

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 (46°54'S, 37°45'E) during summer and winter, comparing commitment to foraging areas across seasons. Thirty-one females were tracked in 2009-2013 resulting in 111 foraging trips for analyses. Inter-annually, preferred foraging areas in summer were consistently \approx 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 north-east of Marion Island and foraged further afield, around the Del Caño Rise and along the South-west 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 in conserving for this globally

significant, and currently declining, population of Subantarctic fur seals and perhaps other top-predators breeding at Marion Island as well. Differences between winter and summer preferred foraging areas 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; subantarctic; TLoCoH; top predator

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 understand the impacts of varying prey populations, effects of climate change and human harvesting on ecosystems (Furness and 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 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 (e.g. 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 (e.g. Ropert-Coudert et al. 2004). If the parents fail to obtain sufficient resources for their offspring, immediate survival (pre-weaning or -fledging) as well as subsequent (post-weaning or -fledging) survival are jeopardised (e.g. Ballard et al. 2010). Additionally, the parents' current and future survival as well as future fecundity may be affected (e.g. 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 (e.g. 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 (e.g. 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 (e.g. Lea et al. 2008). Identifying key foraging areas or reasons for the lack thereof in breeding individuals within populations could guide conservation efforts (e.g. Augé et al. 2014) and be used to plan marine protected areas (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. 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 therefore 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 the temporal interplay too with special consideration of life histories (e.g. Hooker and Gerber 2004, James et al. 2005). Roberts et al. (2003) also supports 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). Subantarctic fur seal females (*Arctocephalus tropicalis*) are central-place foragers with protracted provisioning periods (10 months, Kerley 1983). During winter they have to provision for the current and future pup (aside from her own demands), all the while dealing with altered resource distribution and availability (Beauplet et al. 2004; Womble and 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 investigated how foraging site fidelity of conspecifics from the same colony varies seasonally from summer to winter. The Subantarctic fur seal, with its 10 month lactation period, makes it an ideal study species for such cross-seasonal studies. On Marion Island, 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 north-east 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 two years. It was impossible to quantify individual foraging site fidelity. Any understanding of the two 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 31 individuals, collected over a 5-year 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 (e.g., 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 (Table S1) 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 north eastern coastline of Marion Island (Fig 1; 46°54'S, 37°

