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ORIGINAL PAPER

Starving seabirds: unprofitable foraging and its fitness consequences in Cape gannets competing with fisheries in the Benguela upwelling ecosystem

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Abstract Fisheries are often accused of starving vulnerable seabirds, yet evidence for this claim is scarce. Foraging energetics may provide efficient, short-term indicators of the fitness status of seabirds competing with fisheries. We used this approach in Cape gannets (*Morus capensis*) from Malgas Island, South Africa, which feed primarily on small pelagic fish in the southern Benguela upwelling region, thereby competing with purse-seine fisheries. During their 2011–2014 breeding seasons, we determined body condition of breeding adult Cape gannets and measured their chick growth rates. In addition to these conventional fitness indices, we assessed the daily energy expenditure of breeding adults using a high-resolution time-energy budget derived from GPS-tracking and accelerometry data. For these same individuals, we also determined prey intake rates using stomach temperature recordings. We found that adult body condition and chick growth rates declined significantly during the study period. Crucially, most birds (73 %) studied with electronic recorders spent more energy than they gained through foraging, and 80–95 % of their feeding dives were unsuccessful. Our results therefore point to unprofitable foraging in Cape gannets, with a longer-term fitness cost in terms of adult body condition and reproductive performance that corresponds to a local population decline. Based on this evidence, we advocate a revision of regional fishing quotas for small pelagic fish and discuss the possibility of an experimental cessation of purse-seine fishing activities off the west coast of South Africa. These measures are needed for the ecological and socio-economical persistence of the broader southern Benguela upwelling ecosystem.

Introduction

Human activities perturb marine ecosystems on a global scale (Halpern et al. 2008), even in the most remote of areas (Blight et al. 2010; Grémillet et al. 2015). There is currently a major focus on the impacts of climate change on marine ecosystems (Beaugrand et al. 2013), yet fisheries also profoundly affect the majority of marine biota (Pauly et al. 1998; Worm et al. 2009). Overfishing not only threatens targeted fish populations and related human food security (Pauly et al. 2005), its effects also reverberate across marine food webs, towards both lower and higher trophic levels (Travers-Trolet et al. 2014). Marine predators, especially seabirds, are the most visible part of marine ecosystems, and their fate in overfished areas is the subject of intense debate (Lewison et al. 2012). Specifically, fisheries competing with seabirds are often accused of 'starving' seabirds by NGOs and the media, yet demonstrating such

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direct impacts has proved challenging. This is due to difficulties in (1) attributing recent declines in seabird food to overharvesting by fishing activities (Fréon et al. 2008) and (2) demonstrating a negative impact of forage fish declines upon seabird populations (Frederiksen et al. 2004). For both purposes, long-term seabird monitoring is usually employed, in parallel with fish and fishery assessments, to correlate seabird individual survival, reproductive performance and population trends with varying levels of fishing effort and fish availability (Cury et al. 2011). Yet in a rapidly changing environment, policy-makers and managers cannot always await the outcome of multi-decadal monitoring, and shorter-term ecological indexes are needed. Seabird foraging effort has been identified as a proximate factor conditioning population dynamics (Lewis et al. 2006), and hence, seabird foraging energetics may serve as an ecological indicator. Specifically, such energetics approaches allow an assessment of the daily energy balance of individual birds by comparing their energy intake through food, with their energy expenditure. Birds showing a negative energy balance (more energy spent than acquired) are predicted to show reduced reproductive success and eventually lower adult survival (Drent and Daan 1980). Despite their great potential, foraging energetics have seldom been used to inform the biological conservation of seabird populations exposed to anthropogenic impacts (Lovvorn and Gillingham 1996; Green et al. 2009a). Here, we used foraging energetics to test the profitability of feeding trips in a seabird that competes with industrial fisheries for diminishing fish stocks.

We studied Cape gannets (*Morus capensis*), which are endemic to the Benguela upwelling ecosystem off southern Africa. Cape gannets predominantly feed on small pelagic fish (sardines *Sardinops sagax* and anchovies *Engraulis encrasicolus*) which are naturally abundant in the region due to intense marine productivity (Moloney et al. 2013). These stocks nonetheless show large spatio-temporal variability in their biomass and occurrence, resulting in contrasting levels of prey availability to seabirds (Sabarros et al. 2012; Crawford 2013). The exact causes of such fluctuations are being debated and are currently attributed to the combined effects of multi-decadal ecosystem dynamics, climate change and fisheries (Coetzee et al. 2008). Notably, overfishing has been demonstrated to be the cause for a major collapse in sardine stocks in the 1960s, accompanied with ecosystem changes in the Northern Benguela (Heymans et al. 2004). The combined effects of climate change and fisheries are also suspected to have triggered an ecosystem shift in the early 2000s (Coetzee et al. 2008; Grémillet et al. 2008a), which resulted in competition between seabirds and fisheries for access to diminishing fish stock off the west coast of South Africa. (Okes et al. 2009), reducing the fitness of Cape gannets (Cohen et al. 2014). Despite the fact that the purse-seine fishery targets scarce fish stocks within the foraging areas of declining populations of endemic seabirds (Cape gannets, African penguins *Spheniscus demersus* and Cape cormorant *Phalacrocorax capensis*), it still has a total annual catch (TAC) of >600,000 metric tonnes based on the abundance of fish throughout South African shelf waters. However, there is a spatial mismatch between fishing effort and fish distribution. Most fish biomass occurs on the eastern Agulhas Bank, far from traditional fishing centres and outside the foraging ranges of seabirds breeding at islands off the west coast (Jarre et al. 2015). Because most fishing vessels still operate from west coast harbours, 80 % of fish are caught west of Cape Agulhas, whereas 80 % of fish biomass is found east of Cape Agulhas (Blamey et al. 2015).

