Foraging behaviour and energetics of Cape gannets *Morus capensis* feeding on live prey and fishery discards in the Benguela upwelling system

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ABSTRACT: We compared the foraging ecology of Cape gannets *Morus capensis* attending 2 colonies of equivalent size, yet with contrasting diet and population trends. One colony, on the west coast of South Africa, is decreasing in size and its occupants feed mainly on fishery wastes, whereas the other colony, on the south coast of South Africa, is growing and its occupants feed exclusively on natural prey (pelagic fish). In October and November 2005, we examined the diet, at-sea behaviour, and energy requirements of breeding gannets using direct observations, miniaturised GPS loggers, and time-depth recorders attached to foraging adults. Concurrent hydroacoustic surveys allowed us to assess the distribution and abundance of their preferred prey (the sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*). Birds from the declining west coast colony foraged in areas containing very low abundances of pelagic fish. They fed primarily on low-energy fishery discards. They increased their foraging effort and exploited a greater area than birds from the growing colony, which took advantage of abundant pelagic fish stocks in their foraging range. A marked eastward shift of pelagic fish initiated in the late 1990s has resulted in the shortage of natural prey to Cape gannets on the west coast, strongly suggesting that the local population trend is driven by food availability during the breeding season. A bioenergetic model showed that enhanced availability of low-energy fishery discards does not seem to compensate for the absence of natural prey. Added to the predation pressure by the Cape fur seal *Arctocephalus pusillus* and the great white pelican *Pelecanus onocrotalus*, those threats weigh heavily on a vulnerable seabird population.

KEY WORDS: Bioenergetic modelling · Fishery waste · GPS tracking · Hydroacoustic survey · Marine management · Pelagic fish · Seabird

INTRODUCTION

To survive and reproduce, adult seabirds have to gather food at sea in a highly variable environment (Bakun 1996). Their ability to adapt to this variability and forage efficiently determines their population trajectories (Lewis et al. 2006). On an evolutionary time scale, seabird life-history traits are adapted to cope with environmental stochasticity through slow chick growth rates, long breeding seasons, delayed maturity, and long lifespans. On a shorter time scale, as during the breeding season, adult seabirds show flexible foraging behaviour, which should help them cope with labile prey distributions (e.g. Lescroël & Bost 2005). Studies of seabird at-sea behaviour are currently booming thanks to rapid advances in biotelemetry technology. However, very few field studies have simultaneously investigated the foraging behaviour

and predatory efficiency of seabirds relative to the distribution and abundance of their prey (Grémillet et al. 2004a). This is because seabirds often forage over huge oceanic areas, and population studies of their prey (mainly fish) require at-sea investigations on board research vessels, which are both expensive and time-consuming.

Beyond natural environmental variability, seabirds also face the impact of human activities, of which the most profound are probably industrial fisheries. These fisheries often deplete marine fish stocks, diminishing the availability of food for numerous seabird species (Furness & Tasker 2000). Conversely, they may also generate large volumes of fish waste, upon which many seabird species have learnt to make a living (Garthe 1996). Several studies have investigated the impact of fishery discards on seabird behaviour, ecology, and population dynamics (Arcos & Oro 1996, Oro et al. 2004), but no study has compared the foraging behaviour of a seabird species feeding either on its natural live prey or on fishery discards and discussed the consequences of these different foraging options on population processes.

We performed such a study on the Cape gannet *Morus capensis*, a large coastal seabird endemic to the Benguela upwelling system; the birds primarily feed by plunge diving on small pelagic fish (Berruti et al. 1993). The Benguela, characterised by high productivity due to the vertical transport of cold, nutrient-rich waters to the surface, extends from southern Angola (17°S) to the southern tip of Africa (34°S) and eastwards to East London, South Africa (28°E). It is one of the most productive ocean areas in the world (Shannon & O'Toole 2003), but is also heavily exploited by fisheries that target small pelagic fish, such as the sardine *Sardinops sagax* and the anchovy *Engraulis encrasicolus*, as well as demersal whitefish such as the hake *Merluccius* spp. (Crawford et al. 1987). Fisheries compete with seabirds by depleting stocks of their natural prey (Crawford 1999), but also produce large amounts of waste, some of which is consumed by seabirds. In the 1980s, hake fishery discards represented 15% of seabird consumption in the Benguela (i.e. 65000 t yr^{-1}, Crawford et al. 1991). Towards the end of the 1990s, approx. 9000 t of hake were still discarded annually off the west and south coasts of South Africa (Walmsley et al. 2007).

