Fine-scale foraging behaviour of southern Buller's albatross, the only *Thalassarche* that provisions chicks through winter

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ABSTRACT: Predators generally time their reproductive events to match the peak in prey resource availability in order to sustain the elevated energy requirement of offspring provisioning. Consequently, most temperate/polar seabirds breed in spring/summer, including the majority of small albatross species that have short breeding cycles. In contrast, the southern Buller's albatross *Thalassarche bulleri bulleri* has a delayed breeding schedule, with chick-rearing extending throughout the entire austral winter. In the present study, the fine-scale at-sea movements and trophic niche of chick-rearing southern Buller's albatross were determined at Hautere/Solander Island (New Zealand, 46° 35' S, 166° 54' E) during the 2016 and 2017 chick-rearing periods to investigate the winter foraging strategy used during this nominally challenging period. The tracks recorded by 15 males (n = 43) and 11 females (n = 21) revealed that foraging behaviour accounted for only a small proportion of time at sea, primarily influenced by the time of day. Foraging occurred mainly in the neritic waters of New Zealand's South Island shelf, with individuals undertaking consistent short trips (≤230 km from the colony) or alternating short and long trips up to 1500 km from the colony. Fine-scale tracking data revealed that males spent more time foraging, during shorter trips than females. Their isotopic niches were small, with overlap between sexes, but with males having higher $\delta^{15}N$ values than females. Time spent foraging was influenced by both static and dynamic oceanographic variables. These findings suggest that southern Buller's albatross foraging behaviour, despite having to sustain chick provisioning in winter, is similar to that of summer-breeding congeners.

KEY WORDS: Foraging behaviour · Winter breeding · Bio-logging · Albatross · *Thalassarche bulleri bulleri* · New Zealand

1. INTRODUCTION

Trophic resource acquisition, the fundamental process on which all allocation of energy expenditure in an animal's life depends, varies according to nutritional demand and resource availability in the environment (Boggs 1992). During offspring provisioning, 'income-breeding' species increase their nutritional intake to meet the elevated energy requirements of both offspring and self-maintenance. Such demand can be satisfied by matching the timing of reproduction with a period of high food availability

(Lack 1968) and altering the time/energy allocation of behaviours (Gittleman & Thompson 1988). Correspondingly, food supply and parental foraging are both selection pressures on individual fitness, shaping the evolution of breeding (Thomas et al. 2001).

The marine environment is highly temporally and spatially dynamic, and scale-dependent interactions between oceanographic and biological processes lead to a heterogeneous seascape of productivity and prey (Haury et al. 1978). This complexity is thought to shape the extreme life history traits of marine predators (low offspring production, delayed maturity and long life expectancy; Ashmole 1971). However, predictable seasonal variations occur in polar and temperate regions, with ocean primary productivity and consumer biomass rising in spring/summer and decreasing in autumn/winter (Atkinson & Peck 1990). Hence, the breeding schedule of many marine predators in these ecosystems is centred on summer.

During breeding, seabirds become central-place foragers and behave to maximise their energy gain from the time-constrained transport of prey between feeding areas and the nest. For the albatrosses, this trade-off is accomplished using dynamic soaring flight powered by the wind (Richardson 2011). This flight allows them to cover considerable distances with minimal energetic cost (Bevan et al. 1995) and to maximise their prey encounters (Weimerskirch et al. 2005). Feeding mainly upon cephalopods, fish and crustaceans by surface-seizing (Cherel & Klages 1998), albatrosses are constrained by the availability of prey near the surface. As visual predators, they follow a diel activity pattern, searching in flight and landing on water to feed mainly during the day and become less active at night when they raft on the water surface (Weimerskirch & Wilson 1992, Catry et al. 2004b).

To locate favourable foraging conditions, albatrosses can use different oceanographic cues at meso-scales, such as eddies (Nel et al. 2001) and continental shelves (Cherel et al. 2000, Hedd et al. 2001), that individuals can exploit with environmental specialisation (Bonnet-Lebrun et al. 2018). In addition, some species have different foraging strategies between sexes (Phillips et al. 2004, Pereira et al. 2018). Furthermore, the presence of conspecifics (Silverman et al. 2004), marine mammals (Sakamoto et al. 2009b) and fishing vessels (Torres et al. 2011) has been reported to influence their foraging behaviour, demonstrating their complex interactions with the marine environment.

Large albatrosses (*Diomedea* spp., 6–11 kg body mass) lay an egg in spring/summer, which hatches in late summer/early autumn. The chick is provisioned by both parents during 9 mo to reach its fledging size and to become heavier than adults (Weimerskirch & Lys 2000). During winter, the breeders display an asymmetrical parental investment, reduce the time spent with the chick and increase their proportion of long trips, resulting in a feeding rate decrease while the parents' body condition deteriorates (Weimerskirch & Lys 2000). Pairs with chicks have to forage with greater effort at this stage (Shaffer et al. 2003), and will not be able to breed the next year (Jouventin & Dobson 2002).

In contrast, the smaller albatrosses nesting in subantarctic and temperate latitudes (e.g. *Thalassarche* and *Phoebetria*, 2–5 kg) breed with a shorter chick-rearing period (4–5 mo) coinciding with summer–autumn, with 1 exception. In New Zealand, the endemic Buller's albatross *T. bulleri* occurs with 2 genetically distinct subspecies (Wold 2017). The breeding distribution of the northern Buller's albatross (NBA) *T. b. platei* is restricted to the Three Kings (34° S) and the Chatham Islands (43° S), while the southern Buller's albatross (SBA) *T. b. bulleri* nests at only the Solander (46° S) and the Snares Islands (48° S). Whereas NBAs have a breeding period similar to other *Thalassarche* species, SBAs have a delayed breeding season by 3 mo. SBAs lay eggs in midsummer (January), hatch in autumn and display the longest chick-rearing period of the genus (167 d, Sagar & Warham 1998), which forces SBAs to sustain chick provisioning through the entire austral winter. Previous studies showed SBA foraging around New Zealand and the Tasman Sea (Stahl & Sagar 2000a,b); these waters undergo cooling and structure changes in winter in association with the Antarctic circumpolar ocean–atmosphere system (White & Cherry 1999).

While breeding constraints during the austral winter are avoided by other small albatrosses, or imply negative carry-over effects for the large *Diomedea* (Prince et al. 1994b), the small population of winter-breeding SBAs (13 625 pairs) can sustain an average breeding success of 70% with an adult survival rate >90% (Sagar et al. 2002, Francis & Sagar 2012). Although this Near Threatened species (IUCN 2019) is subject to environmental changes in its foraging range (Matear et al. 2013), and has experienced a recent decline in adult survival (Francis & Sagar 2012), little is known about its fine-scale foraging behaviour and activity budget. How SBA parents sustain the chick-rearing food requirements is not well understood and is crucial to understanding the species' interactions with its environment. Hypothet-

ically, its winter food requirements may involve greater foraging effort in comparison to other albatrosses, or with adaptation of activities to daylight reduction (9–10 h of daylight d^{-1} during SBA chick-rearing vs. 11–15 h for summer-breeding albatrosses at similar latitudes). Alternately, its food requirements may not require additional effort, thanks to a winter prey resource. The objectives of the present study, therefore, were to determine: (1) fine-scale at-sea movements and activity budget, (2) foraging behaviour and trophic niche, and (3) influence of sex and environmental factors on foraging behaviour of SBAs during the chick-rearing period.