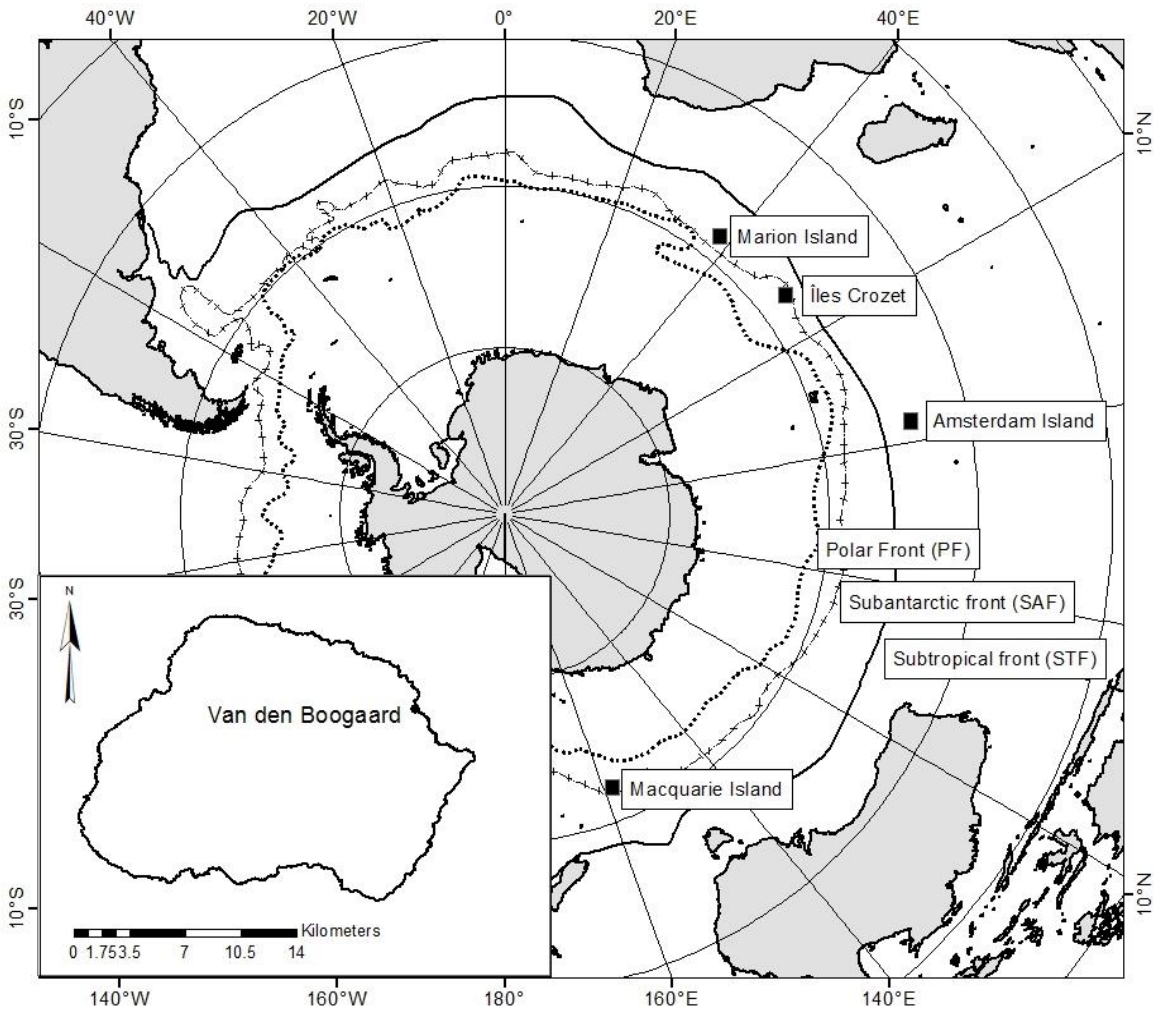


Figure 1: Marion Island's position in the Southern Ocean in relation to Îles Crozet, Amsterdam Island & Macquarie Island as well as the Polar Front, Subtropical Front and the Subantarctic Front. The location of Van den Boogaard beach (study beach) on Marion Island is shown (inset)

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 Ltd.). 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 months) 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 two-state, behaviourally switching state-space models (SSM) were fitted to Argos tracks (Jonsen et al. 2005). SSMs filtered out erroneous location estimates and interpolated 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 hours was chosen based on median number of Argos location points per day (9-10 points per day). We ran two 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 two 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 two parts of the algorithm: a) during nearest neighbour selection (the time-scaled distance); and b) 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 three methods and we chose the more robust adaptive a -method (Getz et al. 2007) 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 -percent 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 revisitation 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 hours in the present study. Thus points within a hull that are 24-hours apart are considered separate visits. A 24 hour IVG was selected because Subantarctic fur seals from Marion Island dive exclusively at night (Wege 2013) and travel during the day. Individuals that 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, would 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 (this 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. These percentiles were chosen 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's 50% isopleth overlaps 20% (0.2) with animal id28, but id28's 50% isopleth overlaps 68% (0.68) with id13. We created multi-level categorical identifiers based on the interaction between 1) season ("season interaction") and 2) year ("year interaction") each of the two overlapping individuals occurred in. This means that for the "season interaction" between individuals there are four 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's; whereas winter-summer refers to a winter animal's proportion overlap with a summer animal's. The same logic applies to "year interaction" (2009...2013-2009...2013), which resulted in 25 factor levels. To simplify this we created a third two-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 and 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 each season within a year (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, Pentraeth, UK). 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 one female Subantarctic fur seals produced 111 tracked foraging trips (range: 1 – 8 trips per female) of which 98 were complete and 13 incomplete, distributed over 5 winters [2009W (n = 10), 2010W (n = 19), 2011W (n = 9), 2012W (n = 6), 2013W (n = 4)] and 3 summers (2011S (n = 21), 2012S (n = 22), 2013S (n = 19)]; table S1: supplementary data). 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: supplementary data). The 111 unique foraging trips produced 22600 location estimates after filtered and interpolated by means of SSMs. Of these 10178 (45%) location estimates were classified as restricted search, 12405 (54.8%) were classified as travelling behaviour and only 17 (<1%) locations could not be classified.. There were no over-night foraging trips by any of the 31 females. Of the 111 (98 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 two females in each year doing two 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 – 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 location estimates in a hull (3.8 hrs – 242.2 hrs) and a mean (\pm sd) of 20.6 ± 15.01 location estimates (51.4 ± 37.5 hrs). 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

