

Foraging behaviour and habitat use of a short-ranging seabird, the crested tern

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ABSTRACT: We used satellite tracking technology on the crested tern *Sterna bergii*, a seabird weighing <400 g. GPS units weighing <22 g were deployed on adult terns brooding young chicks. Individuals typically commuted to foraging grounds <40 km from the colony where their travel speeds slowed to ≤ 10 km h⁻¹, presumably as prey encounter rates increased. Individuals undertook trips up to 4 h 17 min in length and 118 km in distance, and trip duration was positively correlated with the maximum distance and total distance traveled. Foraging behaviour, examined in relation to habitat characteristics (benthic habitat type, depth, sea surface temperature [SST], chlorophyll *a* [chl *a*]), was typically associated with warm (19 to 21°C), shallow (<20 m depth) waters that were relatively high in chl *a* (>0.5 mg m⁻³). The most well-supported model (generalised linear mixed model) of foraging behaviour indicated a positive relationship between time spent at sea, distance travelled and chl *a*, suggesting individuals spent relatively more time foraging at greater distances from the colony in zones of higher primary production. The timing and location of crested tern breeding may be linked to the 2-fold increase in primary production near Troubridge Island over the austral summer. Individual differences in the length (distance and duration) of foraging trips may reflect either prior knowledge of where prey aggregations exist, distinctions in individual niche use driven by the types or sizes of prey available, and/or alternate behavioural states (self feeding and provisioning). The restricted foraging range of crested terns while breeding may make them sensitive to competition with fisheries that operate within their foraging range.

KEY WORDS: Bio-logging · Foraging ecology · Seabird · GPS · Habitat partitioning · *Sterna bergii*

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INTRODUCTION

As central-place foragers during the breeding season, marine predators, such as seabirds or otariid seals, must balance their energetic requirements with those of their offspring (Orians & Pearson 1979). As a result, characteristics of their foraging behaviour reflect the fasting abilities of their offspring and conditions of prey availability near breeding sites (Swihart & Johnson 1986, Cairns 1987, Burger & Piatt 1990). For seabirds, which are further constrained by the need to provision their young with whole or macerated prey, parents would be expected to forage as near to the colony as prey conditions and energetic

requirements allow. However, the availability of prey near colonies may be influenced by density-dependent effects caused by the collective foraging behaviour of conspecifics (Davoren et al. 2003), and large colonies of breeding seabirds may deplete prey resources around a colony (Ashmole 1963, Birt et al. 1987). Prey availability is also influenced by the habitat characteristics near to colonies and several studies have related the foraging behaviour of seabirds to biological and physical features (e.g. bathymetry, sea surface temperature [SST], chlorophyll *a* [chl *a*]) (Guinet et al. 1997, Becker & Beissinger 2003, Suryan et al. 2006, Peltonen et al. 2007, Weimerskirch et al. 2008).

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The linkage between habitat use and the foraging behaviour of large seabirds (>400 g) has received particular attention in recent years due to the development of animal-borne telemetry devices and remote sensing techniques (Guinet et al. 1997, Gremillet et al. 2004, Suryan et al. 2006, Pinaud & Weimerskirch 2007). These studies have indicated that seabird foraging responses vary between species and populations due to local biophysical conditions that enhance productivity and prey availability. Foraging behaviour also differs between individuals as a product of foraging-site fidelity and breeding phenology. Individuals that best modify their foraging behaviour in response to existing prey conditions may be conferred a selective advantage through increased breeding success (Lea et al. 2002). Consequently, the foraging behaviour of individuals may vary within one general 'mode' of behaviour. Characterising the different foraging tactics exhibited by conspecifics may provide insights into the factors that shape the evolution of foraging behaviour and life history strategies, and is important in identifying the significance of prey 'hotspots' (Lea et al. 2002).

The size of bio-logging devices has precluded research of the fine-scale patterns of foraging behaviour of smaller seabird species (<400 g), and the foraging behaviour of terns remains one of the most poorly resolved aspects of their biology. Previous research is limited to radio-telemetry studies, diet analyses or vessel-based surveys (Becker et al. 1993, Surman & Wooler 2003, Rock et al. 2007). These studies suggest that terns are generally restricted in their foraging range while breeding. The recent development of GPS loggers <25 g in size allows the foraging behaviour of smaller species such as terns to be better described and modelled in relation to habitat variables that can be incorporated in models as covariates.

During the breeding season adult crested terns *Sterna bergii* lay a single egg that they incubate for approximately 28 d (Langham & Hulsman 1986). After hatching, chicks are provisioned by both parents for approximately 5 wk at the breeding colony. Crested terns are long lived and in South Australia have a well-defined breeding season (McLeay et al. 2009b). Previous research identified that crested terns may be sensitive to large scale decreases in prey (McLeay et al. 2009b). Chicks reared in years when sardine *Sardinops sagax* abundance was low exhibited smaller adult morphology and recruited at lower rates (McLeay et al. 2009b). A move towards an ecosystem-based management system for marine resources requires information about the distribution and abundance of apex predators that is spatially explicit. Sardine form the target of Australia's largest volume purse-seine fishery, the South Australian Sardine Fishery, and are a major component

of the diet of crested terns (Ward et al. 2001, Dimmlich et al. 2004, McLeay et al. 2009a). Data on the foraging ecology of crested terns may help to identify areas near colonies where resource competition from fishing is most likely to occur.

In this study we reported on the use of the latest satellite tracking technology on a seabird weighing <400g, the crested tern. We used newly developed GPS tracking technology to investigate the foraging behaviour of crested terns while provisioning young chicks in South Australia. We examined the foraging behaviour of crested terns in relation to the physical and biological habitats most used by individuals while undertaking foraging trips during the breeding season. We predicted that the foraging behaviour of crested terns would correlate with the physical and/or biological conditions characteristic of near-colony waters, and that individuals will display differences in foraging behaviour within a general mode of behaviour to minimise competition for resources.

MATERIALS AND METHODS

Study site. The study was undertaken at Troubridge Island, southern Gulf St Vincent, South Australia (35° 4' S, 137° 49' E) in the austral summers of 2006 and 2007 (November/December) (Fig. 1). Troubridge Island is a conservation park of ~260 ha composed of sand. The surrounding waters of Gulf St Vincent are relatively protected and shallow (5 to 40 m depth), and characterised by benthic habitats composed of bare sand, seagrass and rocky reefs (Tanner 2005). The crested tern colony at Troubridge Island is the largest in South Australia with 3000 to 3500 breeding pairs (L. J. McLeay unpubl. data).