2. MATERIALS AND METHODS

2.1. Field procedures

The study was conducted at Hautere/Solander Island (46.569° S, 166.896° E), which hosts 5280 SBA breeding pairs, i.e. ca. 37% of the entire population (Thompson et al. 2017). Birds from accessible nests of the West Bay area were selected at random during the post-guard stage of the 2016 and 2017 breeding seasons. One adult per nest (n = 20 in May 2016 and 19 in July 2017) was captured by hand after having fed its chick, and weighed in a cloth bag with a suspension scale (±25 g, Pesola). To monitor their at-sea movements and fine-scale behaviour, individuals were equipped with 2 data loggers: (1) a GPS i-gotU model GT−600 (Mobile Action Technology) 45 × 39 × 13 mm, sampling locations at 2 min intervals, and (2) a tri-axial accelerometer GCDC X16-mini (Gulf Coast Data Concepts) 47 × 22 × 9 mm, sampling at 25 Hz. Both devices were encapsulated separately in heat-shrink tubing and attached to the central dorsal feathers with waterproof tape (Tesa 4651). For all individuals, the loggers were consistently positioned between the wings, with the accelerometer behind the neck and the GPS lower on the back. The total package weighed 52.8 g (2.1 ± 0.2% of body mass), a mass reported to have no measurable effect on trip duration (Sagar & Weimerskirch 1996) and likely to have minimal impact on individual behaviour (Phillips et al. 2003).

Following instrumentation, individuals were returned to the nest to resume normal behaviours. Two days later, nests were visually monitored during local daylight hours, and individuals that had returned to provision their chick were recaptured to retrieve the data loggers. Body mass was recorded upon return (during or after chick feeding, depending on the indi-

viduals), and a 0.3 ml blood sample was obtained by venepuncture of a tarsal vein, for genetic sex determination (Parentage and Animal Genetic Services Centre, Massey University, Wellington) and for stable isotope analyses. Handling time at capture and recapture did not exceed 15 min.

2.2. Data processing

The GPS data were plotted in GIS (ArcMap 10.2, ESRI) to remove the locations on the island, and define trips as the time spent at sea between the departure and the return of the birds. The resulting trips were processed in the R statistical environment v. 3.4.2 (R Core Team 2017). A speed filter was used to remove potential erroneous locations, with a cut-off threshold of 110 km h^{-1} (Catry et al. 2004a), as stormy conditions occurred during the deployments. Trip metrics (duration, maximum distance from the colony, total distance travelled, average speed) were calculated with the 'adehabitat HR' package (Calenge 2006), and tracks were linearly interpolated to 1 s intervals using the 'zoo' package (Zeileis & Grothendieck 2005). The period of day (dawn, day, dusk, night) was assigned for each time–location combination, using solar elevation with the 'maptools' package (Bivand & Lewin-Koh 2017) and nautical twilight (i.e. sun 12° below the horizon) to define dawn and dusk. At night, the illuminated fraction of the moon was retrieved with the 'lunar' package (Lazaridis 2014).

The acceleration data aligned with these at-sea trips were analysed within IGOR Pro software v.7 (Wavemetrics) to infer behaviour at each second of the trip. The raw acceleration data on the 3 axes were separated between their static and dynamic components, resulting, respectively, from body angle and from movement (Yoda et al. 2001). The static component, i.e. raw data smoothed with a running average over 1 s, was subtracted from the raw data to obtain the dynamic component (Wilson et al. 2006). Static and dynamic components were used to calculate, respectively, the body pitch and the vectorial dynamic body acceleration, an index of whole-body activity (Gleiss et al. 2011). A 3-step process then identified 4 key behaviours (see Fig. S1A in the Supplement at www.int-res.com/articles/suppl/m652 p163_supp.pdf): soaring flight, flapping flight, rafting (floating) on water and foraging on water. Firstly, time spent flying or on the water was determined by travelling speed obtained from the GPS track, with speeds <10 km h^{-1} defining the time on water

(Weimerskirch et al. 2002). Landings were inferred when birds stopped a behaviour in the air to start another on water. Secondly, a *K*-means clustering conducted on the heave axis data separated the time when the acceleration was steady (non-active bird) from the time when it was variable (active bird), using the 'Ethographer' package (Sakamoto et al. 2009a). Thirdly, as *Thalassarche* albatrosses feed predominantly on near-surface prey grasped by surface seizing (98% of the feeding observations made by Harper 1987), and can submerge briefly to a depth of several metres (Prince et al. 1994a), prey encounters are expected to involve a negative body pitch of <−20° (Warwick-Evans et al. 2015) associated with sharp and rapid movement to reach prey from the surface. After visual inspection of the data, we used a negative body pitch <−30° on water associated with vectorial dynamic body acceleration peaks >1 *g* (Fig. S1B) during the bout to infer foraging behaviour. The frequency distribution of time between foraging behaviour revealed a sharp decrease for intervals >1 s (68% of all intervals <1 s, Fig. S2), and hence, this threshold was assumed to represent separate foraging events. As SBAs were observed rafting and preening at sea in front of the colony, only trips >3 km from the colony and including foraging behaviour were considered to be foraging trips.

To investigate the environmental parameters influencing the foraging activity of SBAs, the foraging trips were expressed as a standardised proportion of time spent foraging in 0.1° × 0.1° grid cells. The relationships between this foraging intensity index and bio-physical oceanographic variables, considered to directly or indirectly influence marine predators and their prey (Reisinger et al. 2018), was analysed with remotely sensed variables. Static (depth, seafloor slope) and dynamic (sea-surface wave height, sea surface temperature, mixed layer depth, sea water velocity, mean sea surface chl *a* concentration, wind speed) oceanographic variables (bathymetry obtained from GEBCO [www.gebco.net] and other datasets from Copernicus [http://marine.copernicus.eu/]; Table S1) were spatio-temporally overlaid with these cells using the 'raster' package (Hijmans & Van Etten 2016).

Stable isotope analysis of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$), a proxy of trophic ecology (Jaeger et al. 2010), was used to infer the trophic level of individuals and to quantify their niche width (Bearhop et al. 2004). Analysis was conducted on whole blood, a tissue integrating the assimilated diet over the 4–5 wk prior to sampling for albatrosses (Ceia et al. 2015). Samples were oven-dried at 60°C for 24 h,

ground and homogenized, and ~0.5 mg were packed into tin capsules for combustion on a Eurovector elemental analyser coupled to an Isoprime mass spectrometer (GV Instruments) at the National Isotope Centre (GNS Science, Lower Hutt, New Zealand). Isotopic ratios are reported in the δ notation relative to the international standards (Vienna Pee Dee Belemnite [VPDB] limestone for carbon, atmospheric N_2 for nitrogen). Their isotopic deviation is defined as $\delta(‰) = [(R_s − R_{ref}) / R_{ref}]$, where R_s is the isotopic ratio measured for the sample and R_{ref} is the reference standard. Internal laboratory standards (leucine, $\delta^{13}C$: −28.30‰ and $\delta^{15}N$: +6.54‰; EDTA, $\delta^{13}C$: −31.12‰ and $\delta^{15}N$: +0.58‰; caffeine, $\delta^{13}C$: −38.17‰ and $\delta^{15}N$: −7.82‰; cane sugar, $\delta^{13}C$: −10.33‰) calibrated to primary reference materials (RMs; IAEA-N1, $\delta^{15}N$: +0.43‰; IAEA-N2: $\delta^{15}N$: +20.41‰; IAEA-CH6, $\delta^{13}C$: −10.449‰; and IAEA-CH7, $\delta^{13}C$: −32.151‰) relative to $\delta^{13}C_{VPDB}$ and $\delta^{15}N_{Air}$ indicated an analytical precision of ±0.1‰ for $\delta^{13}C$ and ±0.2‰ for $\delta^{15}N$. The SBA isotopic niche was estimated using the ellipse-based metrics implemented in the 'SIBER' package (Jackson et al. 2011), with standard ellipse areas corrected for sample size (SEA_c) and Bayesian standard ellipses areas (SEA_B). Iterative posterior draws (10^4) estimated the SEA_B and were used to statistically compare the niche width and niche overlap between sexes. Overlap was calculated from the overlap area between maximum likelihood fitted ellipses, converted to a percentage of the total ellipse.

2.3. Statistical analyses

All statistical analyses were conducted within the R statistical environment v. 3.4.2 (R Core Team 2017). Different analyses were conducted on the mass, GPS trip metrics, activity budget, isotopic and foraging behaviour data according to their respective characteristics. Data normality and variance homogeneity were respectively assessed with Shapiro-Wilk and Bartlett tests. To compare the individuals' body mass and mass gain estimations (1 data point per individual) between sex and year, we used Wilcoxon–Mann-Whitney *U*-tests and *t*-tests, respectively. Linear mixed models (LMMs) were used to compare the GPS trip metrics (duration, maximum distance to the colony, total distance travelled and mean trip speed) between sex and year (see Table 1, Table S2). They were fitted with individual identity as a random effect, to account for the hierarchical structure of tracking data and pseudo-replication of repeated measures with the package 'nlme' (Pinheiro et al.

