 g d<sup>-1</sup> in 2005 (Table 7). By comparison, in 2011 foraging trips lasted an average of 19.2 hours (below average), travelling 374 km (below average), no study chicks were left alone at the nest (Table 7), and chick growth rates averaged 67.3 g d<sup>-1</sup> (Table 7). Thus, it appears that breeding gannets may be able to compensate for a reduction in sardine and anchovy only if a suitable alternative prey is available close enough to their colony to avoid extended foraging trips, which cause a reduction in provisioning rates to chicks as well as poorer nest attendance (and thus higher predation and mortality). It is also important to note that gannets are expert predators and often appear to locate prey that surveys and fisheries are unable to find (Grémillet et al. 2008b). This may have been the case in recent years, when sardine and anchovy constituted a large portion of the gannet's diet yet acoustic surveys reported low biomasses of these species (see Fig. 2). However, there could have been a decrease in

absolute sardine and anchovy consumption, which would not be apparent as we measured percent composition. These findings highlight the need for spatial management of competing fisheries, and the fact that the behavioural flexibility of foraging gannets is constrained by the demands of their chicks.

## CONCLUSIONS

Limits of seabird behavioural flexibility vary depending on a species' life history traits and its geographic constraints (Grémillet & Charmantier 2010). Despite flexibility in adult foraging strategy, poor feeding conditions are likely to cause low chick growth and survival rates, eventually leading to low breeding success and recruitment, and colony-level population declines. If poor conditions persist, colony-level population declines may lead to global declines, as some breeding sites may be abandoned while others reach carrying capacity. Because gannets do not breed until their third or fourth year, the effects of poor breeding conditions may not arise until several years later. Hence longitudinal monitoring of both seabird and prey populations is essential.

Long-term studies across varying environmental conditions are essential to improve our knowledge of the complex responses of Cape gannets and other seabirds to environmental change. The persistence of a population depends on the ability of individuals to cope with changes in their environment, so a clearer understanding of the limits of the behavioural flexibility of Cape gannets should lead to more effective management strategies in light of inevitable continued changing conditions. Malgas Island is pro-

tected within the West Coast National Park Marine Protected Area (BirdLife International 2012b), but the gannets' foraging trips extend hundreds of kilometres from Malgas Island, overlapping extensively with South Africa's pelagic fisheries (Okes et al. 2009). The implementation of no-take fishing zones or reduced Total Allowable Catches during years where the abundance of sardine and anchovy falls below a certain threshold or is located relatively far from Malgas Island may help breeding gannets to reduce their foraging effort in search of quality prey. This type of Ecosystem Approach to Fisheries, taking into consideration minimum requirement for seabirds in the calculation of the Total Allowable Catches (Cury et al. 2011), would surely benefit the Benguela ecosystem.

An understanding of how well Cape gannets cope with varying conditions not only helps to conserve gannets and other seabirds, but may reveal how seabirds can be used to monitor the status of the Benguela ecosystem and its pelagic fish populations, thus improving fisheries management of some of South Africa's economically key fish species. Using seabirds as indicators of ecosystem change has been suggested as a cheaper, potentially more effective method of monitoring than current survey methods (Cairns 1992, Berruti et al. 1993, Monaghan 1996). However, since seabirds generally exhibit some degree of behavioural flexibility, understanding that life history traits are affected differently depending on the severity of conditions is important when using seabirds as indicators of ecosystem health (Grémillet & Charmantier 2010). Cape gannets should be valued as both functional components (as top predators) of the Benguela ecosystem and as potentially useful environmental sentinels. It is critical that long-term monitoring and anti-predator control measures continue and that appropriate conservation action in response to changing environmental conditions is taken to prevent further population declines.

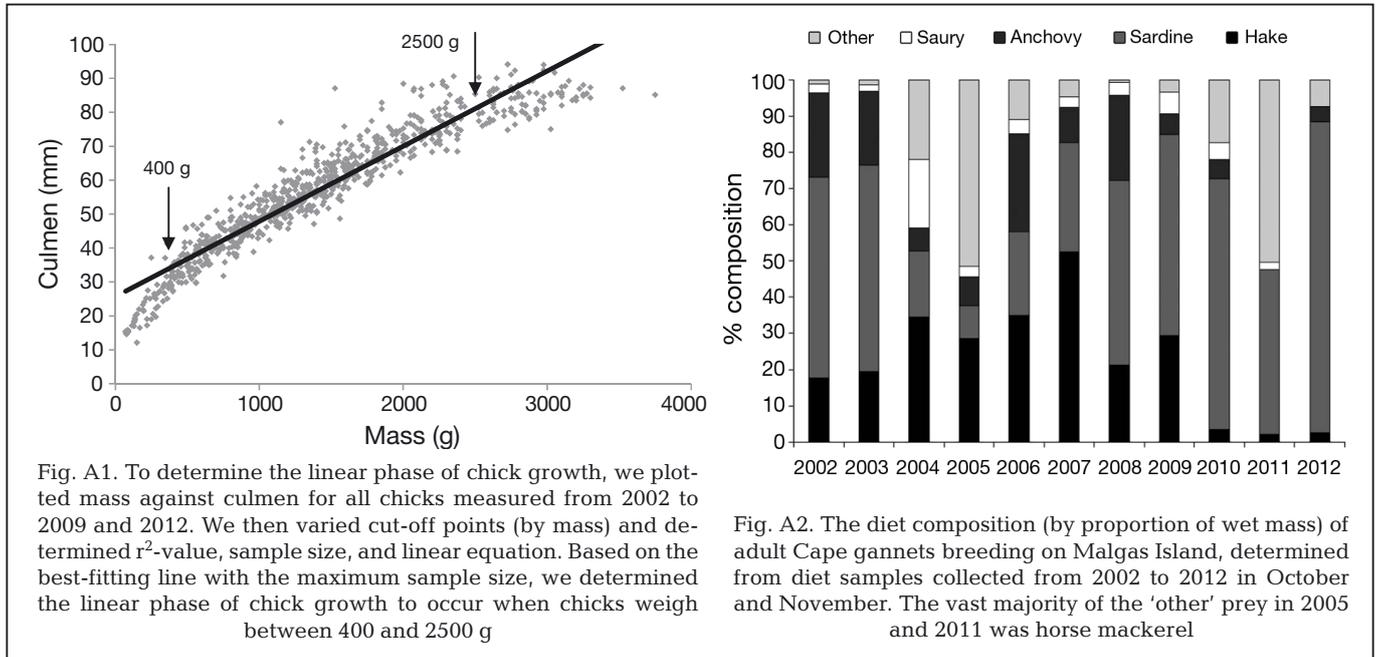
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**Appendix.** Additional data on Cape gannet chick growth and diet composition



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