

Factors influencing the habitat use of sympatric albatrosses from Macquarie Island, Australia

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ABSTRACT: Differences in habitat use of sympatric species are influenced by variability in functional morphology and life history trade-offs and are expected to shape species resilience to environmental change. To determine differences in year-round habitat use and gain insight into how morphological and life history traits influence foraging of an albatross community from subantarctic Macquarie Island, Australia (54.6° S, 158.9° E), we quantified the physical features associated with high residence time for 10 black-browed *Thalassarche melanophris*; 10 grey-headed *T. chrysostoma*; 15 light-mantled *Phoebastria palpebrata*; and 12 wandering albatrosses *Diomedea exulans* tracked in 1994–2009. Overlap among the 4 species was greatest close to the island during the breeding season, extending north into the Tasman Sea. Nevertheless, black-browed albatrosses ranged more locally than the other species, perhaps because they have a shorter breeding cycle and morphological traits that result in less efficient flight and greater capacity to outcompete other species for prey. Nonbreeding albatrosses showed high variability in habitat use across wide ocean expanses, but all used productive frontal regions and mesoscale eddies. Increased residence times during the breeding and nonbreeding periods were associated with moderate wind speeds for all species (excluding breeding black-browed albatrosses), indicating that birds used areas where aerodynamic performance was enhanced. Given patterns in residence time at sea, and the functional and life history adaptations of each species, we suggest that black-browed albatrosses breeding on Macquarie Island will be more vulnerable to expected future climate-driven changes to wind patterns in the Southern Ocean, and potential latitudinal shifts in the Subantarctic Front.

KEY WORDS: Environmental models · Foraging ecology · Habitat overlap · Macquarie Island · Residence time · Seabirds · Southern Ocean · Tracking

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1. INTRODUCTION

The functional morphology and life history traits of a species represent evolutionary trade-offs that determine the ability of individuals to exploit their

environment to maximise energy acquisition and minimise energy expenditure. As oceanographic shifts drive changes in environmental structure across the distribution of an animal, its behavioural plasticity, influenced by functional morphology and life history

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traits, determines the extent to which it can adapt and successfully reproduce (Lescroël et al. 2010, Carneiro et al. 2015). Understanding the capacity of individuals and populations to respond to changes in the environment is critical, given the scale of recent and unprecedented ecosystem shifts driven by global climate change (Descamps et al. 2016, Abadi et al. 2017).

Variability in habitat use within a community of species reflects the diversity in functional morphology and life history adaptations (Costa 1991, Zhang et al. 2007). The ability to use alternative habitats or exploit altered environmental conditions determines the vulnerability of each species to climate change and anthropogenic threats, providing essential information for evidence-based conservation planning (Waldron et al. 2006, McGowan et al. 2017). Community-level assessments of habitat use can also reveal areas of high ecological significance where the distributions of multiple species overlap. These may indicate regions of greater biodiversity and thus could be targeted as candidate areas for protection (Raymond et al. 2015, Tancell et al. 2016, Thiers et al. 2017). Ultimately, determining the characteristics among key foraging areas of a community of species allows better quantification of links between environment, functional morphology, life history and population dynamics.

In the Southern Ocean, productivity is unevenly distributed in space and time; rather, it is concentrated in areas where available nutrients and light permit phytoplankton growth (Sullivan et al. 1993, Pakhomov & McQuaid 1996, Moore & Abbott 2000). For marine predators, macro- (100–1000s of km) and meso-scale (10s of km) oceanographic features, such as frontal regions and eddy structures, are associated with aggregated prey resources (Bost et al. 2009, Dragon et al. 2010, Scales et al. 2014). Nutrient retention and enrichment of surface waters through upwelling and mixing at frontal and mesoscale cyclonic eddy features can support greater phytoplankton concentration relative to surrounding waters (Mitchell et al. 1991, Sokolov & Rintoul 2007). As climate change continues to influence the oceanographic characteristics and productivity of the Southern Ocean (Sarmiento et al. 2004, Turner et al. 2014), understanding the constraints on distribution set by the morphological and life history traits of predators may help us to forecast climate-mediated futures for their populations (Constable et al. 2014).

Morphologically, albatrosses are adapted to fly efficiently over long distances. Their long narrow wings (high aspect ratio, i.e. the square of the wings-

pan divided by the wing area) promote maximum flight efficiency by ensuring great aerodynamic lift and less induced drag (Pennycuick 2008). Furthermore, the high body mass, long wingspan and large wing area of albatrosses allow them to achieve high glide ratios, enabling maximum forward speed with minimum sink speed. With a high body mass and associated high wing loading, they can reach relatively fast flight speeds, enabling access to prey resources that can be far from breeding colonies (Warham 1977, Suryan et al. 2008). Albatrosses exploit wind shear generated by gradients between surface and low-altitude winds and pockets of lighter winds between waves, to achieve dynamic soaring flight, gaining momentum with little energetic expenditure (Sachs 2005).

In terms of their life history characteristics, albatrosses are extreme *K*-strategists, with long life expectancy, a slow breeding cycle and low fecundity (Warham 1990). The combination of a long reproductive cycle and morphological traits that favour economic long-distant flight allows albatrosses to forage across vast areas to find patchily distributed prey (Lack 1968). Within the Southern Ocean, albatrosses are known to feed at oceanographic features that are often far from their colonies, including shelf edges (Deppe et al. 2014), mesoscale eddies (Nel et al. 2001) and frontal zones (Scales et al. 2016).

Variations in life history characteristics (e.g. longevity, breeding frequency, breeding-season duration; see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m609p221_supp.pdf) and morphology (e.g. body mass, wingspan, wing area) affect aerodynamic performance and reproductive costs of albatrosses, and, ultimately, their capacity to buffer the effects of environmental variability (Weimerskirch et al. 1986). Relative differences in flight costs may predispose species which expend more energy to reach distant foraging areas to be more vulnerable to environmental stochasticity; alternatively, species that exhibit greater flexibility in foraging strategy may be more resilient to ecosystem perturbations (Kappes et al. 2010).

Four species of albatross, representing 3 of the 4 genera of the family Diomedidae, breed at subantarctic Macquarie Island, Australia: black-browed *Thalassarche melanophris*, grey-headed *T. chrysoloma*, light-mantled *Phoebastria palpebrata* and wandering albatrosses *Diomedea exulans*. The populations within this community have differing long-term trends; 2 species are increasing (black-browed and light-mantled), 1 is decreasing (wandering), and 1 has a stable population trajectory (grey-headed, DPIPWE 2014). With different energetic costs associ-

ated with flight and reproduction, we expected that the 4 species would show differences in habitat use and higher residence times associated with oceanographic features that aggregate prey. We aimed to: (1) determine the environmental features influencing habitat use and (2) understand how morphology and life history traits influence distribution and consequently, vulnerability or resilience to environmental variability.

2. MATERIALS AND METHODS

2.1. Field data collection

Four species of albatrosses (black-browed, $n = 10$; grey-headed, $n = 10$; light-mantled, $n = 15$; and wandering, $n = 12$) from Macquarie Island (54.6°S , 158.9°E) were tracked throughout their breeding and nonbreeding periods between November 1992 and December 2009 (Fig. 1, Table S1) using global location sensing (GLS) tags (British Antarctic Survey) or platform terminal transmitters (PTTs; Microwave Telemetry). The GLS tags (4.5 g, $25 \times 18 \times 7$ mm) sampled light each minute and stored the greatest value at the end of each 10 min period. They also recorded the water temperature after 20 min of salt-water immersion. The GLS tags were calibrated at Macquarie Island for 6 d before being deployed. These tags were attached to 40 mm plastic Darvic bands using epoxy glue and a cable tie, and then fastened to the tarsus of each individual while holding the bird away from its nest. The PTTs (30 g, $50 \times 15 \times 15$ mm) were attached to 3 small groups of feathers with Tesa[®] 4651 tape to the mantle region between the wings, with the antennae extending to the anterior of the bird (Wilson et al. 1997, Terauds et al. 2006). The PTTs were programmed to transmit every 90 s.

