

Foraging distribution of Cape gannets in relation to oceanographic features, prey availability and marine protected areas

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ABSTRACT: Seabirds forage in a dynamic environment of heterogeneously distributed prey resources. Many seabird species use oceanographic features that promote prey aggregation, as a means of locating prey patches. The combination of tracking data, remote-sensing data and estimates of prey availability is useful in determining how seabirds locate prey. GPS tracks of foraging Cape gannets *Morus capensis* were collected across 3 breeding seasons and tested for inter-annual changes in home range size and foraging effort, and compared against the availability of their predominant prey (sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus*) as determined from acoustic surveys. Biophysical features associated with foraging were compared to a random point dataset using a binomial general linear mixed model, while foraging distributions of Cape gannets were compared against the placement of marine protected areas (MPAs). The total home range of foraging Cape gannets, breeding at Bird Island, South Africa, propagated westwards over the 3 breeding seasons, which coincided with a concurrent westward contraction in the distribution of sardine and anchovy. Foraging effort showed an apparent increase in response to low prey densities and occurred mostly outside MPAs. Although gannets seemed to forage in relatively cold waters, biophysical features were generally unreliable predictors of gannet foraging distribution. The relationship between home range and prey distribution, coupled with recent declines in local prey availability, demonstrates the ability of gannets to track the distribution of their prey resources. However, the ephemeral and dynamic nature of these prey resources places a major constraint on conservation-based spatial planning involving Cape gannets.

KEY WORDS: *Morus capensis* · Agulhas Bank · Home range · Predator–prey relationships · Productivity · Marine protected areas

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INTRODUCTION

Seabirds have long been thought to forage in a large, unpredictable environment, with patchily distributed prey resources (Ashmole 1971). However, recent findings suggest that at a large and medium scale, the distribution of prey can be predicted fairly accurately (Weimerskirch 2007). This is especially true for shelf systems where bathymetry drives perennial processes such as shelf edge upwelling (Probyn et al. 1994). These processes may act as nu-

clearing points for prey, which tend to be aggregated through physical forcing (e.g. Friedlaender et al. 2006, Sokolov 2008). Seabirds often track such oceanographic features, which are indicative of productivity, and hence prey availability (e.g. Bost et al. 2009). Consequently, oceanographic features tend to be fairly reliable predictors of seabird foraging distribution (Weimerskirch 2007, Bost et al. 2009).

Zones of relatively low sea surface temperature (SST) and high productivity are often targeted by foraging seabirds and could be useful in identifying can-

didate areas for conservation-based spatial planning. This has become increasingly important due to the dire status of numerous seabird species (Croxall et al. 2012), resulting from, amongst other factors, declines in prey availability (Okes et al. 2009) and accidental capture as fishery bycatch (Petersen et al. 2009). In order to both protect threatened habitats and biota and manage fisheries, there has been movement towards spatially explicit conservation (Halpern 2003), which has largely been focused on immobile ecosystems (e.g. coral reefs; McClanahan et al. 2007) and their associated species. However, there is increasing need for conservation approaches that benefit highly mobile and far-ranging species such as marine top predators (Louzao et al. 2006, Game et al. 2009). This could potentially be achieved by identifying predator foraging distributions and modelling habitat preferences, which can be used to highlight areas of key importance (Louzao et al. 2006).

The Cape gannet *Morus capensis*, a large pelagic seabird endemic to the south and west coasts of South Africa and Namibia (Crawford et al. 1983), is a medium-distance forager capable of covering several hundreds of kilometres in a single foraging trip (Grémillet et al. 2004, Pichegru et al. 2007). Its natural diet consists of small shoaling pelagic fish, predominantly sardine *Sardinops sagax*, anchovy *Engraulis encrasicolus* and saury *Scomberesox saurus* (Green et al. 2015). Since the mid-1950s, the size of the Cape gannet population has undergone a severe decline, reportedly related to decreased prey availability (Crawford et al. 2007a). This, together with its restricted breeding range, has resulted in the Cape gannet's classification as Vulnerable by the IUCN (BirdLife International 2013). The Cape gannet colony at Bird Island, Algoa Bay, South Africa, has in contrast increased over recent decades, from about 19 100 pairs in 1955/1956, to approximately 98 000 pairs in 2005/2006 (Crawford et al. 2007a), and is now fairly stable (Oceans and Coasts, South Africa unpubl. data).

Cape gannets breeding on the west and south coasts of South Africa experience very different foraging conditions. For example, gannets breeding at Bird Island eat predominantly live prey (Moseley et al. 2012, Green et al. 2015), whereas along the west coast, fishery discards (mainly hake *Merluccius* spp.), a suboptimal prey source (Mullers et al. 2009), make up a much larger proportion of the diet. Similarly, on the west coast of South Africa, Grémillet et al. (2008a) found that Cape gannets foraged in waters that were neither significantly more productive, nor cooler than those of the overall home range. However, productiv-

ity on the eastern Agulhas Bank tends to be more transient and localised (Probyn et al. 1994) than it is on the west coast (Andrews & Hutchings 1980).