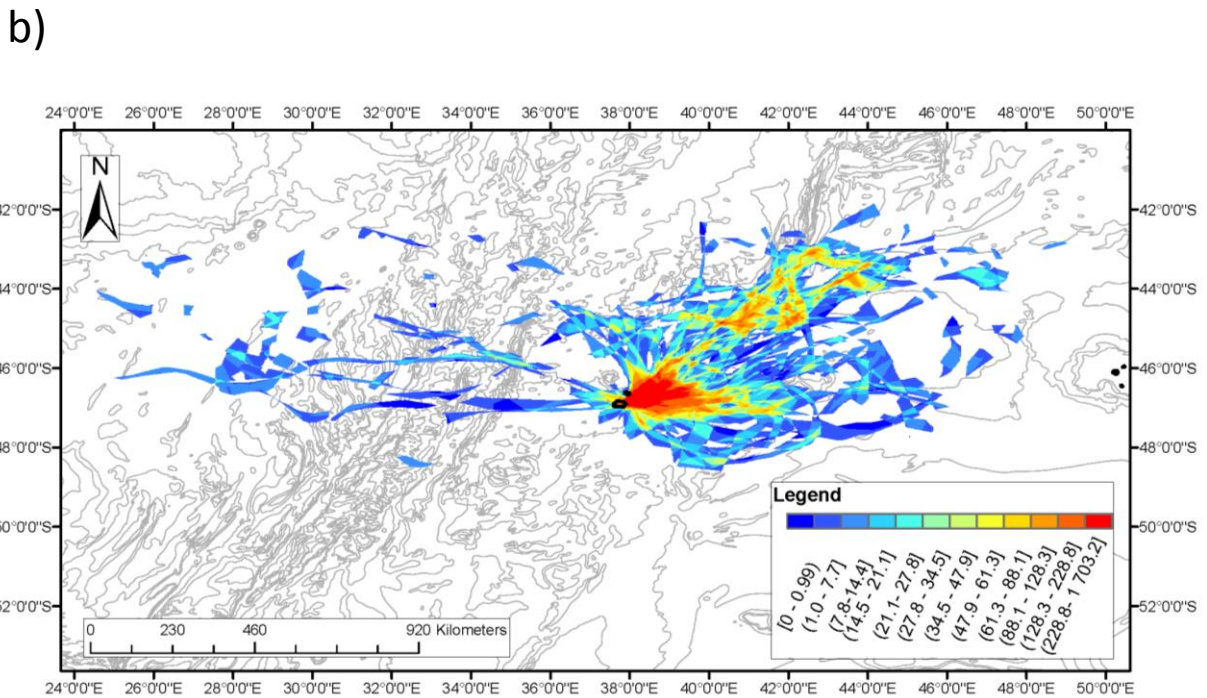
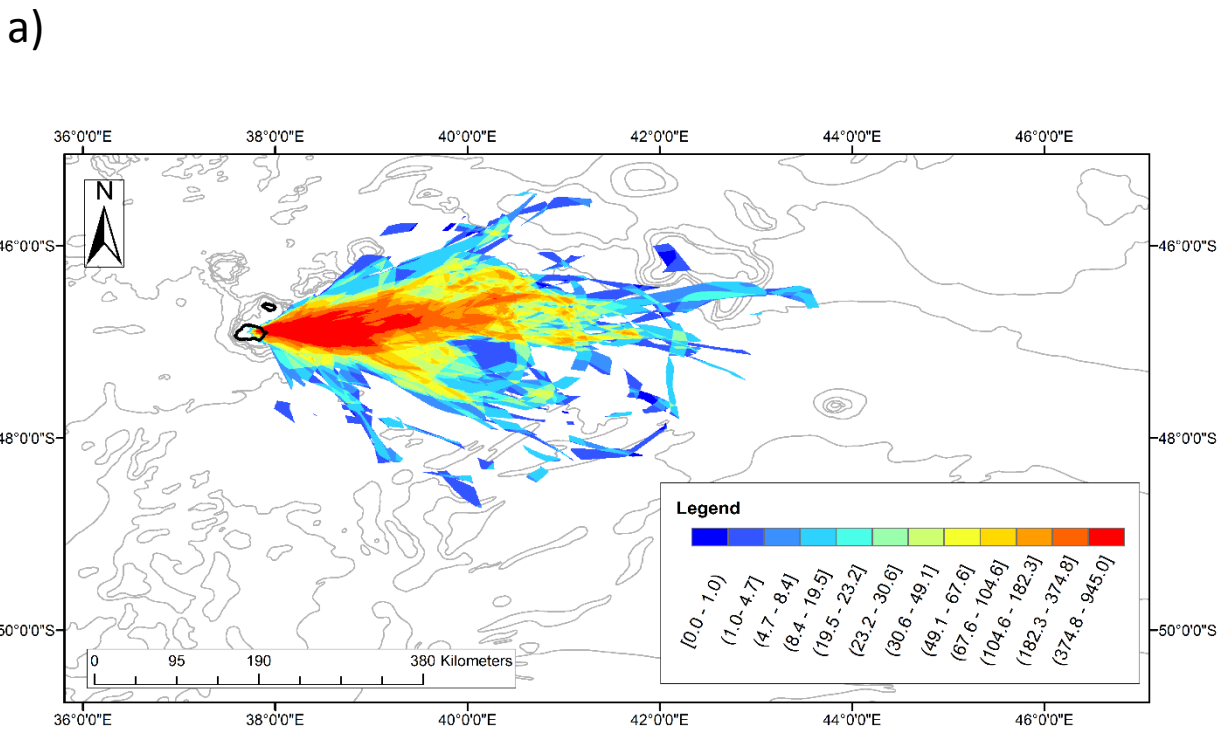


Figure 2: Home range (95% isopleth) of satellite tagged Subantarctic fur seals at Marion Island between 2009-2013 during a) summer and b) winter. Isopleths of individuals were overlay and summed together within a 1km² grid raster. Colour breaks based on quantiles of summed values. Home range data are presented with a one arc-minute bathymetry overlay (IOC IHO, BODC 2003).

hull in winter (61.9 ± 38.1 hours) than in summer (23.4 ± 14.9 hours). 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 GLM model 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 32.84% (95% Confidence intervals CI: 24.53% - 41.94%). Secondly, summer individuals' core distribution overlapped by 16.81% (CI 12.16% - 22.27%) with 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 Figure 3. The proportion value in each cell is interpreted as row individual overlap with column individual. Clustering was based on Euclidean distances between any two observations.

Table 1: Summary of binomial generalised linear model (GLM) comparisons: (a) GLMs of the 50% isopleths' and (b) 95% isopleths' proportion overlap between individuals; "prop50" = proportion of overlap of the 50% isopleth, "prop95" = proportion of overlap of the 95% isopleth; "season_interaction" = the season in which each of the two overlapping individuals were tracked

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

Only models with a $\omega AIC > 0$ are presented and the accepted model is presented in bold. *k*, number of parameters; LL, log-likelihood; AICc, Akaike's Information Criterion corrected for finite sample sizes; ΔAIC , difference in AICc from that of the best fitting model; ωAIC , AIC weight.