2.2. Data processing

The GLS tag data were extracted and decompressed using BASTrak software ('Communicate' and 'Decompressor'; Fox 2010). Subsequently, twice-daily locations were estimated using the R packages 'SGAT' and 'BAStag' (<https://github.com/SWotherspoon/SGAT>, <https://github.com/SWotherspoon/BAStag>). Geolocation is more accurate if it is based on unobstructed sampling of light data during the twilight periods, which allows the determination of sunrise and sunset times. However, it is common for light records from birds to exhibit shading by feathers or nesting behaviour, which may delay or advance the estimated timing of sunrise or sunset, respectively. We implemented a pre-processing step to minimise the effects of shading. By identifying the onset or end of twilight as the crossing of a set threshold light level, we could interactively assess whether the light data were shade-free or not. When shading disrupted the onset of the recorded twilight, we advanced or delayed the timing to the correct twilight time (i.e. only if the shading ceased before the end of the twilight).

Initial twilight times were determined using the threshold method applied to pre-processed light data and locations estimated at local noon and midnight (Hill & Braun 2001, Ekstrom 2004). A Bayesian framework was used to estimate the most likely location (and 95% CI) using light data and a set of 3 priors. The first prior (a gamma distribution of observed speeds with a maximum straight-line travel speed between 2 twilight locations (sunrise/sunset, set as 90 km h^{-1}) was used to constrain consecutive locations. The second prior (a beta distribution of twilight errors, in minutes from actual twilight) addressed unresolvable shading. The third prior (a Gaussian distribution of remotely-sensed sea surface tempera-

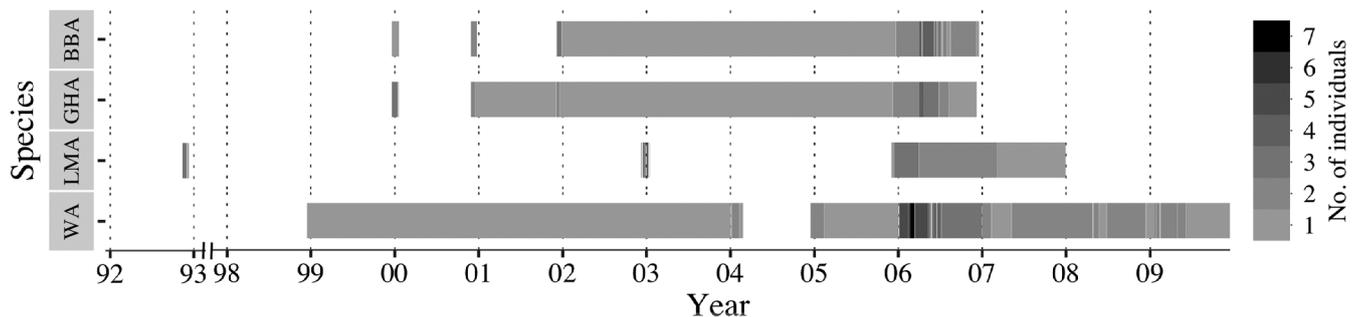


Fig. 1. Timeline of platform terminal transmitters (PTT) and global location sensing (GLS) tag deployments on black-browed (BBA, $n = 10$), grey-headed (GHA, $n = 10$), light-mantled (LMA, $n = 15$) and wandering albatrosses (WA, $n = 12$) from Macquarie Island, Australia, showing temporal changes in the number of individuals tracked

ture (SST) with erroneous high temperatures excluded during pre-processing) increased latitudinal resolution associated with SST. Locations of tagged albatrosses that encountered 24 h daylight during the polar summer were constrained to regions south of a maximum latitude based on predicted photoperiods. For data from GLS tags ($n = 4$) that showed irreconcilable noise in the light data, an alternative twilight-free method was used to estimate primary location following Bindoff et al. (2018). For both methods, the likely path represents the final posterior mean of the primary locations (Sumner et al. 2009).

The PTT locations in Argos location class 'Z' were removed, and the remainder filtered according to flight speed using a forward-backward averaging algorithm based on the maximum travel speed of 90 km h^{-1} (McConnell et al. 1992), using the R package 'trip' (Sumner et al. 2009). All data processing and analysis were completed within R version 3.1.1 (R Core Team 2016).

2.3. Statistical analysis

Residence time was estimated by first calculating the time spent by each tracked bird in each 100 km square cell, then taking the average of these values for each cell across all individuals. This avoids 'halo' effects around breeding sites resulting from high aggregate residence times in nearby cells due to the many transits, albeit brief, by commuting birds. Prior to inclusion in the residence time analysis, the processed PTT and GLS locations were combined, and a half-hourly interpolation was applied to capture use of cells corresponding to each individual track. The relatively coarse scale of the square grid cells enables PTT and GLS datasets to be integrated and analysed in the same way. We used the presence of an egg or chick in the nest to define the breeding period for each individual, with the nonbreeding period commencing at fledging or nest failure. The timing of laying, failure or fledging was established through regular nest monitoring and examination of the light data from the GLS tags (with incubation and guard periods easily identifiable from the frequent periods of shading). Tracking data from PTTs deployed on 2 juvenile black-browed, grey-headed and wandering albatrosses were combined with the data from nonbreeding adults in the residence time analysis, as their movements would have been similarly unconstrained by the demands of breeding. Despite differences in foraging behaviour and experience between juveniles and adults, juvenile albatrosses are

likely to be similarly constrained by morphology influencing flight and foraging efficiency to adults during the nonbreeding period (Wunderle 1991, Fayet et al. 2015). Furthermore, juvenile albatrosses previously tracked following fledging (as in this study) displayed habitat overlap with adults and similar flight paths and behavioural characteristics (de Grissac et al. 2016). For comparison, tracking data from juvenile albatrosses included in the nonbreeding dataset from this study are presented in Fig. S2. Although black-browed, grey-headed and wandering albatrosses show some sexual segregation at other sites (Shaffer et al. 2001, Phillips et al. 2004, Froy et al. 2015), due to the small number of deployments in our study, tracks from male and female albatrosses were pooled in the analysis (Fig. S3). For nonbreeding black-browed, grey-headed and light-mantled albatrosses, the tracking data included in the analysis represent a small number of deployments ($n = 4, 4$ and 2 , respectively) and are unlikely to be representative of the distribution of the population.

To identify the environmental characteristics of the areas used by the albatrosses, we used generalised additive models (GAMs) with a log link, gamma distribution and maximum likelihood (ML) smoothness selection to the time spent grids. Daily oceanographic and atmospheric data (chlorophyll *a* [chl *a*] concentration, eddy kinetic energy, bathymetric gradient, SST gradient, sea surface height anomaly and wind speed) extracted from global databases and averaged over the parent grid cells from the spatial and temporal domain of interpolated tracking data for each species and period were included as the explanatory variables (Table S2). Oceanographic features such as frontal zones and eddy features were represented in the models as regions of higher SST gradient, eddy kinetic energy and sea surface height anomaly. As the data were highly skewed, the covariate eddy kinetic energy was log-transformed. A latitude, longitude smoothed term was included as a covariate to account for spatial structure and spatial autocorrelation in the data. This method represents one of several approaches to dealing with autocorrelation in tracking datasets, which if left unaddressed can lead to errors in interpreting ecological relationships (Dormann 2007, Hawkins 2012). The trade-off for implementing this method is that some environmental relationships may remain unidentified because the spatial smoother explains a large amount of variability (Webb et al. 2014).