The Cape gannet breeds at 6 island colonies from central Namibia to the southeast coast of South Africa (Fig. 1). We studied the foraging ecology of birds from the 2 southernmost colonies located on opposite sides of Cape Agulhas: Malgas Island on the west coast of South Africa and Bird Island on the south coast (Fig. 1). These colonies were of equivalent size at the time of our study (approx. 65000 pairs on each island), together supporting 80% of the world breeding population of Cape gannets (Crawford 2005). However, they have experienced different population trends: the population on Bird Island has shown a positive growth rate since the start of monitoring in the 1950s (Klages et al. 1992), whereas that on Malgas Island grew more slowly until 1996 (Crawford 1999) and has recently declined (Crawford et al. 2007). The colonies grew thanks to the progressive cessation of guano activities and reduction of human disturbance (Griffiths et al. 2004). Studies of the diet of Cape gannets were conducted on both islands in the 1980s. Birds from Bird Island fed exclusively on natural prey (i.e. sardines, anchovies, and saury *Scomberesox saurus*) (Klages et al. 1992), whereas birds from Malgas fed on both live prey and fishery discards (Berruti et al. 1993). Because a recent study suggested that Cape gannet population trends are driven by food availability during the breeding season (Lewis et al. 2006), we investigated the foraging strategies of Cape gannets from Malgas Island and Bird Island to test the hypothesis that contrasting food abundance and quality (live prey versus fishery waste) contribute to the contrasting population trends at the 2 different colonies. We compared the foraging behaviour and diet of gannets from each island with the abundance and distribution of their principal prey (small pelagic fish: the sardine *Sardinops sagax* and the anchovy *Engraulis encrasicolus*) as determined during an acoustic survey conducted concurrently with our studies on the birds. We then estimated the energetic needs of Cape gannet for breeding successfully on each island using a bioenergetic model.

MATERIALS AND METHODS

We studied the foraging behaviour of Cape gannets breeding at Malgas Island (Saldanha Bay, 33°03'S, 17°55'E) in the Western Cape and at Bird Island (Nelson Mandela Bay, 33°50'S, 26°17'E) in the Eastern Cape of South Africa (Fig. 1). Observations were conducted from 9 to 31 October 2005 on Malgas Island and from 21 to 29 November 2005 on Bird Island, under permits issued by South African National Parks. Cape gannets on Bird Island typically breed 1 to 2 months later than those on Malgas Island, and therefore birds from the 2 colonies were at the same breeding stage.

Recording seabird foraging behaviour. On each island, 30 adult birds raising small chicks (1 to 3 wk old) were caught on their nest site prior to a foraging trip and fitted with electronic devices. The birds were caught when both partners were at the nest site, so that 1 partner could stay on the nest to guard the chick. Birds were caught with a hook mounted on a telescopic pole, which allowed us to capture birds nesting away from the margins of the colony.
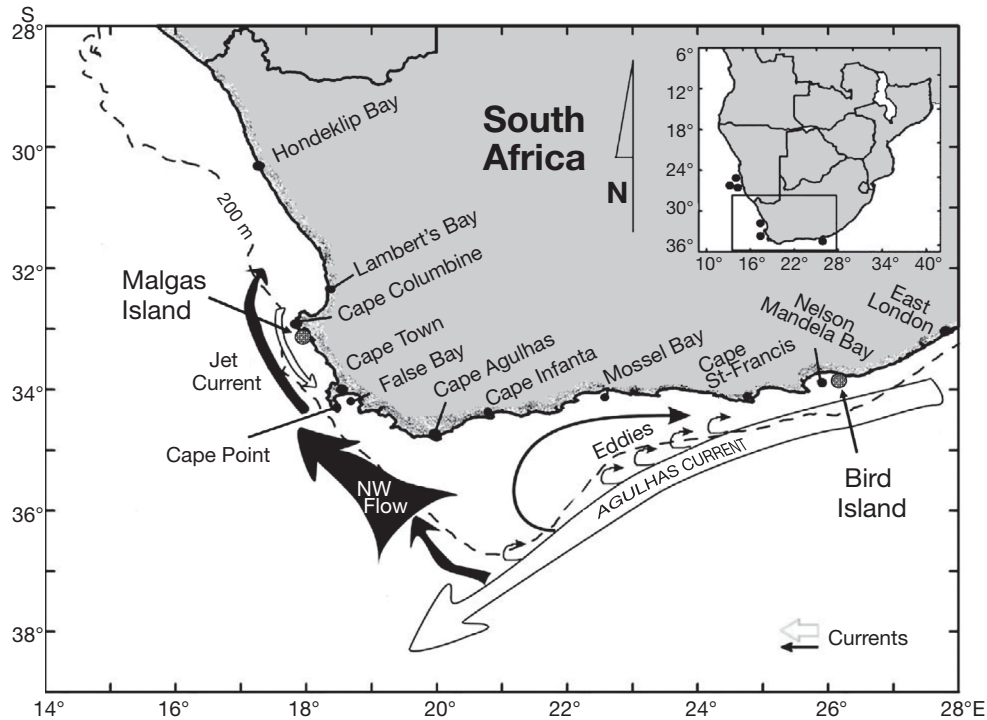
Fig. 1. *Morus capensis*. Distribution of 6 colonies (inset) and main ocean currents in Southern Africa (modified from Miller et al. 2006)