Animal capture and logger deployment. Crested terns that were attending chicks <5 d old were captured at their nests at sunrise (~05:30 h) each day with handheld nets. Crested terns do not forage at night and consequently adults present on their nest at this time were likely to undertake a foraging trip in the following 12 h (L. J. McLeay unpubl. data). To prevent chicks from leaving their nests while GPS units were being attached to their parents, we constructed a 20 cm high fence made of 5 mm wire mesh around each chick. A 15 cm band of shade-cloth was attached to the bottom of each fence to prevent injury to chicks and the fence incorporated enough vegetation to afford chicks shade and cover from predators. GPS units were attached with Loctite 401 glue (Intek Adhesives) to the feathers on the backs of 21 adults, and each individual was marked with the dye, Nyanzol D, and colour-banded to aid individual recognition. Attachment of GPS units required <5 min from capture

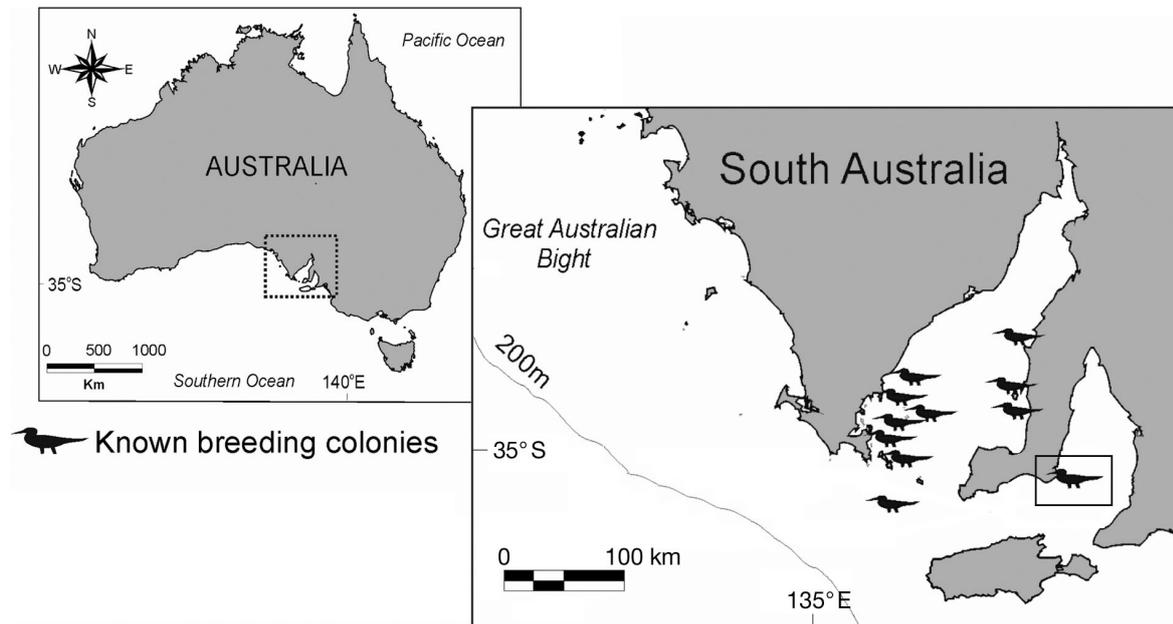


Fig. 1. Study area in South Australia, shown in map enlargement on right, with 200 m depth contour and known crested tern breeding colonies. Box indicates Troubridge Island study site

to release. Nests were monitored every 15 min at a distance of 30 to 40 m with binoculars (Leica, 10×42 magnification) until the adult returned, at which point it was recaptured and had the unit removed by cutting it away from the feathers with scissors. The attachment of GPS units to seabirds may potentially affect normal brooding and/or foraging behaviour. Only adults weighing >350 g (mean \pm SD, 365 ± 15.1 g) were used in this study to minimise the GPS unit mass to body mass ratio. Nonetheless, GPS loggers represented between 5.2 and 6% of adult body mass for the individuals used in the study, which is at the upper limit of what is generally recommended for tracking wild birds (Caccamise & Hedin 1985, Cochran 1980). For this reason we attempted to minimise deployment times by catching individuals once they had returned from their first trip of the day. Adults showed no signs of handicap or distress following capture/recapture (i.e. they did not exhibit intensive preening behaviour) and returned to their chicks within 5 min of being released (Wilson et al. 1990). To further assess any effect of GPS unit attachment on behaviour we recorded the nest departure and arrival times (assumed foraging trip duration) of individuals with and without GPS units attached (Davoren & Montevecchi 2003).

Data collection. GPS units: We used micro-GPS units (μ GPS, Sirtrack) with an integrated antenna and housed within a urethane waterproof case. The overall weight of the unit when packaged was 21 g, outer dimensions: $\sim 37 \times 22 \times 19$ mm). Units were pro-

grammed on a continuous loop duty cycle to record positions at 1 min intervals to ensure data were recorded for 12 to 24 h. The accuracy of GPS is typically <5 m (Ryan et al. 2004).

Habitat variables: SST ($^{\circ}\text{C}$) and fluorescence data (chl a , mg m^{-3}) were obtained from the Ocean Biology Processing Group (OBPG) at NASA Goddard Space Flight Center (GSFC) (www.oceancolor.gsfc.nasa.gov). We used data collected daily by the moderate resolution imaging spectroradiometer (MODIS) at 500×500 m resolution (MODIS-Aqua sensors, Level 0). Data were processed to Level 3 by applying the OC3M/MSI12 v. 5.2.3 empirical algorithm with SeaDAS software (Baith et al. 2001, Franz 2006). This algorithm identifies and minimises the atmospheric effects on remotely sensed data with information collected on the different MODIS-Aqua spectral bands. Since cloud cover on many days during field work prevented daily measurement of SST and chl a , we used the weekly average of data (centred on the day of sampling). There was no significant difference between SST and chl a data collected in concurrent 7 d periods during the study period, so where 7 d averages were not available for a particular week, we used MODIS-derived data from the previous week.

Data relating to the type of benthic habitat surrounding Troubridge Island were obtained from Tanner (2005) who had assessed the benthic community structure by means of remote video surveys every 2 nautical miles along east–west transects in Gulf St Vincent.