The correlations between predictor terms were investigated using a Pearson's correlation matrix, and a threshold of 0.8 was applied to remove highly corre-

lated terms. Separate models were built for each species and period (breeding vs. nonbreeding season), incorporating all environmental predictors, followed by a stepwise model selection process, where the least significant terms were sequentially dropped, and the model refitted. All mean values are presented \pm SE, unless otherwise indicated.

3. RESULTS

3.1. Breeding period

During the breeding period, all species displayed constrained central-place foraging with a predominant north–south distribution, with the capacity to disperse limited by the demands of incubation or chick-rearing at the colony (Fig. 2a). Mean daily displacements calculated from the filtered tracking data varied among species, with the shortest distances covered by wandering albatrosses (mean: 191 ± 8 km d^{-1}) and the longest by grey-headed and light-mantled albatrosses (respective means: 427 ± 18 and 404 ± 12 km d^{-1} ; Tukey's: $p = 0.66$; ANOVA: $F_{3,2664} = 99.71$, $p < 0.001$). Contrasting patterns in the daily maximum distance from the colony resulted in black-browed albatrosses (mean: 326 ± 22 km) having greater residence times closer to Macquarie Island, compared with wandering albatrosses, which typically foraged farther from the island (mean: 942 ± 21 km, ANOVA: $F_{3,2664} = 110.1$, $p < 0.001$; Table 1). The greatest overlap in distribution among species during the breeding period occurred along the Macquarie Ridge and into the Tasman Sea (Fig. 3a, Fig. S4).

For breeding black-browed albatrosses, the optimal model explained 85% of deviance in residence time, with greater SST gradient, greater sea surface height anomaly, and low to moderate (<10 m s^{-1}) wind speeds best explained greater residence times during breeding (Table 2, Fig. 4), where greater residence time occurred closest to the breeding colony, primarily around the Subantarctic Front (SAF, Fig. 5) at Macquarie Ridge, and extending north into the south Tasman Sea (Fig. 2a). The mean daily displacement for black-browed albatrosses was 266 ± 13 km d^{-1} (Table 1).

Breeding grey-headed albatrosses also had greater residence times in the Tasman Sea and the SAF to the east of Macquarie Island (Fig. 2a), with the latter used by 7 of 8 tracked individuals, all of which displayed directed trajectories to this area followed by greater residence times in the region (Fig. S5). The optimal model included only wind speed and ex-

plained 63% of deviance in residence time, with moderate speeds corresponding to greater residence times. No significant effects were found for any of the oceanographic covariates (Table 2, Fig. 4).

Light-mantled albatrosses showed the most extensive breeding distribution at sea and the most southerly range. Light-mantled albatrosses concentrated their time at sea within frontal regions including the Antarctic Polar Front (APF) to the south of Macquarie Island and the southern boundary of the Antarctic Circumpolar current (ACC, Fig. 5). For light-mantled albatrosses, greater chl *a* concentration, greater eddy kinetic energy, low bathymetric gradient and low to moderate wind speeds explained 63% of deviance in residence time (Fig. 4, Table 2).

Habitat use by wandering albatrosses during the breeding season was predominantly to the west of Macquarie Island (Fig. 2a), with the greatest residence times concentrated along the APF. Wandering albatrosses used areas further from the colony (mean: 942 ± 21 km), but travelled a shorter distance (mean: 191 ± 8 km d^{-1}) each day than any other species tracked. The optimal models for this species included only wind speed, which explained 53% of total deviance in residence time; no oceanographic covariates had a significant effect on residence time during the breeding period (Table 2, Fig. 4).

3.2. Nonbreeding period

All species dispersed more widely during the nonbreeding period and exhibited circumpolar distributions characterised by patchy, isolated areas of longer relative residence times at sea (Fig. 2b). Despite the larger overall distribution, the daily displacement distances travelled were significantly shorter than those during the breeding period for all species, except black-browed albatrosses, which displayed a mean daily flight distance of 351 ± 14 km d^{-1} (32% greater than during the breeding period; ANOVA: $F_{3,7143} = 49.02$, $p < 0.001$). Wandering albatrosses moved the shortest daily distances (mean: 153 ± 4 km d^{-1}), and black-browed albatrosses moved the greatest distances (mean: 351 ± 14 km d^{-1}). Overlap of all 4 species (corresponding use of individual 100×100 km grid cells), was restricted to a small region close to the breeding colony and several isolated groups of grid cells in the south-west Pacific basin and the Drake Passage (Fig. 3b).

During the nonbreeding period, the best models included multiple environmental covariates and showed that despite large differences in spatial habitat use,

