

Cross-seasonal foraging site fidelity of subantarctic fur seals: implications for marine conservation areas

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ABSTRACT: Marine top predators show fidelity to foraging areas with predictable high-quality food patches. Areas of predictable prey yield are of conservation importance, and telemetry data aid in identifying such areas. This study examined colony-specific and intra-individual foraging site fidelity of lactating subantarctic fur seals *Arctocephalus tropicalis* from Marion Island, Southern Ocean (46° 54' S, 37° 45' E), during summer and winter, comparing commitment to foraging areas across seasons. Thirty females were tracked in 2009–2013, resulting in 109 foraging trips for analyses. Inter-annually, preferred foraging areas in summer were consistently ~200 km due east of Marion Island towards the Gallieni Rise. Summer individuals' core utilization areas overlapped by an estimated 32.84 % (CI: 24.53–41.94 %). Seals responded to a decrease in regional productivity in winter by foraging in more distant, alternative areas. In winter, individuals changed their travelling direction to northeast of Marion Island and foraged further afield, around the Del Caño Rise and along the Southwest Indian Ridge. Despite preferring some foraging areas in winter, there was a low amount of overlap 6.03 % (CI 4.02–9.16 %) of individual core utilization areas. The foraging grounds identified in this study have not been included in prior conservation assessments and are important for conserving this globally significant, and currently declining, population of subantarctic fur seals and perhaps other top predators breeding at Marion Island as well. Differences between foraging areas preferred in winter and summer highlight the importance of sampling during different seasons when using telemetry data for the identification of potential pelagic conservation areas.

KEY WORDS: *Arctocephalus tropicalis* · Directional preference · Foraging tactic · Habitat utilization · Marine protected area · Marion Island · Satellite telemetry · T-LoCoH

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INTRODUCTION

Identifying marine areas that are of conservation concern requires an intimate knowledge of the processes that link the marine food web (Douvere 2008, Game et al. 2009). Top predators in marine ecosystems provide potentially important platforms to help understand the impacts of varying prey populations, climate change and human harvesting on ecosystems (Furness & Greenwood 1993, Bowen 1997). The consistent use of foraging grounds, i.e. foraging site fidelity, by top predators provides an indirect way to understand the distribution and aggregation of prey ('hot spots') as well as the consistency and overall productivity of

marine resources (e.g. Weimerskirch 2007). Furthermore, conservation plans to mitigate and monitor potential threats to top predators (Harwood 2001) such as Pacific blue-fin tuna *Thunnus orientalis* (Block et al. 2011), leatherback turtles *Dermochelys coriacea* (James et al. 2005), Steller sea lions *Eumatopias jubatus* (Gende & Sigler 2006) and sevengill sharks *Notorynchus cepedianus* (Barnett et al. 2011) have been developed using such data.

High-latitude marine predators live in distinctly seasonal environments where resources are patchily distributed (e.g. Boyd et al. 1994). These predators face challenges in finding food because prey resources can vary seasonally and are often located far

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away. In addition, such prey is also utilized by other marine predators, which impose limitations on the foraging success of individuals, influencing the viability of fidelity to foraging grounds. Despite this heterogeneity in resource distributions, long-distance migrations to and from specific foraging grounds are not uncommon (Stewart & DeLong 1995, Block et al. 2001, Pütz et al. 2006), and many seabird and pinniped species exhibit foraging site fidelity (Bradshaw et al. 2004, Chilvers 2008, Lowther et al. 2012, Augé et al. 2014, Baylis et al. 2015).

Breeding individuals are under greater pressure than non-breeders because they are restricted by the demands of their offspring, either prior to parturition or egg laying or when providing for dependent offspring (Ropert-Coudert et al. 2004). If the parents fail to obtain sufficient resources for their offspring, immediate survival (pre-weaning or pre-fledging) as well as subsequent survival (post-weaning or post-fledging) are jeopardised (Ballard et al. 2010). Additionally, the parents' current and future survival as well as future fecundity may be affected (Weimerskirch et al. 2001, Pistorius et al. 2004, Ballard et al. 2010). Most land-breeding marine predators in the subantarctic are income breeders, which means mothers mainly rely on resources obtained during offspring rearing (Boness & Bowen 1996, Boyd 1998) and alternate foraging trips with periods of suckling or feeding offspring (e.g. albatrosses, fur seals, and penguins; Ashmole 1971, Ricklefs 1983, Boness & Bowen 1996). Female fur seals are limited in the duration of foraging by the fasting capabilities of their pups and their own nutritional demands (Costa 1991, Verrier et al. 2009). Because females commute between foraging grounds and their rookery (i.e. breeding colony beach), prior knowledge of consistently good foraging areas would be advantageous (Boyd et al. 2002). Individuals must decide if the benefits of utilising known foraging patches (albeit of low or average quality) encountered early in the foraging phase outweigh the costs and risks associated with continued searching for higher quality foraging patches in a transient environment (Bonadonna et al. 2001).

Seals and sea lions from the same colonies tend to forage in colony-preferred foraging areas (Bonadonna et al. 2000, Beauplet et al. 2004, Call et al. 2008) and within this larger colony-preferred area, individuals often visit the same areas repeatedly, i.e. individual-preferred foraging areas (Bonadonna et al. 2001, Boyd et al. 2002, Biuw et al. 2009). Fidelity to specific foraging grounds is often associated with local upwelling or productive features in the region

(Skern-Mauritzen et al. 2009, Baylis et al. 2012). Therefore, understanding foraging plasticity is key to understanding foraging strategies of individuals from different colonies and populations (Lea et al. 2008). Identifying key foraging areas or reasons for the lack thereof in breeding individuals within populations could guide conservation efforts (Augé et al. 2014) and be used to plan marine protected areas (MPAs) (Harwood 2001).

However, most of the aforementioned studies on foraging site fidelity were restricted to summer foraging behaviour of lactating females (e.g. Bonadonna et al. 2000, Beauplet et al. 2004, Call et al. 2008). In summer, prey aggregations are more predictable and productivity is higher, especially in high-latitude seasonal environments. Only a few studies on winter foraging site fidelity exist, such as on Antarctic fur seals *Arctocephalus gazella* (Arthur et al. 2015) and king penguins *Aptenodytes patagonicus* (Baylis et al. 2015). Antarctic fur seal females have a short lactation period and are free in winter from the constraints imposed by a pup, but the opposite is true for other otariids that have lengthy lactation periods, e.g. subantarctic fur seals (Kerley 1983). For adequate marine spatial planning, we therefore need to consider not only the spatial interplay between predators and their environment but also the temporal interplay with special consideration of life histories (Hooker & Gerber 2004, James et al. 2005). Roberts et al. (2003) also support the protection of the sensitive life stages of species to conserve marine biodiversity.