Three types of data logger were used:

(1) GPS-TD loggers (earth & Ocean Technologies) are miniaturised GPS devices combined with time-depth recorders (see Ryan et al. 2004 for details). Latitude and longitude were recorded at 2 min intervals to an accuracy of approximately 10 m, and depth and temperature were recorded at 1 s intervals to the nearest 0.1 m. Loggers were housed in waterproof and pressure-tight, streamlined fibre-composite containers closed with an O-ring cap (96 × 39 × 26.5 mm; mass 75 g, i.e. 2.4% of adult body mass).

(2) GPS data loggers (Technosmart) were also housed in the same type of waterproof and pressure-tight, streamlined containers as above (95 × 48 × 24 mm; mass 65 g, i.e. 2.1% adult body mass; see Grémillet et al. 2004b for details). Position data (latitude, longitude, and altitude) were recorded at 10 s intervals, with an accuracy of 10 m.

(3) Time-depth recorders (TDR, M190-D2GT, 12-bit resolution, 60 × 15 mm, 15 g; Little Leonardo) were deployed in conjunction with the GPS loggers. These devices monitor depth and temperature every second with an absolute accuracy of 0.1 m (see Ropert-Coudert et al. 2004 for details). The GPS + TDR package weighed 80 g, i.e. 2.5% of adult body mass.

All birds were equipped for a single foraging trip to minimise pseudo-replication problems. The GPS device was attached to the bird's lower back, using 3 central tail feathers, while TDRs were attached underneath the tail. All devices were fixed with Tesa tape, which allows the loggers to be removed with minimal damage to the plumage. Handling lasted 4 to 7 min from capture to release and took place under shade to avoid heat stress, while the bird's head was covered to reduce handling stress. Although these techniques have been used on several occasions on Cape and Northern gannets *Morus bassanus* (Grémillet et al. 2004b, 2006, Lewis et al. 2006) without any apparent impact on the welfare of the animals, we checked for potential biases resulting from human handling or impacts from the presence of loggers. Ten birds from control nests with comparable chick age were marked using biocompatible dye on a paintbrush fixed to a pole. Marking took place without handling the birds. Control and experimental nests were then monitored every hour from dawn to dusk until a complete foraging trip had been performed by each partner. We assumed that the foraging trip of equipped birds would be modified in case of disturbance (Adams & Klages 1999). Control nests were then checked every hour for 4 further complete consecutive foraging trips to assess the variability of the foraging environment through the regularity of trip duration. We assumed that in a predictable environment, birds have more regular foraging trips and regular daily feeding rates of young (Schreiber & Burger 2002). We compared the standard deviations of the mean duration of the 5 foraging trip durations between the 2 colonies.

Analysis of electronic data set and spatial analysis. Dive profiles were analysed using IGOR Pro (v. 4.01, Wavemetrics), with a dive defined as when a device recorded a depth ≥0.5 m for ≥1 s. We determined the number of dives per h of foraging trip, the average dive duration, and the average maximum dive depth for each of the foraging trips (see details in Ropert-Coudert et al. 2004).

Using the GPS positions, we determined and compared the foraging range of the birds from the 2 colonies. Foraging range was determined from filtered GPS positions known to be associated with feeding behaviour, i.e. positions where the birds were flying (speed > 10 km h^{-1}) and displaying a sinuous path (see details in Grémillet et al. 2004b). This method discards commuting sections, thus minimising pseudo-replication, and has been validated by Grémillet et al. (2006). Positions obtained from GPS loggers recording at 10 s intervals were sub-sampled to have 1 position every 2 min to be comparable with data obtained from the GPS-TD loggers.

Adaptive kernel analyses of bird foraging positions were used to assess the time spent per unit area. Analyses were conducted using Arcview GIS 3.2 with the smoothing factor chosen according to the Least Square Cross Validation (LSCV) method (Girard et al. 2002). Contour levels covering 10 to 90 % of the foraging locations were estimated. The surface of the foraging range was calculated through the concave polygon method with Ranges VI (Anatrack). We also calculated the average density of sardines and anchovies present in the foraging area of the birds from both islands.

Energetic modelling. We used the algorithm of Enstipp et al. (2006) to assess the daily energy requirements (kJ d^{-1}), daily food intake (g d^{-1}), and metabolic scope (average metabolic rate expressed as a multiple of the basal metabolic rate [BMR]) of Cape gannets. We used time budget information gained from the GPS data loggers, such as the foraging trip duration and the time spent flying, and field data for the body mass and chick age.