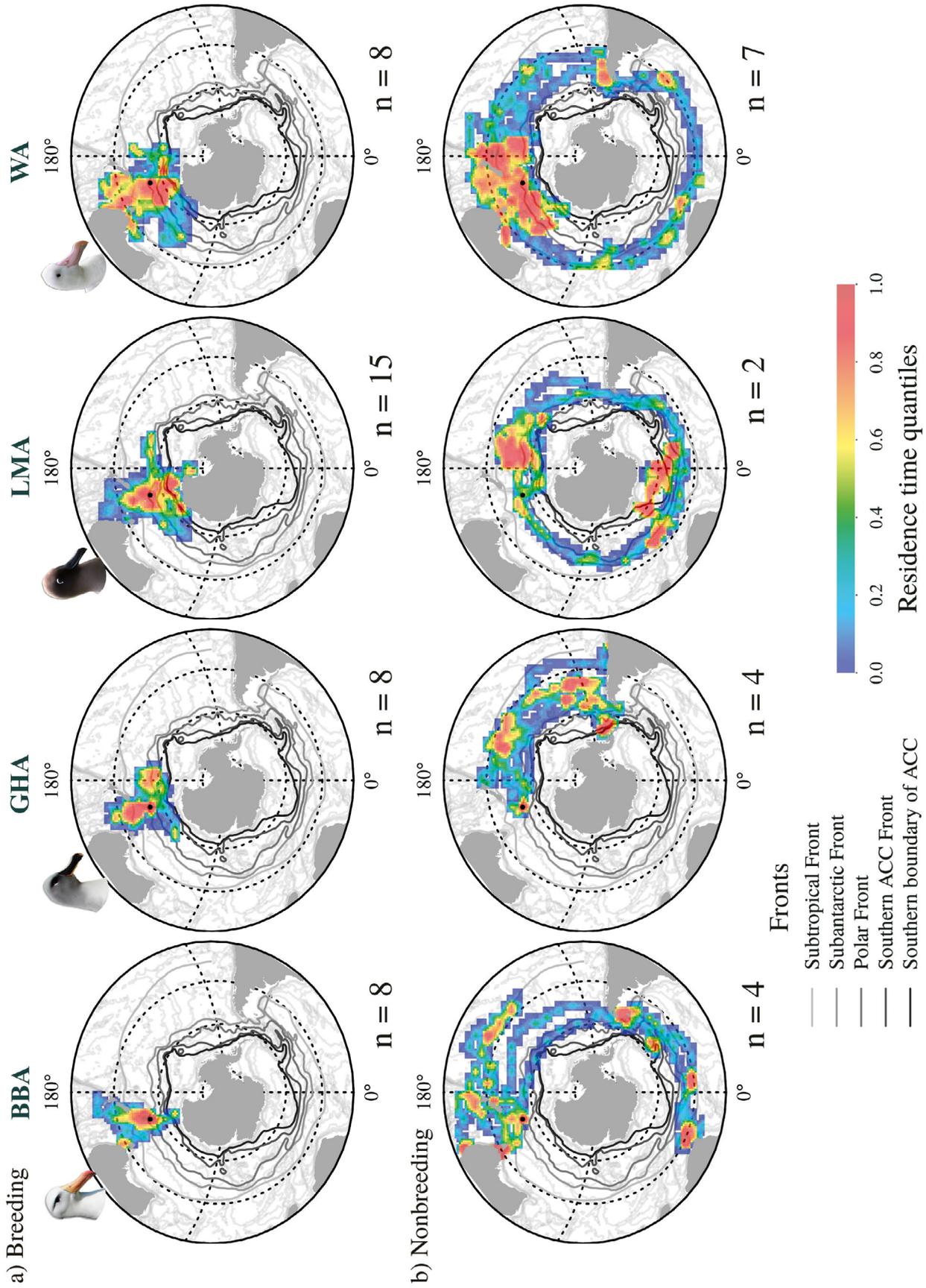


Fig. 2. Residence time quantiles of black-browed (BBA), grey-headed (GHA), light-mantled (LMA) and wandering albatrosses (WA) tracked from Macquarie Island during (a) breeding and (b) nonbreeding periods. Residence time was based on a 100×100 km grid. The major Southern Ocean frontal features are based on Orsi et al. (1995)

Table 1. Summary of deployments and foraging behaviour of black-browed (BBA), grey-headed (GHA), light-mantled (LMA) and wandering albatrosses (WA) tracked from Macquarie Island, Australia, between 1992 and 2009. PTT: platform terminal transmitter, GLS: global location sensing tag

		BBA	GHA	LMA	WA
Number of tracked individuals		10	11	15	12
PTT deployed		8	9	12	8
GLS deployed		2	2	3	4
Number of days of tracking data	Breeding	501	325	738	1081
	Nonbreeding	557	567	815	2515
Mean \pm SE daily displacement (km d ⁻¹)	Breeding	266.2 \pm 12.7	426.5 \pm 17.5	403.8 \pm 12.4	191.1 \pm 8.1
	Nonbreeding	351 \pm 14	266 \pm 9	265 \pm 11	153 \pm 4
Mean \pm SE daily maximum distance from colony (km)	Breeding	326 \pm 22	812 \pm 35	811 \pm 23	942 \pm 21

greater residence times were associated with similar oceanographic features (Table 2, Fig. 4), for example, mesoscale eddy structures (high eddy kinetic energy) and thermal fronts (high SST gradient). Furthermore, the relationship of residence time to wind speed was similar to the breeding period for grey-headed, light-mantled and wandering albatrosses, with a general pattern of low to moderate winds corresponding with greater residence times (Table 2, Fig. 4). Despite some similarities, environmental models did indicate differences among species in their responses to environmental covariates.

Black-browed albatrosses had greatest residence times in isolated regions with greater chl *a* concentration, greater eddy kinetic energy, and more pronounced sea surface temperature gradients (Table 2, Fig. 4). The optimal model was found to explain 49% of the deviance in residence time. Wind was not a significant predictor of residence time for nonbreeding black-browed albatrosses.

For nonbreeding grey-headed albatrosses, the optimal model described 41% of deviance in residence time, with areas with greater eddy kinetic energy and more pronounced bathymetric gradients (i.e. slope) corresponding with greater residence times (Table 2, Fig. 4). These results reflect the habitat characteristics of the central southern and south-east Pacific basin, south of the Subtropical Front (STF, Fig. 5). We found no significant difference in mean daily flight distances between grey-headed and light-mantled albatrosses during the nonbreeding period (respective means: 265 \pm 9 and 265 \pm 11 km d⁻¹; Tukey's: $p = 0.66$; ANOVA: $F_{3,4479} = 128.8$, $p < 0.001$), although they used quite different areas at sea. There was contrast, however, in their responses to bathymetric gradient, indicated by positive and negative linear relationships for grey-headed and light-mantled albatrosses, respectively (Table 2, Fig. 4). Of the 2 tracked nonbreeding light-mantled

albatross, one showed a circumpolar distribution, and the other may have completed a circumpolar movement; however, the geolocator failed at approximately 10° W. The optimal model for the 2 tracked light-mantled albatrosses showed that the greatest residence times were explained by greater chl *a* concentration, high eddy kinetic energy and low bathymetric gradient (deviance = 52%, Table 2, Fig. 4) in the central southern Pacific and south-east Atlantic Oceans (Fig. 2b).

Wandering albatrosses had the shortest mean daily distances travelled during the nonbreeding period (Table 3), with the optimal model showing greatest residence times in areas of greater eddy kinetic energy and more pronounced SST gradients (deviance = 50%, Table 2, Fig. 4) in the south-west Pacific basin, close to the breeding colony (Fig. 2b). Six of the 7 individuals tracked had a broadly resident migration strategy with greater use of the south-west Pacific basin region (Fig. S3). The remaining individual circumnavigated Antarctica twice during 1 nonbreeding period (complete trips lasted 201 and 55 d).

4. DISCUSSION

This study presents the entirety of albatross tracking data from Macquarie Island collected to date, comprising a small number of deployments over several years. Although there was some overlap among species in habitat use across both the breeding and nonbreeding periods, there was also evidence for spatial segregation and foraging niche specialisation (i.e. preferences for particular oceanographic features). This is in agreement with a previous study of at-sea activity patterns of the same 4 species tracked from South Georgia during the nonbreeding season (Mackley et al. 2010).

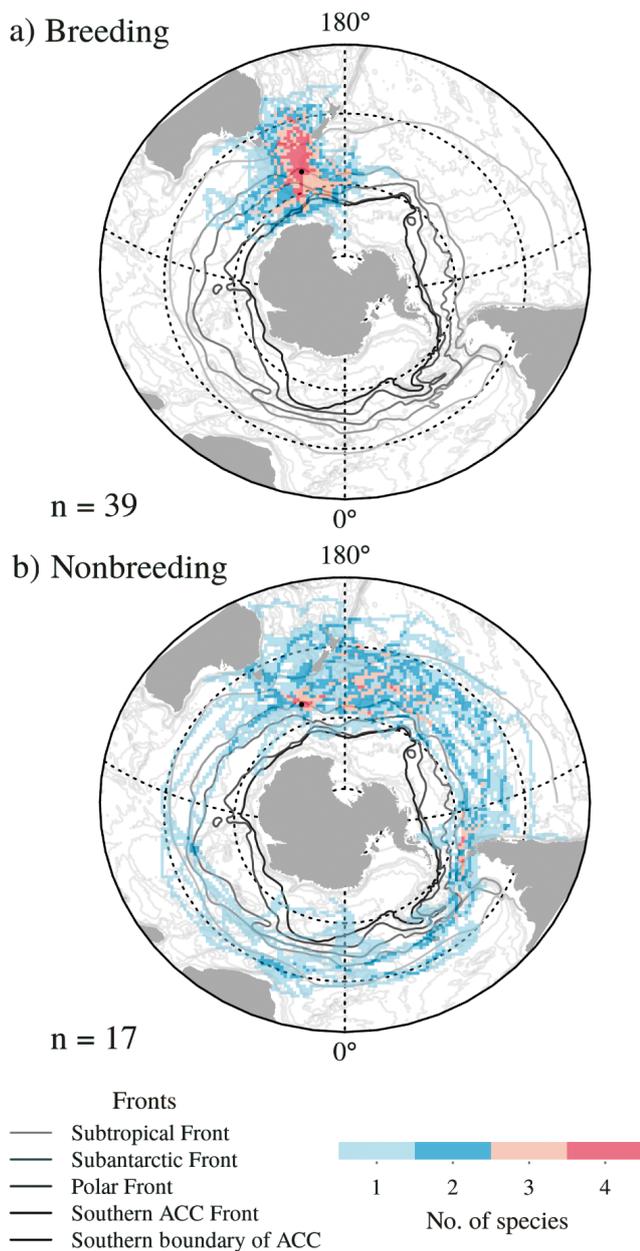


Fig. 3. Gridded (100 × 100 km) (a) breeding and (b) nonbreeding overlap of albatrosses tracked from Macquarie Island (black-browed, grey-headed, light-mantled and wandering albatrosses) in relation to major Southern Ocean frontal features (from Orsi et al. 1995)

4.1. Breeding season movements and habitat associations

We evaluated environmentally-explicit models for 4 sympatric albatross species during the breeding and nonbreeding periods to examine the relationships between habitat use and environmental parameters (bathymetry, oceanography and wind speed).