2014). Similar LMMs were also used to investigate the influence of sex, year, period of day and moon illumination on the birds' activity budget (see Table 1, Table S2). Accounting for repeated measures has not been developed in circular statistics, hence, we selected the first trip of each individual to compare the destination bearings of the trips using a circular ANOVA implemented in the package 'circular' (Agostinelli & Lund 2017). First trip hours of departure from and arrival to the colony were compared between sex and year with Wilcoxon–Mann-Whitney U-tests. Isotopic results were tested for potential differences between sexes and years with ANOVA. For foraging behaviour, the geographic distance between foraging periods was modelled with another LMM to investigate the influence of sex, year, period of the day and marine habitat (see Table 3, Table S2). Finally, the environmental factors influencing foraging were investigated using generalised additive mixed models (GAMMs) implemented in the package 'mgcv' (Wood 2018), with the standardised time spent foraging (% of time spent foraging within a cell relative to the total time spent foraging during the entire trip) as the response variable and the oceanographic variables as explanatory variables. Prior to modelling, the oceanographic data were scaled and checked to avoid cross-correlation with a cut-off of $|r^2| < 0.5$. Model selection, for all LMMs and GAMMs, was conducted by candidate model comparisons of their Akaike's information criterion (AIC) values using the package 'MuMin' (Bartoń 2016). The best supported model, or by default the most parsimonious model, was identified by a model-averaging procedure among the equally supported models with ΔAIC < 4 (Burnham et al. 2011) and retained (Table S2) after validation based on the examination of residuals (Zuur et al. 2009). Unless otherwise stated, all data are reported as means ± SE.

3. RESULTS

3.1. At-sea movements and activity budget

GPS data were obtained from 33 individuals undertaking 77 trips, and due to device malfunctions, were reduced for combined GPS and accelerometer foraging trips data to 26 individuals and 64 trips (15 males/43 trips; 11 females/21 trips) totalling 3700 h at sea. These individuals departed from and returned to the colony mostly during daylight (96%), with the maximum activity occurring at 15:00 h. This timing was not significantly different between departures/returns, sex and year (Wilcoxon tests, W = 2867, 2642, 3112, respectively). Individuals departed with a body mass of 2.65 ± 0.03 kg, with no significant differences between sex and year (Wilcoxon tests, W = 89 and 93, respectively). At recapture, their mass gain estimation was not significantly different between sexes (t-test, t_{18} = −0.6) but showed a higher value in 2016 with 219 ± 43 g than in 2017 with 32 ± 54 g (t-test, t_{29} = 2.6, p = 0.01).

Foraging trips varied greatly in duration (2–315 h), with a skewed distribution towards short trips (mode = 3 h). Brief single-day trips (2–9 h, 26% of the trips) were undertaken close to the colony (6–82 km away) around the narrow peri-insular shelf enclosing this volcanic island (Fig. 1A). Short overnight trips (12–29 h, 27%) were used to forage further (up to 231 km) off the southwest corner of New Zealand's South Island, in neritic, shelf-slope and oceanic waters (Fig. 1B). Multi-day trips (3–14 d, 46%) reached distant locations (up to 1575 km away) in various regions of the New Zealand and Australian shelves, Tasman Sea, south Pacific Ocean and subantarctic waters (Fig. 1C). Nearshore coastal habitats were also used by individuals foraging within the channels between the coastal islands of south-eastern Tasmania, Fiordland and Otago Peninsula (Figs. 1B,C & 3B). Both sexes in both years conducted all 3 types of foraging trips, with sample sizes showing independence between these factors (chi-squared test, χ^2 = 4.3 and 0.6, respectively). In the same way, the trip direction bearing did not differ significantly between sex or year (circular ANOVA, p > 0.1 in both cases). Models investigating the influence of year and sex on the trip parameters revealed no significant influence for single-day and overnight trips, but significant influences for multi-day trips (Table 1). Multi-day trips by males had a shorter duration by 54 ± 23 h (p < 0.05), covered shorter total distance by 1565 ± 494 km (p < 0.01) and reached closer maximum distance from the colony by 411 ± 124 km (p < 0.05) compared to females, but travelled at the same mean trip speed. Year influenced only the mean trip speed (Table 1), with long trips in 2017 slower by 3.4 ± 1.6 km h⁻¹ (p < 0.05) than in 2016. When recorded, successive trips indicated the presence of multiple foraging strategies. Primarily, a dual short–long trip strategy was noted for 14 individuals, alternating 1 multi-day trip with 1 or several shorter ones towards different areas (Fig. 3A). Secondarily, short-term consistency was noted for 4 individuals repeating trips within the same areas (Fig. 3B). The remainder (3 individuals) undertook 2–3 single-day and overnight trips with no clear patterns.
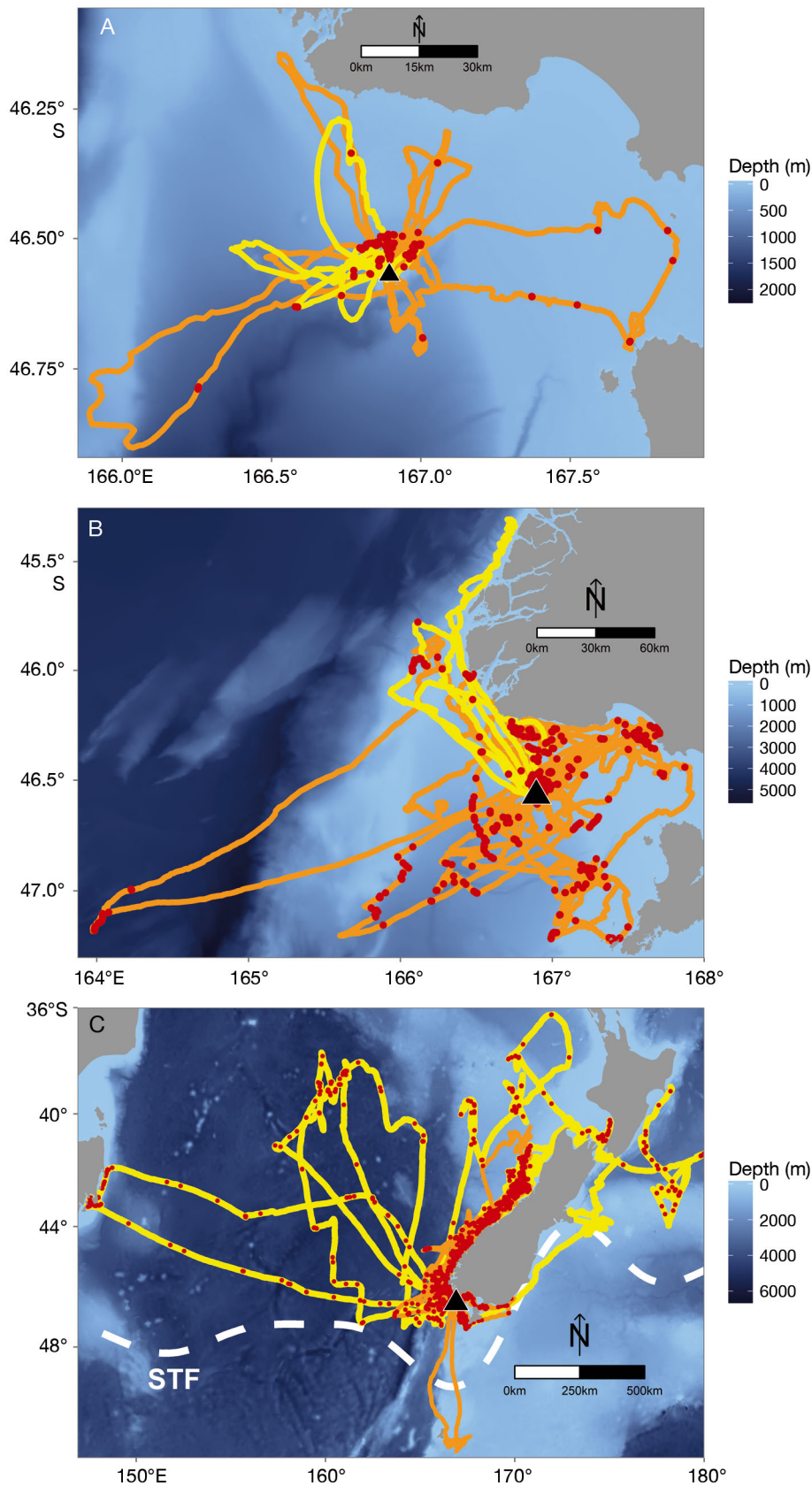
Fig. 1. At-sea movements of breeding southern Buller's albatrosses during the post-guard stage at Hautere/Solander Island in 2016 and 2017: (A) single day, (B) overnight and (C) multiple-day trips. Line colours represent sex (orange: males, yellow: females) overlaid with red dots representing the foraging events when acceleration data were available. Land is shaded in grey and the colony site is shown by the black triangle. In panel C, the dashed white line represents the average position of the subtropical front (STF), estimated by the 10°C sea surface temperature isotherm (Heath 1985) observed during the tracking periods. Note the different scales in each panel

