



## Foraging behaviour and habitat use by Indian Yellow-nosed Albatrosses (*Thalassarche carteri* breeding at Prince Edward Island)

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### ABSTRACT

Demographic parameters of wild animals are often closely associated with their foraging distribution and behaviour, and understanding these attributes can assist in identifying causes of population changes. The Indian Yellow-nosed Albatross (*Thalassarche carteri*) is endangered but little information is available on its at-sea distribution and behaviour. It breeds only in French (Iles Amsterdam, St Paul, Kerguelen and Crozet) and South African (Prince Edward Island, PEI) territories in the south-west Indian Ocean, with PEI supporting about 20% of the global population. This study aimed to investigate the at-sea distributions of adult Indian Yellow-nosed Albatrosses provisioning chicks at PEI and to compare them with distributions of Yellow-nosed Albatrosses breeding at other localities. Using satellite transmitters, we identified two areas that were particularly favoured for foraging. Parents whose partners were brooding small chicks frequently moved north-east of PEI to shallow, productive waters where cold, nutrient-rich water upwells and results in enhanced levels of chlorophyll-a. By contrast, parents with older chicks that could be left unattended often foraged along the Agulhas Bank where eddies and shear forces promote vertical mixing. The at-sea distribution of birds breeding at PEI was located between those reported for Indian Yellow-nosed Albatrosses breeding at Ile Amsterdam and Atlantic Yellow-nosed Albatrosses (*T. chlororhynchos*) breeding at Gough Island, so that birds from these localities may face different threats at sea. Our study is the first to highlight key feeding areas for Indian Yellow-nosed Albatrosses from PEI and to demonstrate partitioning of foraging grounds by Yellow-nosed Albatrosses from different localities.

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## Introduction

The numbers of many seabird species have declined over the past few decades (Croxall *et al.* 2012). For some of these, the population decreases have been associated with conditions at foraging grounds (e.g. Frederiksen *et al.* 2006; Crawford *et al.* 2017), emphasising the importance of understanding the foraging distributions of seabirds, drivers thereof and threats prevailing while foraging. The use of foraging habitat by wild animals is determined by the distribution of food resources, mediated by the physiological capabilities of the animals, their memory and learned behaviours, intra- and inter-specific interactions, and requirements for activities other than foraging, such as reproduction or migration (Kappes *et al.* 2015).

Studies of seabird distributions based on tracking technology indicate that seabird foraging patterns largely reflect the distribution, predictability and movement of prey items (e.g. Wanless *et al.* 1998; Wakefield *et al.* 2009). The distribution of food resources in the open ocean is influenced by both physical and biological processes (Zavalaga *et al.* 2010). Ocean structures such as fronts (Shaffer *et al.* 2006), eddies (Weimerskirch *et al.* 2004; Hyrenbach *et al.* 2006), upwelling areas (Peery *et al.* 2009; García-Reyes *et al.* 2014; Bakun *et al.* 2015) and tidal zones (Irons 1998) often have enhanced productivity, attracting predators such as seabirds and marine mammals (Pakhomov *et al.* 1996; Zavalaga *et al.* 2010). Partitioning of feeding grounds between colonies of the same or closely related species has been reported previously and likely serves

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to decrease intra- and inter-specific competition (e.g. Weimerskirch *et al.* 2009; Masello *et al.* 2010; Kappes *et al.* 2015).

Albatrosses and petrels display conservative life histories, with low reproductive rates, slow chick development, delayed onset of breeding and high adult survival (Warham 1996; Phillips *et al.* 2016). These life history adaptations result largely from the limited rate at which adults can provide food to their chicks, given their large foraging ranges (Lack 1968; Regular *et al.* 2013). Prey resources may be sparse, patchy and unpredictable in their distribution (Ashmole 1971), although some habitats such as sectors of shelf edges appear more predictable than others, e.g. oceanic waters (Weimerskirch 2004). Successful and efficient foraging by seabirds depends on the spatial and temporal distribution of their prey and the search strategies used to find them (Regular *et al.* 2013). This has particular relevance during the breeding season when adults are spatially constrained, as they must commute between the colony and their feeding grounds (Ashmole 1971; Weimerskirch *et al.* 2008). However, many oceanic species travel hundreds or thousands of kilometres from their colonies to remote locations, which are preferred due to their high productivity or on account of niche specialisation (Wakefield *et al.* 2009).