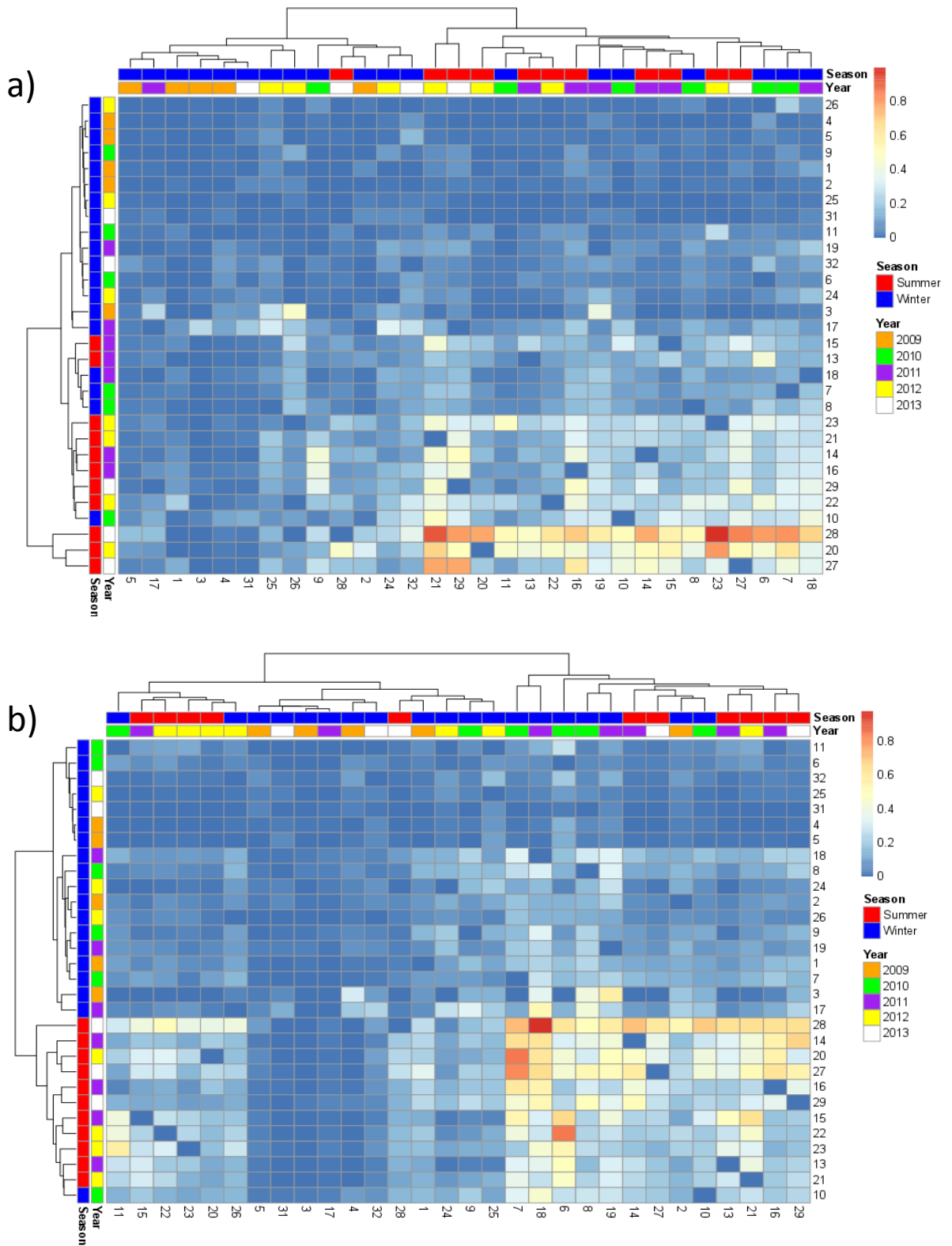


Figure 3: The proportion overlap in the a) 50% and b) 95% isopleth between individuals where the value presented is the proportion of overlap the animal given in a row overlaps with the animal in the column. The numbers in the columns and rows denote individual animal id's (refer to Table S1 or S2 for 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 two observations.

Table 2: Consistency in all Subantarctic fur seal females' mean foraging trip direction within a season using a Moore's modified Rayleigh test. Grand mean gives 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.

Season	n	Grand mean	Rho	Moore's Modified R	P-value
2009W	4	303.38°	0.032	0.25	> 0.05 N.S
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 N.S
2013S	4	84.03°	0.947	1.24	< 0.005
2013W	2	305.83°	0.798	1.06	< 0.025

Table 3: Consistency in individual Subantarctic fur seal female's mean foraging trip direction between consecutive foraging trips within a season using a Moore's modified Rayleigh test. Grand mean gives 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.

Season	Seal ID	n	Grand mean	Rho	Moore's Modified R	P-value
2009W	1	2	76.688°	0.81	0.935	> 0.05 N.S.*
2009W	5	2	267.69°	0.869	0.989	> 0.05 N.S.*
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 N.S.*
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 N.S.*
2012S	20	2	97.636°	0.984	1.053	> 0.05 N.S.*
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 N.S.*
2012W	25	2	330.784°	0.191	0.401	> 0.05 N.S.*
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 N.S.*

Individual and colony preferred foraging direction

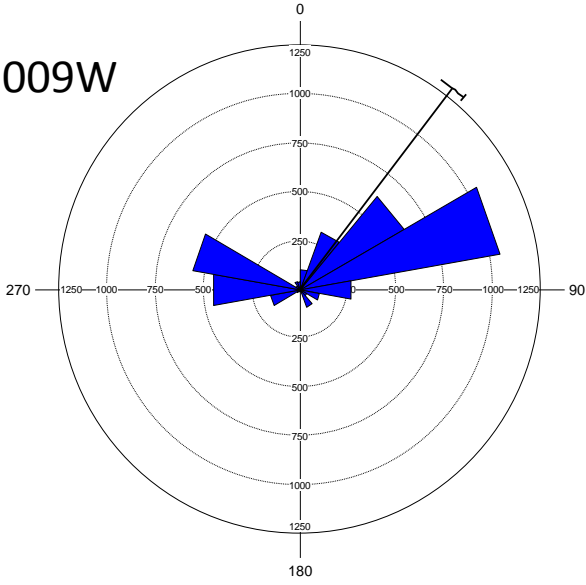
Mean foraging trip directions in all years were predominantly east in summer and north-east in winter from Marion Island with the overall mean bearing from the island being 19.99° and 95.03° in winter (Fig. 4) and summer (Fig. 5) respectively. Seasonally, mean foraging trip direction varied only during 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 31 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