Blastocyst implantation occurs in autumn for pinnipeds, and females need to make judicious decisions regarding energy expenditure (Bester 1995). Female subantarctic fur seals *Arctocephalus tropicalis* are central-place foragers with protracted provisioning periods (10 mo; Kerley 1983). During winter they have to provision for the current and future pup (aside from their own demands), all the while dealing with altered resource distribution and availability (Beauplet et al. 2004, Womble & Sigler 2006). Understanding how preferred foraging locations for a marine top predator changes from summer to winter (i.e. from one critical life phase to the next) when resources are less predictable would help build our theoretical knowledge base on how species' life-history could influence marine conservation spatial planning.

To date no study has investigated how foraging site fidelity of conspecifics from the same colony varies seasonally from summer to winter. The subantarctic fur seal, with its 10 mo lactation period, is an ideal study species for such cross-seasonal studies. On

Marion Island, Southern Ocean, female subantarctic fur seals showed no clear seasonal difference in colony-based preferred foraging areas (de Bruyn et al. 2009). Females mostly had direct foraging trips to the northeast of the island predominantly over the Del Caño Rise in 2006/2007, while only a few foraging trips were directed to the west of Marion Island, which were longer and more tortuous (de Bruyn et al. 2009). However, these results were based on a single trip per female of 16 females across 2 years. It was impossible to quantify individual foraging site fidelity. Any understanding of the 2 different colony-preferred foraging areas would have been overshadowed by individual variation in a small sample.

In this study we ask the following: (1) Do lactating subantarctic fur seals display both individual and colony-level foraging site fidelity in both summer and winter? (2) How does the degree of loyalty to a foraging area change from summer to winter? (3) What are the key areas of habitat preference? (4) How does the preferred foraging areas change from summer to winter?

These questions were addressed using spatial telemetry data from 30 individuals, collected over a 5 yr period (2009–2013), with multiple trips recorded per individual. Antarctic fur seal females often forage

along set routes, foraging as they encounter prey instead of foraging in one specific patch or area (Bonadonna et al. 2000, Staniland et al. 2004). For this reason we not only make use of habitat utilization models to identify key foraging areas but also look at preferred travelling directions of subantarctic fur seals from Marion Island.

MATERIALS AND METHODS

Animal handling, instrumentation

Argos satellite-linked data loggers (see Table S1 in the Supplement; www.int-res.com/articles/suppl/m554p225_supp.pdf) were deployed on lactating subantarctic fur seals with dependant pups between the austral winters of 2009 and 2013. Deployments took place at Van den Boogaard beach on the northeastern coastline of Marion Island (Fig. 1; 46° 54' S, 37° 45' E) (see Table S1 for a summary of deployment details). Seals were captured and restrained using a hoopnet, and devices were attached on the dorsal midline pelage just below the scapulae of the animal by means of a double-component, quick-setting epoxy resin (Araldite AW2101, CIBA-GEIGY). Animals

were restrained for a maximum of 30 min to allow the epoxy resin to set (Field et al. 2012) while minimising stress to individuals. Seals carried the devices for the duration of the battery life (on average 4 mo) after which they were recaptured, and the devices were removed by carefully shaving the guard hairs of the fur underneath each device with a scalpel. Summer deployments spanned December to March and winter deployments from April to October.

Filtering tracking data by means of state-space models

Location information relayed through the global ARGOS satellite system contains inherent errors and some erroneous data. To account for this observation error 2-state, behaviourally switching state-space models (SSM) were fitted to Argos tracks (Jonsen et al. 2005). SSMs filtered out erroneous location estimates and interpolated

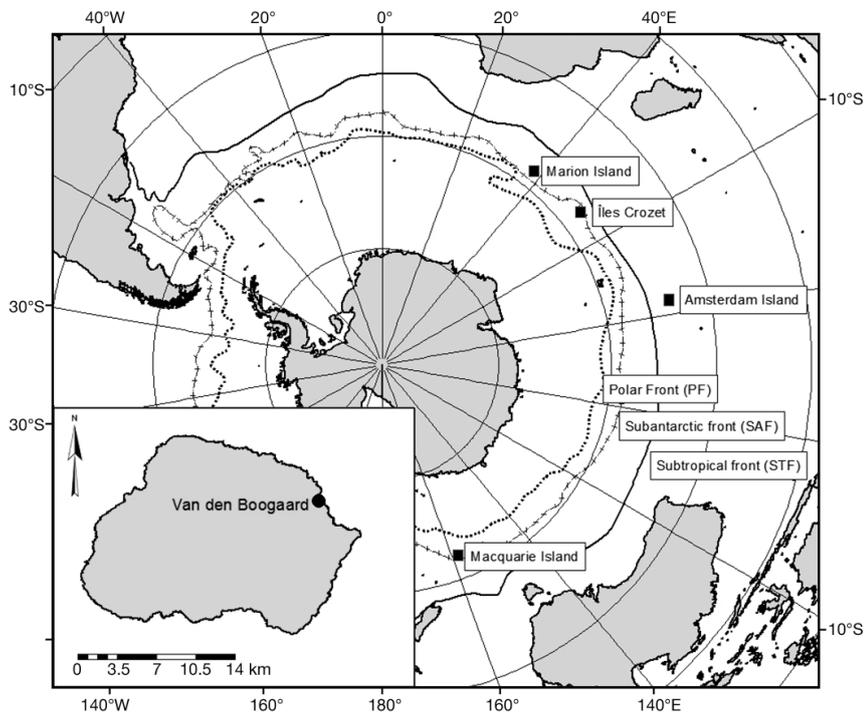


Fig. 1. Position of Marion Island in the Southern Ocean in relation to Îles Crozet, Amsterdam Island and Macquarie Island as well as the Polar Front, Subtropical Front and the Subantarctic Front. Inset: Location of Van den Boogaard beach (study beach) on Marion Island

tracks at a set time interval. SSMs also produce behavioural mode estimates, where one mode corresponds to searching/foraging behaviour and the second mode to travelling behaviour. Prior to analyses all seals' tracks were split into individual foraging trips. Bayesian SSMs were fitted using Markov chain Monte Carlo in 'rjags' (Plummer 2016), via the 'bsam' package (Jonsen et al. 2014), implemented in programme R (R Core Team 2014). A hierarchical formulation allows for estimation of parameters for multiple animals and their individual foraging trips (Jonsen et al. 2006). An inter-step duration of 2.5 h was chosen based on median number of Argos location points per day (9–10 points d^{-1}). We ran 2 Markov chains in parallel, each of 50 000 iterations, using only every 200th value, while the first 10 000 values (i.e. burn-in) were excluded. Diagnostic plots were used to assess converging and appropriate mixing of the 2 Markov chains (Jonsen et al. 2013).