This study aimed to determine the at-sea distribution of adult Indian Yellow-nosed Albatrosses (IYNAs; *Thalassarche carteri*) provisioning chicks at Prince Edward Island (PEI) during the brood-guard and post-guard stages, in relation to oceanographic features. Indian Yellow-nosed Albatrosses only breed at islands in the south-west Indian Ocean: PEI (South Africa), the western Crozets and Ile Amsterdam (France), with a few pairs at Kerguelen (France). Prince Edward Island (46 km<sup>2</sup>) is the smaller of the two main islands of the Prince Edward Islands (PEIs, 46°50' S, 37°50' E); Marion Island (290 km<sup>2</sup>) is the larger island but IYNAs do not breed there (Ryan *et al.* 2003).

We compared the distribution of IYNAs breeding at PEI to those of IYNAs from Ile Amsterdam (Agreement on the Conservation of Albatrosses and Petrels 2009) and that of the sibling species, the Atlantic Yellow-nosed Albatross (*T. chlororhynchos*), breeding at Gough Island (FitzPatrick Institute unpub. data). Atlantic Yellow-nosed Albatrosses only breed at the Tristan da Cunha Archipelago and Gough Island (UK territories) in the central South Atlantic Ocean. Both species are listed as globally endangered (IUCN 2017). The total population of IYNAs is about 42 000 pairs, of which *ca.*7500 (~20%) breed at PEI; the overall population of Atlantic Yellow-nosed Albatrosses is 27 000–41 000 pairs (BirdLife International 2017). The Endangered status of the IYNA

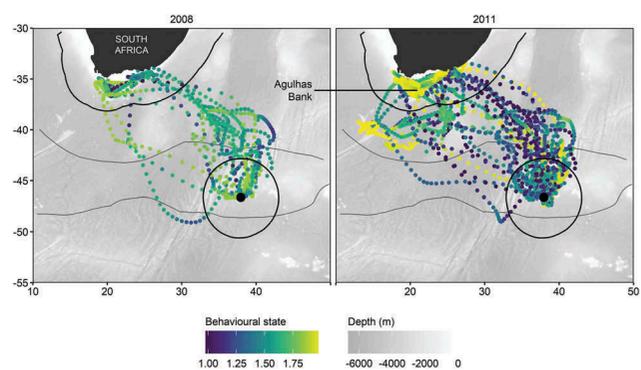
is based largely on the decreasing population trend observed at Amsterdam Island, attributed to accidental fishing mortality and introduced diseases (Weimerskirch 2004; BirdLife International 2017). Disease is not thought to be an issue at PEI, which is among the least disturbed of sub-Antarctic islands, and the population at PEI is thought to be stable (Ryan *et al.* 2009). We predicted that IYNAs breeding at PEI would feed closer to the island during the brood-guard period than later in the season. When chicks are small, frequent meal delivery is required and only one adult can forage at a time. If there was competition during breeding between different colonies of IYNAs for food, there might be segregation of their foraging grounds, although distances from colonies could also influence such separation.

## Methods

### Study site

The PEIs lie *ca.*1800 km south-east of South Africa (Figure 1) in the dynamic oceanic environment between the Subantarctic Front (SAF) and the Antarctic Polar Front (APF) (Lutjeharms and Ansorge 2008). They are home to globally important colonies of marine top predators and fall within the PEI Marine Protected Area (MPA), which was proclaimed in South Africa's territorial waters around the islands, *inter alia* to sustain the foraging requirements of seabirds and marine mammals that breed at the islands (Lombard *et al.* 2007).