Foraging distances of the albatrosses tracked from Macquarie Island were limited during breeding by incubation and chick-rearing duties, which impose a central-place foraging constraint (Table 1; see also Ashmole 1963). This presumably explains the greater inter-specific overlap in habitat use at this time compared with the non-breeding period. Habitat use was predominantly associated with oceanographic features to the north of the colony, along transit corridors to the Macquarie Ridge and north into the Tasman Sea (Fig. 2a). These features provide seasonally productive habitat (Tilburg et al. 2002, Sokolov & Rintoul 2007), which are also used by other marine predators, e.g. Macquarie Ridge: southern elephants seals *Miromunga leonina* (Hindell et al. 2016) and subantarctic *Arctocephalus tropicalis* and Antarctic fur seals *A. gazella* (Robinson et al. 2002); Tasman Sea: Buller's albatrosses *Thalassarche bulleri* (Sagar & Weimerskirch 1996, Stahl & Sagar 2000a,b), Cook's petrels *Pterodroma cookii* (Rayner et al. 2008) and antipodean (Gibson's) albatrosses *Diomedea antipodensis gibsoni* (Walker & Elliott 2006).

Although our small samples make it difficult to make population-level inferences about core distributions, the differences in habitat use at sea corresponded well with the differences among species in life history, and their morphological adaptations. Despite greater overlap during the breeding season, we determined inter-specific differences in habitat use. Species with adaptations for more energetically efficient flight (higher glide ratio, higher aspect ratio, less induced drag, increased lift) and with longer breeding periods travelled further from the colony. Conversely, the species with higher flight costs (lower glide ratio, lower aspect ratio) and a shorter breeding period used areas at sea closer to the colony during the breeding season. Differential responses indicated by the environmental modelling results provide additional evidence of resource partitioning during the breeding period.

Black-browed albatrosses made use of local neritic waters associated with the Macquarie Ridgeline and the SAF (Fig. 2a). The SAF represents a region of high SST gradient, an important predictor of residence time for this species. However, despite high residence time detected over the Macquarie Ridgeline, bathymetry was not detected as an important predictor in the analysis. Perhaps this result is an artefact of scale, where shelf edge waters and associated steep gradients in bathymetry occur over a smaller scale than the 100 km grid cell resolution used in the modelling. Neritic foraging is typical of this species at Macquarie Island (Terauds et al. 2006)

Table 2. Optimal general additive model results showing significant relationships between residence time (hours) of black-browed (BBA), grey-headed (GHA), light-mantled (LMA) and wandering albatrosses (WA) tracked from Macquarie Island, and environmental variables: chlorophyll *a* concentration (chla), eddy kinetic energy (eke), bathymetric gradient (gbathy), sea surface temperature gradient (gsst), sea surface height anomaly (ssha) and wind speed (wind). A longitude–latitude smoothed term (Long. lat.) is incorporated to address spatial autocorrelation

Species	Smoothed term	Estimate	<i>F</i>	<i>t</i>	<i>p</i>	R ²	Deviance
Breeding							
BBA	Intercept	10.1875		186.1937		0.2706	0.8512
	Long. lat.		15.5791		<0.001		
	ssha		11.0138		0.0011		
	wind		4.8871		0.0023		
GHA	gsst		3.5673		0.015		
	Intercept	10.3509		175.9226		0.0233	0.6299
	Long. lat.		8.7488		<0.001		
	wind		2.4716		0.0418		
LMA	Intercept	10.6691		253.1974		0.4268	0.6302
	Long. lat.		19.0563		<0.001		
	eke (log)		6.8701		<0.001		
	chla		11.9919		<0.001		
	wind		3.3481		0.0015		
	gbathy		4.2591		0.0397		
WA	Intercept	10.9249		213.037		0.0647	0.5268
	Long. lat.		14.9203		<0.001		
	wind		3.7916		0.004		
Nonbreeding							
BBA	Intercept	10.0548		278.537		0.2276	0.4873
	Long. lat.		13.3514		<0.001		
	eke (log)		4.8312		<0.001		
	chla		9.8216		0.0017		
	gsst		3.0436		0.0132		
GHA	Intercept	10.4761		295.4269		0.219	0.4102
	Long. lat.		13.0776		<0.001		
	wind		5.4755		<0.001		
	gbathy		15.8203		<0.001		
	eke (log)		2.6937		0.0287		
LMA	Intercept	10.2028		252.5517		0.2235	0.5247
	Long. lat.		23.0428		<0.001		
	gbathy		11.3853		<0.001		
	gsst		5.4396		0.0199		
	wind		2.4211		0.0273		
	chla		1.6085		0.178		
WA	Intercept	10.8688		376.1416		0.233	0.5037
	Long. lat.		43.114		<0.001		
	wind		9.6689		<0.001		
	gsst		5.8276		<0.001		
	eke (log)		5.3217		<0.001		

and other colonies (Cherel & Weimerskirch 1995, Weimerskirch et al. 1997a, Wakefield et al. 2012). Their comparatively low aspect ratio results in higher drag during flight, more use of flap-gliding and increased energetic costs for long-distance travel (Pennycuik 1982). Combined with a lower wing loading, which facilitates improved manoeuvrability and aerodynamic lift at lower wind speeds, black-browed albatrosses have greater take-off performance and are known to outcompete other albatross species for prey in multi-species feeding aggregations (Table 3;

Warham 1977, Pennycuik 1983, Harrison et al. 1991, Weimerskirch & Guionnet 2002). This is reflected in their at-sea activity patterns, i.e. shorter flight bouts and a larger proportion of time spent on the water compared to the other species (Mackley et al. 2010). Localised foraging by black-browed albatross is coupled with faster recovery of adult body condition, shorter incubation shifts and a higher meal delivery rate such that the chick-rearing period is shorter than in the other species (Table 3; Huin et al. 2000, Waugh et al. 2000, Phillips et al. 2003).