Determining foraging site fidelity and habitat utilisation overlap by means of T-LoCoH

To determine intra-individual and inter-individual habitat utilisation, the Time Local Convex Hull method (T-LoCoH) (Lyons et al. 2013) was used and implemented in programme R with the '*tlocoh*' package (Lyons et al. 2013, R Core Team 2014). T-LoCoH is based upon the non-parametric utilisation distribution construction method: the Local Convex Hull method (LoCoH) (Getz & Wilmers 2004, Getz et al. 2007). LoCoH aggregates nearest neighbour points around each point and constructs minimum convex polygons (local hulls) for each point and then ranks these hulls according to density (Getz & Wilmers 2004, Getz et al. 2007). T-LoCoH reshapes the LoCoH algorithm by incorporating a time stamp of each point at 2 parts of the algorithm: (1) during nearest neighbour selection (the time-scaled distance, a); and (2) sorting of the hulls. The time-scaled distance parameter (s) controls the balance between exclusively space–distance ($s = 0$) and exclusively time–distance ($s = 1$) nearest neighbour selection. We chose s such that 50% of hulls would be time-selected. Other habitat utilization studies, based on kernel density estimation, would discard 'travelling' locations produced by SSMs (e.g. Arthur et al. 2015). However, given the incorporation of time into the T-LoCoH algorithm, we decided to retain all locations regardless of behaviour mode. T-LoCoH nearest neighbours are selected by means of one of 3 methods (Getz et al. 2007), and we chose

the more robust adaptive a -method whereby all points that fall within the time-scaled distance a of the parent point are selected. Variable a was user-defined based on visual methods given in detail by Lyons et al. (2013). Thereafter, hulls are sorted from smallest to largest (size based on number of points enclosed) and then cumulatively merged. Once a union of hulls enclosed $i\%$ of points, the union is saved as the i th isopleth and continues until it reaches an estimate of the 100th percent isopleth (Getz & Wilmers 2004, Getz et al. 2007).

Intra-individual foraging site fidelity: revisitation to and time spent in individual hulls

A time-stamp is incorporated into the T-LoCoH algorithm by sorting of hulls according to re-visitation rates (number of times a hull was visited on separate occasions either within or between foraging trips) and duration of visits (mean number of visits to each hull). These are calculated based on a user-defined inter-hull-visitation-gap (IVG) of 24 h in the present study. Thus, points within a hull that are 24 h apart are considered separate visits. A 24 h IVG was selected because subantarctic fur seals from Marion Island dive exclusively at night (Wege 2013) and travel during the day. If an individual spent the night diving within a hull, did not swim outside the border of the hull, but remained there until the next night of foraging, this was considered to constitute 2 separate visits to the hull. This enables the incorporation of within-foraging trip fine-scale preferences of foraging areas. Those hulls where an individual remained for several days, or foraged one night and returned to it several days later, would constitute important foraging areas. This is an advance over previous foraging site fidelity studies, where foraging trips were treated as singular time–space units (e.g. Bonadonna et al. 2001) which could not consider within-foraging trip site fidelity, as we can (present study).

Inter-individual foraging site fidelity: differences in core and home-range utilization distribution overlap

To compare overlap of foraging areas, the proportion of 50 and 95% isopleth overlap was calculated between individuals. We chose these percentiles because they represent the core area of use and the home-range of an individual, respectively (Burt 1943,

Barraquand & Benhamou 2008). This matrix of overlapping proportions is asymmetrical which means that, for example, Animal ID13 overlaps 20% (0.2) with Animal ID28, but Animal ID28 overlaps 68% (0.68) with Animal ID13. We created multi-level categorical identifiers based on the interaction between (1) season ('season interaction') and (2) year ('year interaction') each of the 2 overlapping individuals occurred in. This means that for the 'season interaction' between individuals there are 4 possible levels: summer–summer, summer–winter, winter–summer, winter–winter. The season given first is the season in which the first animal's 50 or 95% isopleth overlaps with the second animal's season in which it was tracked, i.e. summer–winter refers to a summer animal's proportion overlap with a winter animal, whereas winter–summer refers to a winter animal's proportion overlap with a summer animal. The same logic applies to 'year interaction' (2009 ... 2013–2009 ... 2013), which resulted in 25 factor levels. To simplify this, we created a third 2-level factor ('yes''no') variable for the proportion of overlap between animals tracked in the same year ('yes') and animals tracked in different years ('no'). Binomial generalised linear models with a logit-link function described the relationship between the proportion of isopleth overlap (50 and 95%) between individuals (response variables) and season, year and repeated tracking in the same year (predictor variables). Models were selected by a stepwise selection process, and support for different candidate models was assessed using Akaike's information criterion adjusted for small sample size (AICc) and Akaike weights. The model with the lowest AICc value and highest Akaike weight was considered best model (Burnham & Anderson 2002). Analyses were performed in programme R (R Core Team 2014).

Foraging trip directional preference

All points within a 10 km radius from Marion Island were discarded to exclude 'on land' or 'thermoregulatory swimming' location fixes. A compass direction in degrees from Van den Boogaard beach was calculated for each location and a first order circular mean was calculated to identify the mean direction of travel from the island for each foraging trip. A second order mean and vector length (given by Rho) was computed for all trips made by each individual and all trips made within a year each season (W: winter; S: summer) (e.g. 2009W; hereafter year_season). Moore's modified Rayleigh test (Zar 1998) was used

to determine if mean foraging direction was randomly distributed around Marion Island or not, at an individual (i.e. foraging trip number within an individual as predictor variable) and colony level (i.e. year_season as predictor variable) scale. Variation in mean foraging direction was analysed for all trips made by each individual and all trips made within a year_season. This was done in Oriana 4 for Windows® (Kovach Computing Service). Moore's modified Rayleigh test (Zar 1998) uses the points within the predictor variable (i.e. individual tag or year_season) and tests whether those points are randomly distributed or has directional preferences within that individual/year_season's points.

RESULTS

Thirty female subantarctic fur seals produced 109 tracked foraging trips (range: 1–8 trips per female) of which 96 were complete and 13 incomplete, distributed over 5 winters (2009W, $n = 10$; 2010W, $n = 19$; 2011W, $n = 8$; 2012W, $n = 6$; 2013W, $n = 4$) and 3 summers (2011S, $n = 21$; 2012S, $n = 23$; 2013S, $n = 18$); Table S1 in the Supplement. Incomplete tracks occur when satellite-linked data loggers stop transmitting at sea. Incomplete tracks were excluded from all trip summaries and further analyses (Table S2 in the Supplement). The 109 unique foraging trips produced 22 600 location estimates after being filtered and interpolated by means of SSMS. Of these 10 178 (45%) location estimates were classified as restricted search, 12 405 (54.8%) were classified as travelling behaviour and only 17 (<1%) locations could not be classified. There were no overnight foraging trips by any of the 30 females. Of the 109 (96 complete) foraging trips, only 11 (7 complete) were to the west of Marion Island. These trips were made in the winters of 2009 ($n = 4$), 2010 ($n = 1$), 2011 ($n = 1$), 2012 ($n = 1$) and 2013 ($n = 4$). Multiple westerly trips in 2009W and 2013W are the result of 2 females in each year doing 2 foraging trips each to the west of Marion Island (Fig. 2).