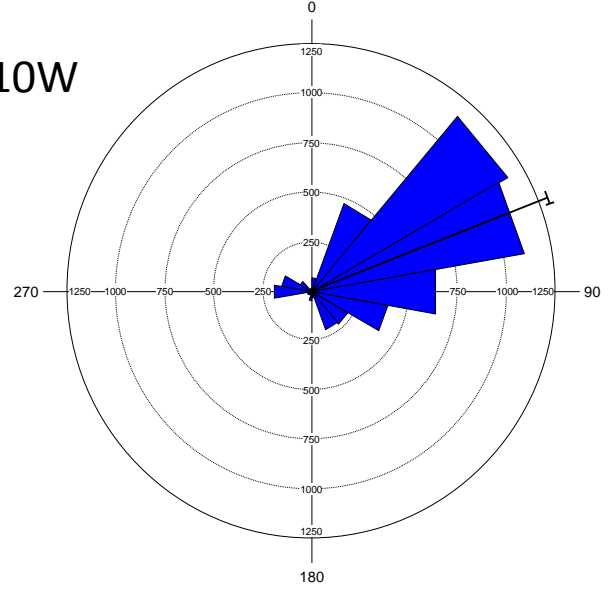
This study assessed both individual and colony level foraging site fidelity changes from summer to winter in Subantarctic fur seals - a central-place forager with a protracted lactation period. We used habitat utilization models as well as preferred direction of travel from Marion Island and found season to be 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 summer preferred foraging areas were consistently in a due-east direction towards the Gallieni Rise, stopping short