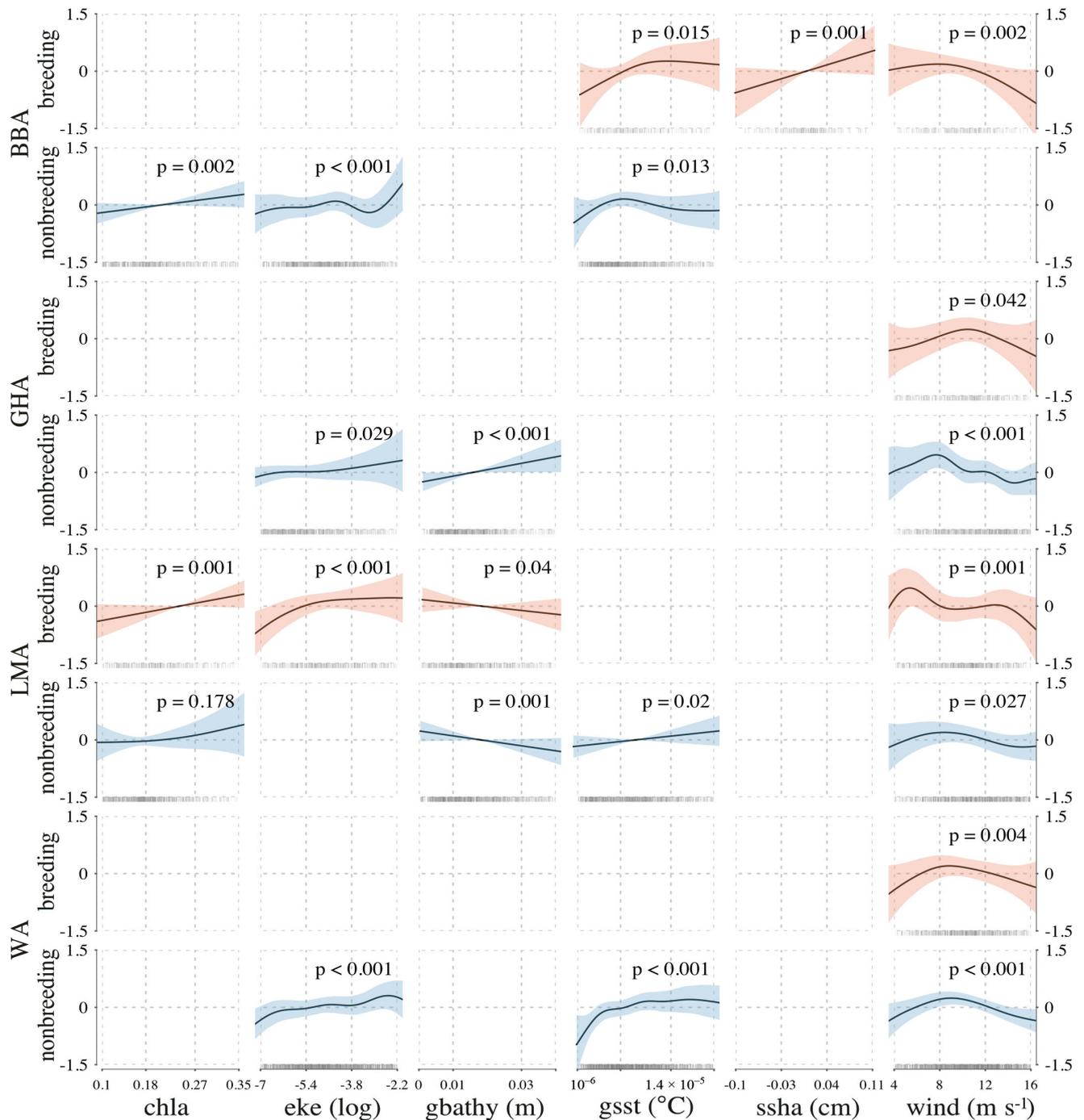


Fig. 4. General additive model response curves (shading: SE) showing significant relationships between residence time (hours) of breeding (red) and nonbreeding (blue) black-browed (BBA), grey-headed (GHA), light-mantled (LMA) and wandering albatrosses (WA) tracked from Macquarie Island, and environmental variables: chlorophyll a concentration (chla), eddy kinetic energy (eke), bathymetric gradient (gbathy), sea surface temperature gradient (gsst), sea surface height anomaly (ssha) and wind speed (wind)

In contrast, grey-headed albatrosses travel greater distances, have longer intervals between incubation shifts (Table 3; see also Terauds 2002) and chick feeds, and exhibit slower chick development (Huin et al.

2000, Waugh et al. 2000, Phillips et al. 2003). As at Macquarie Island, breeding grey-headed albatrosses at other sites also associated with large-scale frontal systems (which represent regions of concentrated

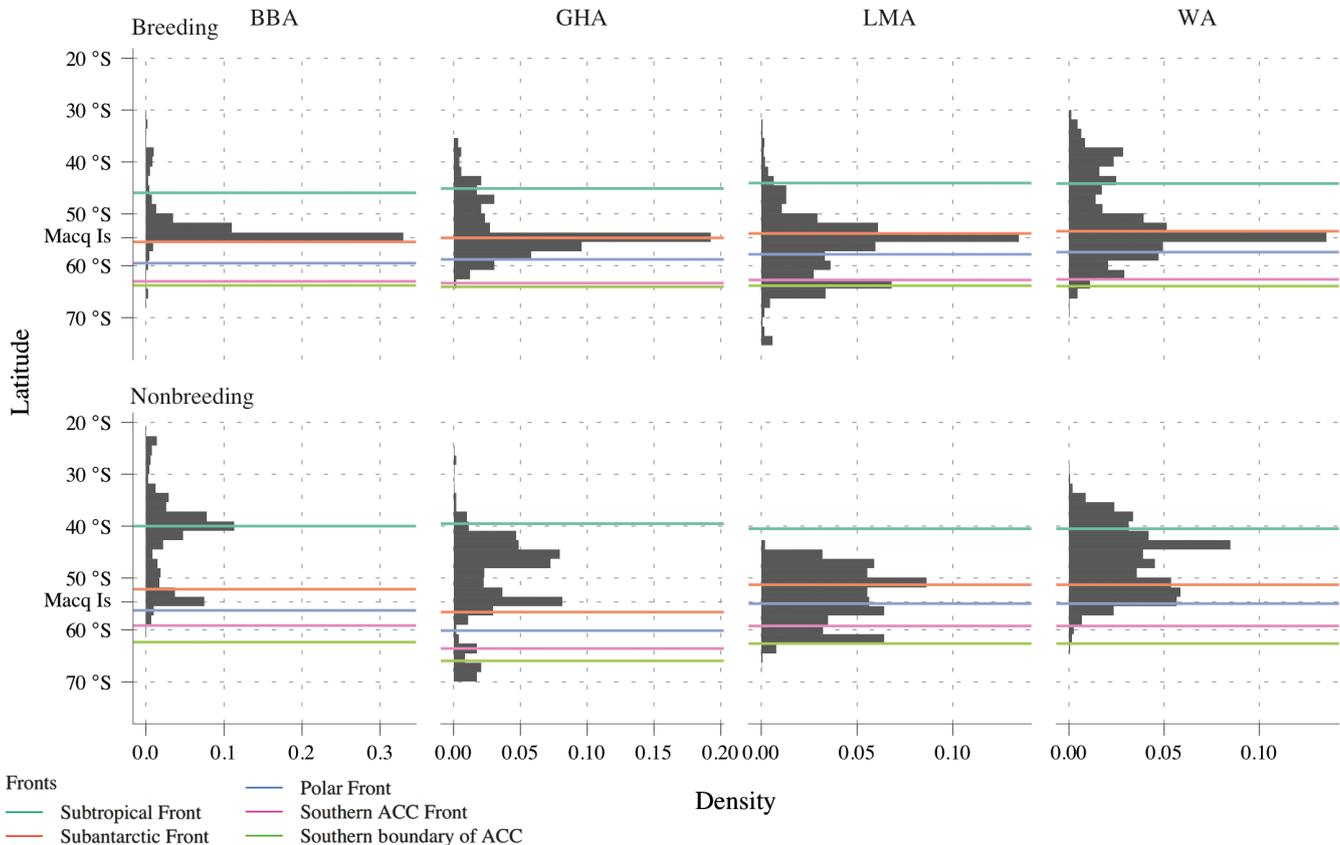


Fig. 5. Locations of tracked breeding and nonbreeding albatrosses from Macquarie Island by latitude, in relation to the mean positions of major Southern Ocean frontal systems, averaged across the species distribution (from Orsi et al. 1995)

productivity and higher prey availability) (Waugh et al. 1999, Scales et al. 2016). Despite concentrated habitat use along the SAF (Fig. 5), to the east of Macquarie Island (Fig. 2), no relationship between residence time and SST gradient was evident among birds tracked from Macquarie Island, potentially due to a small sample size and individual variability in habitat use.