Habitat types were assigned based on the predominant type of taxa recorded at each site. This resulted in the classification of 8 benthic habitat types: ascidian, ascidian/bryozoan, bryozoan, *Pinna* (a bivalve mollusk), sand, scallops, seagrass/*Pinna* and seagrass. Bathymetric data were obtained from GeoScience Australia 1 × 1 km grid. The bathymetric depth values for each location were interpolated as functions of their distance from the nearest nodes and assigned to each 5 s of time travelled along a foraging path.

Trip and wind direction: To assess the direction of the foraging areas most visited by adult terns, in 2007/08 we recorded the number and bearing of adults returning from a foraging trip. Observations were made in a 360° search pattern with binoculars (Leica, 10 × 42 magnification) for 10 min periods between 09:00 and 11:00 h from a vantage point of ~4 m above the colony. The numbers of birds that were carrying fish in their bills returning from distances >500 m was recorded within 45° sectors. Data relating to the prevailing wind direction during the study were provided by the Australian Bureau of Meteorology (recorded at Edithburgh, 35° 06' S, 137° 44' E, ~10 km from Troubridge Island).

Data analysis. GPS data were downloaded and filtered with the package 'timeTrack' (now named package 'Trip') (v. 1.1–5, M. Sumner, University of Tasmania, Hobart) within R statistical software (v. 2.3.0, R Development Core Team, R Foundation for Statistical Computing) according to the methods of McConnell et al. (1992) and based on a maximum horizontal flight speed of 60 km h⁻¹. GPS did not always record a position every minute as they were programmed to do and actual locations may have provided a biased sample of the temporal and spatial distribution of foraging activity. To determine the proportion of time spent in area (TSA) by each individual we assumed a constant horizontal flight speed between filtered locations and interpolated a new position for every 5 s of time travelled along the individual's track by using the R statistical software and timeTrack package. This ensured we did not bias our sampling to places where we received the most GPS locations. In a predetermined grid the number of interpolated positions within a cell of 250 × 250 m (62 500 m²) were summed and assigned to a central node. To ensure the duration of individual trips did not bias analyses, TSA data were converted to a proportion of the total time spent in each cell for each individual. Several other variables, described as follows, were calculated from the GPS data to summarise the foraging behaviour of each individual. (1) Trip duration, defined as the time an individual left the colony to the time it returned. (2) The total distance travelled (km), calculated as the sum of the dis-

tance (km) between all interpolated GPS positions along each individual's track. (3) Maximum distance from the colony, calculated from the nest to the distal point reached on each foraging trip. (4) Elongation coefficient, which is the 'straightness' of the track and is measured as the ratio of the maximum straight line distance from the colony relative to the actual path (Guinet et al. 1997). Elongation ratios may have a maximum of 0.5, which indicates little change in overall flight direction over the course of the track, whereas lower ratios indicate more turning. (5) Median bearing, which is the median compass bearing from the nest to each interpolated position (calculated with Oriana, v. 2.02, Kovach Computing Services). (6) Mean flight speed (km h⁻¹), determined as the distance between consecutive interpolated GPS locations divided by the duration (5 s). (7) Concentrated foraging behaviour, defined as the proportion of time spent in flight at speeds ≤10 km h⁻¹. Low transit speeds are commonly used to identify foraging behaviour for marine predators (Nel et al. 2001, Gremillet et al. 2004, Awkerman et al. 2005, Weimerskirch et al. 2005, Simmons et al. 2007). To determine this value we examined a frequency distribution of the speeds of individuals between each interpolated position. A distinct peak in the frequencies was noted at speeds ≤10 km h⁻¹. Unlike many seabirds, crested terns do not spend more than a few seconds sitting on the sea surface and seldom roost on floating debris during foraging trips. Consequently, speeds ≤10 km h⁻¹ are likely to indicate birds that have located prey or are in the process of acquiring prey.

Two approaches were used to describe the physical and biological habitats used by adult crested terns while foraging. Firstly, we extracted data relating to depth, benthic habitat type, SST and chl *a* from each 250 × 250 m cell visited by individuals in 2007. Mapinfo v. 8 (Mapinfo) was used to link physical and biological data to TSA data. We then used generalised linear mixed models (GLMMs) in R to fit a series of models including physical (depth, SST), biological (benthic habitat type, chl *a*) and distance from shore to the TSA data. To account for variation in the foraging behaviour of individuals we included 'individual' as the random effect. The proportion of TSA by each individual in each 250 × 250 m cell visited was used as the response variable and we applied Akaike's information criteria (AIC) to select the best models from a set of candidate models developed *a priori*. Gaussian, gamma and binomial response models were considered with appropriate identity, inverse, logit and complementary log–log link functions. AIC is useful as a comparative measure for models that are developed with different link and distributional assumptions (Bradshaw et al. 2004). Smaller AIC model values are

preferred. Spatial autocorrelation of foraging behaviour may result from individuals passing through near-colony areas. Moreover, MODIS data collected in near shore (<2 km) shallow waters (<5 m depth) was considered unreliable due to potential error caused by bottom reflection, so GPS locations and their associated environmental data were removed for locations <2 km from the colony (Awkerman et al. 2005). Absence of strong co-linearity between predictor variables is also an important assumption of generalised linear modelling procedures, so we investigated correlation between all variables by using principal components analysis in SPSS (v. 15). Bathymetry was highly correlated with distance from colony and chl *a* (bathymetry eigenvalue, 0.089). Consequently, we separated these factors in all GLMMs fitted to foraging (TSA) data. In the second approach, to compare general habitat use as a function of habitat availability, we overlaid circles centred on Troubridge Island, with each circle's radius centred on the maximum distance travelled by individual birds from Troubridge Island. We then calculated the

TSA for all individuals over each habitat (depth, benthic habitat type, SST, chl *a*) and compared it with the proportion of each habitat available within the circle (modified from Awkerman et al. 2005).

Four individuals returned successive tracks. Of these, the first track from 3 individuals was typically shorter, and may have reflected short-term behavioural adjustments to the logger. Consequently, our analyses used the second track from individuals that conducted multiple trips. This also avoided the potential analytical problems associated with temporal autocorrelation of foraging behaviour. Short trips (<5 km) conducted by 2 other individuals (Tracks 14 and 18, Table 1) may have also reflected short-term adjustments to the logger and were omitted from all habitat analyses.

To test for differences in nest attendance patterns we performed a *t*-test in SPSS v. 15. SPSS was also used to check all data for assumptions of normality and homoscedasticity using Komolgorov-Smirnov/Shapiro-Wilk's tests and Levene's test. The values of foraging parameters are presented as average \pm SD.