In this context, we tested the hypothesis that Cape gannets breeding at a west coast colony, competing with the west coast purse-seine fleet, exhibit a negative energy balance. Specifically, we compared the daily food intake of individual chick-rearing Cape gannets with their daily food requirements. Cape gannets are a particularly appropriate species for this type of short-term energetics approach, for two reasons. Firstly, their foraging trip durations and effort are highly repeatable from one trip to the next (Rishworth et al. 2014). Unlike many petrel species, they do not alternate short, unprofitable foraging trips, with longer trips during which parents raising chicks replenish their body reserves (Chaurand and Weimerskirch 1994). Second, Cape gannets do not perform adaptive mass loss (sensu Croll et al. 1991) during the breeding season; they rather keep steady body masses across the chick-rearing period (Bijleveld and Mullers 2009), especially when feeding conditions are good (Mullers and Tinbergen 2009). Hence, the energy balance of birds during a particular foraging trip is a reasonable estimate of foraging profitability at the scale of the breeding season.

Overall, our study allowed us to track the most recent impacts of environmental change on Cape gannet foraging and fitness and to formulate novel recommendations for the conservation of seabirds and of the broader southern Benguela upwelling ecosystem.

Methods

The study was conducted on Malgas Island (33.05°S, 17.93°E) in the Western Cape, South Africa, one of the six breeding sites for Cape gannets globally. Malgas Island hosts approximately 22,000 pairs of Cape gannets, ca. 30 % of the world population, but the population has decreased from more than 50,000 pairs in the late 1990s (Crawford et al. 2014). Each year in October 2011–2014, the post-absorptive body mass (±10 g), wing length (±1 mm) and

Table 1 Cape gannet activity-specific energy expenditure (W) and corresponding standard error of estimate (SEE, in W). All values estimated following Green et al. (2009a, b, 2013). Energy expenditure (in W, hence J s^{-1}) was used as input values for daily energy expenditure (DEE) calculations, and their respective SEE for Monte Carlo simulations (see "Methods")

Activity	Energy (W)	SEE energy (W)
Nest	9.1	0.8
Dive	55.2	9.3
Take-off	85.9	12.6
Flight	42.0	4.5
On water	26.5	2.5

bill measurements (±0.1 mm) of adult Cape gannets raising chicks were measured, and their body condition index was calculated as body mass divided by wing chord (g.mm^{-1}), following Cohen et al. (2014). Growth parameters of their chicks were determined during their linear growth phase, following Cohen et al. (2014), as the difference in a chick's mass between two consecutive measurements divided by the number of days between those two measurements. In October 2012 and 2014, another set of breeding adult Cape gannets was caught at the nest before starting a foraging trip and fitted with three data loggers: (1) a GPS recorder (CatTrack1, Catnip Technologies, Hong Kong, PRC, 44 × 28 × 13 mm, 20 g) attached to the lower back with waterproof Tesa® tape (Product No. 4651), which recorded position and speed at 1-min intervals; (2) a device recording body acceleration (20 Hz) and time at depth every second (in 2012: G6A, CEFAS Technology Limited, Lowestoft, UK; 40 × 28 × 15 mm, 18 g; in 2014: M190-D2GT, Little Leonardo, Tokyo, Japan, 60 × 15 mm, 20 g) attached with Tesa® tape underneath the tail; and (3) a stomach temperature logger (MiniTemp logger, Earth&Ocean Technologies, Kiel, Germany; 70 × 15 mm, 18 g) recording temperature every second, and which was fed to the birds and remained in the stomach until recovered, or was voluntarily regurgitated by the bird. The total mass of the three devices was 56–58 g, i.e. 2.2–2.3 % of the bird body mass. All devices were recovered after 1–2 foraging trip lasting a few hours to 2 days. For external devices, all tape was removed with the loggers, ensuring minimal impact to the plumage. The stomach temperature recorder was removed using a purpose-made grab, following Wilson et al. (1998). This method has been used successfully on various penguins, albatrosses, cormorants and gannets (Wilson et al. 1998; Grémillet et al. 2001, 2003, 2012).

Data analysis

We did not test for sex-specific differences, due to a moderate sample size. However, previous studies showed that our sampling protocol (random capture of birds at the nest during changeovers) results in well-balanced samples in terms of sex ratio (Lewis et al. 2002). GPS records were used to visualize Cape gannet foraging paths, which were annotated using information on diving events and feeding events provided by the other loggers. For instance, the acceleration and time–depth recorders identified the exact time and depth of each dive. Foraging trip characteristics (distance, speed, duration, range) were calculated from GPS tracks whereby distances were calculated using great circle distances.