Table 1. Summary of the model outputs used to assess the trends in activity budget and foraging trip parameters of breeding southern Buller's albatrosses at Hautere/Solander Island. These linear mixed models include individual identity as random effect. **Bold:** explanatory variables with significant p-values

Response variable	Explanatory variables	Parametric coefficients			p
		Est.	SE	*t*	
% time spent rafting on water	Intercept	6.9	3.4	2.0	0.04
	Sex (male)	4.2	3.4	1.2	0.22
	Year (2017)	4.8	3.3	1.4	0.16
	Period of the day (day)	**6.3**	**2.3**	**2.6**	**<0.01**
	Period of the day (dusk)	**8.1**	**2.5**	**3.2**	**<0.01**
	Period of the day (night)	**48.8**	**2.3**	**20.3**	**<0.001**
% nocturnal time spent rafting on water	Intercept	32.9	5.5	5.9	<0.001
	% moon illuminated	18.8	7.7	2.4	0.01
	Year(2017)	**−10.5**	**4.8**	**−2.1**	**0.03**
% time spent foraging	Intercept	0.17	0.04	4.3	<0.001
	Sex (male)	**0.13**	**0.03**	**3.6**	**0.001**
	Year (2017)	**−0.08**	**0.03**	**−2.3**	**0.02**
	Period of the day (day)	**0.11**	**0.03**	**3.03**	**0.002**
	Period of the day (dusk)	−0.04	0.04	−1.04	0.3
	Period of the day (night)	−0.02	0.03	−0.5	0.5
Nocturnal landing rate	Intercept	1.2	0.1	7.7	<0.001
	Moon illumination	0.2	0.2	0.9	0.3
	Year(2017)	**0.5**	**0.1**	**3.0**	**0.005**
Trip duration (single day)	Intercept	2.9	0.8	3.6	0.004
	Sex (male)	0.75	0.9	0.8	0.4
	Year (2017)	0.5	0.9	0.6	0.5
Trip duration (overnight)	Intercept	17.3	3.0	5.7	<0.001
	Sex (male)	4.2	3.1	1.3	0.2
	Year (2017)	−0.8	2.2	−0.3	0.7
Trip duration (multiple days)	Intercept	154.4	21.3	7.2	<0.001
	Sex (male)	**−54.7**	**23.2**	**−2.3**	**0.02**
	Year (2017)	−8.9	22.6	−0.4	0.6
Total distance travelled (single day)	Intercept	35.8	24.8	1.4	0.1
	Sex (male)	22.6	27.9	0.8	0.4
	Year (2017)	49.8	27.9	1.7	0.1
Total distance travelled (overnight)	Intercept	323.0	96.5	3.3	0.006
	Sex (male)	−36.5	71.6	−0.5	0.6
	Year (2017)	−1.6	101.3	−0.01	0.9
Total distance travelled (multiple days)	Intercept	3686	452	8.1	<0.001
	Sex (male)	**−1565**	**494**	**−3.1**	**0.004**
	Year (2017)	−858	484	−1.7	0.08
Max. distance from the colony (single day)	Intercept	13.9	11.6	1.1	0.2
	Sex (male)	15.3	13.0	1.1	0.2
	Year (2017)	7.3	12.7	0.5	0.5
Max. distance from the colony (overnight)	Intercept	115.3	27.5	4.1	0.001
	Sex (male)	−39.8	28.9	−1.3	0.2
	Year (2017)	−19.3	20.4	−0.9	0.3
Max. distance from the colony (multiple days)	Intercept	738	112	6.5	<0.001
	Sex (male)	**−411**	**124**	**−3.3**	**0.02**
	Year (2017)	51	122	0.4	0.6
Average trip speed (single day)	Intercept	12.7	4.3	2.9	0.01
	Sex (male)	9.4	4.8	1.9	0.07
	Year (2017)	4.8	4.7	1.0	0.3
Average trip speed (overnight)	Intercept	19.2	3.5	5.4	<0.001
	Sex (male)	−4.8	3.7	−1.3	0.2
	Year (2017)	−1.6	2.6	−0.6	0.5
Average trip speed (multiple days)	Intercept	23.0	1.4	15.5	<0.001
	Sex (male)	−2.3	1.6	−1.4	0.1
	Year (2017)	**−3.4**	**1.6**	**−2.1**	**0.04**

Individuals spent most of their time at sea in soaring flight (53.3 ± 2.6%), followed by rafting (floating) on water (42.0 ± 2.4%). Flapping flight represented 4.3 ± 0.5% of the time and foraging behaviour only 0.30 ± 0.03%. Birds spent most of their time engaged in behaviours with low vectorial dynamic body acceleration (Table 2). LMMs revealed that the percentage of time spent on water was not influenced by sex or year, but was significantly influenced by the period of the day with an increase of >40% at night (p < 0.001, Table 1) at the expense of flying behaviours (Table 2). Conversely, the proportion of time spent foraging was significantly influenced by sex, year and period of the day, with higher proportion for males than females (p = 0.001), higher proportion during the day than other periods of the day (p < 0.01), and lower proportion in 2017 than 2016 (p = 0.02, Table 1). The time spent foraging and the landing rate showed similar trends during a day (Fig. 2). Individuals displayed an average landing rate of 0.70 ± 0.02 h^{-1} during their trips, that reached 0.99 ± 0.04 h^{-1} during daylight and that decreased to 0.61 ± 0.05 h^{-1} at twilight and to 0.51 ± 0.02 h^{-1} at night. During night-time recorded through all the moon phases, LMMs showed that the illuminated fraction of the moon had no significant influence on the percentage of time spent foraging and the landing rate, but positively influenced the percentage of time spent flying (p = 0.01, Table 1).