Table 1. *Sterna bergii*. Summary data for individual tracks collected from adult crested terns via GPS in 2006 (n = 2) and 2007 (n = 23). Data provided for Track 16 are calculated up to when the GPS unit failed on an incomplete trip. Dates given as day/month/year. CFE: concentrated foraging effort

Track no.	Date	No. GPS locations	Trip duration (h:min)	Total distance travelled (km)	Maximum distance from colony (km)	Mean flight speed (km h ⁻¹)	Median bearing	Elongation coefficient	CFE (proportion of time \leq 10 km h ⁻¹)	Foraging group
1	30/11/2006	101	1:41	41.7	13.3	25.2	338°	0.32	0.07	5
2	17/12/2006	257	4:17	99.4	38.9	23.5	266°	0.39	0.32	2
3	22/11/2007	110	1:51	41.3	9.5	22.8	350°	0.23	0.10	5
4	21/11/2007	16	0:16	9.5	4.7	35.2	61°	0.50	0.01	3
4.1	21/11/2007	177	3:08	40.4	11.5	12.6	338°	0.28	0.61	5
5	22/11/2007	81	1:22	38.6	17.6	28.9	130°	0.45	0.02	5
6	22/11/2007	6	0:07	4.5	2.3	42.0	126°	0.50	0.00	4
6.1	22/11/2007	63	1:05	24.5	8.3	23.1	8°	0.34	0.17	5
7	26/11/2007	75	1:17	28.0	8.2	22.0	347°	0.29	0.16	5
8	26/11/2007	34	1:05	31.8	15.5	29.8	173°	0.49	0.00	5
9	27/11/2007	257	4:16	118.0	28.7	28.1	186°	0.24	0.09	1
10	28/11/2007	101	2:03	41.8	17.4	20.2	196°	0.42	0.29	5
11	5/12/2007	132	2:19	64.3	17.4	28.2	56°	0.27	0.12	5
11.1	5/12/2007	69	1:24	40.9	16.6	29.7	171°	0.40	0.25	5
12	5/12/2007	41	0:41	23.0	11.1	33.8	158°	0.48	0.05	5
12.1	5/12/2007	65	1:08	36.4	16.3	32.7	171°	0.45	0.14	5
13	6/12/2007	107	1:50	59.4	27.9	32.9	120°	0.47	0.04	5
14	6/12/2007	8	0:10	6.7	3.3	39.4	5°	0.50	0.00	4
15	11/12/2007	39	0:40	25.4	11.2	38.2	135°	0.44	0.00	5
16	11/12/2007	84	1:27	43.4	34.4	30.5	120°	Trip incomplete		5
17	11/12/2007	48	0:48	29.5	14.2	37.2	154°	0.48	0.04	5
18	12/12/2007	14	0:14	8.3	4.1	35.4	229°	0.50	0.01	3
19	12/12/2007	42	0:42	18.5	6.8	26.5	347°	0.36	0.05	5
20	13/12/2007	27	0:28	17.4	8.0	37.5	213°	0.46	0.00	5
21	13/12/2007	247	4:15	97.3	35.2	23.2	138°	0.36	0.33	2

RESULTS

The GPS data collected from 25 foraging trips made by 21 adult crested terns is summarized in Table 1. In total, 2201 unfiltered GPS locations were recorded. The pilot study undertaken in 2006 returned 2 foraging tracks. In 2007, 23 tracks were recorded from 19 individuals (4 individuals returned 2 tracks). Individuals foraged in neritic waters <40 km from the colony. Adults travelled between 2.3 and 38.9 km (average, 15.3 ± 10.3 km) from the colony and the total distance travelled by individuals ranged between 4.5 and 118 km (average, 39.6 ± 29.0 km) (Table 1, Fig. 2). The average flight speed of individuals ranged between 12.6 and 42.0 km h⁻¹ and foraging trip duration ranged from 6 min to 4 h 17 min (average, 1h 33 min \pm 1h 17 min), and was positively correlated with the maximum distance from the colony ($r^2 = 0.730$, $df = 23$, $p < 0.001$) and the total distance travelled ($r^2 = 0.896$, $df = 23$, $p < 0.001$) (Table 1). The duration of foraging trips for GPS-equipped individuals was lower compared with individuals without GPS units attached (2 h 38 min \pm 1h 48 min versus 3 h 20 min \pm 1 h 33 min) but the difference was not significant ($t = 1.514$, $df = 52$, $p = 0.14$).

Foraging paths and areas of concentrated foraging

Individuals moved away from the colony on a specific bearing before reaching their distal point, where flight

speed decreased to ≤ 10 km h⁻¹ as a product of concentrated foraging behaviour (Figs. 2 & 3). Once concentrated foraging behaviour was initiated, individuals increased their turning rate and often circled back to locations previously visited (e.g. Track 4.1, enlargement of inset, Fig. 3). The outward and inward parts for most foraging trips were generally straight and parallel as indicated by the relatively large (68%) proportion of trips with high (>0.35) elongation coefficients (Table 1, Fig. 2). One individual conducted a more 'looping' flight path, returning to the colony from a different bearing to its outward phase (Track 9, Fig. 3).

Most individuals (>80%) spent <20% of their time at speeds ≤ 10 km h⁻¹ (Table 1). Four individuals conducted short trips <10 km in length and spent <1% of their time conducting concentrated foraging (Tracks 4, 6, 14 and 18, Table 1). These tracks were also characterised by maximum attainable values in the coefficient of elongation (0.5), indicating little change in overall flight direction over the course of their track and may have been indicative of short-term behavioural adjustments to the logger (Table 1).