Among breeding light-mantled albatrosses, greater residence times were associated with lower wind speeds ($\sim 6 \text{ m s}^{-1}$) compared with the other species (Fig. 4). Their lower wing loading and high aspect ratio (Table 3) provides greater aerodynamic lift, superior glide ratios and more economic flight at lower wind speeds, allowing efficient foraging south of 61°S where wind speeds are lower and less consistent (Young 1999). This is underlined by their limited use of closer waters around the APF (between 56° and 61°S , Fig. 5), where wind velocities are greater. Similarly, breeding birds tracked from Heard Island, Crozet and South Georgia typically forage far south of the APF (Phillips et al. 2005a, Lawton et al. 2008, Delord et al. 2014). By undertaking long incubation shifts and employing a bimodal foraging strategy in

chick-rearing (Terauds & Gales 2006), light-mantled albatrosses from Macquarie Island can not only exploit local foraging habitat close to the colony, but they can also make use of tailwinds to travel to distant, productive waters (high chl *a*) associated with the southern boundary of the ACC (Weimerskirch & Robertson 1994, this study).

Wandering albatrosses are much larger than the other species at Macquarie Island and consequently, the adults have greater energy reserves and chicks have a longer fasting capability, enabling more distant foraging trips by parents (Table 3) (Arnould et al. 1996, Berrow & Croxall 2001). The shorter daily displacement distances of the tracked birds (Table 1) and characteristic prolonged looping flights reflect a foraging strategy that involves searching large areas, maximising encounters with patchily distributed prey (Weimerskirch et al. 1997b, Wakefield et al. 2009). Their high aspect ratio, wing loading and glide ratios support efficient dynamic soaring, enabling exploitation of distant resources at little energetic cost (Table 3; see also Shaffer et al. 2001). However, these traits reduce efficiency during take-off and landing (Weimerskirch et al. 1997b, Mackley et al. 2010). Conse-

Table 3. Summary of functional and life history parameters of black-browed, grey-headed, light-mantled and wandering albatrosses (abbreviations as in Table 2) from Macquarie Island. Values are means \pm SE. M: males; F: females; NA: not available

Attribute	BBA	GHA	LMA	WA	Reference
Status	44	88	2151	7	DPIPWE (2014)
Breeding pairs (2013/14)	Increasing	Stable	Increasing	Decreasing	
Population trend					
Mass (kg)	M: 3.67 \pm 0.23 F: 3.05 \pm 0.17	M: 3.52 \pm 0.25 F: 3.07 \pm 0.18	2.84	M: 9.44 \pm 0.59 F: 7.84 \pm 0.18	Pennycuik (1982), Shaffer et al. (2001), Phillips et al. (2004)
Wingspan (cm)	M: 228.8 \pm 5.3 F: 221.8 \pm 3.4	M: 221.2 \pm 4.0 F: 216.0 \pm 5.5	218	M: 311.0 \pm 4.0 F: 299.0 \pm 5.0	
Wing area (cm ²)	M: 3900 \pm 150 F: 3660 \pm 90	M: 3555 \pm 135 F: 3395 \pm 135	3380	M: 6260 \pm 270 F: 5860 \pm 230	
Wing loading	M: 92.3 \pm 5.3 F: 81.7 \pm 4.0	M: 97.1 \pm 7.0 F: 88.6 \pm 5.9	82.4	M: 148.0 \pm 10.0 F: 132.0 \pm 11.0	
Aspect ratio	M: 13.4 \pm 0.3 F: 13.4 \pm 0.3	M: 13.8 \pm 0.3 F: 13.8 \pm 0.5	14.1	M: 15.5 \pm 0.6 F: 15.3 \pm 0.6	
Maximum glide ratio	21.7	22.0	22.4	23.2	
Reproduction	Annual	Biennial	Biennial to triennial	Biennial	Terauds (2002)
Breeding frequency	Late Sep–early May	Early Oct–late May	Mid-Oct–mid-June	Early Dec–early Jan (13 mo)	
Breeding season	25 Sep–31 Oct	6 Oct–30 Oct	Oct–17 Nov	8 Dec–14 Jan	
Laying date	3.1 \pm 0.1	5 \pm 0.2	NA	8.8 \pm 0.4	
Early incubation shift length (d)	3.6 \pm 2.7	7.5 \pm 4.0	10.5 \pm 4.6	8.8 \pm 4.9	
Late incubation shift length (d)	68.9 \pm 0.2	71.7 \pm 0.1	66.5 \pm 0.3	79.2 \pm 0.2	
Mean incubation length (d)	22.4 \pm 0.4	24.8 \pm 0.3	22.4 \pm 0.5	30.1 \pm 0.8	
Mean brood guard length (d)	118 ^b	135 ^b	139.7 \pm 2.6	273.6 \pm 3.6	
Chick rearing length (d)	43.4 \pm 12.4	52.0 \pm 12.5	48.6 \pm 12.3	63.85 \pm 19.8	DPIPWE (2014)
Mean breeding success (1994–2014, %)					

^aData from colonies other than Macquarie Island; ^bmedian values

quently, wandering albatrosses land less frequently than other albatrosses and remain on the water for longer periods (Croxtall & Prince 1994, Weimerskirch et al. 1997b, Mackley et al. 2010).

4.2. Nonbreeding season movements and habitat associations

Despite the small number of nonbreeding individuals tracked in our study, during the nonbreeding period, when central-place constraints disappear, residence time at sea among all species tracked from Macquarie Island indicated broadly similar responses to environmental parameters indicative of thermal fronts and mesoscale eddy structures. All 4 species overlapped in the south-east New Zealand Exclusive Economic Zone, where light-mantled and wandering albatrosses, in particular, had high residence times. Here, the SAF tracks the subantarctic slope on the edge of the Campbell Plateau (Morris et al. 2001); this creates a frontal region of high current velocity that continues eastwards and results in high surface eddy kinetic energy (Sallée et al. 2011) and high biological productivity (Murphy et al. 2001). This area is also used by Antipodean albatrosses (Walker & Elliott 2006), Campbell albatrosses (Waugh et al. 1999), Chatham petrels (Rayner et al. 2012) and southern elephant seals (Pascoe et al. 2016).

Nonbreeding albatrosses from Macquarie Island concentrated at distant regions of elevated primary productivity (high chl *a* concentration), mesoscale eddy structures (high eddy kinetic energy) and thermal fronts (high SST gradient, Fig. 4). Oceanic fronts were preferred by black-browed, light-mantled and wandering albatrosses, and mesoscale eddy structures by black-browed, grey-headed and wandering albatrosses. Both frontal regions and eddy structures can aggregate prey through physical structuring and concentration of primary productivity and zooplankton biomass, offering predictable resources for higher trophic-level predators (Mitchell et al. 1991, Sokolov & Rintoul 2007, Bost et al. 2009).