Considering the global significance of the Bird Island Cape gannet colony, it is vital that we understand what drives foraging behaviour in birds of this population, and furthermore, whether the current marine protected area (MPA) network holds any conservation value for the colony. In this study, changes in the foraging distribution, home range and proxies of foraging effort of Cape gannets breeding at Bird Island, Algoa Bay, were assessed over 3 consecutive breeding seasons. To test for habitat selectivity, foraging distribution was compared with both prey distribution and biophysical features (SST, chlorophyll *a* [chl *a*], bathymetry and slope). Because upwelling processes along the south coast are much less extensive than along the west coast, areas of high productivity were expected to be localised, acting as nucleating points for prey. In addition, as a means of testing whether the current MPA network coincides with important gannet foraging areas, the spatial distribution of foraging locations was compared against the distribution of MPAs within the potential foraging range of gannets at Bird Island. The results of this study may be useful as a guide for future expansions of the region's MPA network. Due to the size of the potential foraging range of Cape gannets, and their tendency to forage offshore, it was predicted that foraging would show minimal overlap with MPAs.

MATERIALS AND METHODS

Study site

Fieldwork was conducted over 3 consecutive breeding seasons (2010/2011 breeding season: 8–25 December and 14–22 January; 2011/2012 breeding season: 8–26 December and 28 January–4 February; 2012/2013 breeding season: 4–14 December and 17–28 January) at Bird Island, Algoa Bay (33° 50' 26" S, 26° 17' 10" E), situated on the eastern Agulhas Bank within the Agulhas bioregion. Bird Island lies approximately 65 km east of Port Elizabeth and 8 km off the mainland at Woody Cape, the eastern margin of Algoa Bay (Fig. 1).

MPAs

Within the potential foraging range of the Bird Island gannet colony are 3 established marine re-

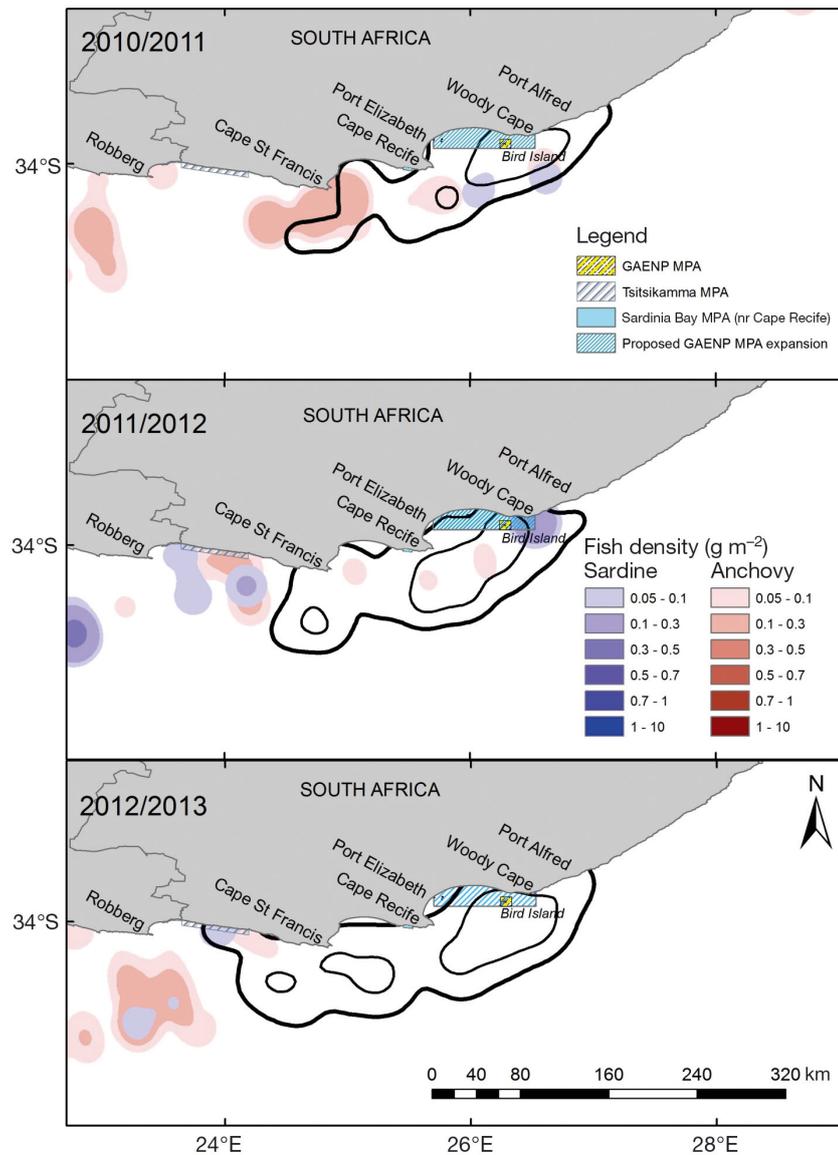


Fig. 1. Kernel home ranges for Cape gannets *Morus capensis* breeding over 3 seasons (2010/2011, 2011/2012 and 2012/2013) at Bird Island, Algoa Bay, in relation to the distribution of marine protected areas (MPAs) along the coast, and estimates of sardine and anchovy densities. Home range contours represent the 50% (thin black lines) and 95% (thick black lines) utilization densities. GAENP: Greater Addo Elephant National Park

serves, namely the Greater Addo Elephant National Park MPA (GAENP MPA), Sardinia Bay MPA and the Tsitsikamma National Park MPA (Fig. 1). These reserves are no-take zones in which no commercial exploitative activity is permitted. A fourth reserve has been proposed, i.e. an expansion of GAENP (A. Oosthuizen pers. comm.), which would incorporate the current MPA along with the majority of Algoa Bay (Fig. 1).