Intra-individual foraging site fidelity: revisitation to and time spent in individual hulls

Individuals revisited the same hull between 1 and 16 times, with a mean (\pm SD) of 2.3 ± 2.02 separate visits per hull per female seal. Individuals spent anywhere between 1.5 and 97 locations estimates in a hull (3.8 – 242.2 h) and a mean (\pm SD) of $20.6 \pm$

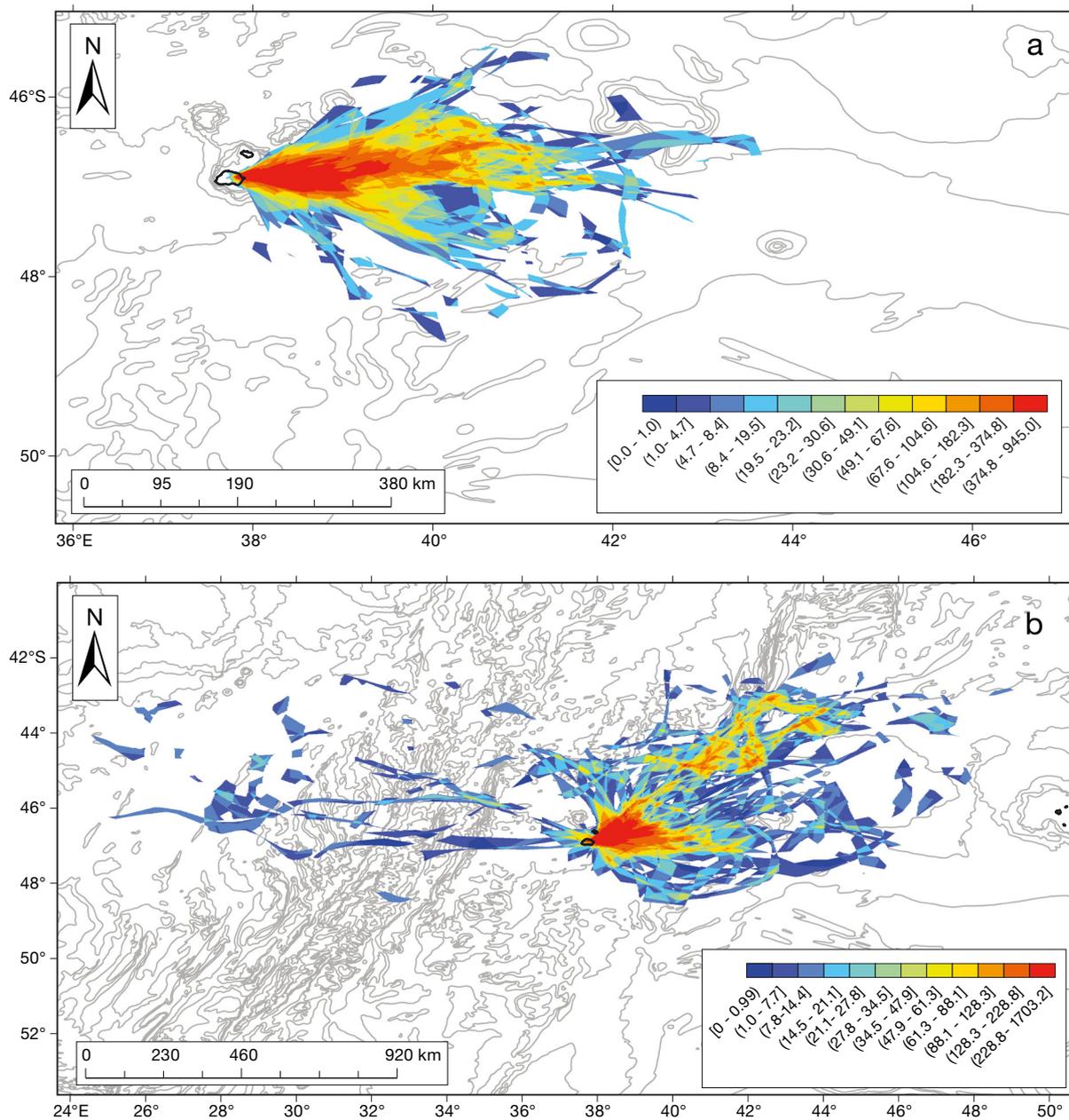


Fig. 2. Home range (95% isopleth) of satellite-tagged subantarctic fur seals at Marion Island between 2009 and 2013 during (a) summer and (b) winter. Values presented are the sum of the number of hulls within a 1 km² grid raster. Colour breaks based on quantiles of summed values. Home range data are presented with a 1 arc-min bathymetry overlay (IOC, IHO and BODC 2003)

15.01 location estimates (51.4 ± 37.5 h). Individuals revisited the same hulls less in winter (1.9 ± 1.3 number of separate visits) than in summer (3.4 ± 3.0 number of separate visits). Conversely, they stayed longer in a hull in winter (61.9 ± 38.1 h) than in summer (23.4 ± 14.9 h). No annual variation in number of separate visits or number of locations to hull was apparent.

Inter-individual foraging site fidelity: core and home-range utilization distribution overlap

The best-ranked generalised linear model (GLM) of proportion of overlap between individuals' 50% isopleths only retained season as a predictor variable (Table 1). This model indicated the core distributions of summer individuals overlapped an estimated

Table 1. Binomial generalised linear model (GLM) comparisons: GLMs of the proportional overlap of (a) 50 % isopleths and (b) 95 % isopleths individuals. prop50: proportion of overlap of the 50 % isopleth; prop95: proportion of overlap of the 95 % isopleth; season_interaction: season in which each of the 2 overlapping individuals were tracked. *k*: number of parameters; LL: log-likelihood; AICc: Akaike's information criterion corrected for finite sample sizes; Δ AIC: difference in AICc from that of the best fitting model; ω AIC: AIC weight. Only models with a ω AIC > 0 are presented and the accepted model is presented in **bold**