3.2. Foraging behaviour and trophic niche

During these at-sea movements, a total of 6658 foraging behaviour events were inferred, between 1 and 551 trip^{-1} according to their duration. These foraging events lasted between 1 and 60 s, with a highly skewed distribution towards short durations (94% of events were <10 s, mode = 2 s). They were spread along the entire trip, with no clear bias between the outward, central and inward phases of the trips
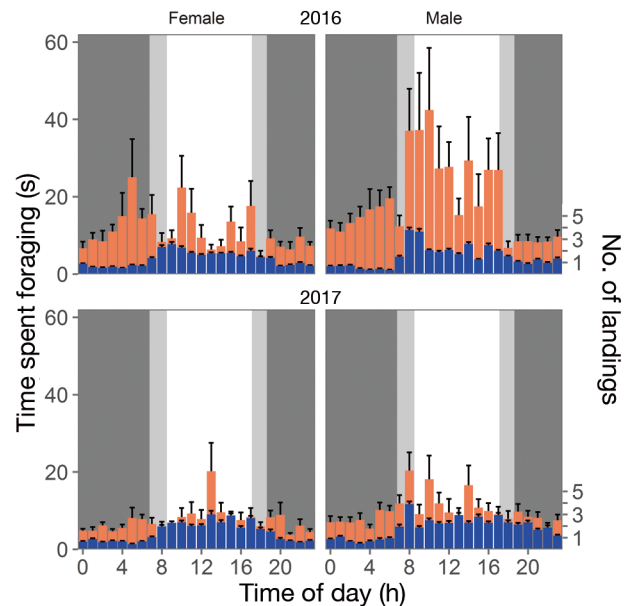

Fig. 2. Temporal distribution of average (mean ± SE) foraging time (orange) and landing rate (blue) during southern Buller's albatross foraging trips during the chick-rearing stage. Shaded areas in the background represent the twilight periods (dawn and dusk, light grey) and night (dark grey) during the tracking periods. Time of day is New Zealand local time

(Fig. 1). These foraging events occurred in short periods of activity (bouts), with the time interval skewed towards short values. Inspection of the time interval distribution indicated that events separated by less than 660 s were likely to be clustered within the same foraging period (Fig. S3). Applying this threshold, SBA foraging occurred at a rate of 0.44 ± 0.02 periods h^{-1} that were separated by a variable geographic (straight line) distance between 0.09 and 490 km. LMM revealed that this distance was not significantly influenced by year and sex (Table 3).

While individuals spent their overall time at sea in neritic waters (<200 m, 38.2%), in slope waters (200–1000 m, 36.4%), in bathyal waters (1000–2000 m, 8.0%) and in abyssal waters (17.2%), their time spent

Table 2. Activity patterns during southern Buller's albatross foraging trips and associated vectorial dynamic body acceleration (VeDBA) values (mean ± SE) sampled at post-guard stage (n = 26 individuals, 64 trips, 3700 h at sea). Values in **bold** highlight the majority of time in each period of the day

Behaviour	Proportion of time at sea (%)				VeDBA s^{-1} (g)
	Dawn	Day	Dusk	Night	
Floating	11.1 ± 0.8	23.5 ± 1.2	17.7 ± 1.0	**60.4 ± 1.3**	0.16 ± (4 × 10^{-5})
Soaring flight	**85.6 ± 0.9**	**72.2 ± 1.3**	**79.7 ± 1.1**	38.1 ± 1.3	0.17 ± (5 × 10^{-5})
Flapping flight	2.9 ± 0.3	3.6 ± 0.2	2.2 ± 0.2	1.1 ± 0.1	0.26 ± (9 × 10^{-5})
Foraging	0.25 ± 0.02	0.48 ± 0.03	0.22 ± 0.02	0.24 ± 0.008	0.47 ± (2 × 10^{-3})

Table 3. Summary of the model outputs used to assess the trends in foraging behaviour of breeding southern Buller's albatrosses at Hautere/Solander Island. The linear mixed model (LMM) and generalised additive mixed model (GAMM) include individual identity as a random effect; edf: estimated degrees of freedom. (–) Not applicable. **Bold**: explanatory variables with significant p-values (p < 0.05)

| Model	Response variable	Explanatory variables	Parametric coefficients			Approximate significance of smooth terms		p
			Est.	SE	t	edf	F	
LMM	Interval distance between foraging events	Intercept	47.2	6.4	7.3	–	–	<0.001
		Sex (male)	−5.7	3.9	−1.4	–	–	0.16
		Year (2017)	−0.2	3.8	−0.07	–	–	0.9
		Period of the day (day)	9.9	5.1	1.9	–	–	0.05
		Period of the day (dusk)	**17.2**	**6.5**	**2.6**	**–**	**–**	**0.009**
		Period of the day (night)	4.0	5.1	0.7	–	–	0.4
		Marine habitat (neritic)	**−35.3**	**3.9**	**−8.8**	**–**	**–**	**<0.001**
		Marine habitat (slope)	**−25.0**	**4.0**	**−6.2**	**–**	**–**	**<0.001**
		Marine habitat (bathyal)	−15.9	3.9	−1.4	–	–	0.1
GAMM	Log(standardised time spent foraging)	Wave height	–	–	–	2.6	2.3	0.06
		Sea surface temperature	**–**	**–**	**–**	**6.1**	**6.5**	**<0.001**
		Mixed layer thickness	**–**	**–**	**–**	**4.4**	**3.6**	**<0.01**
		Depth	**–**	**–**	**–**	**3.5**	**6.5**	**<0.001**
		Seafloor slope	**–**	**–**	**–**	**1.0**	**11.4**	**<0.001**
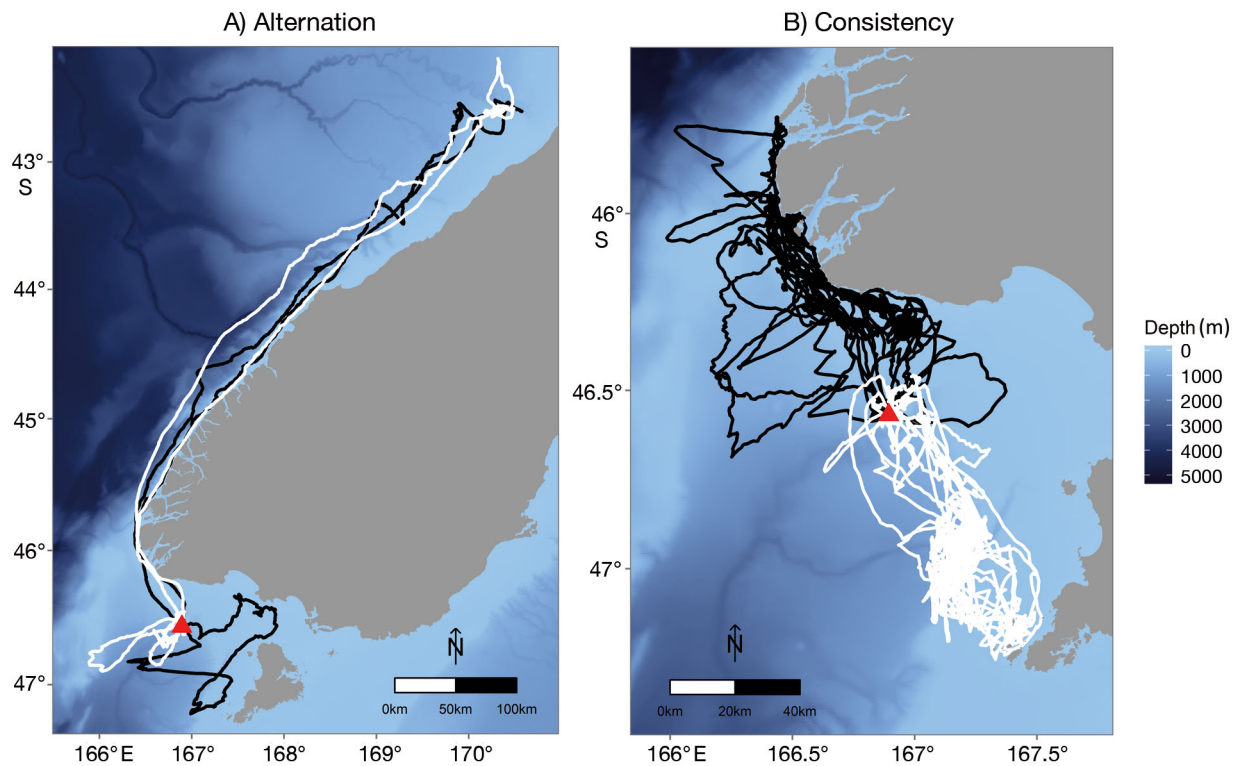
Fig. 3. Foraging strategies used by southern Buller's albatrosses (2 representative individuals, black and white tracks [different individuals shown in each panel]) over several successive foraging trips: (A) alternation of short/long trips; (B) consistency of the individuals' foraging patterns. Red triangle: colony location. Note the different scales in each panel

foraging was concentrated in neritic waters (47.9%), followed by slope (34.6%), abyssal (10.5%) and bathyal waters (6.9%). These marine habitats significantly influenced the geographic distance separating foraging periods (p < 0.001), with the greatest dis-