GPS deployments

Resin-encased GPS Loggers (I-gotU GT-600, Mobile-Action-Technology) were deployed on chick-rearing Cape gannets during the breeding seasons (December to February) of 2010/2011, 2011/2012 and 2012/2013. Attendant parents whose partner had returned were caught, prior to departure, by means of a crook fixed to the end of a telescopic pole. The miniaturised GPS Logger was then fitted onto the base of the tail by means of water-proof Tesa® tape. Loggers weighed 39 g, or approximately 1.5% of average adult body mass. Previous studies have found no significant impact of such devices on the foraging behaviour of Cape gannets (Grémillet et al. 2004, Pichegru et al. 2007). Handling time was minimised to reduce stress and observer impacts. Following deployment, the bird's nest was monitored hourly, during daylight hours, until the bird returned, at which point the logger was immediately removed.

For 2010/2011 and 2011/2012, loggers were programmed to record a position every 10 s provided the bird was travelling at speeds greater than 10 km h^{-1} . At lower speeds, positions were logged every 5 s. In 2012/2013, the loggers were programmed to record positions every 10 s, regardless of speed. In total, 115 tracks (35 in 2010/2011, 40 in both 2011/2012 and 2012/2013) were collected over the 3 breeding seasons of this study. For the respective breeding seasons, a total of 29, 36 and 40 tracks were complete, or showed battery failure shortly before the bird's return to the

colony. The lower numbers of complete tracks obtained during the first 2 breeding seasons are attributable to the higher position-fix frequency. Despite being programmed to log at set frequencies, device fix rates were not always regular. To correct for differences in fix rates, all tracks were standardised to 10 s intervals using the 'adehabitatLT' (v.0.3.12) package in R, whereby missing points were derived through linear interpolation of the original track.

Tracks were subsequently analysed in ArcMap 10.1 (Environmental Systems Research Institute).

Home range

To reduce the effect of differing sample sizes between breeding seasons, 35 tracks from each season were randomly selected for computation of the annual colony home range. Incomplete tracks were included to reduce the bias associated with including only shorter, complete tracks during the first 2 breeding seasons. Home ranges were generated by means of a Kernel Home Range analysis using the package 'adehabitatHR' in R, with the ad hoc method as a smoothing parameter. Two contour levels were selected to represent the total (95 %) and the core (50 %) ranges of the colony. Areas (km²) were then calculated for both levels (95 and 50 %) as a basic means of assessing annual change.

Area-restricted search

Foraging locations, or positions of area-restricted search (ARS), can be isolated by means of a track sinuosity index (Grémillet et al. 2004, Mullers & Navarro 2010). Sinuosity was calculated as the ratio between the cumulative distances covered between 4 fixes and the displacement between the first and last fix. Sinuosity values greater than 3.3 were assumed to represent active foraging by birds (Grémillet et al. 2004). At speeds below 10 km h⁻¹, gannets were assumed to be sitting on the water. Consequently, all fixes corresponding to speeds lower than 10 km h⁻¹ were removed. The isolated ARS locations therefore represent areas where gannets were assumed to be foraging, although possible surface feeding when birds sit on the water (which has not been observed in Cape gannets) cannot be accounted for in these data. Inter-annual change in foraging effort was tested using 5 proxies, namely mean and maximum distance of ARS from the colony, commuting distance (distance from colony until first onset of ARS), mean track sinuosity (of all fixes associated with flying) and proportion of flight associated with ARS. These parameters were first tested for within-breeding season differences using Student's *t*-tests, or Mann-Whitney *U*-tests, which indicated no significant differences. Thereafter, differences between breeding seasons were tested using either analysis of variance (ANOVA) or Kruskal-Wallis tests, depending on data normality. Pairwise compar-

isons were performed using either Tukey's HSD tests or non-parametric multiple contrast tests (nprmc, type='Tukey', package 'nparcomp'). Sample sizes for the above analyses were standardised across breeding seasons according to the breeding season with the lowest sample number. All means are reported together with standard deviation (SD).

Pelagic fish densities

Sardine and anchovy biomass and distribution were extracted from South African Department of Agriculture, Forestry and Fisheries (DAFF) acoustic survey data (Coetzee et al. 2008) and mapped for 2010/2011, 2011/2012 and 2012/2013 using a density analysis in ArcView 3.2.