Candidate models	<i>k</i>	LL	AICc	Δ AIC	ω AIC
(a) GLMs with 50 % isopleth					
prop50 ~ season_interaction	4	-143.060	294.2	0	0.715
prop50 ~ season_interaction + same	5	-142.967	296.0	1.84	0.285
(b) GLMs with 95 % isopleth					
prop95 ~ season_interaction	4	-181.807	371.7	0	0.74
prop95 ~ season_interaction + same	5	-181.843	373.8	2.09	0.26

32.84 % (95 % CI: 24.53–41.94 %). Secondly, summer individuals' core distribution overlapped by 16.81 % (CI 12.16–22.27 %) with that of winter individuals. Lastly, in the winter the estimated amount of overlap for individuals' core distribution foraging areas was the same whether they were overlapping with winter (6.03 %; CI 4.02–9.16 %) or summer (6.27 %; CI 3.33–9.80 %) individuals. The best-ranked GLM model of proportion of overlap between individuals' 95 % isopleth (home range) also only retained season as a predictor variable (Table 1). This model indicated that the home range of summer individuals overlapped by an estimated 29.48 % (CI: 21.50–38.41 %). Secondly, summer individuals' home range overlapped by 20.84 % (CI 15.74–26.68 %) with winter individuals' home range (Fig. 3). Lastly, in the winter the estimated amount of overlap for individuals' home range were very similar whether they were overlapping with winter (9.19 %; CI 6.43–12.56 %) or summer (6.33 %; CI 3.55–10.17 %) individuals (Fig. 3). The proportion of overlap between individuals' core- (Fig. 3a) and home-range (Fig. 3b) distributions are graphically represented by means of a clustered heatmap in Fig. 3. The proportion value in each cell is interpreted as row individual overlap with column individual. Clustering was based on Euclidean distances between any 2 observations.

Individual- and colony-preferred foraging direction

Mean foraging trip directions in all years were predominantly east in summer and northeast in winter from Marion Island with the overall mean bearing

from the island being 19.99° in winter (Fig. 4) and 95.03° summer (Fig. 5). Seasonally, mean foraging trip direction varied only during 2009W and 2012W with females not travelling in a preferred direction from Marion Island (Moore's modified Rayleigh test; Table 2, Fig. 4). Of the 30 females tracked, there is more than one complete track for 23 females. Moore's modified Rayleigh test indicated that of those 23, only 8 (all winter females) did not swim in a preferred direction on consecutive trips (Table 3), but the other 13 females showed preference in foraging direction from Marion Island.

DISCUSSION

This study assessed both individual and colony-level foraging site fidelity changes from summer to winter in subantarctic fur seals, which are central-place foragers with a protracted lactation period. We used habitat utilization models as well as preferred direction of travel from Marion Island and found season is a strong modulator of levels of foraging site fidelity and colony-preferred foraging areas.

During summer, lactating subantarctic fur seals displayed both individual and colony-level foraging site fidelity as well as a high level of consistency in travelling direction between consecutive foraging trips, within and between individuals. Inter-annually, the foraging areas preferred in summer were consistently in a due-east direction towards the Gallieni Rise, stopping short of the Africana Rise with 32.84 % (CI: 24.53–41.94 %) of summer individuals' core utilization area (50 % isopleth) overlapping with each other. Foraging site fidelity was also present within and between individuals in winter, albeit to a lesser degree. In winter, individuals still travelled in a preferred direction, but foraging trips were longer and more tortuous. The colony-preferred travelling direction changed from due-east to northeast of the island along the Southwest Indian Ridge and around the edges of the Del Caño Rise. Despite these preferred foraging areas, there was little overlap between winter individuals. We found that only 6.03 % (CI 4.02–9.16 %) of winter individuals' core utilization areas overlapped with each other.

In winter some females also foraged to the west of Marion Island, similar to findings of de Bruyn et