For all individuals, the proportion of time spent at speeds ≤ 10 km h⁻¹ was significantly and positively correlated with trip duration ($r^2 = 0.225$, $p = 0.019$) and total distance travelled from the colony ($r^2 = 0.188$, $p = 0.030$). Of the 4 individuals that recorded 2 foraging trips, one returned to the same foraging area (Tracks 12 and 12.1, Table 1). The other 3 individuals moved away from the colony at a different bearing from their pre-

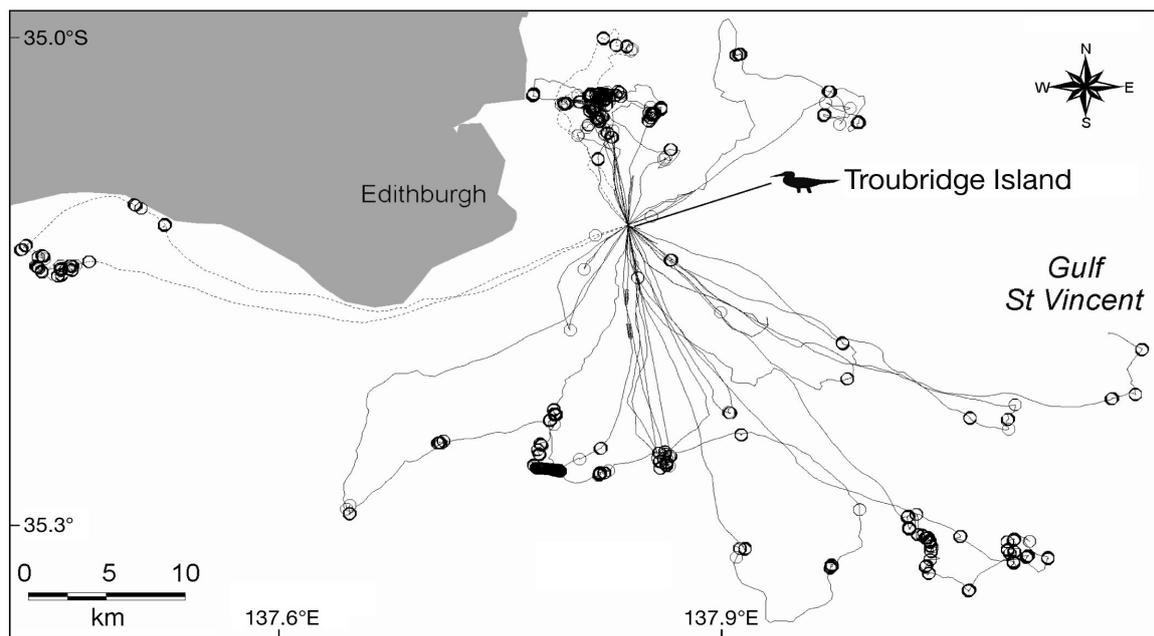


Fig. 2. *Sterna bergii*. Foraging trips of individual crested terns (no. individuals = 21, no. tracks = 25) recorded via GPS. Circles: areas of concentrated foraging. Lines: tracks recorded in 2006 (dashed; $n = 2$) and 2007 (solid; $n = 23$)

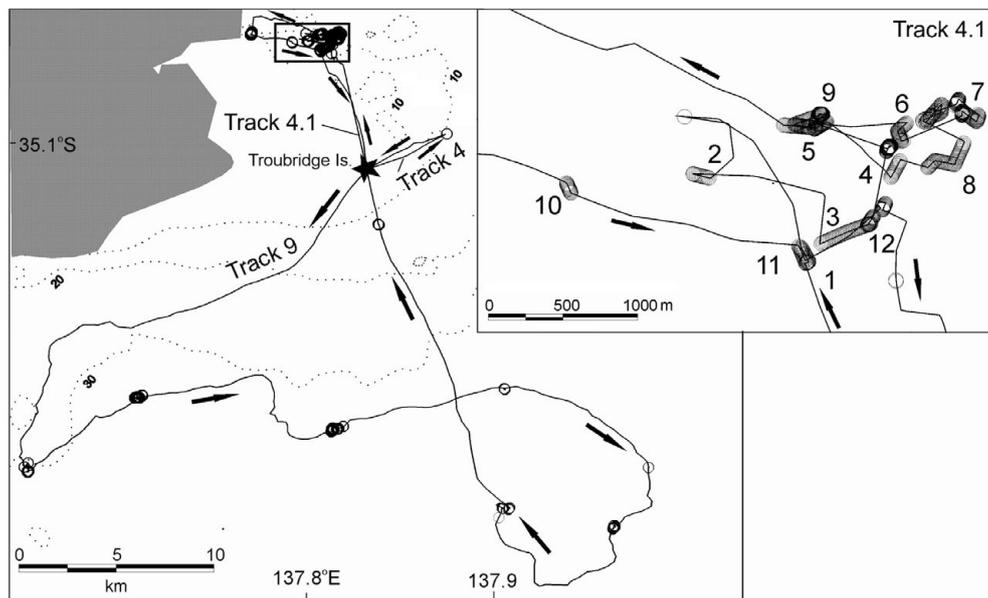


Fig. 3. *Sterna bergii*. Short and long commuting trips (Tracks 4 and 4.1, respectively) and looping trip (Track 9) of adult crested terns from Troubridge Island. Inset: close up of Track 4.1 with numbers 1 to 12 ordering the direction of travel. Circles: areas where flight speed was $<10 \text{ km h}^{-1}$, i.e. concentrated foraging. Arrows: direction of travel. Star: Troubridge Island. Dotted lines: depth contours (10 m increments): All tracks were derived from micro-GPS data, which were recorded at 1 min intervals, with positions interpolated every 5 s with timeTrack.

ceding trip and travelled up to 5.4 times the distance (Tracks 4 and 4.1, 6 and 6.1, and 12 and 12.1, Table 1).

Trip direction versus wind direction

Remote binocular observations of individuals returning to Troubridge Island indicated that over 90% of adult crested terns returned from bearings between 45° and 270° (NE to W) (median 135°). Similarly, 72% of adult crested terns fitted with GPS devices returned from foraging trips at bearings between 45° and 270° (NE to W) (median 130°). During the study period in 2007 the wind direction was mainly from the SSE (median 157°) indicating that individuals generally foraged into the prevailing wind and returned downwind from foraging grounds.

Physical and biological habitats

Depth

Approximately 60% of the waters used by crested terns within a 38.9 km radius of Troubridge Island (maximum foraging distance, Table 1) are 30 to 40 m deep (Fig. 4). Adult crested terns foraged predominantly ($>60\%$ TSA) over waters <20 m in depth, which was significantly shallower than waters available

within their entire foraging range ($\chi^2 = 544.0$, $df = 3$, $p < 0.001$) (Fig. 4).

Benthic habitat

Approximately 72% of foraging occurred over sand habitat which comprised the majority of available benthic habitat in waters NE to SW (bearing 45° to 270°) of Troubridge Island (Fig. 5). Individuals also spent $\sim 20\%$ of their time foraging over ascidian, bryozoan, scallop and seagrass habitats located in waters within 20 km, and SW to NE (bearing 270° to 360°) of the colony, but no time foraging over *Pinna* or seagrass/*Pinna* habitats (Fig. 4). Although foraging was typically random over benthic habitats, individuals spent more time foraging over ascidian and ascidian/bryozoan benthos, and less time foraging over *Pinna* and *Pinna*/seagrass than expected ($\chi^2 = 100.1$, $df = 7$, $p < 0.001$) (Fig. 4).