Physical variables

SST (°C) and chl *a* (mg m⁻³) maps were derived from the moderate-resolution imaging spectroradiometer (MODIS) Aqua satellite run by NASA (<http://oceancolor.gsfc.nasa.gov>). These represent daily averages of the conditions within the surface layers of the water column at a spatial resolution of 1 km². Bathymetry data were derived from the global digital elevation model (DEM) GTOPO30, at a resolution of 30 arc seconds (approximately 1 km²). Estimates of slope were generated from the DEM using the spatial analyst extension in ArcMap 10.1. To assess habitat selectivity, the conditions experienced by foraging gannets were compared against the conditions available within the breeding home range. For this, a random dataset of 10 000 points was created within the calculated home range of the colony during each breeding season. For each day, the nearest (<1 km) SST, chl *a*, bathymetry and slope values were assigned to the foraging locations and random datasets. On many of the days, cloud cover obscured much of the study area, with physical data only available for those points that overlapped with cloud-free areas. For this reason, only days with minimal cloud cover were used in the analysis. Although the effects of cloud cover could be overcome by averaging the data over days or weeks, this would remove the ephemeral nature of physical processes on the continental shelf, making it unacceptable for the purpose of this study. For every presence location, 3 points with associated physical conditions were randomly selected from the random dataset of the same day. We used a binomial generalised linear mixed effects

Table 1. Comparisons of the mean foraging location characteristics for foraging Cape gannets *Morus capensis* during 3 consecutive breeding seasons at Bird Island, Algoa Bay, South Africa. ARS: area-restricted search. Values in **bold** are significant ($p < 0.05$); ns: not significant

Parameter	2010/2011			2011/2012			2012/2013			Significance (p-values)		
	Mean	SD	n	Mean	SD	n	Mean	SD	n	2010/2011 vs 2011/2012	2010/2011 vs 2012/2013	2011/2012 vs 2012/2013
Mean foraging distance from colony (km)	44.24	34.59	35	65.45	42.46	35	78.78	60.77	35	0.05	0.05	ns
Max foraging distance from colony (km)	66.83	43.04	35	91.89	59.23	35	108.96	80.67	35	ns	ns	ns
Commuting distance (km)	49.62	34.72	35	53.31	49.61	35	25.49	22.29	35	ns	0.01	<0.001
Mean sinuosity value	1.22	0.10	22	1.17	0.10	22	1.29	0.14	22	ns	ns	<0.01
Proportion of flight associated with ARS (%)	1.77	1.08	22	1.23	0.89	22	2.20	1.21	22	ns	ns	<0.01

model (package 'lme4' in R) to assess differences in physical conditions between where birds were present and random points (Aarts et al. 2008, Wakefield et al. 2009). Resultant data were then modelled as a function of SST, chl *a*, bathymetry and slope, using breeding season, date and individual as random effects. The model was assessed using the 'dredge' function, and the resultant model with the lowest Akaike's information criterion (AIC) value was selected.

RESULTS

Across the 3 breeding seasons, gannets breeding at Bird Island foraged mostly on the continental shelf, with only a few birds ($n = 5, 9$ and 3 in 2010/2011, 2011/2012 and 2012/2013, respectively) venturing as far as the shelf margin. All but 3 remained over waters of less than 800 m depth. In general, birds foraged well offshore (average of 26 ± 13 km from the coast), but over waters generally shallower than 200 m. Most foraging took place to the west and southwest of Bird Island (Fig. 1). Some birds reached almost as far as Robberg Peninsula, a straight line distance of 270 km west of Bird Island, and to about halfway between Port Alfred and East London, 115 km to the east.

Home range

The home range of Cape gannets breeding at Bird Island increased progressively in size during the study period ($12\,753$ km² in 2010/2011, $15\,933$ km² in 2011/2012 and $19\,992$ km² in 2012/2013; Fig. 1). This increase seems to have been propagated westwards, with considerable portions of the home range in 2011/2012 and 2012/2013 being situated west of Cape St Francis. In 2010/2011, the core (50% utiliza-

tion density) of the home range was centred on Bird Island, with a localised core southeast of Cape Recife (Fig. 1). These 2 cores merged during the westward expansion of the home range in 2011/2012, and another localised core opened south of Cape St Francis. Further expansion in 2012/2013 led to the development of a third core off the coast of Tsitsikamma (Fig. 1).

The average distance of gannet ARS from the colony was significantly greater in both 2011/2012 ($p = 0.05$) and 2012/2013 ($p = 0.05$) than in 2010/2011 (Table 1). However, there was no significant difference between breeding seasons based on the farthest position from the colony (Table 1). On average, commuting distance was significantly lower during the 2012/2013 breeding season than during both 2010/2011 ($p < 0.01$) and 2011/2012 ($p < 0.001$) (Table 1), but not significantly different between 2010/2011 and 2011/2012 (Table 1). Both average track sinuosity and the proportion of flying locations associated with ARS were significantly higher in 2012/2013 than 2011/2012 ($p < 0.01$), but not significantly different between either 2010/2011 and 2011/2012, nor 2010/2011 and 2012/2013 (Table 1). This suggests an increase in foraging effort in 2012/2013, with birds initiating ARS sooner, but on average foraging farther away from the colony and spending a greater proportion of time searching for prey.

Distribution of pelagic fish

Sardine and anchovy showed a progressive westward contraction in distribution from 2010/2011 until 2012/2013 (Fig. 1). During 2010/2011, the average density of sardine and anchovy within the home range was 5.33 and 14.37 g m⁻² respectively. At this time, 2 cores of sardine and anchovy biomass were situated off Algoa Bay, and a large, dense core of anchovy was located around Cape St Francis (Fig. 1).