Daily food intake (DFI) was calculated from stomach temperature recordings. Ingestion of cold fish, which have body temperatures equivalent to ambient seawater, causes precipitous stomach temperature decreases in homoeothermic gannets (Wilson et al. 1995). The occurrence of such decreases indicates prey ingestions, and the amplitude and duration of temperature decreases indicate prey mass (Wilson et al. 1995). We calculated the mass of ingested prey using equation (4) in Wilson et al. (1995):

$$M = \frac{\mathrm{INT}}{m \times \mathrm{SHC_f} \times (T_\mathrm{a} - T_\mathrm{f})}$$

where M is prey mass (g), INT the integral of the surface above the temperature decrease (Wilson et al. 1995, Fig. 1a), m a constant, $\mathrm{SHC_f}$ the specific heat capacity of water (J °C^{-1} g^{-1}), T_a the temperature of the stomach (°C) and T_f the temperature of the ingested food (°C). For our calculations, m was set to 0.16 ± 0.09 (Wilson et al. 1995, Table 3), the recommended value for active birds feeding on single prey, which is the case for foraging Cape gannets. $\mathrm{SHC_f}$ was taken to be that of water, 4.17 ± 0.1 J °C^{-1} g^{-1}, while T_a was set to 40 ± 1 °C based on our recordings of stomach temperature in post-absorptive, active Cape gannets, and T_f was set to 15 ± 1 °C, corresponding to the thermal preferences of small pelagic fish in the southern Benguela region (N. Twatwa et al., unpublished data).

Daily food requirements (DFR) were calculated using a time-energy budget. We first used accelerometry data to reconstruct accurate Cape gannet time budgets (±1 s), following Ropert-Coudert et al. (2004). By using activity-specific acceleration signals, we identified five activity categories: (1) at nest, (2) flying, (3) diving, (4) on water and (5) taking off. Using this information, we estimated individual daily energy expenditure (DEE in kJ day^{-1}), on the basis of activity-specific average energy expenditures determined by Green et al. (2009b, 2013) for closely related Australasian gannets (*Morus serrator*). We transformed activity-specific average heart rates (beats min^{-1}) from Green et al. (2009b, Table 1), into activity-specific levels of oxygen consumption (O_2 l min^{-1}), and their estimated standard errors (Table 1) using the calibration curve from Green et al. (2013, Fig. A1). Bird-specific daily oxygen consumption was then transformed into DEE (kJ day^{-1}) using an energy equivalent of 20.1 ± 0.8 kJ per litre O_2 (Enstipp et al. 2006). We also calculated the DEE of each gannet chick whose parents were equipped with data loggers, following equations provided in Navarro et al. (2015), who determined mass-specific (m in g) energy expenditure of Cape gannet chicks using the doubly labelled water method as:

$$\text{DEE} = 1.23m^{0.923}$$

with estimated confidence intervals of 0.70–3.04 for the intercept and 0.78–1.01 for the exponent. Chick DEE was split equally between the two parents, to estimate each parent's DEE (kJ day^{-1}) while breeding. This value was transformed into daily food requirements (g wet fish mass) using an assimilation efficiency of 77 ± 1 % (Enstipp et al. 2006), and mass-energy equivalents of bird diets (kJ g^{-1} fish). Those were calculated using the diet of birds which regurgitated food while being handled during our field study. Average calorific values of the different prey species were derived from Batchelor and Ross (1984) and Pichegru et al. (2010b) and gave weighted averages (for wet fish mass) of 6.8 ± 1.6 kJ g^{-1} in 2012, and 6.1 ± 1.6 kJ g^{-1} in 2014.

To estimate error ranges (%) in daily food intake (DFI) from stomach temperature measurements and daily food requirements (DFR) from time-energy-budget analysis, we used Monte Carlo simulation models (Manly 1997) for individual Cape gannets. Simulations were run 10,000 times, randomly drawing input values for DFI and DFR from the observed range. Time-budget input values were auto-correlated, so we modelled them with a single, joint error margin of ±1 s across all simulations.