Sea surface temperature (SST)

The typical pattern of SST around Troubridge Island during the brooding period in 2007 is depicted in Fig. 5A. SST ranged between 17.1 and 20.4°C but temperatures were generally 1 to 2°C warmer in inshore coastal waters compared with waters of central Gulf St Vincent (Fig. 5A). Adults showed a preference for for-

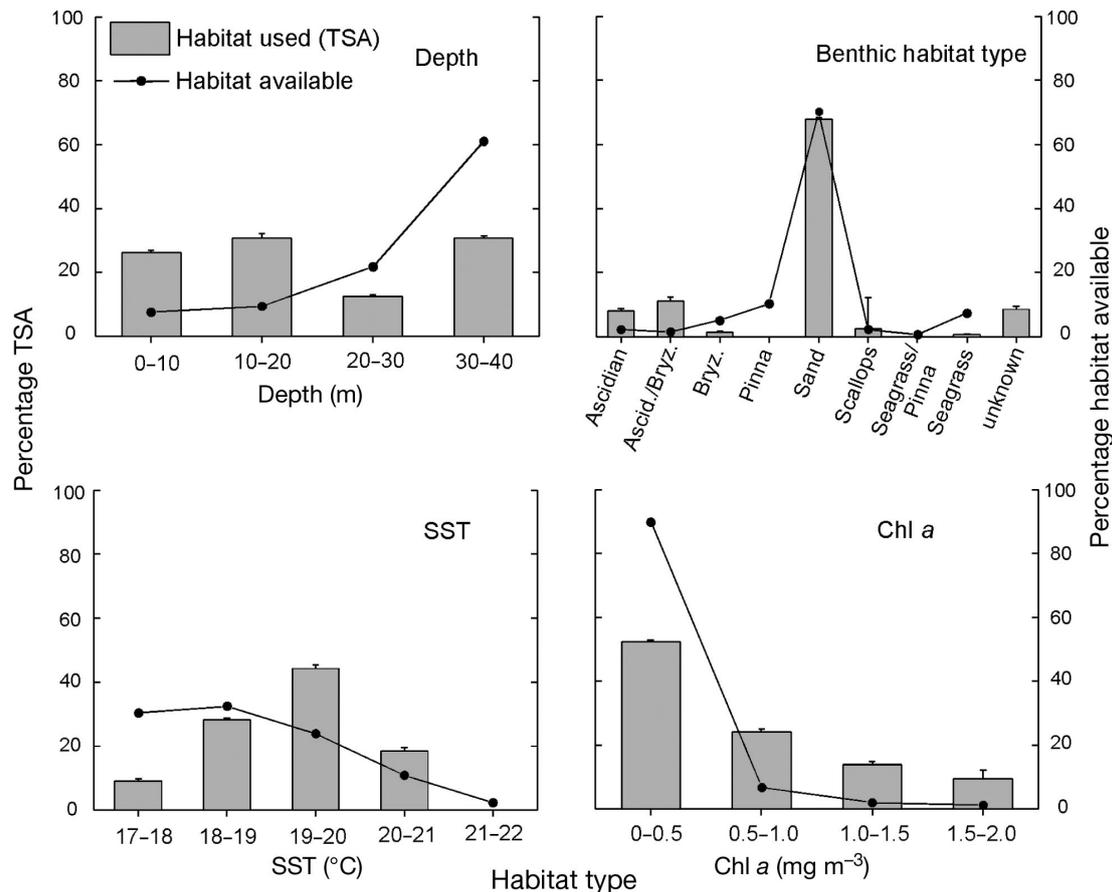


Fig. 4. *Sterna bergii*. Percentage of time spent in area (TSA) at different physical and biological habitat types for individuals tracked using micro-GPS in 2006 and 2007 (error bars are SD of percentage TSA)

aging over waters ranging between 19 and 21°C. These areas were significantly warmer than the areas available within their entire foraging range ($\chi^2 = 36.0$, $df = 3$, $p < 0.001$) (Fig. 4).

Chl a

Data derived from MODIS satellite imagery for the brooding period in 2007 indicated that chl a within the foraging range of adult crested terns ranged between 0.18 and 1.94 mg m^{-3} (average $0.60 \pm 0.47 \text{ mg m}^{-3}$), but was typically low ($< 0.5 \text{ mg m}^{-3}$). Primary production was higher (chl a $> 0.5 \text{ mg m}^{-3}$) in shallow inshore coastal waters and coincident with the thermal front located in waters between the SW and NE (bearing of 270° to 45°) of Troubridge Island (Fig. 5A,B). Adults spent a high proportion of time (55%) foraging over waters with chl a levels $> 0.5 \text{ mg m}^{-3}$. These areas had significantly higher primary production compared with other habitats available within their entire foraging range ($\chi^2 = 293.7$, $df = 3$, $p < 0.001$) (Fig. 4).

Generalised linear model selection

Residual plots and AIC values indicated that the most suitable GLMM incorporated a Gaussian error structure and identity link function to model the proportion of TSA as a function of the habitat variables (Table 2). A complementary log–log transformation was used to capture the strong right skew of TSA. The best (top 7) models from the full candidate set of models, and 'full' and null models are presented in Table 2. The most well supported model included distance from colony and chl a. This model explained 6.1% of the deviance from the null model [i.e., $100 \times (1801.14 - 1691.06)/1801.14$] (Table 2), and there was strong support for the effects of distance from shore and chl a on TSA (chl a, $G^2 = 7.6$, $df = 1$, $p = 0.006$; distance from shore, $G^2 = 76.6$, $df = 1$, $p < 0.001$). In addition, models that included distance from shore outperformed models that included bathymetry independently. These results indicate that the TSA increased mainly as a function of distance from the colony and in response to increased levels of primary production (chl a). There