Table 2. Comparison of mean chlorophyll *a* (chl *a*), sea surface temperature (SST), bathymetry and slope at foraging locations compared to a random point dataset within the home range of Cape gannets *Morus capensis* breeding at Bird Island, Algoa Bay. ARS: area-restricted search

Breeding season	Dataset	Chl <i>a</i> (mg m ⁻³)		SST (°C)		Bathymetry (m)		Slope (°)	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD
2010/2011	ARS	2.88	3.14	18.85	0.97	93.87	20.21	0.25	0.19
	Random	2.20	3.42	19.58	1.71	126.65	142.31	0.54	0.98
2011/2012	ARS	0.91	0.74	19.61	1.27	117.50	35.67	0.42	0.67
	Random	1.60	3.39	19.93	1.66	208.61	341.28	0.82	1.57
2012/2013	ARS	1.24	0.99	21.49	1.34	109.52	49.13	0.54	1.02
	Random	0.98	0.82	21.77	1.86	206.85	317.56	0.98	1.96

In 2011/2012, the abundance of sardine within the gannet home range increased to an average of 10.14 g m⁻², while anchovy decreased to 11.82 g m⁻². However, apart from a dense core of sardine off Woody Cape and 3 small cores of low anchovy density distributed between Woody Cape and Cape St Francis, much of this biomass was situated west of Cape St Francis (Fig. 1). By 2012/2013, the distribution of both species had shrunk well west of Cape St Francis, with average densities of 2.86 g m⁻² (sardine) and 3.86 g m⁻² (anchovy) within the home range of the gannet study population. These distributional changes seem to have been followed by a westward expansion in the gannet home range (Fig. 1) and increased foraging effort by Cape gannets in terms of average distance of foraging from Bird Island, distance travelled until onset of ARS, track sinuosity and proportion of foraging associated with ARS (Table 1).

Productivity within the study area was relatively low (Brown 1992, Demarcq et al. 2003), and appeared to decrease over the 3 breeding seasons (Table 2). Foraging gannets utilized waters averaging 20.49 ± 1.7°C (range: 17.25–25.6°C), with an average chl *a* of 1.49 ± 1.8 mg m⁻³ (range: 0.2–12.7 mg m⁻³; Table 2). Overall conditions for the random datasets were slightly warmer for temperature (20.86 ± 2.0°C) and slightly lower in terms of chl *a* concentrations (1.38 ± 2.4 mg m⁻³; Table 2). During all 3 breeding seasons, gannets seemed to forage in colder waters than those associated with the random datasets (Fig. 2). This difference was significant in 2010/2011 ($p < 0.001$), but not across the 3 breeding seasons. There were no significant differences or clear patterns with regard to chl *a*. Overall, model comparison showed that the combination of SST and bathymetry, accounting for breeding season as a random effect, provided a model with the lowest AIC value. During the first 2 breeding seasons, gannets foraged mostly in waters of 20°C or less, with modal

temperatures of 18 and 19.5°C for 2010/2011 and 2011/2012, respectively (Fig. 2). However, in 2012/2013 there was an apparent shift in the frequency distribution of environmental SST, with a new modal temperature of 22.5°C, and as a result, the majority of foraging was conducted in considerably warmer waters (>20°C; Fig. 2). Throughout the study, gannets foraged in relatively shallow waters (mean depth: 108 ± 42 m) and over a largely flat sea-floor (mean slope: 0.45 ± 0.84°; Table 2).

MPA boundaries

Over the 3 breeding seasons, most of the foraging locations occurring within MPAs were situated within the boundaries of the proposed expansion of the GAENP MPA (Table 3). During the latter 2 breeding seasons, in particular 2012/2013, there was some overlap with the Tsitsikamma National Park MPA (Fig. 1). The current formal protected area network, through potential protection of prey species in areas where no fishing is allowed, has provided little benefit (<4% of foraging locations) to foraging gannets over the course of the study (Table 3). The overall overlap of foraging locations with all MPAs (including the expanded GAENP MPA) was highest during 2010/2011 (13.1%) and 2012/2013 (10.4%), but considerably lower in 2011/2012 (3.5%) (Table 3).

DISCUSSION

The home range of Cape gannets breeding at Bird Island expanded fairly rapidly over the 3 yr study period. This was accompanied by an apparent increase in foraging effort in terms of average distance of foraging from Bird Island, distance travelled until onset of ARS, track sinuosity and proportion of foraging associated with ARS as a response to changes