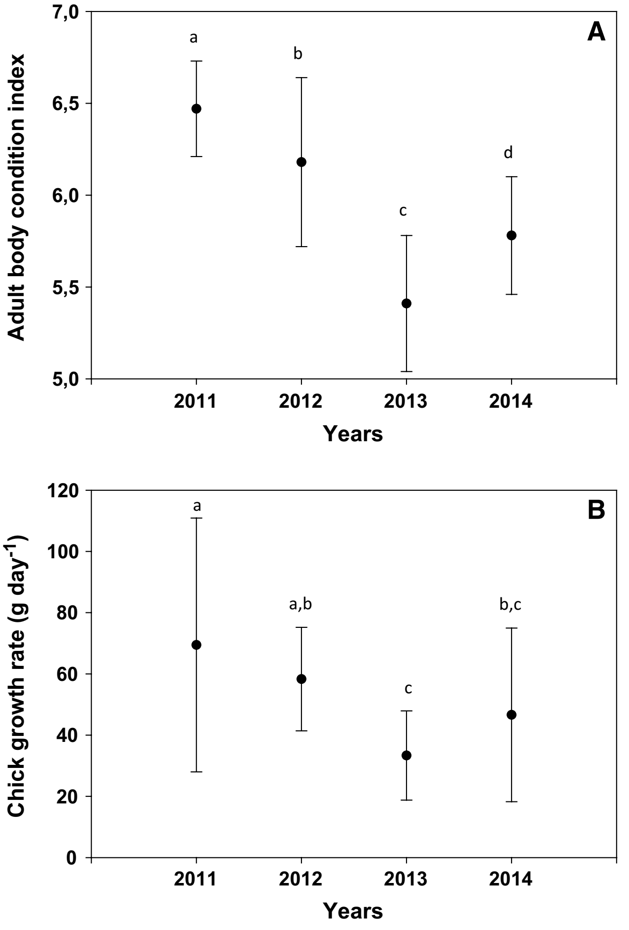

Fig. 1 Annual average body condition index of breeding Cape gannets (**a**) and annual average growth rates of their chicks (**b**) across 2011–2014 ($n = 103$ in total, 18–35 nests per year). In both cases, annual averages are decreasing significantly across the study period ($F_{3,102} = 36.7$, $p < 0.0001$ and $F_{3,102} = 8.54$, $p < 0.0001$, respectively). Different letters above histogram bars denote significant differences between years. Error bars correspond to standard deviations

Results

A total of 103 breeding adults and their chicks were weighed and measured in October from 2011 to 2014 (18–35 nests per year). Adult body condition decreased significantly during this period ($F_{3,102} = 46.96$, $p < 0.0001$; Fig. 1a) and was lowest in 2013 (post hoc Tukey's tests: $p < 0.05$ to all years). Annual chick growth rates also decreased significantly from 2011 to 2014 ($F_{3,102} = 8.54$, $p < 0.0001$; Fig. 1b) and was lower in 2013 than in 2011 and 2012 (post hoc Tukey's tests: 2011–2013: $p < 0.001$; 2012–2013: $p < 0.01$). Fourteen birds were equipped with GPS, accelerometer/TDR and stomach temperature loggers (six in 2012 and eight in 2014). One accelerometer malfunctioned in 2012, so we obtained activity results for five birds that year (Table 2). All GPS and accelerometry/TDR devices were recovered after foraging trips lasting 5–49 h (Table 2). In 2014, two birds regurgitated their stomach temperature loggers away from the nest and those were lost, but all others were recovered (Table 2). During the recovery of the stomach temperature logger from the last bird in 2014, its stomach wall was injured and the bird died from internal bleeding. This was the first such incident recorded in hundreds of deployments on a variety of seabirds by the same personnel; nonetheless, we immediately stopped deploying stomach temperature loggers. All other studied birds continued breeding normally after the experiments.

Most birds performed one-day trips at a maximum distance of 100–150 km from the colony and travelled between 250 and 500 km in total (Table 2). In 2012, one bird performed two short trips (6 h) and another spent 2 days at sea, reaching waters 200 km south of the colony. The number of dives per trip varied greatly between individuals (12–218 dives trip^{-1}), whereas the number of prey

Table 2 Foraging trip parameters of Cape Gannets tracked in 2012 and 2014 using GPS loggers

Year	Id bird	Id trip	Start date	End date	Trip duration (h)	Range (km)	Average speed (m s^{-1})	Max speed (m s^{-1})	Distance travelled (km)	No. dives	Mean dive duration (s)	No. prey ingestions
2012	Bird03	1	11/10/2012 12:23	12/10/2012 8:51	20.5	91.4	3.7	19.4	277.5	25	2.2 ± 1.5	5
	Bird04	1	11/10/2012 13:27	12/10/2012 10:44	21.3	117.4	5.0	19.3	383.6	–	–	4
	Bird09	1	13/10/2012 10:55	14/10/2012 14:44	27.8	103.3	4.0	21.0	404.9	41	3.1 ± 2.1	2
	Bird10	1	13/10/2012 10:50	13/10/2012 16:16	5.4	45.8	7.4	26.1	144.3	16	7.6 ± 8.4	1
	Bird10	2	14/10/2012 3:52	14/10/2012 10:13	6.3	89.2	10.2	19.8	231.6	12	3.2 ± 1.7	2
	Bird15	**1**	**15/10/2012 10:21**	**17/10/2012 11:40**	**49.3**	**206.1**	**5.0**	**30.4**	**893.1**	**69**	**5.0** ± 3.7	**9**
	Bird16	1	15/10/2012 12:30	16/10/2012 13:36	25.1	72.4	3.0	24.7	272.3	57	3.5 ± 3.2	2
2014	Bird1	1	12/10/2014 9:17	13/10/2014 9:36	24.3	115.9	4.5	20.9	398.5	218	3.2 ± 1.3	5
	Bird2	1	12/10/2014 9:44	13/10/2014 8:26	22.7	144.7	5.1	22.9	418.2	63	2.5 ± 1.4	7
	Bird4	1	13/10/2014 7:43	14/10/2014 11:47	28.1	148.4	5.1	21.7	515.6	92	4.2 ± 2.0	8
	Bird5	1	13/10/2014 8:24	13/10/2014 16:29	8.1	68.3	6.9	21.0	198.7	47	2.7 ± 1.2	2
	Bird8	**1**	**14/10/2014 8:37**	**15/10/2014 13:51**	**29.2**	**141.9**	**4.5**	**23.1**	**475.2**	**105**	**3.0** ± 3.0	**7**
	Bird9	**1**	**14/10/2014 9:15**	**15/10/2014 8:01***	**22.8**	**175.7**	**4.3**	**18.9**	**348.1**	**75**	**5.4** ± 7.1	**4**