Birds equipped with loggers were weighed before attaching the devices and again when back at the nest, after removal of the devices, i.e. 1 to 2 h after the bird returned to its nest. This method allowed us to minimise the food loss due to the bird regurgitating during its handling and to standardise the amount of food already fed to the chick (R. Navarro unpubl. data). Adult gannets were weighed to the nearest 25 g using a spring balance (Salter Brecknell Super Samson, RACO Industries). There was no difference in adult body mass before a foraging trip between gannets from the 2 islands ($F_{1,56}$ = 3.67, p = 0.061). Diet samples of gannets were collected during our study by Marine and Coastal Management staff from 20 to 22 October on Malgas Island and from 14 to 17 November on Bird Island. Prey types and their proportions by mass in the overall diet samples were assessed. We assumed that food brought back to the nest by birds (i.e. the difference in bird mass before and after a foraging trip) would be composed of prey in the same respective proportions as in the overall diet samples. We then calculated the energetic value of the food brought back by each bird according to calorific values from the literature (Batchelor & Ross 1984).

Fish distribution and abundance. Sardines and anchovies are the preferred prey of Cape gannets (Adams & Klages 1999) and can constitute >90 % of their diet (Crawford 2005). Information on the abundance and distribution of these small pelagic fish species over the period of observations of gannet foraging was obtained from a hydroacoustic survey conducted by Marine and Coastal Management from 18 October to 5 December 2005. This survey mapped the distribution and estimated the abundance of anchovies, sardines, and the redeye round herring *Etrumeus whiteheadi* off South Africa between Hondeklip Bay on the west coast and East London on the east coast (Fig. 1). It consisted of transects oriented perpendicular to the coast and extending across the continental shelf from close inshore to the 200 m isobath. Echo-integration techniques were used to estimate fish density along survey transects, and midwater trawling was used to determine the species composition and size frequency distributions of pelagic fish. A full description of the methods is given in Barange et al. (1999).

Statistical analyses. The threshold for statistical significance, α, was 5 %. To fulfil the criteria of normality, trip duration was calculated excluding the nighttime (from the ephemerid), given that gannets do not fly at night (Ropert-Coudert et al. 2004, pers. obs.). However, in order to be comparable with other studies, nighttime was included in the calculation of the foraging trip duration versus foraging path length regression.

To compare variables between the 2 islands, we performed balanced ANOVA, with all the variables as responses and islands as model when the data had a normal distribution (sometimes after square-root transformation), equal variance, and the same number of values. Otherwise, Kruskal-Wallis tests were performed for each variable.

RESULTS

Seabird foraging behaviour

On Malgas Island, we equipped 21 birds with a single GPS and 9 with a GPS-TD. On Bird Island, we equipped 18 birds with a GPS coupled with a TDR, 5 with a GPS-TD, and 7 with a single GPS. Although

some birds stayed at sea for longer than the loggers' battery capacity, 27 complete GPS tracks were collected from both islands, as well as complete diving activity over a trip for 7 birds from Malgas Island and 14 birds from Bird Island. All data loggers were retrieved after a single foraging trip and all equipped birds continued to breed normally. No difference in the foraging trip duration was found between equipped and control birds at either site (Malgas Island: $F_{1,31} = 0.42$, p = 0.523; Bird Island: $F_{1,57} = 0.86$, p = 0.357).

Gannets from Malgas Island worked harder than those from Bird Island (Table 1). Foraging trips of Malgas Island birds lasted longer ($F_{1,52} = 4.1$, p = 0.048) and showed a greater foraging path length ($F_{1,52} = 6.06$, p = 0.017) compared to trips by Bird Island gannets, and Malgas birds also spent a greater amount of time flying per trip h ($F_{1,52} = 7.88$, p = 0.007). They brought a greater amount of food back to the nest ($H_{1,50} = 5.62$, p = 0.018) whilst diving shallower ($F_{1,52} = 5.84$, p = 0.026), but the mean energy content of their food was not significantly different from that of birds from Bird Island ($H_{1,54} = 0.16$, p = 0.690). The maximum distance travelled from the colony was significantly correlated with foraging trip duration for Malgas birds ($F_{1,25} = 46.78$, p = 0.000, $r^2 = 0.638$: max. distance from colony (km) = 9.7 + [173 × trip duration (h)]), but not for birds from Bird Island ($F_{1,25} = 2.81$, p = 0.106, $r^2 = 0.065$). The mass of food brought back to the colony was significantly correlated with the time spent at sea for both islands, but the correlation coefficient was greater for birds from Malgas

Island ($T_{1,23} = 5.02$, p < 0.001, $r^2 = 0.231$: food brought to nest (g) = 683 − [10.3 × trip duration (h)]) than for birds from Bird Island ($T_{1,23} = 3.06$, p = 0.005, $r^2 = 0.001$: food brought to nest (g) = 203 + [0.41 × trip duration (h)]). Gannets from Bird Island showed less variability in foraging trip duration, i.e. with smaller standard deviations of the average foraging trip durations ($H_{1,54} = 17.11$, p < 0.001) compared to those from Malgas.