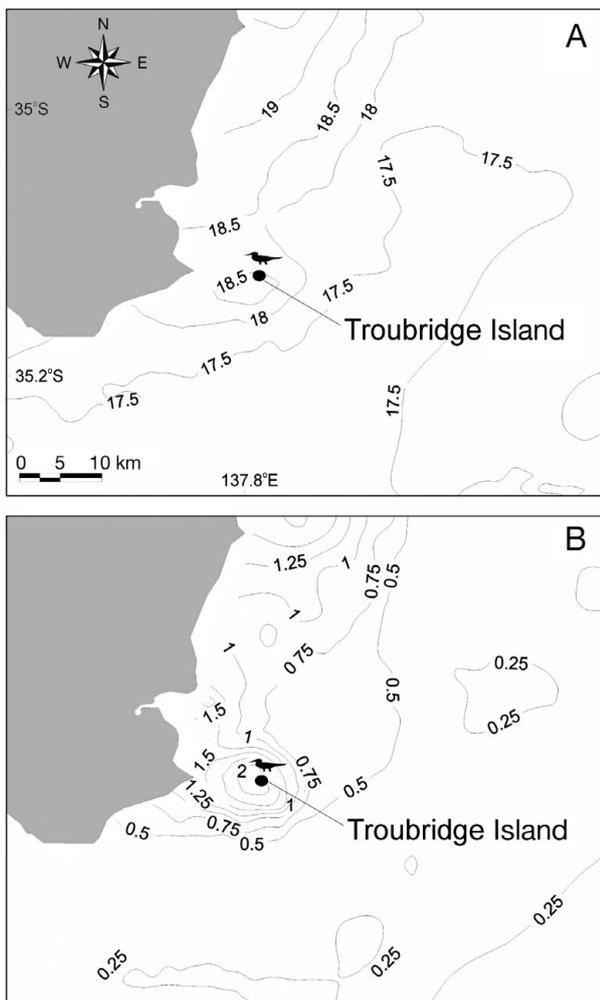


Fig. 5. Typical (A) sea surface temperature (SST) ($^{\circ}\text{C}$) and (B) chl *a* concentration (mg m^{-3}) around Troubridge Island in 2007 (from MODIS satellite data, 7 d average for period 19 to 25 November 2007)

was little support for the effects of SST or benthic habitat type on TSA. When these variables were removed from the full model, AIC values improved by ~ 7.5 and 19.7 points, respectively (Table 2).

DISCUSSION

How organisms use their surrounding habitats while breeding is key to understanding the factors that constrain their reproduction and population growth. This study is one of the first to use GPS to record the fine-scale temporal and spatial foraging patterns and habitat use for a seabird < 400 g in size. The advent of lightweight GPS tracking technology has revolutionised the ability to record the fine-scale foraging behaviour and habitat use of small seabirds. Our results support those obtained via vessel surveys and radio-tracking studies for other tern species while breeding, and showed crested terns conducted short foraging trips close (< 38.9 km) to the colony (Becker et al. 1993, Surman & Wooler 2003, Rock et al. 2007). The fasting ability of offspring is the main factor determining how far parents can travel while foraging. The chicks of many tern species are often provisioned several times a day with small, single prey items (Hamer et al. 2002). This behaviour may reflect the limited gut capacity of tern chicks and contrasts with the provisioning strategies of other seabird species that forage over longer distances and deliver macerated prey.

The mass of GPS loggers (21 g) represented between 5.2 and 6 % of the body mass of individuals used in our study and are at the upper limit of what is generally recommended for birds (3 to 5 % of body mass) (Cochran 1980, Caccamise & Hedin 1985). Although we did not observe any definitive deleterious effects of the GPS loggers on adult behaviour, such effects can

Table 2. *Sterna bergii*. Results of the top 7 GLMMs showing the effect of marine habitat variables on time spent in area (TSA) for crested terns foraging from Troubridge Island. Analyses were undertaken for time spent by crested terns within 250×250 m grid cells (no. cells visited = 2495). 'Individual' was included in all models as a random effect. The environmental variables, chl *a* and SST, were included as fixed effects. Benthic habitat type (benth) was included as a categorical fixed effect. dist: distance from shore; k: number of parameters; Dev: deviance; LL: log-likelihood; ΔAIC : change in AIC between the best and candidate model. The null (intercept only) and full (all factors of interest) models are also listed

Model	k	Dev	LL	AIC	ΔAIC
TSA~dist + chl <i>a</i>	4	1691.06	-855.16	1720.33	0
TSA~dist	3	1702.58	-858.92	1725.83	5.51
TSA~dist + chl <i>a</i> + dist \times chl <i>a</i>	5	1688.44	-857.18	1726.37	6.04
TSA~dist + chl <i>a</i> + SST	5	1691.02	-857.98	1727.97	7.64
TSA~dist + SST	4	1702.21	-861.58	1733.16	12.84
TSA~benth + dist + chl <i>a</i>	9	1689.03	-861.08	1740.15	19.83
TSA~benth + dist	8	1701.04	-865.07	1746.14	25.82
TSA~benth + dist + chl <i>a</i> + SST (full)	10	1688.91	-863.84	1747.67	27.34
TSA~1 (null)	1	1801.14	-902.38	1810.76	90.44

not be discounted and our tracking data should be interpreted with some caution. The duration of foraging trips was shorter for individuals equipped with GPS loggers compared with that of non-equipped birds and it is possible that the behaviour of some individuals may have initially been altered due to logger attachment. Short-term behavioural adjustments may have been apparent in the short trips undertaken when individuals were initially released. For this reason we omitted short trips (<5 km) from habitat analyses. Nonetheless, ~85% of the GPS tracks recorded indicated no signs of altered foraging behaviour and our study is the first to provide high resolution patterns of movement of a tern species in relation to the biophysical characteristics of near-colony waters.

Foraging behaviour and distance

The finding that foraging trip duration was positively related to the total and maximum distance travelled from the colony is common in studies of marine central-place foragers (Harcourt et al. 2002, Page et al. 2006). Individual differences in foraging trip length (distances or duration) may result from variations in prey availability and/or prior knowledge of where prey aggregations exist. Although we did not measure prey abundance, adults typically exhibited a 'commuting' type of foraging strategy while provisioning young chicks (Weimerskirch 2007). This strategy was reflected in the concentrated foraging behaviour displayed by individuals at distances >5 km from the colony, and by the significant effect of distance from colony identified in the GLMM. Commuting strategies are common among seabirds while breeding and may result from behaviour that bypasses a zone of prey depletion that exists around large seabird colonies ('Ashmole's halo') to access denser and more energetically profitable prey aggregations at greater distances (Ashmole 1963, Birt et al. 1987, Weimerskirch et al. 2005, Gaston et al. 2007, Elliott et al. 2009).