Dive behaviour was estimated from depth recorder on accelerometers and prey ingestion using stomach temperature recorders. Individuals in positive energetic balance are in bold. The symbol * indicates that the track was incomplete, with the recording stopping just before the bird got back to the colony (as ascertained via direct observation at the nest), and hence having a minor effect on trip duration and distance travelled. (–) indicates that data were not available due to accelerometer failure

ingested ranged from 1 to 9 per trip (Table 2), so most dives (80–95 %) were unsuccessful. Mean dive duration was short, ranging from 2.2 to 7.6 s among birds (Table 2).

Analysis of stomach temperature traces showed that birds caught prey items which weighed an estimated 10–1010 g each. Estimated individual DFI ranged widely (110–1200 g), and average DFI across birds tended to be lower in 2012 (360 ± 260 g day^{-1}, $n = 6$) than in 2014 (520 ± 440 g day^{-1}, $n = 6$). Monte Carlo simulations estimated DFI average error margins of ±45 %. Equipped birds that regurgitated while being handled had consumed a mixed diet of sardines, Atlantic saury (*Scomberesox saurus*), chokka squid (*Loligo reynaudii*), redeye herring (*Etrumeus whiteheadi*) and hake (*Merluccius* spp.) in both years whereby natural prey and discards represented 84 and 16 % of the diet, respectively.

From our high-resolution time-energy budgets, we estimated the daily food requirements of the 11 birds that were successfully equipped with all three loggers, to which we added those of their chicks (see "Methods"). Overall, parent and chick daily food requirements ranged between 340 and 490 g day^{-1}, and average values were lower in 2012 (412 ± 31 g day^{-1}, $n = 5$) than in 2014 (526 ± 32 g day^{-1}, $n = 6$). Monte Carlo simulations estimated that individual average DFR had average error margins of ±21 %. Comparison of estimated DFI and DFR revealed that eight of 11 birds spent more energy than they gathered through feeding at sea (four birds in 2012 and four in 2014; Fig. 2). Further, the theoretical daily energy requirements of the chick only amounted to only 13.5 % (SD = 5 %) of overall daily food requirements of each individual. Therefore, our results suggest that the observed daily food intake of adult birds is, in most cases, not even sufficient to cover their own energy demand. The only Cape gannet in positive energy balance in 2012 was the one that spent 2 days at sea, travelled the longest distance (893 km) and went farthest from the colony (200 km). This individual dived 69 times and caught nine prey items, mainly south of Cape Point (Fig. 3). The

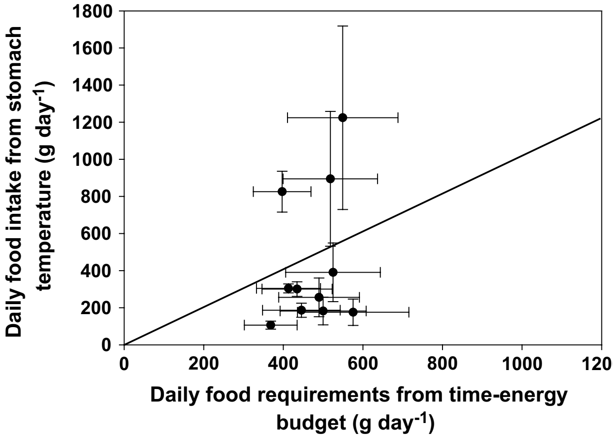

Fig. 2 Comparison of individual daily food requirements (g day^{-1}) of breeding Cape gannets as estimated via high-resolution time-budget analysis, and their daily food intake (g day^{-1}) as estimated through stomach temperature analysis. Bi-dimensional error margins were estimated using Monte Carlo simulations (see “Methods”). The diagonal line indicates values for which food demand and food intake are balanced. Birds with values below this line were in energy deficit