Seabirds and the distribution and availability of their pelagic prey

Raw GPS tracks of the birds from the 2 islands are shown on Fig. 2. Birds from both colonies covered a major axis approx. 500 km long. However, the area

Table 1. *Morus capensis*. Adult body mass and foraging characteristics. *p < 0.05, **p < 0.01, ***p < 0.001, ns: not significant, nd: not determined

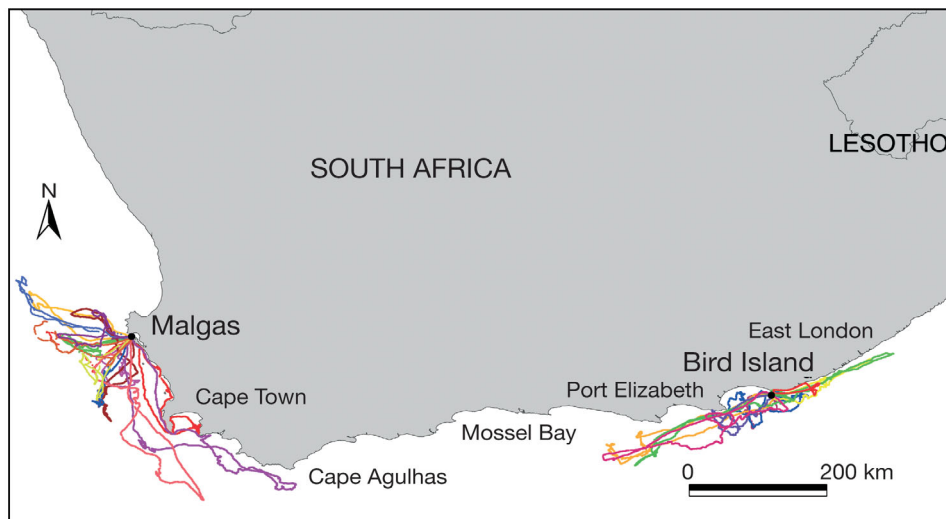| Parameter	Malgas Island	Bird Island	Significance
Body mass (g)	2673 ± 250	2785 ± 190	ns
Trip duration incl. night (h)	29.73 ± 11.1	22.83 ± 10.68	nd
Trip duration excl. night (h)	17.4 ± 7.19	13.8 ± 17.18	*
Foraging path length (km)	504 ± 237	367 ± 232	*
Max. distance to colony (km)	136 ± 64	112 ± 89	ns
Mean speed (km h⁻¹)	48.5 ± 3.14	47.09 ± 5.31	ns
Time spent flying (h)	10.1 ± 4.4	6.55 ± 3.4	**
Time spent flying per trip (%)	60 ± 14	49 ± 15	**
Food brought to nest (g)	361 ± 243	213 ± 141	*
Energy brought back to nest (kJ)	1561 ± 1053	1162 ± 1103	ns
Index of trip regularity	0.71 ± 0.38	0.35 ± 0.15	***
Dives per trip h	2.18 ± 1.3	2.42 ± 2.3	ns
Mean duration of dives (s)	4.58 ± 3.78	5.72 ± 4.38	ns
Mean max. dive depth (m)	3.11 ± 2.48	4.24 ± 2.37	*
Foraging range (km²)	31191	6673	

Fig. 2. *Morus capensis*. GPS tracks of foraging birds. Different colours show tracks from different birds (n = 27 birds from each island)

actively exploited by the foraging birds was 5 times greater at Malgas (31191 km^2) than at Bird Island (6673 km^2) (Table 1). The hydroacoustic survey recorded virtually no sardines or anchovies off the west coast, indicating an almost complete absence of natural prey for gannets from Malgas Island, which foraged from offshore of Lambert's Bay to Cape Agulhas (see Fig. 3). Sardines were distributed from False Bay to Nelson Mandela Bay, with the highest densities (>100 g m^{-2}) located towards the shelf edge around 150 km offshore off Mossel Bay and in Nelson Mandela Bay. Anchovies were distributed over much of the continental shelf between False Bay

and Cape Infanta, towards the shelf edge off Mossel Bay, and inshore near Cape St Francis, with several moderate- to high-density concentrations (50 to >100 g m^{-2}).