Indian Yellow-nosed Albatrosses nest in colonies on the northern cliffs of PEI (Ryan *et al.* 2003). Eggs are



**Figure 1.** Location estimates for the 16 breeding Indian Yellow-nosed Albatrosses tracked from Prince Edward Island (black circle) during 2008–2009 (left panel) and 2011 (right panel). Locations are coloured by the behavioural state (*b*) estimated from a state-space model: higher values correspond with restricted behaviour (likely to include foraging) while lower values correspond with transit behaviour. Black lines show the South African Exclusive Economic Zone. Grey lines show approximate positions of the Subtropical Front and the Subantarctic Front (north to south) from Orsi *et al.* (1995).

laid in September and October and are incubated for *ca.*78 days before hatching in November or December (Agreement on the Conservation of Albatrosses and Petrels 2009). Chicks fledge in March or April after spending approximately 115 days at the nest (Agreement on the Conservation of Albatrosses and Petrels 2009).

### Location data

Sixteen adult IYNAs were equipped with platform transmitter terminals (PTTs; 30 g Pico-100, Microwave Telemetry, Columbia, MD; 35 g SPOT4, Wildlife Computers, Redmond, WA) to track their at-sea distribution. Eight PTTs were deployed on 18 December 2008 on birds that were brooding small chicks and eight were deployed on 10 March 2011 on birds attending large chicks. Tesa® tape and Loctite® glue were used to attach the PTTs to back feathers in 2008, whereas in 2011 they were attached beneath the two central tail rectrices using cable ties and Loctite glue. All transmitter packages (including attachment materials) weighed less than 2% of adult IYNA body mass (*ca.*2.2–2.5 kg).

The number and duration of research visits to PEI are strictly limited (PEIMPWG 1996) so PTTs could not be recovered and were left on birds until they fell or were moulted off. The locations of birds were downloaded via the Argos satellite system (Collecte Localisation Satellites, Toulouse, France). The quality of Argos location data depends on how many Argos satellites are in view at the time of transmission. The data are classified as 3, 2, 1, 0, A or B, using the least-squares Argos algorithm. Positions for classes 3, 2 and 1 are accurate to within 100 m, 250 m and 500–1500 m, respectively. Those in classes 0, A and B are less reliable and have no error estimate (Argos 1996). The quality of location data in this study was controlled using two steps. First, positions on land were eliminated. Second, a sequential filter that considers location data classes, distance between successive locations and a maximum sustained flying speed (*v*Max) of 27.7 m/s (100 km/h) was applied to identify possible unrealistic positions (*argosfilter* R package; Freitas *et al.* 2008; Freitas 2012). These were filtered in an iterative process, removing points that required a velocity > *v*Max, unless it had location class of 1, 2 or 3 as these are known to be accurate to within 1.5 km. The velocities of the four points closest to a removed point were then recalculated and the process repeated until no low-quality point had a velocity above *v*Max (BirdLife International 2004). All analyses were conducted in the R environment (R Core Team 2016).

### Environmental data

To characterise the at-sea environment encountered by IYNAs, we collated 11 environmental variables (Table S1) for each location estimate using the *raster* (Hijmans 2015), *raadtools* (Sumner 2016) and *xtractomatic* (Mendelssohn 2016) packages. Environmental values at a given location were extracted from the grid cell in which that location was situated. The variables were selected based on their frequent use in other studies as proxies or indicators of factors that influence the distribution of prey of marine top predators, or the predators themselves (e.g. Bost *et al.* 2009; Hazen *et al.* 2013; Pistorius *et al.* 2017; Reisinger *et al.* in press).

Values for dynamic variables were obtained daily, with the exception of chlorophyll-*a* (chl-*a*) concentration and primary production (both monthly) and matched to each location's date. For mapping, averages over the entire grid were generated for two periods: December 2008–January 2009 and March–May 2011.

### Analyses

Argos tracking data were analysed using a state-space model, specifically a first-difference correlated random walk with behaviour switching (DCRWS), implemented in the *bsam 1.0.0* package (Jonsen *et al.* 2005). The Argos system estimates positions at irregular intervals, with location errors. The DCRWS model accounts for this – estimating likely positions at regular intervals – while simultaneously estimating a behavioural state (*b*) based on the speed, turning angle and move persistence (auto-correlation) in the track. Values of *b* range from 1.0 to 2.0: straighter, persistent movements with higher speeds have lower *b* values and are considered putative 'transit' behaviour, whereas greater turning angles, less persistent movements and lower speeds have higher *b* values and are considered putative 'restricted' or foraging behaviour (see Jonsen *et al.* 2005, 2007, 2013). The assumption is that the latter characteristics are associated with 'area-restricted search' behaviour, which is predicted to occur when animals encounter prey or favourable foraging conditions in a patchy environment (Kareiva and Odell 1987; Benhamou and Bovet 1989). It is worth emphasising that the behavioural state is estimated as a parameter of a movement model, with some uncertainty, and the nominal behavioural states are inferred from *b*. Further, foraging locations may not accurately be inferred if foraging or search behaviour is characterised by other movement strategies (e.g. Connors *et al.* 2015). We fitted DCRWS models by generating 20 000 samples (retaining every 10th sample) after a burn-in of 40 000 samples. Positions were estimated at 3 h intervals. Trips were identified by inspecting plots of