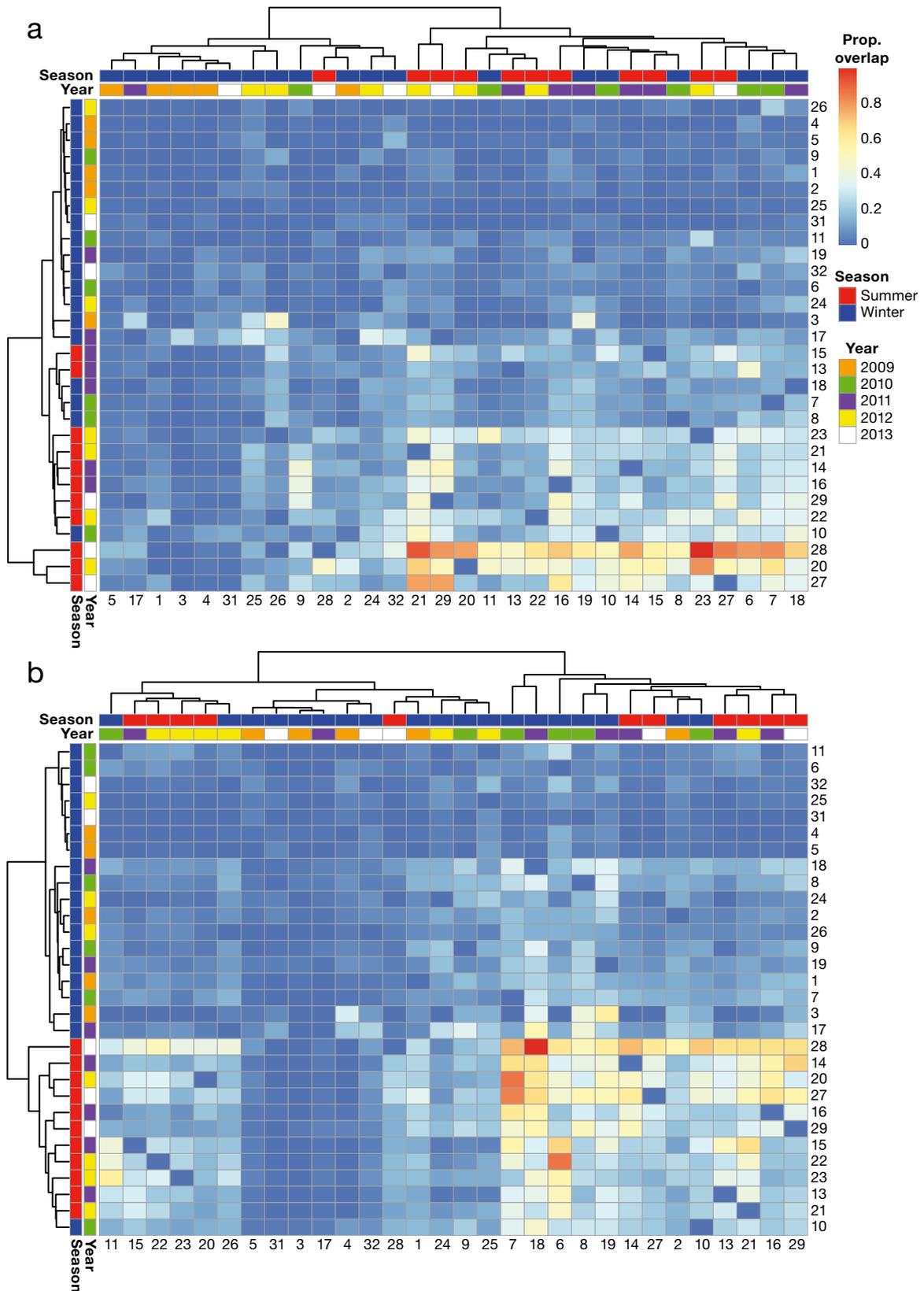


Fig. 3. Proportion overlap in the (a) 50% and (b) 95% isopleth between individuals where the value presented is the proportion the animal given in a row overlaps with the animal in the column. Numbers in the columns and rows denote individual animal IDs (refer to Table S1 or S2 in the Supplement for more information). The year and season in which each of the individuals were tracked are given by colours. Clustering was based on Euclidean distances between any 2 observations

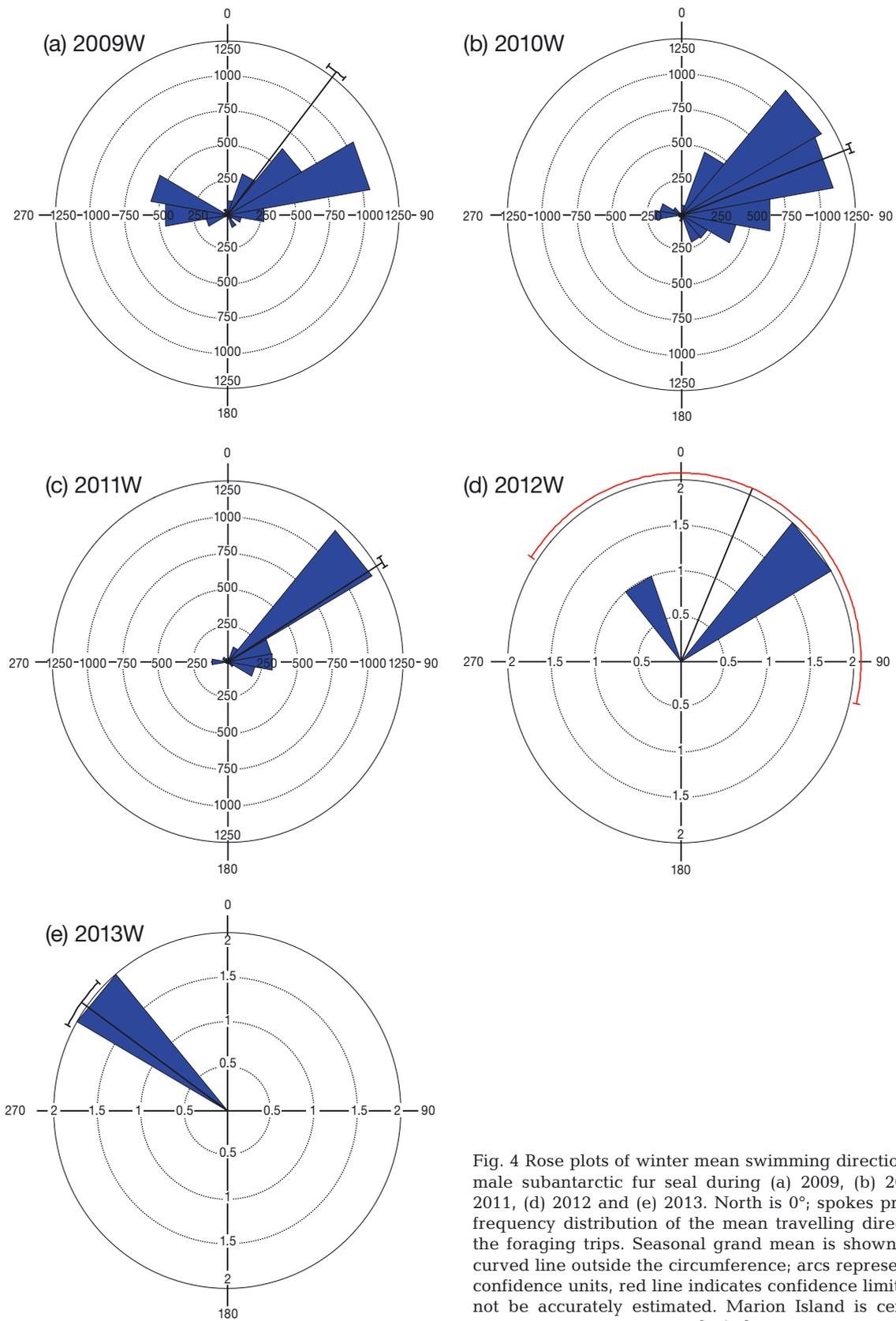


Fig. 4 Rose plots of winter mean swimming direction of female subantarctic fur seal during (a) 2009, (b) 2010, (c) 2011, (d) 2012 and (e) 2013. North is 0°; spokes present a frequency distribution of the mean travelling direction of the foraging trips. Seasonal grand mean is shown by the curved line outside the circumference; arcs represent 95% confidence units, red line indicates confidence limits could not be accurately estimated. Marion Island is central in each circle