Spatial analysis on the foraging range of the birds revealed that most gannets from Malgas Island foraged in areas where few natural prey were observed by the hydroacoustic survey, whereas the foraging core of the birds from Bird Island occurred over a concentration of sardines in Nelson Mandela Bay (Fig. 3). The average density of natural prey located in the foraging area of birds from Malgas Island was 7.2 and 18.0 g m^{-2} for sardines and anchovies, respectively,
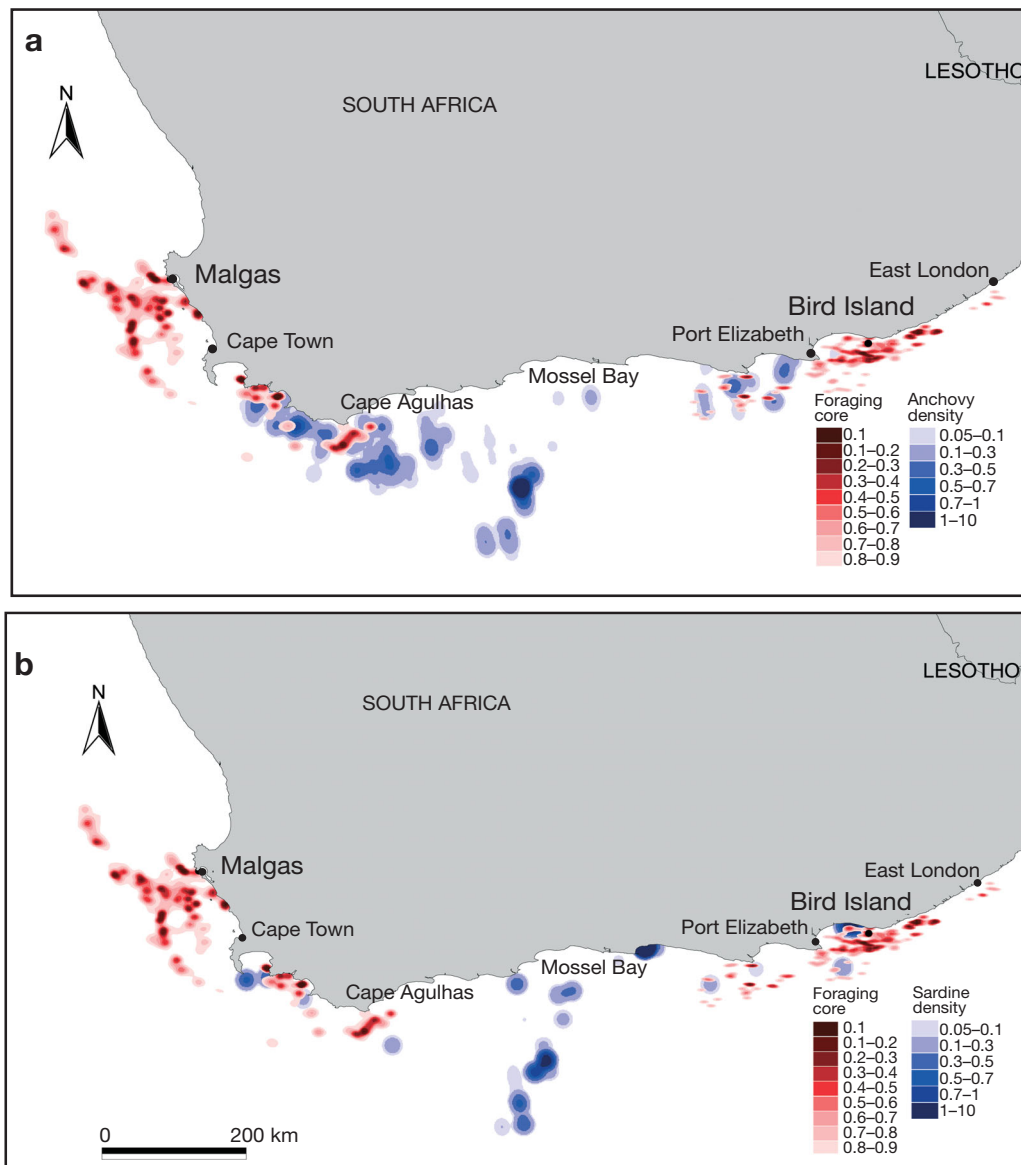

Fig. 3. *Morus capensis*. Foraging range (density of GPS positions associated with feeding behaviour; n = 27 birds from each island) in relation to the distribution and abundance of (a) anchovies and (b) sardines. Colour code for foraging range gives the contour levels covering 10 to 90 % of the locations. Fish density is given in percentile

whereas birds from Bird Island foraged in an area with densities of sardines and anchovies of 17.0 and 15.0 g m^{-2}, respectively. Gannets from Malgas Island had to fly east of Cape Point to feed on sardines or anchovies, corresponding to a round trip of ≥400 km. In contrast, gannets from Bird Island were able to target natural prey much closer to their colony and took advantage of a rich food environment, at least during the study period.