distance from colony vs. time. The maximum distance of an IYNA from its colony and the minimum (cumulative) distance it travelled while tracked were calculated using great-circle distances (Phillips *et al.* 2005a, 2005b).

To understand the relationship between behaviour and environmental variables, we used random forest regression models (Breiman 2001), modelling the continuous behavioural state estimates ( $b$ ) at a location as a response to the set of environmental variables at that location. These are an ensemble statistical learning method where many (100s–1000s) decision trees – each based on a bootstrap sample of the data and a small, random subset of the available predictors – vote (Hastie *et al.* 2009). We implemented these in the *randomForest* package (Liaw and Wiener 2002), growing 1000 trees using two predictors for each tree. The random forest was visualised using a feature contributions method implemented in the *forestFloor* package (Welling *et al.* 2016). To avoid collinearity among variables, when a pair of variables had an absolute Spearman's  $r > 0.7$ , we removed the variable with the higher average correlation to other variables (Dormann *et al.* 2013), resulting in a final set of eight environmental predictors. The mean decrease in the Gini index produced by each of these eight variables was used to assess their importance in predicting the behavioural state of the 16 tracked IYNAs. Variables with a higher mean decrease in Gini index are more important. Main effects were then plotted to examine which parameter values predicted restricted and transit behaviours of IYNAs. A 'goodness-of-visualisation' measure ( $R^2$ ) was calculated to measure how well the contribution of each variable to the model was visualised in two dimensions (see Welling *et al.* 2016 for details).

### Comparing the ranges of Yellow-nosed Albatrosses

In order to compare the at-sea distribution of IYNAs breeding at PEI with those of IYNAs breeding at Ile Amsterdam (BirdLife International 2004) and Atlantic Yellow-nosed Albatrosses at Gough Island (FitzPatrick Institute unpub. data) a non-parametric kernel density estimator was used to identify areas of 50%, 70% and 90% probability of occurrence (Wood *et al.* 2000). The kernel density analysis was carried out by pooling all the data for each population in a single dataset, then applying the 'kernelUD' function in R package *adehabitat* for each dataset (Calenge 2006).

### Results

Locations were obtained from PTTs fitted to IYNAs at PEI for periods lasting from 8 to 55 days (mean 28 days; Table S2). Instruments deployed during brooding transmitted for shorter periods (8–32 days,

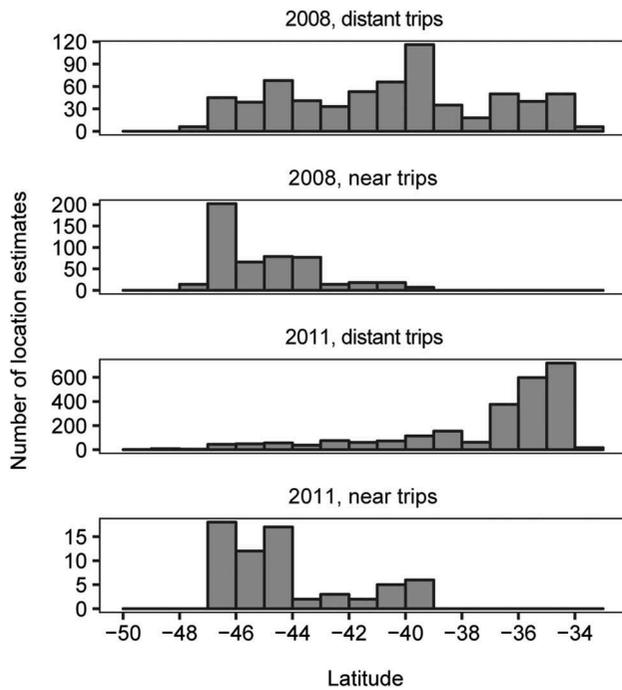
mean 19 days) than those deployed during the post-guard stage (30–55 days, mean 39 days), perhaps because a better attachment technique was used in the post-guard period. Positions were obtained between 18 December 2008 and 19 January 2009 and between 10 March and 4 May 2011, the bulk of the transmissions being received in December and April. For eight of the sixteen birds tracked, the maximum distance from the colony was  $>2000$  km, for five it was between 1000 and 2000 km and for three it was  $<1000$  km (Table S2).