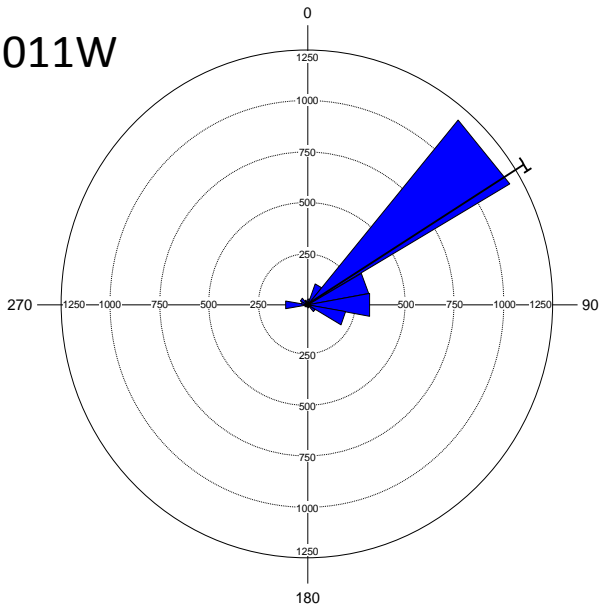
2009W



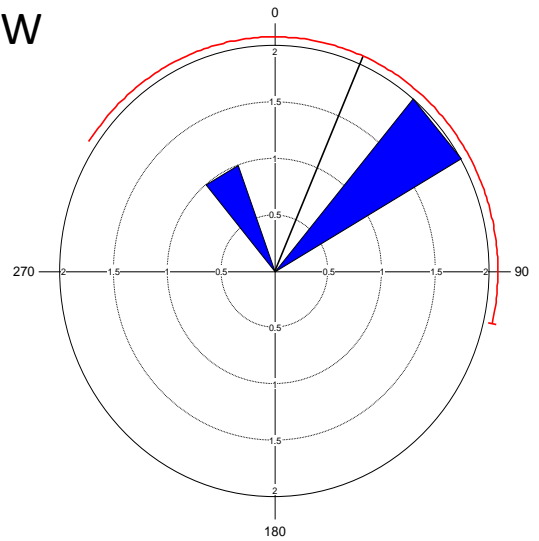
2010W



2011W



2012W



2013W

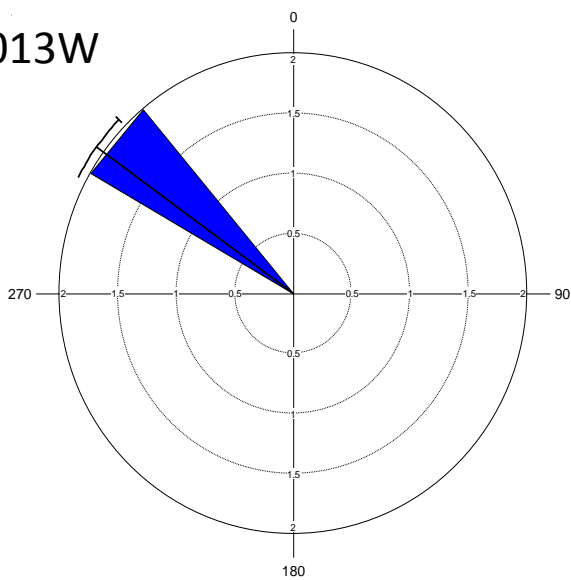
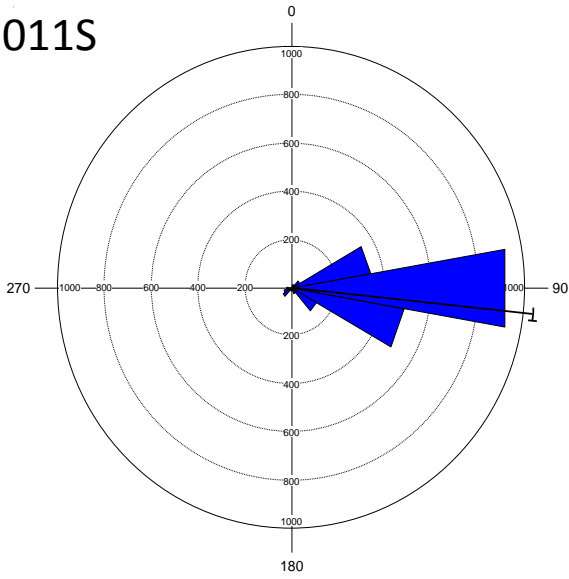
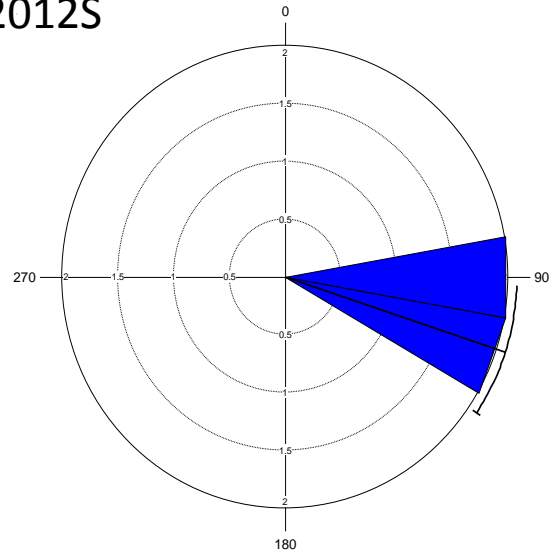


Figure 4: Rose plots of winter mean swimming direction of Subantarctic fur seal females during a) 2009, b) 2010, c) 2011, d) 2012 and e) 2013. North is 0° , the bars present a frequency distribution of the number of foraging trips' mean travelling direction and the seasonal grand mean is given by (-). Marion Island is central in each circle.

2011S



2012S



2013S

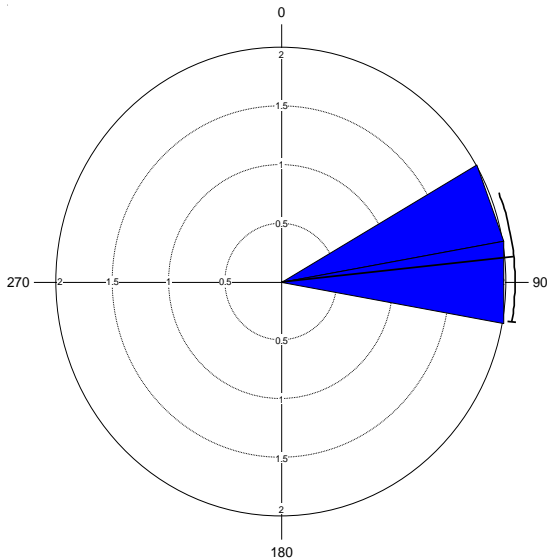


Figure 5: Rose plots of summer mean swimming direction of Subantarctic fur seal females during a) 2011, b) 2012 and c) 2013. North is 0° , the bars present a frequency distribution of the number of foraging trips' mean travelling direction and the seasonal grand mean is given by (-). Marion Island is central in each circle.

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 north-east of the island along the South-west 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 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 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 north-east. These trips are unlikely to represent an alternative foraging strategy (*cf.* Bonnadonna 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 north-east coast Van den Boogaard beach did more than one consecutive foraging trip to the west.

Subantarctic fur seal females did not carry out over-night 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, Beauplet 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 31 females, with 111 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 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 fluctuations 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 a specific area, covering a larger area 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 for 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), 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, preferred colony foraging direction seems to coincide with local bathymetry and frontal structures (de Bruyn et al. 2009, this study), with certain features such as the Gallieni Rise and South-west Indian Ridge, Africana Rise and Del Caño Rise, being the most prominent. The two 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 downstream close to the islands (Smith & Fronemann 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 winter and summer preferred foraging areas, in winter the Discovery II Fracture Zone along the South-west Indian Ridge was identified as a unique area of high use. Winter foraging areas are more extensive and varied than summer areas even though

they are in the same general direction from the study colony. Recently, Kirkman et al. (2016) also found that model-predicted suitable habitat summer and autumn foraging areas of Subantarctic fur seals from neighbouring Prince Edward Island fall within the designated MPA. 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 Marine Protected Area's (MPA's), 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, such as species life-history and local oceanic processes and productivity, which influence foraging site fidelity, 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 captured by the current MPA but the Discovery II Fracture Zone and the area surrounding the Del Caño Rise, winter preferred foraging areas, 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 north-east of the island, especially the Discovery II Fracture Zone and the Del Caño Rise, by Subantarctic fur seals (de Bruyn et al. 2009, this 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 has decreased more than 50% between 2004-2013 (Wege et al. 2016). The exact reasons 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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Ethics

All the above procedures have ethics clearance from the Animal Use and Care Committee (AUCC) of the Faculty of Natural and Agricultural Sciences, University of Pretoria, South Africa, under AUCC 040827-023.