Seabird energetics

Diet sampled during the study was dominated by the deep-water hake *Merluccius paradoxus* for Malgas birds (78% by mass), and by sardines for birds from Bird Island (73% by mass, Fig. 4). Hake consumed by Cape gannets from Malgas occurs in waters 200 to 1000 m deep and is the primary target species of a demersal trawl fishery (Fairweather et al. 2006). The hakes taken by gannets are scavenged from behind trawlers. Sardines, by comparison, are epipelagic fish, which represent natural, live prey for Cape gannets (Berruti et al. 1993). The bioenergetics model (Enstipp et al. 2006) estimated the daily metabolism of Cape gannets breeding on Malgas to be $3.21 \times BMR$, with a necessary daily food intake of 1250 g of fish for the parent alone and 1415 g for 1 parent and its chick. On Bird Island, gannets had an estimated daily metabolism of $2.88 \times BMR$, with a predicted daily food requirement of 620 g of fish for self-maintenance and 710 g when including the chick's needs. These results emphasise the energetic consequences of higher foraging effort in birds from Malgas and the lower calorific value of their prey compared to those from Bird Island; hakes have a calorific value of 4.07 kJ g^{-1} and sardines 8.59 kJ g^{-1} (Batchelor & Ross 1984). Breeding birds from Malgas Island have a daily food demand of >50% of their body mass.
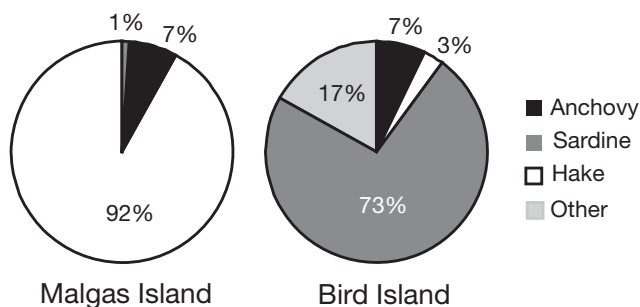

Fig. 4. *Morus capensis*. Percentage contribution by mass of prey items in the birds' diet (n = 28 birds from each colony)

DISCUSSION

Our study shows that Cape gannets are able to adapt their foraging effort according to food availability within the marine environment. Facing a scarcity of prey, birds increased their foraging effort but also turned to scavenging behind trawlers, taking prey of lower energy content. They were forced to invest more energy in reproduction, which was deemed hardly sustainable by our bioenergetics model. We suggest that low foraging efficiency is one of the factors underlying the decline in numbers of Cape gannets breeding on Malgas Island (Crawford et al. 2007). Our study confirms that estimates of foraging effort during the breeding season provide a powerful index of population health (Grémillet et al. 2006).

The acoustic survey located very few anchovies and sardines off the west coast of South Africa during our study, with most sardines located in Nelson Mandela Bay (Fig. 3). Birds from the 2 colonies thus exploited contrasting foraging environments, with birds from Malgas facing a scarcity of natural prey, while the environment in Nelson Mandela Bay was more profitable. In a rich environment, birds from Bird Island could afford to spend more time resting at sea and flew less. The lack of a significant regression between foraging path length and foraging trip duration among Bird Island birds is unique compared to results found for other colonies of Cape and Northern gannets (Hamer et al. 2001, Lewis et al. 2006). By comparison, with few pelagic fish available, birds from Malgas were forced to increase their foraging effort substantially (Fig 3). They stayed longer at sea, travelled further, and spent longer periods flying per hour at sea than gannets from Bird Island, increasing their total foraging range 5-fold (Table 1). Birds from Malgas spent more time searching for their preferred prey. This finding is supported by the stronger regression between the amount of food returned to the colony and the time spent at sea for Malgas birds. However, they resorted to feeding behind trawlers (predominance of shallow dives; Table 1), bringing back fishery discards to the colony (Fig. 4). Finally, the greater variability in foraging trip duration of birds from Malgas Island indicated greater uncertainty in their foraging environment (Table 1), which accords with the high degree of variability of the overall Benguela system higher up in the food web (van der Lingen et al. 2006).