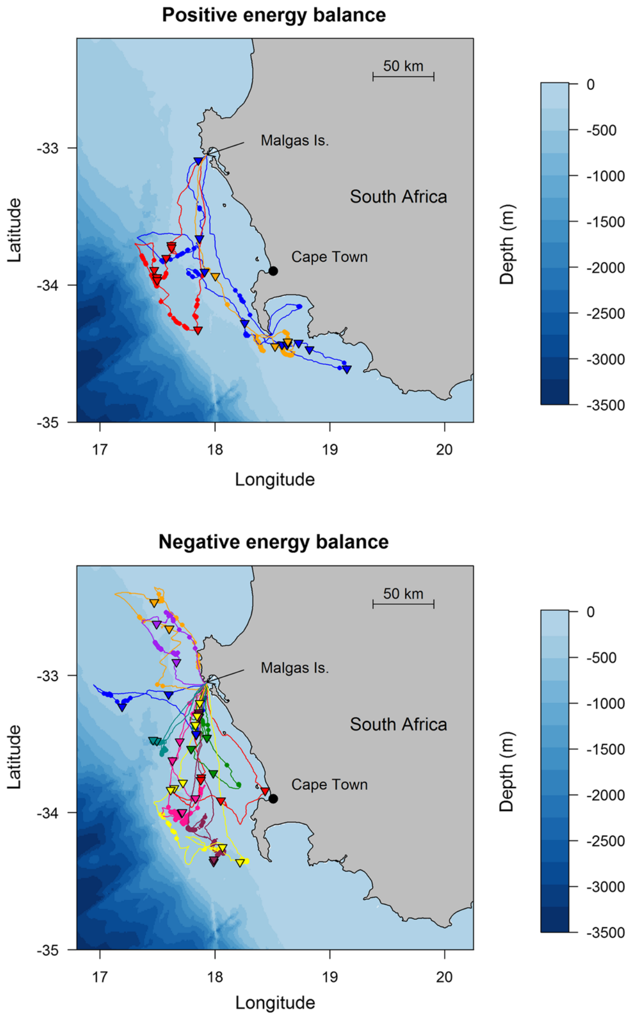

Fig. 3 GPS tracks of Cape Gannets from Malgas Island foraging in 2012 and 2014. Birds with a positive energy balance (*top*) and those with a negative energy balance (*bottom*). *Dots* refer to diving locations, and *triangles* are prey ingestion events. Individuals are colour-coded within each graph

two birds in positive energy balance in 2014 also travelled longer (29.2 and >22.8 h) compared with the other birds tracked that year (20.8 h, $n = 4$). These two birds dived 105 and 75 times and caught seven and four prey items, respectively (Table 2). Their prey ingestion rate was similar to other birds, but their feeding locations differed. One bird went south to the same area as the bird in positive balance in 2012 (Fig. 3), and the other went west to waters between 250 and 500 m deep, close to the slope of the continental shelf (Fig. 3). Interestingly, all birds in negative energy balance fed within 5 h of departure in an area about 50 km SW of the colony, and 55 % of them did not catch any prey items during the 5 h prior to returning to the colony (Fig. 4). By comparison, the two birds with complete tracks that had a positive energy balance fed during the last 5 h of their trip (Fig. 4).

Discussion

Our four-year study revealed that Cape gannet fitness, in terms of reproductive performance and adult body condition, declined at Malgas Island from 2011 to 2014 (Fig. 1), and that in 2012 and 2014, 73 % of the birds studied had a negative energy balance during the chick-rearing period (Fig. 2). It is, to the best of our knowledge, the first time that unprofitable foraging has been demonstrated in a marine predator competing with industrial fisheries. We discuss the limitations and conservation implications of our findings, which lead us to propose essential management measures for purse-seine fishing activities targeting small pelagic fish off the west coast of South Africa.

Methodological aspects

As mentioned in the introduction, Cape gannets do not alternate short and long foraging trips (Chaurand and Weimerskirch 1994), and the characteristics of one particular foraging trip tracked by GPS are therefore representative of the overall foraging effort of the animal (Pettex et al. 2012; Patrick et al. 2014). Further, previous studies showed significant inter-annual variability in Cape gannet foraging, but relatively low intra-annual, inter-individual variability (Tew Kai et al. 2013; Cohen

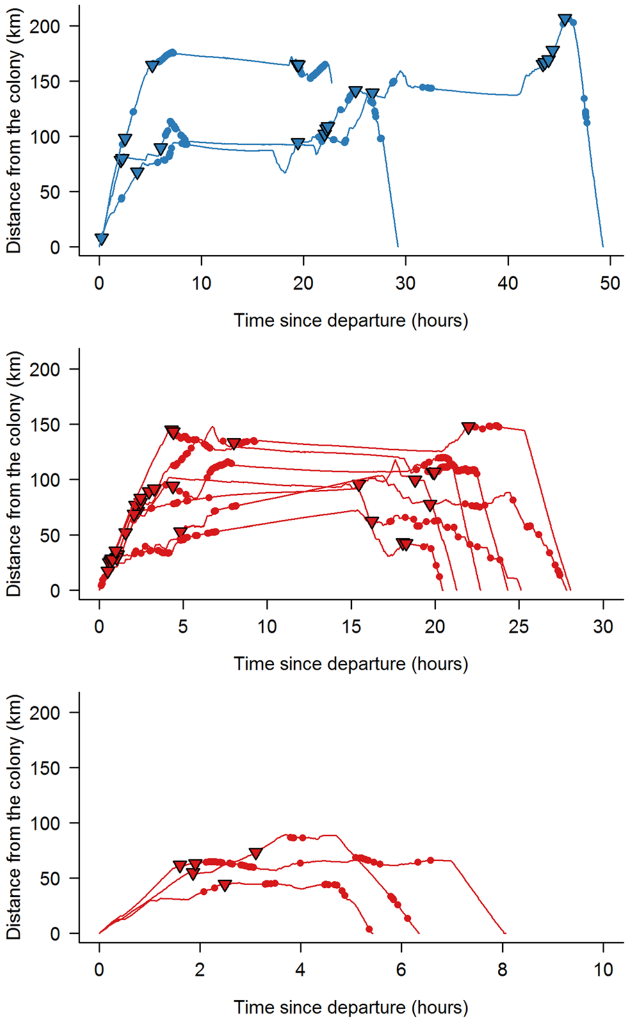

Fig. 4 Distance from the nest (km) as a function of time since departure (hours) in foraging Cape gannets with a positive (*blue*) and negative (*red*) energy balance during the chick-rearing period. *Dots* show the timing of diving events, and *triangles* show the timing of feeding events. Birds in energy deficit (in *red*) are shown in two separate graphs to adequately display long/short foraging trips