In total, 4980 at-sea locations were estimated. Of all locations, 50% ( $n = 2478$ ) were within South Africa's 200 nm Exclusive Economic Zone (EEZ) around the African continent, and this area contained 85% of putative foraging locations. By comparison, only 20% ( $n = 1009$ ) of locations were from the EEZ around the PEIs, 38% (384) of which were within the PEIs MPA. Restricted behaviour (foraging) locations seldom occurred in the PEIs EEZ (7%, of which 41% were within the MPA) or on the high seas (8%; Figure 1).

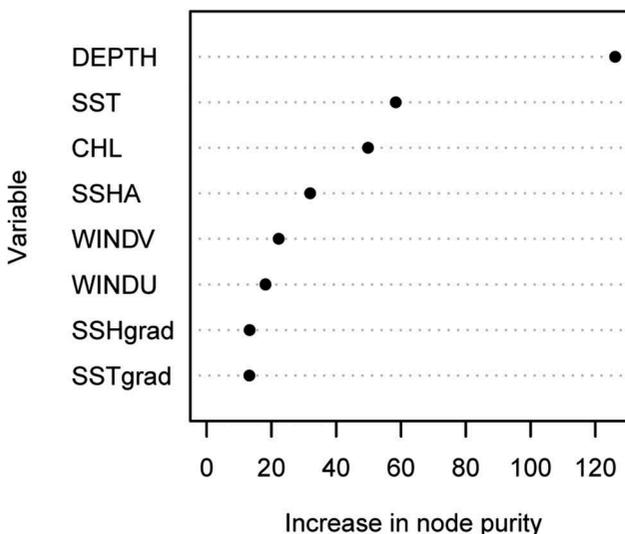
After leaving PEI, birds almost invariably headed northwards (supplementary Figure S1). Their foraging trips could be grouped into two types: long trips ( $n = 14$ ) that reached the warm Agulhas Current, which runs south of Africa (Figure S2), and shorter ( $n = 20$ ) trips that typically were centred between the SAF and the Subtropical Front (STF). Both long and short trips were evident during early and late chick provisioning (Figures S2, S3), but during early provisioning most foraging occurred south of  $39^\circ$  S, whereas during the late-chick stage trips were often north of this latitude (Figure 2). Favoured foraging grounds were in waters of relatively shallow depth north of PEI and along the outer edge of the Agulhas Bank immediately north of the Agulhas Current (Figure 1).

The random forest model performed well, explaining 89.9% of the variance with a root mean square error of 0.1. The main predictor variable was ocean depth (DEPTH), followed by sea surface temperature (SST), chlorophyll-a concentration (CHL-a) and sea surface height anomaly (SSHA) (Figure 3). Meridional and zonal wind strength and gradients in SST and SSH were of lesser importance.

The forest-floor main effect plots showed a clear increase in prediction of restricted (foraging) behaviour as water became shallower; transit behaviour was mostly predicted at depths  $>2000$  m (Figure S4). With regard to SST, temperatures of  $ca. 5$ – $8^\circ$ C and  $ca. 17$ – $23^\circ$ C predicted restricted behaviour and other values transit behaviour. Foraging was more likely to occur at chlorophyll-a concentrations  $>ca. 0.3$   $mg/m^3$  and in areas with negative SSHA (Figure S4). These four



**Figure 2.** Latitudinal distributions of estimated locations of breeding Indian Yellow-nosed Albatrosses tracked from Prince Edward Island in early (2008–2009) and late (2011) chick-rearing periods. Tracks are distinguished as distant (>1000 km from colony) or near (<1000 km from colony) trips.