Foraging in an unpredictable environment

The low abundance of sardines and anchovies off the west coast during spring 2005 (Fig. 3) followed recent changes in the distribution of small pelagic fish, partic-

ularly sardines, off South Africa, with a progressive southern and eastward shift since the mid-1990s (van der Lingen et al. 2005). The distribution of anchovy spawners on the Agulhas Bank has also shown an eastward shift, initiated in 1996, with the bulk of spawners observed during acoustic surveys now being found east of Cape Agulhas, whereas most were west of Cape Agulhas before 1996 (van der Lingen et al. 2002). The timing of this progressive eastward shift of both small pelagic fish species in the mid to late 1990s coincides with the start of the decrease in gannet population size on Malgas Island (Crawford et al. 2007), strongly suggesting that the 2 processes are linked. Moreover, decadal variation in the size of the Malgas Island breeding population (Crawford et al. 2007) can be explained by the fluctuations of anchovy and sardine populations (Schwartzlose et al. 1999), supporting the assumption that population growth is driven in part by food availability during the breeding season (Lewis et al. 2006). These fluctuations of small pelagics could be of great importance in marine ecosystems where these fish are predominant prey species, such as in the Benguela (Lluch-Belda et al. 1989), with known repercussions on top predators that depend on those prey, including Cape gannets (Crawford 1999).

Impact of fisheries on seabirds

The Cape gannet diet reflects environmental variation in the abundance of sardines and anchovies (Berruti et al. 1993, Crawford 1999). In the early 2000s, the proportions of both species in gannet diet at west coast colonies decreased, with a concomitant increase in offal discarded from bottom trawlers (Marine and Coastal Management unpubl. data). The relative proportion of fishery wastes in gannet diet is not correlated with the amount of hake caught by the demersal fishery (Berruti et al. 1993), suggesting that hake is not a preferred prey item. Such prey-switching behaviour is one way in which seabirds may cope with environmental variability (Crawford 1999), but hake is of low calorific value compared to anchovies and sardines (Batchelor & Ross 1984). Gannets from Malgas Island were able to compensate for this to some extent by bringing back larger loads to the nest, resulting in meals with energetic values similar to those of the loads brought back by birds from Bird Island (Table 1). However, they were probably handicapped by the larger loads they were forced to carry. Moreover, previous studies have shown that feeding nestlings on a lipid-poor diet negatively impacts the fledglings' body condition and cognitive abilities (Batchelor & Ross 1984, Kitaysky et al. 2005), which culminates in a higher mortality rate. A regime switch from lipid-rich

to lipid-poor prey can be responsible for changes in breeding success and population structure of piscivorous seabirds (the 'junk-food hypothesis', Anderson & Piatt 1999, Wanless et al. 2005).

Fishery discards have become the main resource for some populations of breeding seabirds when natural prey stocks are depleted (Garthe et al. 1996, Votier et al. 2004). It has been hypothesised that increased fishing pressure in the 20th century and the associated increase in waste availability may have changed the structure and abundance of certain seabird communities (Abrams 1985), and it is known that such artificial food resources can affect foraging parameters and/or reproductive characteristics of birds (Arcos & Oro 1996, Oro et al. 2004). Future changes in fisheries management policies, such as increased use of offal for industrial purposes and reducing the amount of nontarget species being discarded, may further threaten seabird populations reliant on discards (Furness 2003, Votier et al. 2004).

Although some fisheries increase food availability for seabirds through waste, other fisheries compete directly with seabirds when harvesting their main natural prey (Furness 2003). In the southern Benguela ecosystem, the sardines and anchovies that are the main target of the pelagic fishery (van der Lingen et al. 2006) also are the main food resource of several endemic seabirds, including Cape gannets, the African penguin *Spheniscus demersus*, and the Cape cormorant *Phalacrocorax capensis* (Crawford 1999). Obviously, the negative impact of competition between fisheries and seabirds is enhanced when prey becomes scarcer, and a substantial negative impact of fisheries on Cape gannets in the northern Benguela (off Namibia) has been reported previously (Crawford 1999). In the 1950s and 1960s, heavy fishing pressure on sardines without appropriate management policies led to a collapse of 85% of the Namibian populations of gannets, which meant an overall decrease of 40% in the entire Cape gannet population (Crawford et al. 2007).

Conservation implications

Although life-history traits of seabirds act to buffer populations against short-term fluctuations in their food supply, Cape gannets do not seem to be able to cope with recent decadal scale environmental changes, and the overall population of Cape gannets is decreasing. On Malgas Island (which until recently supported 40% of the world population of gannets), the gannet population has started to show a dramatic decrease, arising both from reduced prey availability and increased predation by the Cape fur seals *Arctocephalus pusillus*, which may kill up to 80% of fledg-

lings (Makhado et al. 2006). Great white pelicans (*Pelecanus onocrotalus*) have also recently started feeding on gannet chicks on Malgas Island (L. Pichegru pers. obs.). Together, these threats weigh heavily on a bird already classified as vulnerable (see the 2006 IUCN Red List of Threatened Species, available at www.iucnredlist.org) with a breeding area restricted to only 6 colonies, 5 of which are declining (Crawford et al. 2007). Actions to mitigate these threats are required urgently.

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