tances observed in descending order in abyssal (55 ± 5 km), bathyal (33 ± 5 km), slope (23 ± 1 km) and neritic waters (14 ± 1 km). The period of day also significantly influenced this distance (p < 0.001), that was greater at dusk (p < 0.001, Table 3). Foraging behav-

iour occurred under a wide range of sur-
face oceanographic conditions, varying
in temperature between 9.8 and 20.1°C,
agitated by winds of between 0.2 and
17.7 m s^{-1}, with wave heights between
0.5 and 7.8 m and current speed ranging
from 0 to 0.6 m s^{-1}. The sea surface chl *a*
concentration varied between 0.08 and
3.2 mg m^{-3}, and the mixed layer depth
ranged between 7 and 202 m. The
GAMM revealed that time spent forag-
ing was influenced by the 5 following
oceanographic variables (Table 3): the
mixed layer deepening beyond 50 m
had a positive effect while the wave
height and the seafloor slope (superior
to 2.5°) had a negative effect. The depth
increase had a negative effect in neritic
and slope waters and a variable effect
with large confidence intervals in ba-
thyal and abyssal waters. Sea surface
temperature had contrasting effects,
positive for cold (10–12.5°C) and warm
(17–20°C) temperatures, but negative
between these values (Fig. 4).

There was little variation in δ^{15}N and
δ^{13}C values (Fig. 5). All individuals fed
at a high trophic level characterised by
δ^{15}N = 14.7 ± 0.3‰, with the exception
of 1 individual. This lower outlier (δ^{15}N =
12.8‰, Fig. 5) was the only individual
foraging in subantarctic waters, to
−51.2°S (Fig. 1C). Given the isotopic
baseline variation between subtropical
and subantarctic water masses (Quill-
feldt et al. 2005) biasing their com-
parison, this atypical individual was
excluded from further analysis. In sub-
tropical waters, δ^{15}N values showed mi-
nor differences between sexes (ANOVA,
p < 0.001) with δ^{15}N = 14.9 ± 0.4‰ for

males and 14.5 ± 0.2‰ for females (mean ± SD) but
not between years. δ^{13}C values showed minor differ-
ences between sexes and years (ANOVA, respectively
p = 0.01 and 0.004) with −18.6 ± 0.3 ‰ for females, −18.4
± 0.2 ‰ for males, −18.3 ± 0.2 ‰ in 2016 and −18.6 ±
0.3 ‰ in 2017. Consequently, the isotopic niches were
estimated by ellipses for each sex and year combina-
tions (Table 4, Fig. 5). The ellipse areas ranged from
0.08 to 0.30‰^{2}, with differences between groups; fe-
males were likely to have smaller ellipse areas than
males in any year. Within sexes, opposite inter-annual
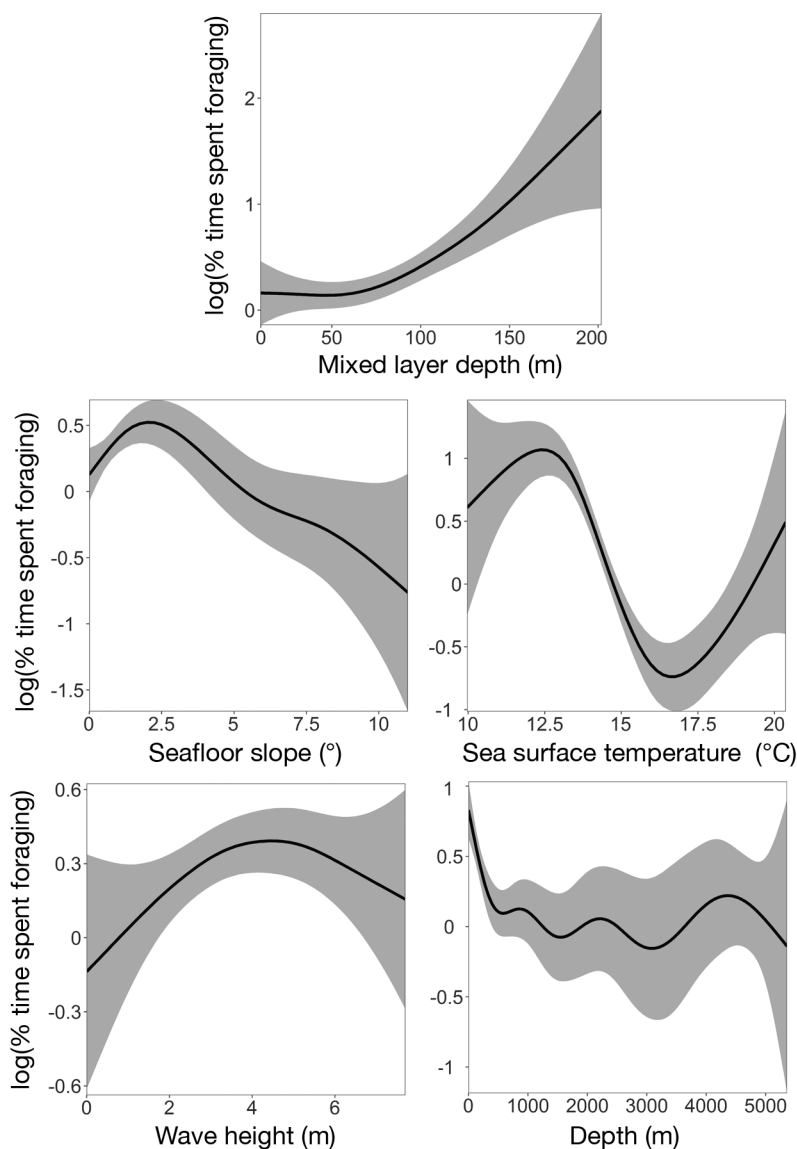differences occurred, with males likely to have a

Fig. 4. Influence of oceanographic variables on the standardised time spent
foraging of southern Buller's albatrosses, predicted by generalised additive
mixed modelling (GAMM) during the post-guard stage at Hautere/Solander
Island. The grey area indicates the 95% confidence interval

smaller ellipse in 2017, and conversely, females likely
to have a smaller ellipse in 2016 (Table S3). The
grouped isotopic results generated ellipse overlaps,
which were, in descending order, greatest for males
between years, sexes within year, sexes between
years and females between years (Table S3).

4. DISCUSSION

Using 2 years of GPS, accelerometer, isotopic and
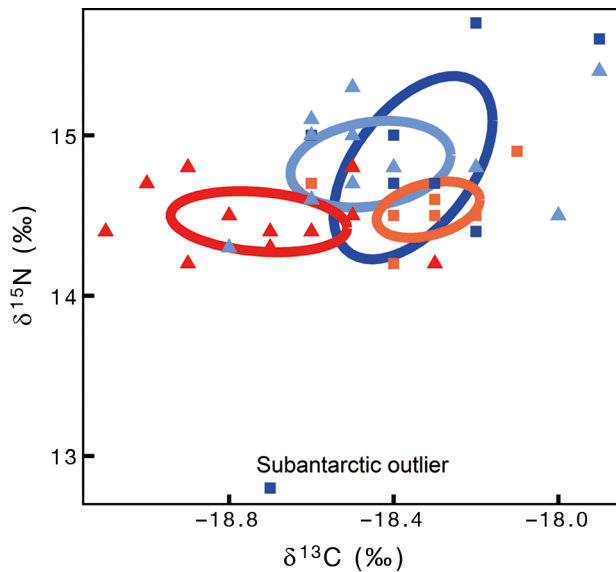oceanographic data, the present study provided fine-

Fig. 5. Isotopic values and niches (from whole blood) of breeding southern Buller's albatrosses provisioning chicks at Hautere/Solander island. Shown are data from males in 2016 (dark blue squares), males in 2017 (light blue triangles), females in 2016 (coral squares) and females in 2017 (red triangles). The isotopic niches of these groups are represented by the 40% corrected standard ellipse area (SEAc)

scale information on the foraging behaviour, and its drivers, of chick-rearing SBAs during winter. Individuals foraged primarily on the New Zealand South Island peri-insular shelf in neritic and slope waters. Parents alternated long and short foraging trips, including repeated trips within the same area and very brief single-day trips in waters surrounding the colony. During their trips, their activity budget was typical for albatrosses, and was primarily influenced by the period of the day. Foraging behaviour represented only a small proportion of their time, and occurred in short bouts spread over an entire trip, with increased foraging during daytime. Although males and females shared this foraging strategy in both years, some differences between the sexes occurred. Males were engaged in shorter long trips and spent

more time foraging than females. The isotopic results were clustered together and showed only minor variation for $\delta^{13}C$ and $\delta^{15}N$ between sexes and years. While their foraging effort was comparable to other albatross species, time spent foraging was influenced by static and dynamic oceanographic variables, including depth, seafloor slope, mixed layer thickness, wave height and sea surface temperature.