**Figure 3.** Importance, measured as the mean decrease in node impurity (Gini index), of the four most influential variables used in a random forest model to predict the behavioural state of 17 Indian Yellow-nosed Albatross tracks. Variables with a higher mean decrease in node impurity are more important. DEPTH: ocean depth (m); SST: sea surface temperature ( $^{\circ}\text{C}$ ); CHL-a: chlorophyll-a concentration ( $\text{mg C/m}^3$ ); SSHA: sea surface height anomaly (m).

variables all had goodness-of-visualisation  $R^2$  values  $\geq 0.77$  (Figure S4). Main effects plots were poorer for the other four variables considered and they also

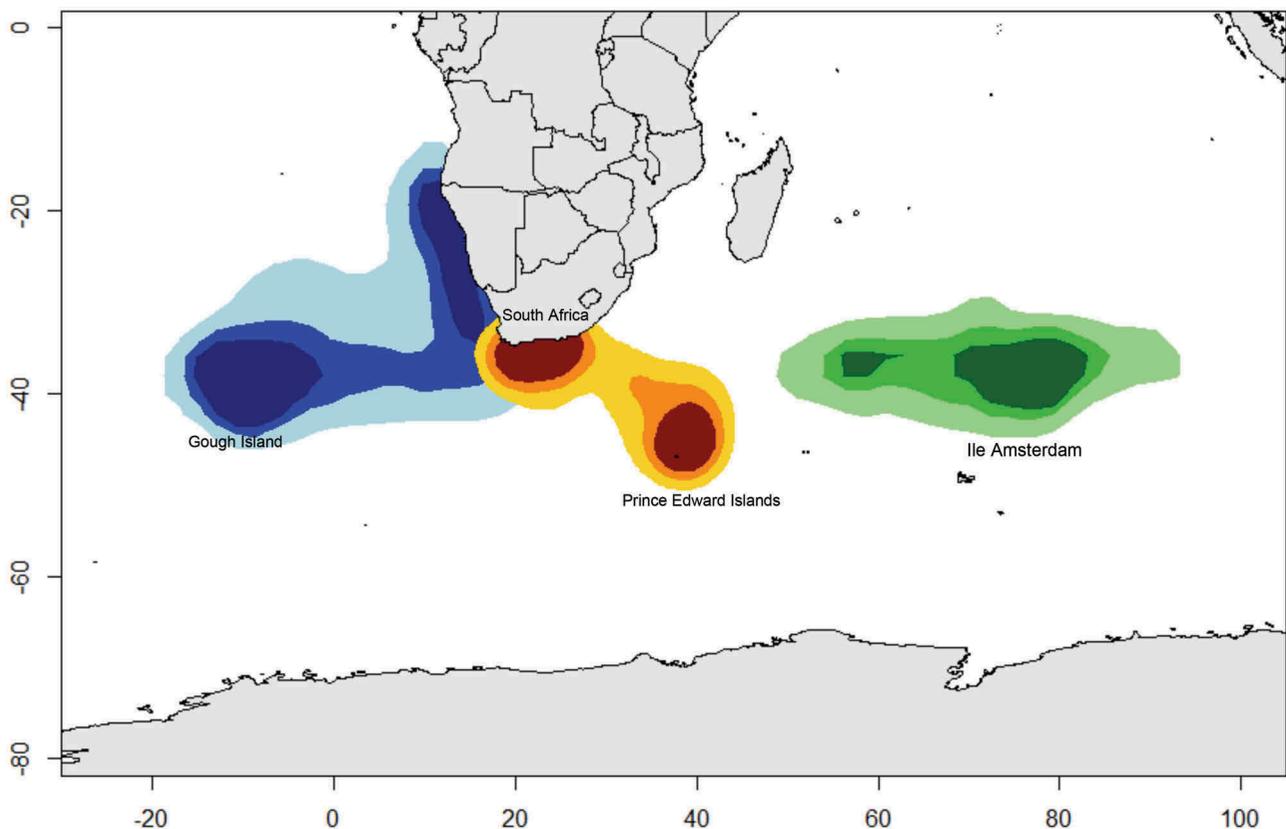
contributed to a lower mean decrease in the Gini index (Figure 3).