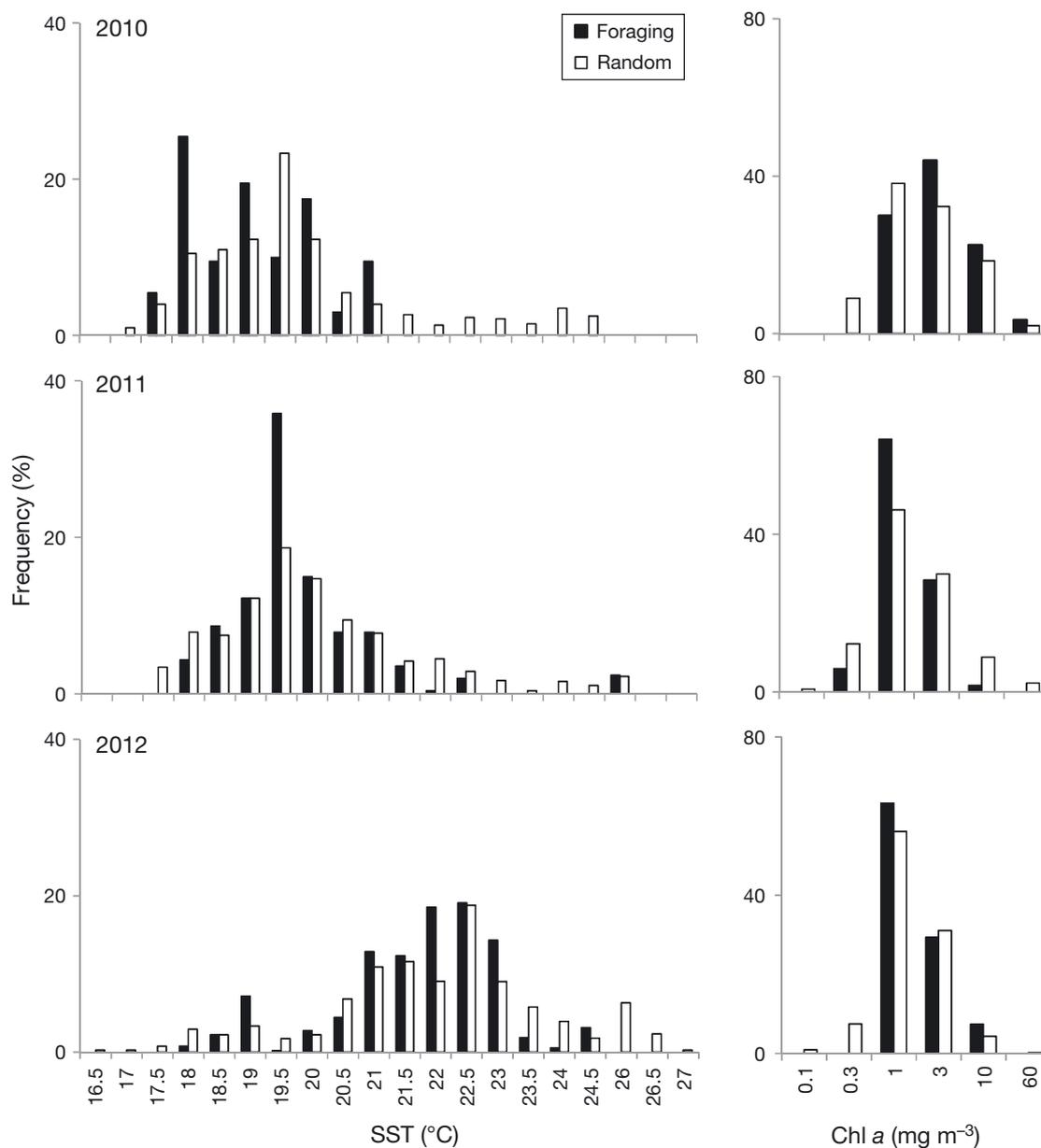


Fig. 2. Frequency distributions comparing 3 breeding seasons of sea surface temperature (SST) and chlorophyll *a* values associated with foraging locations (black bars) of Cape gannets *Morus capensis* breeding at Bird Island, Algoa Bay, against those of a random point dataset (white bars) within the colony home range

Table 3. Seasonal overlap of foraging locations (n, with percentages of total in parentheses) and marine protected areas (MPAs) within the home range of Cape gannets *Morus capensis* breeding at Bird Island, Algoa Bay. GAENP: Greater Addo Elephant National Park. Values for the formal GAENP MPA are also included within those for the proposed GAENP MPA expansion

Breeding season	Sardinia Bay	Tsitsikamma National Park	GAENP	Overall formal	Proposed GAENP MPA expansion	Overall (formal and proposed)	Total foraging locations
2010/2011	0 (0)	0 (0)	8 (1)	8 (1)	156 (13)	156 (13)	1192
2011/2012	0 (0)	0 (0)	1 (0)	1 (0)	35 (4)	35 (4)	993
2012/2013	0 (0)	42 (2)	16 (1)	58 (3)	159 (8)	201 (10)	1928

in the distribution of sardine and anchovy stocks in the study area. Cape gannets foraged exclusively over the continental shelf in waters that were generally colder but not more productive than surrounding waters. Over the 3 breeding seasons, there was a progressive increase in SST in the study area, with an associated decline in productivity. These oceanographic changes appeared to have an influence on the distribution of sardine and anchovy (Fig. 1), and consequently, on the foraging dynamics of Cape gannets. The majority of foraging took place offshore and consequently well outside the boundaries of MPAs.