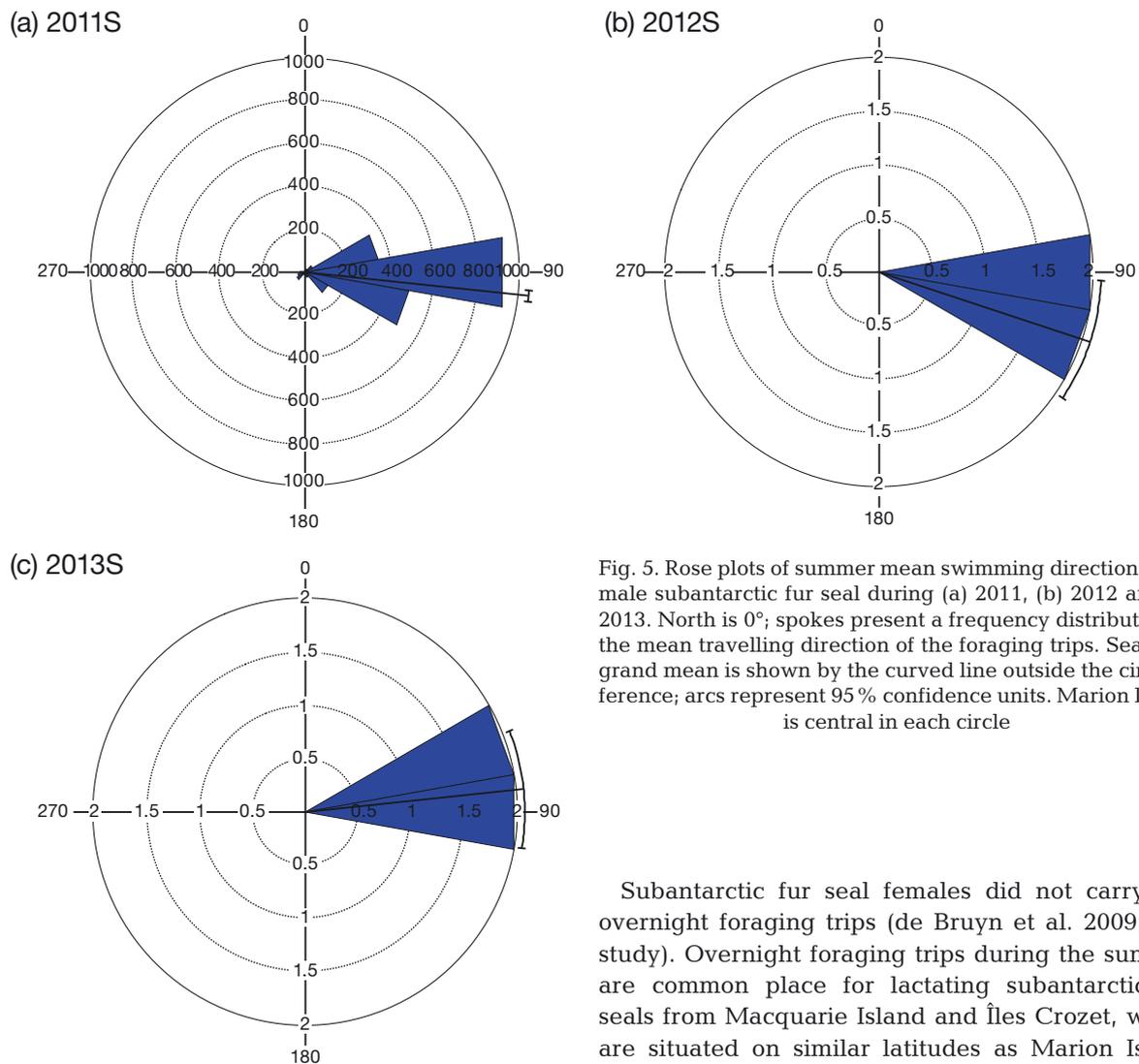


Fig. 5. Rose plots of summer mean swimming direction of female subantarctic fur seal during (a) 2011, (b) 2012 and (c) 2013. North is 0°; spokes present a frequency distribution of the mean travelling direction of the foraging trips. Seasonal grand mean is shown by the curved line outside the circumference; arcs represent 95% confidence units. Marion Island is central in each circle

al. (2009). Foraging trips to the west of the island were longer, further from Marion Island, more tortuous and less frequent than those to the northeast. These trips are unlikely to represent an alternative foraging strategy (cf. Bonadonna et al. 2001, Lea et al. 2008), as they do not occur in a predictable manner or at consistent intervals. The searching behaviour in these westerly trips is probably a short-term response to variable food resources in other preferred areas visited in the preceding foraging trip. Individuals are most likely searching for better prey patches. This might explain why only 4 out of 31 lactating subantarctic fur seal females from the northeast coast Van den Boogaard beach did more than one consecutive foraging trip to the west.

Subantarctic fur seal females did not carry out overnight foraging trips (de Bruyn et al. 2009, this study). Overnight foraging trips during the summer are common place for lactating subantarctic fur seals from Macquarie Island and Îles Crozet, which are situated on similar latitudes as Marion Island (Robinson et al. 2002, Beuplet et al. 2004). The local bathymetry (i.e. lack of or small shelf area) and associated prey resources close to Marion Island do not seem to elicit similar behaviour (de Bruyn et al. 2009).

Although this study incorporates at-sea foraging behaviour of 30 females, with 109 foraging trips, the number of individuals tracked within a 'year_season' is fairly small ($n = 2-6$). This prevented us from exploring any real annual variation in preferred foraging areas. Trips made in the winters of 2009 and 2012 showed no preferred directionality and are most likely the result of a small sample size within those years. Despite the small sample size between years, the consistency in travelling direction from Marion Island across years for both summer and winter periods indicate that, like Antarctic fur seals from Îles Kerguelen, subantarctic fur seals have colony-preferred set foraging

Table 2. Consistency in all female subantarctic fur seals' mean foraging trip direction within a season using a Moore's modified Rayleigh test. Grand mean direction is the mean foraging trip direction from Marion Island; n: number of individuals tracked in the season; Rho: mean vector length; Moore's modified R: test statistic; ns: not significant

Season	n	Grand mean direction (°)	Rho	Moore's modified R	p
2009W	4	303.38	0.032	0.25	>0.05 ^{ns}
2010W	6	82.45	0.800	1.26	<0.01
2011S	4	93.32	0.952	1.23	<0.005
2011W	3	63.81	0.865	1.14	<0.025
2012S	4	107.78	0.915	1.23	<0.005
2012W	3	40.82	0.602	1.02	>0.05 ^{ns}
2013S	4	84.03	0.947	1.24	<0.005
2013W	2	305.83	0.798	1.06	<0.025

routes (Bonadonna et al. 2000). The exact foraging areas along those routes might change between an individual's respective foraging trips or between individuals or even years. This is seemingly due to tracking highly mobile prey, i.e. small-scale fluctu-

Table 3. Consistency in individual female subantarctic fur seals' mean foraging trip direction between consecutive foraging trips within a season using a Moore's modified Rayleigh test. Grand mean direction is the second order mean foraging trip direction from Marion Island; n: number of individuals tracked in the season; Rho: mean vector length; Moore's Modified R: test statistic; ns: not significant