The annual-breeding black-browed albatrosses have a shorter nonbreeding period and travelled farther overall, and flew further each day than the biennial-breeding species (grey-headed, light-mantled and wandering albatrosses, Table 1). With the lowest aspect ratio and the highest glide ratio of the 4 species (Pennycuik 1982), black-browed albatrosses use powered (flapping) flight more frequently and have shorter flight bouts (Mackley et al. 2010). Consequently, they are less reliant on consistent winds, allowing them to exploit waters associated with the STF (Fig. 5), where winds are lighter than at higher latitudes in the Southern Ocean (Young 1999). Macquarie Island black-browed albatrosses showed spatial overlap in Tasmanian and South African shelf waters with conspecifics from Kerguelen (Delord et al. 2014). Furthermore, 1 individual spent a long period on the Patagonian Shelf and in the Benguela Upwelling off South Africa, which are both highly productive regions and represent core foraging areas of black-browed albatrosses from the Falkland Islands (Patagonian Shelf only; Wakefield et al. 2011) and South Georgia (Phillips et al. 2005b, Mackley et al. 2010). This excursion to the Benguela Upwelling represents an unusually long nonbreeding dispersal for this species, which tends to remain within local ocean basins.

Nonbreeding grey-headed albatrosses used waters between the SAF and the STF (Fig. 5), with particularly high residence times in the south-east Pacific basin (Fig. 2). There was considerable spatial overlap in habitat use west of Chile with conspecifics from Marion Island, but little with those from South Georgia (Clay et al. 2016). Like birds from Marion Island, but not South Georgia or Campbell Island (Waugh et al. 1999, Clay et al. 2016), grey-headed albatrosses from Macquarie Island associated with steep bathymetric features such as shelf slopes, which potentially drive nutrient-rich upwelling and support high prey densities.

Nonbreeding light-mantled albatrosses favoured waters between 15° W and 45° E (Fig. 2), demonstrating their capacity to capitalise on high latitude summer productivity associated with the southern boundary of the ACC. They made circumpolar navigations, and like wandering albatrosses (Weimerskirch et al. 2015, this study) and grey-headed albatrosses, exploited the consistent westerly winds to travel long distances east at low cost.

Although they also have the capacity to disperse around Antarctica, nonbreeding wandering albatrosses from Macquarie Island had highest residence times in the south-west Pacific (Fig. 2). Similarly, a

proportion of birds from Crozet and Kerguelen remain resident within the breeding range during the nonbreeding season (Weimerskirch et al. 2015). The nonbreeders from Macquarie used the nearby SAF, or showed a sedentary-with-excursions strategy, making occasional movements to the Campbell Plateau, which also represents a core foraging area for nonbreeding wandering albatrosses from Kerguelen (Fig. 2; see also Weimerskirch et al. 2015). Other birds from Macquarie Island migrated to the Humboldt Upwelling, an area well known for its high biological productivity and diversity of seabirds, including several migrant albatross and petrel species from New Zealand (Spear et al. 2003, Nicholls et al. 2005, Walker & Elliott 2006, Landers et al. 2011), and a proportion of white-chinned petrels from South Georgia (Phillips et al. 2006). Furthermore, there was less evidence of relationships between residence time and environmental variables for nonbreeding wandering albatrosses compared to the smaller albatross species (Fig. 4); this suggests broader habitat preferences, perhaps associated with their large energy reserves and efficient flight morphology.

4.3. Resilience to climate change

For Southern Ocean albatrosses, the consequences of unprecedented global warming and consequent changes in oceanographic and atmospheric conditions are uncertain. However, differences in morphology and life history among species, and hence their behavioural flexibility, are likely to determine their resilience (Jiguet et al. 2007, Maloney et al. 2009, Ficetola et al. 2016). The consistent use of waters to the north of Macquarie Island by breeding black-browed albatrosses may increase vulnerability to climate-induced changes in the latitude of the SAF (Fig. 2). With a southerly shift in the SAF, black-browed albatrosses may need to travel further and expend greater energetic resources to reach prey. The easterly meander of the SAF interacts with the Macquarie Ridge, a region of steep bathymetric gradient running northeast–southwest and generating strong upwelling, which elevates summer chlorophyll concentration (Sokolov & Rintoul 2007), generates eddies (Rintoul et al. 2014) and may support higher trophic connections through entrainment of phytoplankton (Shuckburgh et al. 2009, d'Ovidio et al. 2013). As identified by Flynn & Williams (2012), a southerly shift in the position of the SAF (Sokolov & Rintoul 2009) could result in high flow velocities to the south of the Macquarie Ridge Gap, reducing

down-flow mixing and, potentially, surface productivity in the region.

For 3 species (not nonbreeding black-browed albatrosses), higher residence times were linked to moderate wind speed (Fig. 4). This reflects the balance between enough wind to facilitate aerodynamic lift, and the avoidance of extreme wind speeds that hinder manoeuvrability, in order to achieve economic flight (Jouventin & Weimerskirch 1990). Alternatively, high wind speeds may reduce the capacity of albatrosses to locate food by reducing the ability to detect olfactory cues and the visibility of surface prey. The dependence of albatrosses from Macquarie Island on moderate wind regimes may make them vulnerable to climate-induced changes in wind patterns as the Southern Annular Mode (SAM) becomes increasingly positive (Marshall 2003). In the positive SAM phase, the band of Antarctic circumpolar winds contracts towards the Antarctic continent, resulting in relaxed mid-latitude winds (Hall & Visbeck 2002). Intensified Antarctic circumpolar winds associated with a continuing positive trend in the SAM have benefited wandering albatrosses from Crozet Island by reducing the energetic cost of reaching distant foraging areas, resulting in higher breeding success and body mass (Weimerskirch et al. 2012). For light-mantled albatrosses and breeding wandering albatrosses from Macquarie Island, which target high-latitude waters, a southward shift in wind intensity may prove beneficial by lowering flight costs. However, for breeding black-browed albatrosses, which rely on the Macquarie Ridge and Tasman Sea, and nonbreeding grey-headed and wandering albatrosses that predominantly use waters north of the SAF, a reduction in meridional wind and wind speeds at lower latitudes could reduce flight efficiency and increase energetic costs, presumably with repercussions for breeding performance.

Identifying core foraging areas from small tracking datasets of wide-ranging animals such as albatrosses is inhibited by individual variability in habitat use (Gutowsky et al. 2015). Small tracking datasets, such as the one in this study, may fail to represent important regions for the population where individual variability is pronounced. This is likely to be exacerbated during the overwintering period when home ranges increase (Gutowsky et al. 2015). For this reason, we have constrained our interpretation to broad-scale patterns in habitat use. Understanding how even a small number of individuals use their environment is still valuable, especially for small populations where few data exist, such as in this case.

5. CONCLUSIONS

The habitat use of albatrosses from Macquarie Island reflects foraging strategies that are shaped by functional morphology and life history adaptations. The 2 extremes are a wide-ranging search strategy (wandering albatrosses), which maximises encounter rate with dispersed prey, and a rapid-transit strategy (black-browed, grey-headed and light-mantled albatrosses), whereby individuals forage at oceanographic features associated with more predictable prey. The resulting differences in habitat use have implications for susceptibility to environmental change. For example, black-browed albatrosses, with a more northerly distribution, lower flight efficiency and greater reliance on local productivity, are predicted to be at greater risk of climate-driven shifts in wind patterns and frontal systems. Understanding the links between foraging behaviour, morphology and life history, and the vulnerability or resilience of Southern Ocean albatross species to current and predicted climate-driven atmospheric and oceanographic changes, has the potential to substantially improve forecasts of population viability for a range of seabird species, which is essential information for evidence-based conservation planning.

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