Foraging effort and prey distribution

Prey stock dynamics have elsewhere been shown to have a major influence on Cape gannet foraging distribution and associated effort (Pichegru et al. 2007). At Malgas Island, on South Africa's west coast in the Benguela system, an eastward shift in the centre of gravity of both sardine and anchovy biomass was matched by an increase in the foraging path length of gannets attempting to track the movement of their prey (Pichegru et al. 2007). This same eastward expansion increased the availability of these fish, particularly sardine, for foraging gannets from Bird Island (Crawford et al. 2007b). Sardine biomass in South Africa peaked in 2002, but has since declined as a result of successive years of poor recruitment (Coetzee et al. 2008), which would likely have been accompanied by a range contraction (Lluch-Belda et al. 1989, Barange et al. 2009). This might explain the westward contraction of this species away from Algoa Bay during this study. In 2005, 86% of the diet, by mass, was comprised of sardine, which then decreased to 44% in 2010/2011, 34% in 2011/2012 and almost nothing (3%) by 2012/2013, being almost entirely replaced by anchovy (Green et al. 2015). The 2012/2013 anchovy distribution (Fig. 1) suggests that this species might have undergone a similar westward contraction, possibly worsened by anomalously high temperatures on the eastern Agulhas Bank during the summer of 2012/2013. This persistence of warm, unproductive waters could have been caused by an absence of strong coastal upwelling, a dominant mechanism in which surface waters over the shelf are cooled (W. Goschen pers. comm.). Sardine and anchovy spawn in cold waters (anchovy: 17–23°C, sardine: 16–22°C; Mhlongo et al. 2015), but the modal temperature in the study area during 2012/2013 was 22.5°C, at the upper limit of their pre-

ferred spawning range. Consequently, both species likely moved westward, or migrated to greater depths, away from these largely unfavourable conditions. Should such distributional changes persist, the 2 dominant prey groups could potentially move out of the foraging range of breeding Cape gannets.

It has been suggested that the home range of the gannet colony at Bird Island contracted between the 1950s and 1970s (Klages 1994). Indeed, in the 1980s, Cape gannets were not known to travel much farther than 200 km from Bird Island (Klages et al. 1992). Home range expansion with concurrent increases in search effort could be influenced by intraspecific competition and the consequent depletion of local prey stocks (Lewis et al. 2001). Crawford et al. (1991) estimated that during the 1980s, gannets (estimated at approximately 410 400 adults) foraging along the southwestern African coast consumed 25 800 t of prey during summer (October to March). With this in mind, the total adult population at Bird Island would need to consume some 27 626 t of prey each summer. A rough estimate of small pelagic fish biomass within the home range across the 3 yr study period (2010/2011: 251 234 t; 2011/2012: 349 889 t; 2012/2013: 134 346 t) suggests that gannets consume only a small proportion of biomass within the study area. However, it is possible that a large portion of this biomass remains unavailable to foraging gannets, either due to movement of fish out of the gannet home range, an inability of gannets to track the movement of localised shoals, or shoals being situated at depths exceeding the maximum dive depths of gannets.

Comparisons between the foraging effort of gannets breeding at Bird and Malgas Islands showed that during 2009, both colonies fed predominantly on live prey, but individuals from Bird Island worked harder to locate prey (Moseley et al. 2012). The authors suggested that this was related to a higher level of intraspecific competition at the larger Bird Island colony. A westward contraction in the distribution of prey might aggravate the effects of such competition. While Cape gannets preferentially feed on live prey and increase foraging effort as prey becomes scarce, they are known to scavenge when prey densities are very low (Tew Kai et al. 2013). Prolonged distributional contractions of prey out of the Cape gannet foraging range could drive gannets to scavenge for fishery discards, which are both energy poor and sub-optimal (Grémillet et al. 2008b), particularly for chicks (Mullers et al. 2009), and less available to foraging birds along the south coast than they are along the west coast (Walmsley et al. 2007).

Biological and physical cues

In a western boundary current system such as the Agulhas Current, waters off the shelf edge are typically warm, saline and unproductive (Swart & Largier 1987) supporting low prey abundances. Because of the low energetic rewards associated with such waters, gannets avoid foraging seaward of the shelf margin, despite it being well within their potential foraging range. However, despite gannets generally feeding in relatively cold waters (particularly as observed during 2010/2011) chl *a* was not a reliable predictor of foraging distribution. Grémillet et al. (2008a) found that gannets foraging in the highly productive Benguela system where upwelling is much more extensive showed no preference for colder, more productive waters within their home range. This suggests that, irrespective of the magnitude and spatial extent of upwelling, zones of high chl *a* do not act as a proxy for Cape gannet foraging distribution.

The highly ephemeral nature of upwelling along the south coast may be at too fine a temporal scale to be effective in concentrating prey. Upwelled waters might well be lost to the surrounding environment before they can promote increases in productivity. Consequently, at the relatively fine scale over which gannets forage, it could be more beneficial to make use of alternative foraging cues, such as central information transfer with conspecifics or other marine top predators (Thiebault et al. 2014, Tremblay et al. 2014). In spite of this, there is evidence that Cape gannets can recognise mesoscale fronts (Sabarros et al. 2014). Therefore, under conditions of high upwelling frequency, gannets may be better able to make use of SST and chl *a* as a means of tracking prey distribution, which may in turn explain the relatively high selectivity of cold, productive waters displayed by foraging gannets, particularly in 2010/2011.