4.1. At-sea movements and activity budget

The marine areas exploited in the present study are consistent with those previously reported for the species (Sagar & Weimerskirch 1996, Stahl & Sagar 2000a,b, Torres et al. 2013). However, while previous studies during chick rearing found individuals remaining within a restricted range around the colony (Stahl & Sagar 2000a,b), individuals in the present study covered a wider range that expands the known foraging range of SBAs during the post-guard stage. In addition, some individuals were observed to circumnavigate the New Zealand South Island and frequent the east coast of the North Island, which is consistent with previous ship-borne observations (Stahl et al. 1998). These findings suggest that inter-annual availability in prey distribution may alter the foraging areas of breeding birds. Fine-scale records of single day, overnight and multiple-days trips confirmed the brief, short and long foraging trips described by Stahl & Sagar. (2000b). The finer resolution provided by the GPS in the present study also revealed undocumented very short foraging trips in close proximity to the colony. This strategy seems uncommon for far-ranging large and small albatrosses, which usually forage for several days at greater distances from the colony during chick-rearing (Torres et al. 2011, Pereira et al. 2018, Sztukowski et al. 2018, Thiebot et al. 2018).

Despite foraging areas shared between sexes, the shorter and closer foraging trips undertaken by

Table 4. Isotopic values (whole blood, mean ± SD) of male and female southern Buller's albatrosses provisioning chicks at Hautere/Solander Island recorded in 2016 and 2017. Isotopic niche widths are reported for 40% corrected standard ellipse area (SEAc) and Bayesian standard ellipse area (SEA$_B$). The total did not include the one outlier

Year	Sex	N	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	SEA$_C$ (‰^{2})	SEA$_B$ (‰^{2})
TOTAL (- outlier)		40	−18.4 ± 0.2	14.7 ± 0.3	0.29	0.28
2016	Male	9	−18.3 ± 0.2	14.9 ± 0.4	0.30	0.27
2016	Female	7	−18.3 ± 0.1	14.5 ± 0.2	0.12	0.08
2017	Female	11	−18.7 ± 0.2	14.4 ± 0.2	0.17	0.14
2017	Male	13	−18.4 ± 0.2	14.8 ± 0.3	0.26	0.19

Table 5. Comparative activity pattern (percentage of time, mean ± SD) of albatrosses tracked with activity-recorder loggers. The number of tracked individuals and their chick-rearing (CR) stage is further indicated when available (G: guard; PG: post-guard). In the percentage flying column, values in *italics* represent the values back-calculated from the reported percentage on water reported (100 – percentage). Data are sourced from (1) Prince & Francis (1984), (2) Weimerskirch & Guionnet (2002), (3) Catry et al. (2004b), (5) Hedd et al. (2001) and (6) Kappes et al. (2015); na: data not available

Species	Breeding stage	N	Daytime			Night-time			Source
			Percentage of time Flying	On water	Landings h⁻¹	Percentage of time Flying	On water	Landings h⁻¹	
Grey-headed albatross *Thalassarche chrysostoma*	CR	13	84.9	15.1 ± 9	na	50.1	49.9 ± 14.6	na	1
	PG	4	*84.9*	*15.1*	0.74	*38.1*	*61.9*	0.59	2
	CR	4	*81 ± 16*	*19*	0.99 ± 0.3	*6*	*94 ± 7*	0.14 ± 0.1	3
Black-browed albatross *T. melanophrys*	PG	4	85.7	14.3 ± 6	na	9.5	90.5 ± 4	na	4
	PG	6	*76.0*	*24*	0.98	*32*	*68*	0.67	2
Indian yellow-nosed albatross *T. chlororhynchos*	PG	12	78.9	21.1 ± 7	na	30	70.0 ± 6	na	4
	PG	9	*70.0*	*29.9*	1.26	*16.6*	*83.31*	0.69	2
Shy albatross *T. cauta*	G	21	73.4	26.6 ± 16	na	53.7	46.3 ± 29	na	5
Southern Buller's albatross *Thalassarche b. bulleri*	PG	26	75.8 ± 6	23.5 ± 6	0.99 ± 0.0	39.2 ± 6	60.4 ± 6	0.51 ± 0.0	This study
Dark-mantled sooty albatross *Phoebetria fusca*	G	3	*78.1*	*21.9*	0.40	*39.2*	*60.8*	0.20	2
Light-mantled sooty albatross *P. palpebrata*	PG	3	78.4	21.6 ± 6	na	42.5	57.5 ± 9	na	4
Wandering albatross *Diomedea exulans*	PG	17	67.5	32.5 ± 12	na	28.9	71.1 ± 18	na	4
Laysan albatross *Phoebastria immutabilis*	PG	34	86.8 ± 9	13.2	1.01 ± 0.5	66.8 ± 19	33.2	0.64 ± 0.4	6
Black-footed albatross *P. nigripes*	PG	26	86.9 ± 7	13.1	0.84 ± 0.2	73.0 ± 12	27	0.46 ± 0.1	6

males during the post-guard stage contributed to fine-scale spatial segregation (Pereira et al. 2018) for a species with little sexual dimorphism (Sagar et al. 1998). Shorter trips by males were consistent with earlier observations of the species (Stahl & Sagar 2000b). The tracked individuals displayed some flexibility in their at-sea movements, with usage of different strategies. Alternating between short and long trips is a bimodal strategy observed in many Procellariiformes, and enables parents to maximise food delivery to the chick and restore parental body condition (Baduini & Hyrenbach 2003). Repeated successive short trips consistently within the same area is a strategy used when the environment is predictable (Weimerskirch 2007). Using both strategies, at-sea movements of SBAs appear to be intermediate between the closely related shy albatross *Thalassarche cauta*, a resident species using year-round predictable areas of the south-east Australian continental shelf (Hedd & Gales 2005), and migratory congeners or oceanic species (*Diomedea*) able to adapt to a wider range of oceanographic conditions. Further tracking data over longer durations with accurate measures of chick provisioning and prey content would be required to fully understand the respective advantages of these foraging strategies used by SBAs.

During these at-sea movements, the activity budget obtained from fine-scale acceleration data allowed comparison with previous albatross studies that have inferred time spent in flight, on water and landings from GLS (geo-locator light sensor) wet/dry data loggers. In the present study, SBA flight, landing on water and foraging activities occurred throughout all times of the day and night, but were more frequent during the daylight hours. This activity pattern reflects the constraint of available light for these visual predators (Weimerskirch & Wilson 1992) and is typical for albatrosses (Table 5). The SBA activity budget did not differ between the sexes, as reported for other albatross species (Phalan et al. 2007). Their landing rate (index of foraging activity) and proportion of time spent on water was similar to values reported for shelf-specialised black-browed *T. melanophrys* and shy albatrosses (Weimerskirch & Guionnet 2002, Phalan et al. 2007). In contrast, oceanic species appear more variable, with some displaying higher rates of landings (Indian yellow-nosed *T. chlororynchos*, wandering *D. exulans*, royal *D. epomophora* and Amsterdam *D. amsterdamensis* albatrosses; Weimerskirch & Guionnet 2002, Waugh & Weimerskirch 2003), others displaying lower rates (light-mantled sooty albatross *Phoebetria palpebrata*;

Weimerskirch & Guionnet 2002), and some with different amounts between day and night (grey-headed albatross *T. chrysostoma*; Catry et al. 2004b). These comparisons suggest that SBA landing rate and proportion of time on water did not increase in response to reduced daylight hours (Systad et al. 2000) compared to summer breeding congeners.