Breeding IYNAs tracked from PEI had little overlap with the distributions of breeding IYNAs from Ile Amsterdam and of breeding Atlantic Yellow-nosed Albatrosses from Gough Island (Figure 4). The core latitudinal range of IYNAs from Ile Amsterdam ( $32\text{--}40^{\circ}\text{S}$ ) was similar to the northern foraging latitudes of IYNAs from PEI ( $33\text{--}36^{\circ}\text{S}$ ), but Amsterdam birds generally foraged farther east than those from PEI (Figure 4). Atlantic Yellow-nosed Albatross had a broad latitudinal range ( $25\text{--}45^{\circ}\text{S}$ ) and also foraged along the African continental margin, but usually farther west than IYNAs from PEI (Figure 4).

## Discussion

Although tracking was limited, especially for birds during the early chick-provisioning period, it is likely that the utilisation of ocean habitat by IYNAs breeding at PEI depends on their breeding state. During the early chick-rearing period, when one adult remained with the chick, parents spent more time near to PEI than when chicks were older and could be left unattended (Figure 2). However, the tracks obtained for adults at different stages of breeding were also from different seasons, and environmental variability between seasons cannot be ruled out. Moreover, chicks fledge in late March or April (Agreement on the Conservation of Albatrosses and Petrels 2009), so a portion of the tracking in 2011 represents post-fledging dispersal of adults. Nonetheless, even when chicks were small, parents engaged in long trips (Figures 1 and S3). Long trips may involve self-provisioning; several seabirds alternate between short, frequent foraging trips to maximise food delivery to their young, and infrequent, long trips that serve towards self-maintenance (e.g. Weimerskirch *et al.* 1994; Ropert-Coudert *et al.* 2004a). During the long trips, seabirds may travel farther to areas of known high productivity (e.g. Magalhães *et al.* 2008) or spend more time foraging in the same area that is used during short trips (Ropert-Coudert *et al.* 2004b; Clarke *et al.* 2006).

Areas of restricted movement of IYNAs north-east of PEI were associated with shallow water (<200 m) and low SSTs ( $<8^{\circ}\text{C}$ ; Figures 1, S2 and S4) and were also exploited by lactating female Subantarctic Fur Seals (*Arctocephalus tropicalis*) (de Bruyn *et al.* 2009; Kirkman *et al.* 2016). In these areas sub-surface flow against topographical rises causes upwelling and enhanced productivity (Ansorge *et al.* 2014). In addition, substantial mixing of warmer SAF and colder APF water takes place downstream (east) of the PEIs



**Figure 4.** Kernel density distributions of breeding Yellow-nosed Albatrosses tracked from Gough Island (blue), Prince Edward Island (orange) and Ile Amsterdam (green) showing the substantial partitioning of their foraging grounds. Colour gradients represent, from lighter to darker, probabilities of occurrence of 50%, 70% and 90%. The location of Prince Edward Island is shown by the black dot in the southern portion of the dark orange shading.

(Perissinotto and McQuaid 1992; Ansorge *et al.* 1999). Together with runoff of nutrients and perhaps Aeolian deposits (including iron) from the PEIs (Perissinotto *et al.* 2000), these processes create an area conducive to high marine productivity (Perissinotto and McQuaid 1992). Farther north, IYNAs forage along the edge of the Agulhas Bank at the northern border of the Agulhas Current (Figures 4 and S2). Here, the current may entrain phytoplankton (Lamont and Barlow 2015) as well as zooplankton such as fish eggs and larvae (Hutchings *et al.* 2002), thereby attracting planktivores and enhancing food availability for the albatrosses, which feed on fish, squid and crustaceans (Agreement on the Conservation of Albatrosses and Petrels 2009). Indian Yellow-nosed Albatrosses also scavenge from fisheries in this area, where they are one of the most common albatrosses attending bottom trawlers (Watkins *et al.* 2008). Sea surface temperatures in this region (17–22°C) are cooler than those of the Agulhas Current, across which the albatrosses must move to reach the Agulhas Bank.