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Supplementary Data

Table S1: Summary of tracks obtained of lactating Subantarctic fur seals from 2009 winter (2009W), 2010 winter (2010W), 2011 summer (2011S) and winter (2011W), 2012 summer (2012S) and winter (2012W) and 2013 winter (2013W) at Van den Boogaard beach, Marion Island.

Seal ID	Device	Deployment date	Track duration (days)	Season	No of foraging trips	No of complete tracks	No of incomplete tracks
1	Kiwisat 101 PTT	2009/04/24	134	2009W	3	2	1
2	Kiwisat 101 PTT	2009/04/24	89	2009W	2	1	1
3	Kiwisat 101 PTT	2009/04/24	19	2009W	1	0	1
4	Kiwisat 101 PTT	2009/04/28	96	2009W	2	1	1
5	Kiwisat 101 PTT	2009/04/28	146	2009W	2	2	0
6	Kiwisat 101 PTT	2010/03/07	149	2010W	4	3	1
7	Kiwisat 101 PTT	2010/03/21	142	2010W	4	4	0
8	MK10 Splash Tag	2010/06/02	130	2010W	4	3	1
9	Kiwisat 101 PTT	2010/04/29	85	2010W	2	2	0
10	Kiwisat 101 PTT	2010/05/02	78	2010W	3	3	0

11	Kiwisat 101 PTT	2010/05/05	100	2010W	2	1	1
13	Kiwisat 101 PTT	2011/01/03	76	2011S	6	6	0
14	Kiwisat 101 PTT	2011/01/02	65	2011S	6	6	0
15	Kiwisat 101 PTT	2011/01/02	70	2011S	5	5	0
16	Kiwisat 101 PTT	2011/01/03	62	2011S	4	4	0
17	MK10 Splash Tag	2011/05/15	24	2011W	1	1	0
18	Kiwisat 101 PTT	2011/04/29	119	2011W	4	4	0
19	Kiwisat 101 PTT	2011/04/29	131	2011W	3	3	0
20	Kiwisat 101 PTT	2011/12/23	31	2012S	3	2	1
21	Kiwisat 101 PTT	2011/12/27	88	2012S	7	7	0
22	Kiwisat 101 PTT	2011/12/31	65	2012S	5	4	1
23	Kiwisat 101 PTT	2011/12/23	74	2012S	8	8	0
24	MK10 Splash Tag	2012/05/05	88	2012W	3	3	0
25	Kiwisat 101 PTT	2012/05/05	111	2012W	2	2	0
26	Kiwisat 101 PTT	2012/05/23	75	2012W	1	1	0
27	MK10 Splash Tag	2012/12/22	81	2013S	7	7	0
28	MK10 Splash Tag	2012/12/22	39	2013S	6	5	1
29	Kiwisat 101	2012/12/24	72	2013S	5	5	0

	PTT						
31	Kiwisat 101 PTT	2013/05/15	114	2013W	2	1	1
32	Kiwisat 101 PTT	2013/05/21	49	2013W	2	1	1

Table S2: Foraging trip summaries for each individual complete foraging trip of lactating Subantarctic fur seals from Marion Island.

Season	Seal ID	Foraging trip	Foraging trip duration (days)	Maximum distance reached from MI (km)	Total foraging trip distance (km)	Trip Curvilinear Index	Mean foraging trip direction (°)	Vector length (<i>Rho</i>)
2009W	1	1	20	387.740	1438.920	0.540	108.200	0.900
2009W	1	2	28	407.650	1635.010	0.500	48.010	0.980
2009W	2	1	36	487.720	1946.450	0.500	90.080	0.950
2009W	4	1	37	813.590	2839.710	0.570	265.300	0.980
2009W	5	1	25	460.540	1445.900	0.640	245.350	0.950
2009W	5	2	117	1051.850	5349.780	0.390	290.480	0.930
2010W	8	1	27	510.120	1389.440	0.730	77.440	0.960
2010W	8	2	48	575.660	2495.130	0.460	48.100	0.970
2010W	8	3	32	577.420	1777.220	0.650	46.870	0.990
2010W	6	1	22	552.250	1584.110	0.700	108.310	0.960
2010W	6	2	20	267.820	1169.350	0.460	154.760	0.680
2010W	6	3	31	357.400	1759.590	0.410	134.920	0.930
2010W	7	1	28	664.240	1994.300	0.670	94.550	0.990
2010W	7	2	36	812.270	2380.150	0.680	85.960	0.980
2010W	7	3	12	211.460	774.610	0.550	72.440	0.970
2010W	7	4	57	692.550	3387.440	0.410	47.840	0.970
2010W	9	1	36	858.720	2305.360	0.740	69.260	0.990
2010W	9	2	47	678.650	2457.910	0.550	50.020	0.980
2010W	10	1	17	246.590	1001.280	0.490	70.990	0.900
2010W	10	2	23	390.170	1237.490	0.630	74.540	0.970
2010W	10	3	27	405.340	1694.710	0.480	37.180	0.970
2010W	11	1	19	273.530	1024.670	0.530	123.020	0.960
2011S	13	1	5	104.670	269.370	0.780	121.290	0.950
2011S	13	2	9	340.790	778.730	0.880	94.100	0.990
2011S	13	3	7	212.810	466.300	0.910	102.590	0.960
2011S	13	4	8	217.370	1180.790	0.370	107.880	0.990