et al. 2014). Along these lines, the majority of birds which perform unprofitable foraging are likely to pursue this strategy, to the point of failing their reproductive attempt (Grémillet et al. 2008b). In contrast, a minority of 'better' birds might manage to target pelagic fish at more distant locations, and to achieve a positive energy balance, foraging trip after foraging trip. Unprofitable foraging as demonstrated for 73 % of birds in this study is therefore likely to reflect chronic nutritional stress at the population level for Cape gannets breeding on Malgas Island in recent years.

It is technically challenging to evaluate foraging energetics in free-ranging marine predators, mainly because of the difficulty to estimate prey intake rates. In a few species, this can be observed directly (Anderson et al. 2014), but most species consume prey underwater. Back-mounted cameras (Watanabe and Takahashi 2013) and mandible-opening recorders can be used to document such ingestion events (Wilson et al. 2002), as well as tags recording oesophageal temperature (Ancel et al. 1997), or indirect indices, based on undulations in the depth of dives (Bost et al. 2007). We used stomach temperature recordings, which are adequate to detect the ingestion of single, mid-sized prey items (Wilson et al. 1995), and perform well in comparison with direct measurements of seabird prey intake, such as automatic weighing of individuals at the nest before and after short foraging trips (Grémillet et al. 2000). We estimated energy expenditure in chick-rearing Cape gannets from high-resolution time-energy budgets, and this method was more accurate than the doubly labelled water technique (Fort et al. 2011). Our accelerometry data could also be used to calculate overall dynamic body acceleration (ODBA) as an index of energy expenditure (Wilson et al. 2006), but this would require calibrating ODBA against energy expenditure (using e.g. doubly labelled water), specifically for gannets, and such a calibration study has not yet been performed.

Our estimates of Cape gannet daily food intake (DFI) and daily food requirements (DFR) have non-negligible error margins. In this context, we recommend considering modelled ranges of DFI and DFR, rather than specific average values. However, Monte Carlo simulations showed that, even when taking these error terms into account, most (73 %) of the Cape gannets studied had a negative energy balance (see "Methods" and Fig. 2). The success rate of gannet plunge-dives was also surprisingly low (5–20 %); in comparison, closely related Australasian gannets (*Morus serrator*) investigated by underwater video showed successful prey capture during 93 % of U-shaped dives and 43 % of V-shaped dives (Capuska et al. 2011).

Conservation implications

After a relatively prosperous period in the late 1980s–1990s, Cape gannets breeding off the west coast of South Africa have been confronted with generally deteriorating feeding conditions in the twenty-first century. Notably, an ecosystem shift occurring from the late 1990s reduced the abundance of small pelagic fish off the west coast, despite sustained, high primary productivity in this upwelling region (Moloney et al. 2013; Jarre et al. 2015). Faced with the scarcity of their preferred pelagic fish, Cape gannets switched diets to feed on fishery waste generated by hake trawlers along the edge of the continental shelf (Pichegru et al. 2007; Grémillet et al. 2008b). However, the low calorific value of this surrogate food reduced reproductive performance and body condition (Moseley et al.

2012; Cohen et al. 2014). During the 2000s, Cape gannet experienced some ‘good’ or ‘bad’ years, depending on the short-term availability of pelagic fish during the gannet’s breeding season (Tew Kai et al. 2013; Cohen et al. 2014). In contrast, our results show that, from 2011 onwards, Cape gannets breeding on the west coast have experienced a general decline in their fitness levels (Fig. 1), associated with unprofitable foraging (Fig. 2). Importantly, this occurs while some pelagic fish are still available to the birds, as shown by their diet, yet these resources are now too scarce to allow sustainable Cape gannet foraging at the scale of the Malgas breeding colony. This is confirmed by further field observations: in 2011, and in particular in 2013 and 2014, we recorded some of the lowest body masses measured for breeding adults of this species (e.g. 2.15 kg, while gannets weigh 2.6 kg on average, Hockey et al. 2005).