South African coastal waters and the zone south of the Agulhas Return Current and north of PEI (~40–46° S)

have reasonably high chlorophyll-*a* concentrations compared to the more barren intermediate area across which IYNAs typically transit (Figure S2; Machu *et al.* 2005). South of the Agulhas Return Current there are large eddies, both cyclonic and anticyclonic, whose positions remain relatively stable at the time scale of months, discernable from SSHAs (Figure S2). Negative SSHAs indicate cyclonic eddies that bring cold nutrient-rich water into the euphotic zone and stimulate primary production, whereas positive SSHAs cause downwelling and are consequently not productive (Ansorge and Lutjeharms 2003). The warm anticyclonic eddies are often shed from the Agulhas Current as it moves into the Atlantic Ocean (Pichevin *et al.* 1999), whereas cold cyclonic eddies are generated in the lee of the Agulhas Bank (Penven *et al.* 2001). Areas of restricted movements of IYNAs breeding at PEI were associated with negative SSHAs, whereas positive SSHAs predicted transit behaviour (Figure S4). In general, mesoscale eddies are often considered important to marine top predators because they tend to aggregate prey. For example, foraging by Grey-headed Albatrosses tracked from Marion Island has been linked to eddies (Nel *et al.* 2001). Indian Yellow-nosed Albatrosses from Ile Amsterdam feed at eddies

south of the Agulhas Return Current (Froneman and Pakhomov 2000) and other seabirds also may be associated with eddies in the South Indian Ocean (Hyrenbach *et al.* 2006).

There is substantial partitioning of the feeding grounds of Yellow-nosed Albatrosses breeding at Gough Island, PEI and Ile Amsterdam (Figure 4). Fine-scale GPS tracking of Atlantic Yellow-nosed Albatrosses breeding at Gough Island shows that almost all their foraging occurs along the edge of the African continental shelf (FitzPatrick Institute unpub. data). Their use of the cool Benguela upwelling system off south-west Africa allows them to feed farther north than IYNAs from PEI and Ile Amsterdam. The at-sea distributions of IYNAs breeding at the Crozet Archipelago are unknown, but given the proximity to PEI (~1000 km to the east), they may forage in areas similar to those used by the PEI birds. However, from information currently available, it appears that Atlantic Yellow-nosed Albatrosses and IYNAs from different colonies partition their foraging areas to a considerable extent during breeding. This draws attention to the fact that, if some grounds are more heavily fished than others, at-sea threats to Yellow-nosed Albatrosses may differ between colonies. The IYNA is potentially vulnerable to tuna long-lining in the subtropical Indian Ocean when it forages in subtropical oceanic waters around Ile Amsterdam, where it breeds (Pinaud and Weimerskirch 2005), and in Australasian waters, where it winters (Weimerskirch *et al.* 1986). Recent decreases in long-line by-catch rates by tuna fisheries off South Africa, which were thought to result from the presence of observers on vessels and the imposition of meaningful monetary penalties for catching large numbers of seabirds (Petersen *et al.* 2009; Rollinson *et al.* 2017), suggest that fishing mortality of IYNAs from PEI might be decreasing in this region.

The only trend data for the PEI population of IYNAs suggest that their numbers are stable (Ryan *et al.* 2003, 2009). This contrasts with a rapid decrease in the population at Ile Amsterdam (Agreement on the Conservation of Albatrosses and Petrels 2009), much of which is thought to have resulted from avian cholera (Weimerskirch 2004; Agreement on the Conservation of Albatrosses and Petrels 2009). Hence, factors influencing trends in Yellow-nosed Albatrosses differ on land as well as at sea.

In summary, our results show that IYNAs breeding at PEI forage in productive marine habitats that are used by other predators or exploited by fisheries. However, they differ from the feeding grounds used by Yellow-nosed Albatrosses breeding at Ile Amsterdam and Gough Island. Moreover, when chicks at PEI are large enough to

be unattended, their parents may travel farther to feed than when they are small. Therefore, at-sea conservation of the Yellow-nosed Albatrosses, both species of which are endangered (BirdLife International 2017), will need to cover a wide range of Southern Ocean habitats.

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