Alternatively, gannet foraging distribution could potentially have been focused over productive waters which are situated below the surface layers visible in satellite imagery. Current shear along the shelf edge forces basal waters onto the shelf, and often drives the formation of a productivity maximum ($>1 \text{ mg chl } a \text{ m}^{-3}$) at 1 to 20 m depth (Probyn et al. 1994). Core gannet activity which was located well offshore during the 2011/2012 and 2012/2013 breeding seasons (Fig. 1) might have been focused around this feature, which is quasi-permanent (Chapman & Largier 1989), unlike wind-induced upwelling at the capes (Probyn et al. 1994). Also of note was the problem posed by cloud cover, with many days being excluded due to an absence of data. Upwelling

events are often accompanied by heavy fog (Olivier & Stockton 1989), which can obscure satellite imagery and influence the availability of data. In this way, periods of high productivity may have been under-represented in this investigation.

Conspecifics and other marine top predators might also influence Cape gannet foraging distribution. Individual gannets make use of intraspecific social cues to locate prey patches (Thiebault et al. 2014, Tremblay et al. 2014). In addition, gannets often associate with other marine top predators (e.g. dolphins), which concentrate prey shoals and force them to the surface (Vaughn et al. 2008). Therefore, the distribution of conspecifics and other marine top predators should be considered when interpreting Cape gannet foraging locations.

MPAs and foraging gannets

Across all 3 breeding seasons, there was a distinct spatial mismatch between gannet foraging distribution and MPAs. While core (50%) gannet activity was located well offshore, relatively close to the shelf margin, MPAs were essentially no more than extensions of the mainland. The exceptions were the island reserves, which accounted for the greatest proportion of spatial overlap with gannet foraging distribution. In total, the MPA network (GAENP, Tsitsikamma National Park and Sardinia Bay) accounts for 355 km², some 3% of the total gannet home range in 2010/2011. Hence, current marine reserves clearly provide little direct spatial benefit for this species, apart from protection at the breeding colony on Bird Island. With the addition of the proposed MPA expansion of GAENP, total coverage would increase considerably, to 1454 km² (11% of the 2010 home range estimate). However, this remains outside of the areas of core gannet activity, as it covers much of Algoa Bay, but does not extend farther out over the shelf. Even with the additional coverage of the GAENP expansion, MPAs within the area are unlikely to be effective in protecting prey resources for foraging gannets. This is largely due to the biology of small pelagic fish, which, being highly mobile, would frequently move out of the MPA boundaries.

The efficacy of MPAs with regard to resource competition lies in the reduction of fishing pressure when fish within an area are targeted by both fisheries and top predators. A 20 km experimental fishing closure around St Croix Island in 2008 reportedly increased prey availability for African penguins foraging around the island by removing fishing pressure

(Pichegru et al. 2010). This claim, although debated at the time because of, amongst other factors, confounding effects of prey abundance (Butterworth et al. 2010, Coetzee 2010), has subsequently been confirmed (Pichegru et al. 2012). However, increased fishing pressure at the reserve edge the following year (2010) coincided with increased foraging effort, suggesting that the 20 km reserve was too small an area to adequately buffer against fishing pressure (Pichegru et al. 2012). In contrast, across the large foraging range of Cape gannets breeding at Bird Island, fishing effort and yield remain low (DAFF unpublished data), which likely ensures little competition between the fishery and gannets. As such, the benefits for foraging gannets associated with an MPA would probably be minimal. Furthermore, while the current MPA network excludes commercial fishing, the GAENP MPA extension would be zoned (A. Oosthuizen pers. comm.), with limited, but continued, commercial fishing within the Algoa Bay area.

Pelagic protected areas have been highlighted as a potential solution for conserving marine resources (Game et al. 2009), and may be effective in preserving prey stocks for seabirds in the area. In South Africa, the Offshore Marine Protected Area Project set out to identify key areas of importance for expanding the country's MPA network (Sink et al. 2011). This project has identified 10 focus areas for offshore biodiversity protection. One such area, the Port Elizabeth Focus Area, has within its list of objectives the protection of threatened species and would encompass a large portion of the Cape gannet foraging range, which would likely make it the most effective means of protecting this population. However, as prey distribution seems to be linked to oceanographic conditions (e.g. van der Lingen et al. 2001), long-term environmental change could render spatially explicit MPAs ineffective. This may be overcome by making protected areas more spatially dynamic, in which their position may be annually readjusted based on the distribution of prey stocks as determined by recruitment and spawner surveys (Grantham et al. 2011). Alternatively, conservative management measures such as those currently under development by DAFF (de Moor & Butterworth 2015), whereby fishing pressure is spatially managed, may prove to be more effective in promoting healthy prey resources for seabirds.

Conclusions

Cape gannets breeding at Bird Island have had to increase their foraging effort in order to track chan-

ges in the distribution of their prey. However, given the low levels of exploitation of both sardine and anchovy within the area, it is unlikely that these distributional changes were significantly affected by fishing pressure. Although we provide some evidence that gannets in the Agulhas bioregion forage in relatively cold waters, the lack of predictive power of productivity is surprising. While there is some indication that during periods of intense upwelling and high productivity, gannets may track changes in oceanographic variables, this does not seem a reliable method of predicting foraging distribution of this species. Due to the dynamic nature of their prey, the current MPA network is unlikely to provide much benefit for foraging gannets. While implementation of the proposed GAENP MPA expansion will increase the level of overlap with foraging gannets, it is unlikely to significantly improve feeding conditions due to the spatial mismatch of core gannet foraging areas and MPA positioning and the observed low densities of prey within the MPA boundaries.

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