2011S	13	5	12	335.730	849.830	0.790	98.720	0.980
2011S	13	6	17	674.970	2545.380	0.530	120.550	0.970
2011S	14	1	9	308.400	750.320	0.820	66.600	0.990
2011S	14	2	9	291.460	723.490	0.810	83.600	0.990
2011S	14	3	8	193.450	505.800	0.760	75.690	0.990
2011S	14	4	6	212.870	530.800	0.800	79.660	0.990
2011S	14	5	11	304.360	934.280	0.650	105.310	0.980
2011S	14	6	10	300.260	722.940	0.830	91.010	0.990
2011S	15	1	9	165.720	466.530	0.710	94.451	0.990
2011S	15	2	9	179.560	499.760	0.720	103.661	0.990
2011S	15	3	11	218.360	680.940	0.640	94.171	0.980
2011S	15	4	13	249.950	731.400	0.680	110.280	0.990
2011S	15	5	16	349.100	1069.920	0.650	103.320	0.960
2011S	16	1	8	220.370	516.740	0.850	78.130	0.980
2011S	16	2	13	424.220	1030.740	0.820	83.760	0.990
2011S	16	3	12	389.550	1030.480	0.760	78.440	0.930
2011S	16	4	18	541.770	2262.190	0.480	84.940	0.990
2011W	17	1	14	318.090	2262.190	0.280	53.450	0.990
2011W	18	1	16	307.180	1006.370	0.610	112.780	0.920
2011W	18	2	19	338.450	1324.870	0.510	83.190	0.990
2011W	18	3	22	252.850	1004.910	0.500	48.930	0.980
2011W	18	4	50	853.320	3167.980	0.540	52.950	0.990
2011W	19	1	17	331.620	1173.340	0.570	102.200	0.980
2011W	19	2	33	687.330	2447.980	0.560	58.040	0.930
2011W	19	3	67	632.570	4650.900	0.270	27.030	0.700
2012S	22	1	5	98.388	263.789	0.746	104.758	0.988
2012S	22	2	8	159.772	464.564	0.688	99.151	0.966
2012S	22	3	12	305.778	610.637	1.002	129.905	0.996
2012S	22	4	13	393.321	1307.232	0.602	141.858	0.967
2012S	20	1	3	87.495	192.031	0.911	90.491	0.990

2012S	20	2	4	75.653	180.771	0.837	104.760	0.993
2012S	21	1	3	44.272	100.948	0.877	103.249	0.977
2012S	21	2	7	213.625	512.112	0.834	77.715	0.980
2012S	21	3	13	449.593	1209.382	0.744	74.737	0.993
2012S	21	4	12	430.297	1092.555	0.788	112.789	0.993
2012S	21	5	9	246.606	578.781	0.852	111.128	0.994
2012S	21	6	8	241.531	622.225	0.776	107.559	0.991
2012S	21	7	18	574.291	1673.891	0.686	99.187	0.990
2012S	23	1	6	134.750	541.467	0.498	55.592	0.982
2012S	23	2	5	101.804	360.488	0.565	126.427	0.925
2012S	23	3	7	131.138	466.116	0.563	156.511	0.941
2012S	23	4	7	95.003	368.607	0.515	105.067	0.994
2012S	23	5	9	264.834	686.150	0.772	106.868	0.980
2012S	23	6	13	289.994	868.793	0.668	130.621	0.987
2012S	23	7	3	58.347	117.992	0.989	139.706	0.984
2012W	24	1	29	588.112	1974.630	0.596	76.769	0.973
2012W	24	2	22	212.471	792.605	0.536	17.769	0.888
2012W	24	3	31	683.769	2043.330	0.669	37.344	0.944
2012W	25	1	31	589.326	2305.386	0.511	76.460	0.818
2012W	25	2	77	1258.380	5407.788	0.465	278.230	0.992
2012W	26	1	74	799.956	4683.427	0.342	48.762	0.899
2013S	27	1	3	63.743	167.634	0.760	97.356	0.992
2013S	27	2	7	236.106	476.544	0.991	67.280	0.983
2013S	27	3	5	164.213	310.160	1.059	90.518	0.996
2013S	27	4	9	205.840	451.671	0.911	84.058	0.992
2013S	27	5	5	101.950	222.429	0.917	87.691	0.987
2013S	27	6	7	223.860	403.891	1.109	83.766	0.986
2013S	27	7	14	448.264	994.167	0.902	90.637	0.997
2013S	28	1	8	259.686	646.360	0.804	85.003	0.992
2013S	28	2	5	106.486	200.817	1.061	93.937	0.998

2013S	28	3	4	57.064	128.811	0.886	103.144	0.999
2013S	28	4	4	70.683	184.727	0.765	115.994	0.963
2013S	29	1	10	242.352	579.482	0.836	47.751	0.980
2013S	29	2	11	272.201	725.686	0.750	64.765	0.977
2013S	29	3	9	179.918	601.435	0.598	75.750	0.978
2013S	29	4	12	349.503	912.326	0.766	92.682	0.993
2013S	29	5	14	337.244	1081.074	0.624	97.254	0.947
2013S	30	1	8	135.248	271.986	0.995	70.281	0.973
2013S	30	2	7	236.702	392.158	1.207	79.485	0.971
2013W	31	1	25	547.050	1685.835	0.649	307.682	0.809
2013W	32	1	29	743.788	2519.940	0.590	303.920	0.787