Season	Seal ID	n	Grand mean direction (°)	Rho	Moore's modified R	p
2009W	1	2	76.688	0.81	0.935	>0.05 ^{ns}
2009W	5	2	267.69	0.869	0.989	>0.05 ^{ns}
2010W	6	3	130.188	0.812	1.099	<0.05
2010W	7	4	75.454	0.932	1.212	<0.005
2010W	8	3	57.242	0.943	1.133	<0.025
2010W	9	2	59.708	0.977	1.047	>0.05 ^{ns}
2010W	10	3	60.833	0.904	1.097	<0.05
2011S	13	6	107.388	0.958	1.409	<0.001
2011S	14	6	83.564	0.97	1.41	<0.001
2011S	15	5	101.186	0.977	1.332	<0.001
2011S	16	4	81.374	0.975	1.249	<0.001
2011W	18	4	73.48	0.878	1.17	<0.025
2011W	19	3	66.261	0.75	1.011	>0.05 ^{ns}
2012S	20	2	97.636	0.984	1.053	>0.05 ^{ns}
2012S	21	7	98.186	0.957	1.461	<0.001
2012S	22	4	118.892	0.934	1.204	<0.01
2012S	23	7	118.185	0.845	1.334	<0.005
2012W	24	3	44.555	0.851	1.056	>0.05 ^{ns}
2012W	25	2	330.784	0.191	0.401	>0.05 ^{ns}
2013S	27	7	85.966	0.979	1.504	<0.001
2013S	28	4	99.379	0.969	1.235	<0.005
2013S	29	5	75.628	0.927	1.271	<0.005
2013S	30	2	74.878	0.969	1.058	>0.05 ^{ns}

ations of available food patches within a larger area of predictable food resources (Fauchald et al. 2000, Boyd et al. 2002). Pelagically foraging New Zealand fur seal females also had comparable bearings on consecutive trips, not always foraging in the same specific area, but covering other areas in search of prey (Baylis et al. 2012). Considering that Marion Island females dive every night after leaving the island (Wege 2013), females may swim to a larger preferred foraging area but sample or forage opportunistically en route and return to the island once their energy requirements are met. This is another indication of how smaller-scale preferred areas are nested within larger areas of foraging habitat (cf. Weimerskirch 2007).

The reasons why and cues by which individuals within a colony travel to the same areas are still poorly understood. Some indicators include coastline orientation (Lea et al. 2008, Goldsworthy et al. 2010), local competition (Bonadonna et al. 2001), and direction and distance to physical oceanographic features such as fronts (Georges et al. 2000) or continental shelf edges or ridges (Baylis et al. 2012) as important determinants of colony-preferred foraging areas. At Marion Island, the preferred colony foraging direction seems to coincide with local bathymetry and frontal structures (de Bruyn et al. 2009, present study), with certain features, such as the Gallieni Rise and Southwest Indian Ridge, Africana Rise and Del Caño Rise, being the most prominent. The 2 bathymetrical features where the fur seals forage in the summer months during this study (Africana and Gallieni rises) are typified by extreme mesoscale variability and upwelling over shallower bathymetric features. Summer months are also characterised by increased productivity owing to the proximity of the Subantarctic Front to the island (Pakhomov & Fronemann 1999). Furthermore, the large number of avian predators breeding on Marion Island during the summer results in large quantities of nutrient run-off, which is later associated with phytoplankton blooms and higher productivity down-

stream close to the islands (Smith & Froneman 2008). In winter, the Subantarctic Front moves northwards and is located further away from the island (Pakhomov & Froneman 1999). The lack of predictable resources close to the island in winter may influence the variability of movements observed, the increased trip durations and reduced linearity of movements.

Although there is still overlap between preferred foraging areas in winter and summer, the Discovery II Fracture Zone along the Southwest Indian Ridge was identified as a unique area of high use in winter. Winter foraging areas are more extensive and varied than summer areas even though they are in the same general direction from the study colony. Suitable summer and autumn foraging areas of subantarctic fur seals from neighbouring Prince Edward island also fall within the designated MPA (Kirkman et al. 2016). However, during winter and spring, these areas shifted northwards concurrently with frontal movements. The different characteristics of winter and summer foraging areas have important implications for the conservation of subantarctic fur seals, and potentially other marine top predators such as Antarctic fur seals at Marion Island as shown by Arthur et al. (2015). Therefore, marine spatial planning, for the purposes of designating MPAs, needs to consider habitats important to seals throughout the year and therefore include subantarctic fur seal winter foraging areas. Whilst MPAs need to include specific conservation targets to protect threatened or vulnerable species (Hooker et al. 2011), identifying and protecting important ecological processes are important for protecting pelagic ecosystems (Hooker & Gerber 2004). Augé et al. (2014) suggested land-site fidelity as a proxy for at-sea foraging site fidelity during the seasons when tracking is not possible. Our results contradict this, given the seasonal differences in preferred foraging areas. Various biotic and abiotic factors which influence foraging site fidelity, such as species life-history and local oceanic processes and productivity, need to be considered. We suggest that land-site fidelity as proxy for at-sea foraging fidelity might work for species known to forage close to their haul-out sites, but it is not a useful option for pelagic foragers, like subantarctic fur seals. In this case, using only summer data to inform conservation practices would not adequately capture the species' distributional range while lactating. Protecting a species through marine spatial conservation planning requires at-sea

geographic data year-round from all sexes, age-classes and breeding-stages, which is not always possible.

In 2013, South Africa declared the exclusive economic zone around Marion and Prince Edward islands as an MPA (Lombard et al. 2007). This MPA did not include any fur seal at-sea geographic data or habitat use. Preferred summer foraging areas are included in the current MPA, but the Discovery II Fracture Zone and the area surrounding the Del Caño Rise, foraging areas preferred in winter, are not. The Del Caño Rise links the Prince Edward Islands and the French subantarctic islands, Îles Crozet, and forms part of the movement axis of seabirds from both Marion Island and Îles Crozet (Lombard et al. 2007). The Del Caño Rise is also an area of important fisheries activity (Lombard et al. 2007) forming an important stock of economically important Patagonian toothfish *Dissostichus eleginoides*.

The continued use of this area northeast of the island, especially the Discovery II Fracture Zone and the Del Caño Rise, by subantarctic fur seals (de Bruyn et al. 2009, present study) and Antarctic fur seals (Arthur et al. 2015) from Marion Island has important implications for human fisheries interactions throughout the fur seals' lactation foraging ranges in summer and winter. This region has an important species-specific and ecological role to play in the continued persistence of top predator populations at Marion Island. Both Marion Island and neighbouring Prince Edward Island have declining populations of subantarctic fur seals but growing populations of Antarctic fur seals (Bester et al. 2009, Wege et al. 2016). In fact, the subantarctic fur seal population of Marion Island decreased more than 50% between 2004 and 2013 (Wege et al. 2016). The exact reasons for this are still unknown, which is cause for concern. Whilst individual and colony-level foraging site fidelity could result in competition between individuals and have a population regulatory role on populations, population fluctuations would also occur as a result of decreased food availability. Changing environments may manifest in foraging behaviour as short-term responses to fluctuations in prey availability as well as increased energetic demands by the pups (pre-natal and post-natal). Such short-term responses include altered foraging tactics (e.g. Arnould et al. 1996). Monitoring of fur seal populations from Marion Island may therefore provide important indicators for the persistence of the Del Caño Rise region as an important top predator foraging area.

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