Differences in trip length between individuals may have also been caused by alternate behavioural states of foraging such as provisioning and self feeding. Not all individuals exhibited extended bouts of concentrated foraging behaviour (<10 km h⁻¹) at the most distal parts of their track. Some undertook short trips within 10 km of the colony and returned immediately. Central-place foraging models predict that parents should increase the amount of energy delivered to chicks in line with the amount of time they spend foraging away from the colony (Orians & Pearson 1979). However, the foraging decisions of single prey loaders must also be balanced by what their chicks can physically ingest. The chicks of adults tracked in this study

were all <5 d old and consequently limited to ingesting prey <100 mm in size (McLeay et al. 2009a). If small prey were encountered close to the colony, adults may maximise the net rate of energy acquired and delivered by returning the prey immediately to offspring before undertaking a longer trip for self feeding. Consequently, the short trips exhibited by several adult crested terns in this study may reflect 'size-selective' foraging behaviour mediated by the dietary requirements of offspring during early provisioning.

Variations in trip length may also reflect intra-specific differences in niche use between males and females, differences between individuals in foraging experience or behavioural tactics that minimise competition through the targeting of different habitats. Adults typically foraged over sand habitats at greater distances from the colony, but a few individuals foraged over ascidian and ascidian/bryozoan habitats in inshore waters (<20 km) between the SW and NE of the colony. Our GLMM did not identify benthic habitat type as a significant factor influencing TSA, possibly due to the low resolution of habitat data used, but the differences in trip length and foraging areas visited by adults may be indicative of the types of prey targeted. The small pelagic fish assemblage in offshore waters NE to SW of the colony is characterised by the presence of surface-schooling clupeid fishes such as sardine and anchovy *Engraulis australis* (Rogers et al. 2008). These species are commonly found in the diet of chick and adult crested terns from Troubridge Island and may have been targeted by adults foraging in these areas (McLeay et al. 2009a). Conversely, the large quantities of Degens leatherjacket *Thamnoconus degeni*, garfish *Hyporhamphus melanochir* and blue sprat *Spratelloides robustus*, which are also commonly found in crested tern diets, may reflect foraging behaviour over shallower inshore habitats between the SW and NE of the colony (Gomon et al. 1994, McLeay et al. 2009a).

Foraging behaviour and habitat

Crested terns at Troubridge Island may use tailwinds to return from their foraging grounds. This finding agrees with the hypothesis of Pennycuik (1989) that seabirds should forage upwind and return downwind to facilitate more efficient flight while carrying heavy prey loads. Habitat analyses indicated that adult crested terns typically foraged over warm (19 to 21°C), shallow (<20 m depth) waters that were high in chl *a* (>0.5 mg m⁻³). These biophysical characteristics are likely to reflect the distribution and abundance of their prey. Crested tern chicks may be particularly dependent on small clupeiform fishes (McLeay et al. 2009a).

These fish form a key link in pelagic marine food webs and their distribution and abundance has been correlated with temperature and enhanced levels of primary production (chl *a*) in ecosystems worldwide (Martín et al. 2008, Tsagarakis et al. 2008). By accessing fish aggregations in shallow reliable habitats where production is enhanced, adult crested terns minimise foraging trip durations and maximise foraging success and rates of provisioning while breeding.

The results of our GLMM support our more general habitat analysis and the hypothesis that the foraging behaviour of crested terns is correlated with the biological conditions of waters near the colony. Of the habitat variables included in our candidate model set, chl *a* best explained the increases in time spent foraging within an area (TSA). Central-place foragers commonly use areas where patches of prey are aggregated by physical factors (Guinet et al. 1997, Awkerman et al. 2005, Simmons et al. 2007) and/or elevated levels of primary productivity (e.g. chl *a*) (Hyrenbach et al. 2002, Weimerskirch et al. 2004, Page et al. 2006, Suryan et al. 2006). Previous analyses of chlorophyll data collected from Sea-viewing Wide Field-of-view Sensors (SeaWiFS) in southern Gulf St Vincent indicated that levels of primary production (chl *a*) increase 2-fold over the austral summer (~0.4 mg m⁻³ for October versus ~0.8 mg m⁻³ for February, Petruševics 2008). It is possible that the timing of breeding of crested terns at Troubridge Island is strongly linked to the elevated levels of production in the region during this period.

There is a limited understanding of how physical and biotic processes influence the distribution and abundance of plankton in Gulf St Vincent. Our GLMM did not take into account the possible dilution ('downstream') effects of SST or chl *a* that affect secondary production and the subsequent distribution of prey (Guinet et al. 2001, Bradshaw et al. 2004). Also, the influences of site fidelity on foraging behaviour may dilute the fluid effects of physical or biotic processes that aggregate prey in regions near foraging grounds. While our GLMM could not take these processes into account, predator foraging behaviour eventually depletes prey patches, and predators must relocate foraging effort to areas that are more energetically profitable (Bradshaw et al. 2004). It is likely that the results of our GLMM captured this broad-scale pattern of habitat use.

Management

Crested terns forage from waters <40 km from the colony while provisioning young chicks. The breeding success of crested terns during this study was high (~0.91, L. J. Mcleay unpubl. data); however, the ability

of terns to alter their foraging and provisioning behaviour to maintain high levels of breeding success under poorer food conditions is unknown. Southern Spencer Gulf lies to the west of Troubridge Island and is home to one of the largest aggregations of crested tern breeding colonies in the world (Fig. 1) (L. J. McLeay unpubl.). This region is also targeted by the South Australian Sardine Fishery (SASF), which uses purse-seining methods to catch sardine for use as feed in the southern bluefin tuna *Thunnus maccoyi* mariculture industry near Port Lincoln (see Fig. 2 in McLeay et al. 2009b). In recent years the sardine fishery has expanded in terms of catch, effort and investment, but the trophic effects of fishing on sardine predators are unknown.

The restricted foraging range exhibited by crested terns while breeding may make them sensitive to localised depletion of sardine caused by commercial fishing operations near their colonies. Future data relating to the foraging behaviour, diet, and breeding success at different colonies within this area should be collected concurrently from crested tern populations located inside and outside areas targeted by fishing operations. These data may provide information on the extent of foraging overlap between colonies and may resolve the relationships between foraging behaviour, habitat and density-dependent factors that govern colony size. If this information is combined with spatial analyses of sardine catches it may also indicate whether fishing near breeding colonies is negatively affecting the breeding success and growth of crested tern populations.

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