Cape gannets breeding off the west coast of South Africa have experienced sustained nutritional stress since 2011. As anticipated by Okes et al. (2009) and Pichegru et al. (2009), this situation calls for improved management of marine resources in the southern Benguela off South Africa to ensure the protection of threatened, endemic seabird species. Such conservation action is already underway for the charismatic African penguin, through the exclusion of purse-seine fishing within 20 km of some of its main breeding colonies (Pichegru et al. 2010a, 2012). In this context, it is important to note that Benguela fisheries have actually been adequately managed for decades, with South Africa being a leading nation in terms of establishing an ecosystem-based approach for its fisheries (EAF), ahead of, for instance, countries of the European Union (Shannon and Moloney 2004). Yet, although annual total allowable catch (TAC) for west coast sardine and anchovy is determined through population modelling based upon detailed at-sea surveys of juvenile fish populations (Coetzee 2000), this small pelagic fish fishery is still managed using a single-stock approach (see Fairweather et al. 2006). This is at odds with recent findings, which exposed the likely existence of two stocks of sardines off South Africa, one off the west coast and the other off the south coast (de Moor and Butterworth 2015), whose management as a single stock leads to the over-exploitation and virtual collapse of the west coast stock. Signs of this collapse were visible from the population trends and diet of seabirds of the west coast for the past decade (Pichegru et al. 2007; Grémillet et al. 2008b, Okes et al. 2009; Crawford et al. 2011, 2014). Also, environmental signals visible in Cape gannet foraging energetics and fitness show that the current TAC is too high with respect to small pelagic fish occurring on the west coast of South Africa, at least not to levels preserving adequate food resources for seabirds in this particular region (sensu Cury et al. 2011).

Therefore, in a first step, a minimal measure would be to implement distinct fishing quotas (TAC) for west and south coast small pelagic fish, based on regional fish biomass estimates. This would account for the strongly skewed spatial distribution of small pelagic fish, with low stocks available to seabirds on the west coast. If such local TAC fails to improve the situation, experimental fishing closures should soon be envisaged. Indeed, from the perspective of seabird conservation there is ample scientific evidence that Cape gannets are permanent residents in the Benguela (Grémillet et al. 2008b), are critically dependent upon small pelagic fish across the annual cycle, and that these resources are now too scarce to sustain the Malgas Island breeding colony. Continued large-scale fishing of small pelagic fish off the west coast will therefore inevitably compete with a least 30 % of the world population of threatened, endemic Cape gannets, for which this food resource is vital. These same pelagic resources are equally essential to African penguins, whose world population has shown critical declines in recent years, and may become extinct within the next few decades (Baillie et al. 2004), as well as to a series of other marine predators, including Cape cormorants (Hamann et al. 2012), now also listed as endangered. Because small pelagic fish play a pivotal role in upwelling ecosystems (Cury et al. 2000; Fréon et al. 2008), fully protecting their remaining stocks in the southern Benguela should not only be performed with the objective of seabird conservation, but for the preservation of ecological functioning in the Benguela large marine ecosystem.

From a socio-economic point of view, maintaining a limited level of purse-seine fishing activity may be considered vital for disadvantaged local coastal communities on the west coast of South Africa. However, purse-seine fishing in this region has been only marginally profitable since the 2000s marine ecosystem shift: as Cape gannets, west coast purse-seiners are experiencing reduced catches, and some fish-processing facilities have already relocated to the south coast where the stock of small pelagic fish is still relatively abundant (Jarre et al. 2013). Also, industrial-style purse-seine fisheries only marginally benefit previously disadvantaged workers, since most of the profit flows into white-owned businesses (Jarre et al. 2015). Further, involvement of workers in purse-seine fishing prevents coastal communities from rebuilding more diversified, sustainable, coastal fishing activities, on smaller vessels requiring lower investment (e.g. Belhabib et al. 2015). Such activities target higher-priced fish, with substantially higher profitability and sustainability for coastal communities (Jarre et al. 2015), yet their future success will be linked to the capacity of the different stakeholders to jointly work towards rebuilding coastal fish stocks strongly depleted by traditional line fisheries (Sauer et al. 2003). Finally, ecotourism has become a major source of revenue and a key element of South Africa’s economy (Turpie 2003). For instance, the African penguin colony at Boulders Beach, South of Cape

Town, is visited by >500,000 people each year, generating approximately half a million US$ (Lewis et al. 2012), and the dwindling Cape gannet colony at Lambert's Bay is a mainstay of that town's tourism economy (the once thriving small pelagic fishery having closed down). There is therefore another major incentive for preserving small pelagic fish stocks sufficient to maintain the ecological functioning of the Southern Benguela upwelling ecosystem and its emblematic biodiversity.

Outlook

Seabirds have been used as ecological indicators for millennia, mainly by fishermen in search of fish shoals (Carson 1951), but they have seldom been used to inform operational management decisions with respect to industrial fisheries (Grémillet and Charmantier 2010). A few examples stand out, though. Breeding failures of kittiwakes (*Rissa tridactyla*) from the Isle of May, east Scotland (in conjunction with adverse effects on non-targeted fish species), motivated a closure by British authorities of industrial sandeel fisheries harvesting up to one million tonnes per annum in the western North Sea (Wanless et al. 2007). Further, signals gathered from the diet and reproductive performance of Antarctic marine top predators, especially penguins, are used by the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) to inform krill fisheries (Constable et al. 2000). These management decisions were taken on the basis of long-term monitoring of population trends and reproductive success. Here, we demonstrated how shorter-term state variables, in particular foraging energetics, can efficiently complement information gained from conventional monitoring, to help inform important management decisions.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical standard All experiments were performed under permits from South African National Parks with respect to animal ethics (No. CRC/2015/001—2002), and all protocols were validated by the French Direction des Services Vétérinaires (Permit No. 34-369).

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