4.2. Foraging behaviour and trophic niche

The location of foraging events from acceleration in the present study provided novel insights into how the species obtains its daily food intake, previously estimated at 750 g d^{-1} for similar-sized albatrosses (Catry et al. 2004b). In space and time, foraging behaviour occurred throughout the trips and at any time of the day, suggesting widely distributed prey in space and time. However, foraging bouts occurred mainly in bursts during periods that were separated in space and time by short intervals. These findings suggest feeding on aggregated and patchy prey, which was variable according the period of the day and the marine habitat (intervals were longer at dusk and in oceanic waters). This patchiness is also consistent with the previously reported opportunistic and localised feeding on prey captured by marine mammals (Bräger 1998), in interactions with fishing vessels (Torres et al. 2013) or on offal from shearwater harvesting discharged at sea (Waugh et al. 2017) that can represent an alternative food source for SBAs during the chick-rearing period.

The quantification of the foraging behaviour showed reduced nocturnal foraging activity, while mainly rafting on the sea surface suggests a secondary 'sit and wait' foraging technique (Weimerskirch et al. 1997). The lack of a relationship between moonlight illumination and time spent foraging at night further suggests that this strategy may be opportunistic. Such nocturnal foraging in the grey-headed albatross has been reported to lead to smaller meals with prey of higher water content (e.g. salps, jellyfish; Catry et al. 2004b). Hence, SBAs could focus on bioluminescent and vertically migrating prey reaching the surface at night, such as bioluminescent salps (Swift et al. 1977, Andersen & Sardou 1994), which are reported to be an abundant prey item in SBA diet (James & Stahl 2000). In addition, the quantification of the foraging behaviour revealed a difference between the sexes, with males providing a higher foraging effort than females. In combination with their shorter long trips (and thus, more frequent visits to the chick), these

findings are consistent with the asymmetrical parental investment reported in both summer- and winter-breeding albatrosses, where males engage more frequently in short trips than females, and deliver more food to the chick (Weimerskirch et al. 1997, Weimerskirch & Lys 2000, Hedd & Gales 2005, Phillips et al. 2017). Therefore, male SBAs are likely to be more involved in chick provisioning during winter than females. In addition, inter-annual variation occurred, with less time spent foraging in 2017, in association with a lower mass gain estimation and slower foraging trips. These findings suggest lower food availability in 2017, likely related to inter-annual changes in the marine environment (individuals foraged in waters characterised by sea surface temperatures of 14.9 ± 0.07°C in 2016 vs. 13.9 ± 0.04°C in 2017). However, tracked individuals relied heavily on the shelf and slope waters in both years of the study, a common feature with many summer-breeding congeners: black-browed (Cherel et al. 2000, Wakefield et al. 2011), Chatham *T. eremita* (Deppe et al. 2014), white-capped *T. steadi* (Torres et al. 2011), shy (Hedd et al. 2001), Indian yellow-nosed *T. carteri* (Makhado et al. 2018) and Campbell *T. impavida* (Waugh et al. 1999, Sztukowski et al. 2018) albatrosses. In contrast, the grey-headed albatross exploits deeper pelagic waters in association with the polar frontal zone (Waugh et al. 1999, Nel et al. 2001, Catry et al. 2004b).

The higher foraging activity found in neritic waters in the present study suggests that the New Zealand shelf provides a predictable concentrated winter prey resource, which is likely to induce foraging site fidelity (Stzukowski et al. 2018) in SBAs. Modelling revealed that foraging time was greater on the shelf in areas with shallow depths and gentle seafloor slope, where the mixed layer deepens, with additional influence of sea surface temperature and wave height. These findings reinforce the reliance by the species on the shelf, where dynamic mixing occurs at a fine spatio-temporal scale (Vincent et al. 1991) and is likely to influence the availability of SBA prey.

Prey capture rates in pelagic foraging grey-headed albatrosses were not influenced by wave height (Catry et al. 2004a). In contrast, wave height had a negative influence on time spent foraging by SBAs, which happened primarily in neritic waters. This suggests potentially different environmental drivers of foraging suitability between pelagic and neritic habitats. For the Tasman Sea, the projected response to climate change predicts intensification of currents and increases in eddy activity (Matear et al. 2013). These conditions increased the prey encounter rate

in oceanic-feeding wandering albatrosses, as a result of windier conditions (Weimerskirch et al. 2012). However, whether increased eddies with windier and higher wave regimes mixing the upper ocean more could positively or negatively impact SBA foraging in different marine habitats needs further research.

The isotopic investigation of the trophic niche corroborated the GPS results obtained in the present study, with δ^{13}C values consistent with subtropical/subantarctic water signatures (Cherel & Hobson 2007). The δ^{15}N values were also consistent with the diet of SBAs, composed (by weight) of 65% fishes, 24% salps and 7% cephalopods (James & Stahl 2000); as well as with the δ^{15}N values characterising a fish-dominated diet in New Zealand inshore waters (Flemming & Van Heezik 2014). Despite the SBA generalist diet including 89 prey items from 3 trophic levels (West & Imber 1986, Cherel & Klages 1998, James & Stahl 2000), its isotopic niche measured in the present study was narrow, suggesting a proportional consumption of similar prey types by individuals. In other albatross species, δ^{13}C and δ^{15}N values display a greater variability (Bugoni et al. 2010, Jaeger et al. 2010) and greater ellipse areas (Jiménez et al. 2017), with no difference between sexes from feathers and blood cell isotope data (Phillips et al. 2011). While the difference in δ^{15}N between sexes in the present study is minor (0.4‰), it could relate to the propensity for females to feed more on cephalopods and crustaceans than males (James & Stahl 2000). In addition, while fisheries discards are an important food item of SBAs (James & Stahl 2000), a higher δ^{15}N in male blood by 0.6‰ was reported for the waved albatross *Phoebastria irrorata* when male-biased access to fishery discards occurred (Awkerman et al. 2007). Despite limited SBA interaction with fishing vessels being reported during the guard stage at The Snares Islands (Torres et al. 2013), these findings could indicate more interaction happening at Solander during the post-guard stage. Indeed, this period coincides with the hoki *Macruronus novaezelandiae* trawling season (New Zealand's largest trawl fishery), an SBA prey with high energetic value (Schaafsma et al. 2018) that can be targeted to feed the chick. While feeding on fisheries discards can be beneficial for the population (James & Stahl 2000), SBAs are also considered to be at 'very high risk' of commercial fishing-related mortality (Richard & Abraham 2013). Therefore, further year-round tracking data of both birds and vessels are needed to determine with more accuracy the cost–benefit of this complex interaction.

In summary, the present study revealed that SBAs rely heavily on the neritic and slope waters of the New Zealand South Island to provision their chicks through the austral winter, but also displayed some variability in foraging strategies, with excursions further into oceanic waters. During these trips, there was no evidence of increased foraging effort or nocturnal compensation for shorter day length. Instead, a high foraging event rate and activity level were recorded, comparable to that found in summer-breeding albatrosses. Hence, foraging conditions on the New Zealand shelf are not only favourable for other albatrosses during summer (Waugh et al. 1999), but also during winter for SBAs, which may benefit from the presence of shoaling and spawning prey (Zeldis 1985, Uozumi & Forch 1995, Daponte et al. 2013). In addition, SBAs may benefit from the release of competition with New Zealand summer-breeding species. Indeed, millions of pairs of petrels, shearwaters and prions, as well as >200 000 pairs of *Thalassarche* spp. (Waugh et al. 2013, Jamieson et al. 2016, Miskelly et al. 2019, our unpublished data) vacate their colonies in winter and shift to their non-breeding distributions (Shaffer et al. 2006). Therefore, winter foraging off the New Zealand coast seems an efficient adaptation to the year-round prey availability across the South Pacific basin for this longitudinal migratory species (Stahl & Sagar 2000b).

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