



Foraging habitats of southern elephant seals, *Mirounga leonina*, from the Northern Antarctic Peninsula

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ABSTRACT

Elephant Island (EI) is uniquely placed to provide southern elephant seals (SES) breeding there with potential access to foraging grounds in the Weddell Sea, the frontal zones of the South Atlantic Ocean, the Patagonian shelf and the Western Antarctic Peninsula (WAP). Quantifying where seals from EI forage therefore provides insights into the types of important habitats available, and which are of particular importance to elephant seals. Twenty nine SES (5 sub-adult males—SAM and 24 adult females—AF) were equipped with SMRU CTD-SLDRs during the post-breeding (PB 2008, 2009) and post-moulting (PM 2007, 2008, 2009, 2010) trips to sea. There were striking intra-annual and inter-sex differences in foraging areas, with most of the PB females remaining within 150 km of EI. One PB AF travelled down the WAP as did 16 out of the 20 PM females and foraged near the winter ice-edge. Most PM sub-adult males remained close to EI, in areas similar to those used by adult females several months earlier, although one SAM spent the early part of the winter foraging on the Patagonian Shelf. The waters of the Northern Antarctic Peninsula (NAP) contain abundant resources to support the majority of the Islands' SES for the summer and early winter, such that the animals from this population have shorter migrations than those from most other populations. Sub-adult males and PB females are certainly taking advantage of these resources. However, PM females did not remain there over the winter months, instead they used the same waters at the ice-edge in the southern WAP that females from both King George Island and South Georgia used. Females made more benthic dives than sub-adult males—again this contrasts with other sites where SAMs do more benthic diving. Unlike most other populations studied to date EI is a relatively southerly breeding colony located on the Antarctic continental shelf. EI seals are using shelf habitats more than other SES populations but some individuals still employ open water foraging strategies. Sea-ice was also very influential for PM females with more foraging occurring in heavier pack-ice. Larger females used areas with heavier ice-concentration than smaller females. The study demonstrates the importance of shelf and slope habitat to elephant seals, but also highlighted the influence of sea-ice and fine-scale bathymetry and local ocean condition in determining foraging habitat.

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1. Introduction

The southern elephant seal (SES), *Mirounga leonina*, is one of the most important top predators from the Southern Ocean. The species has a circumpolar distribution with the main breeding colonies found at South Georgia (SG—54°15'S, 36°45'W), Kerguelen (KI—49°15'S, 69°35'E), Heard (53°06'S, 73°31'E), and Macquarie Islands (MCQI—54°37'S, 158°52'E) (Laws, 1994). The only mainland breeding colony is found at Peninsula Valdés

(PV—42°30'S; 63°56'W), Chubut, Argentina (Lewis et al., 1998). The species also breeds at lower concentrations at the Falkland Islands (FI—51°42'S; 57°51'W), Marion Island (MAI—46°54'S; 37°44'E), South Orkneys Islands (SO) and Bouvet Islands (BI) and in several smaller subantarctic islands along the South Shetlands Archipelago (SSA—62°00'S, 58°00'W) (Vergani 1985; Vergani et al., 2004, 2007; Ling and Bryden 1981; Laws, 1994; Carlini et al., 2001; McMahon et al., 2005a, 2005b). Thus the breeding range for the species spans from its southern most colonies at Livingston Island (LI—62°27'30"S; 60°47'17"W) to its northernmost land breeding colonies at Peninsula Valdés, Patagonia. This distance represents about 12 degrees of latitude (approx. 1200 nm).

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The seasonal movements exhibited by elephant seals are not restricted to the areas close to their natal colonies (DeLong and Stewart, 1991; Boyd and Arnborn, 1991; Hindell et al., 1991, 1999; Campagna et al., 1995; Le Boeuf and Laws 1994; Le Boeuf et al., 2000, present study). Rather, southern elephant seals use distant foraging areas which are usually associated with the Antarctic Polar Front (APF), continental shelf margins or the ice edge (Boyd and Arnborn, 1991; Hindell et al., 1991; Fedak et al., 1994; Jonker and Bester, 1998). Their overall displacement shows that most of the Southern Ocean is potentially available to these seals as foraging grounds. It has been suggested that since they migrate long distances, dive to great depths and return to natal areas in a somewhat predictable pattern, elephant seals would appear to be suitable platforms for monitoring ecosystem changes in open oceans (Fedak, 2004; Biuw et al., 2007; Campagna et al., 2006; Charrassin et al., 2008, 2010; Padman et al., 2012).

Elephant seals play an important role in the dynamics of marine food resources as a result of their large populations, wide distribution and large energy demands. Consequently, over the past two decades southern elephant seals have been tracked throughout their distribution range as an attempt to determine key areas from South Georgia (McConnell et al., 1992; McConnell and Fedak, 1996), Iles Kerguelen (Bailleul et al., 2007a, 2007b), Macquarie Island (Hindell et al., 1999; van Den Hoff et al., 2002; Hindell et al., 2003), Elephant Island (EI, Muelbert et al., 2004) and Peninsula Valdes (Campagna et al., 1998, 2000, 2006, 2007). While at sea they encounter different oceanic environments (Biuw et al., 2007) although individuals from different breeding populations sometimes meet on common foraging grounds, such as the West Antarctic Peninsula, which is used by seals from the South Shetland Islands and South Georgia (Biuw et al., 2007). Although on a broad scale, frontal systems and major bathymetric features seem to play an important role for some elephant seal populations (Marion Island, Jonker and Bester, 1998; Macquarie Island, Hindell et al., 1991; Field et al., 2001; Hindell et al., 2003; and Peninsula Valdes, Campagna et al., 2000) other oceanographic features such as fronts and their eddies (Campagna et al., 2006) and as well as features such as ice edge (Bornemann et al., 2000; Bailleul et al., 2007a), and other meso-scale indicators (Campagna et al., 2007; Bailleul et al., 2010; Meredith et al., 2011) are important factors shaping southern elephant seal at sea behaviour.

Elephant seals (*Mirounga* spp.) are also highly dimorphic, proficient divers which exhibit long, deep and often continuous dives (Le Boeuf et al., 1988, 1992; Boyd and Arnborn, 1991; DeLong and Stewart, 1991; Campagna et al., 1995; Hindell et al., 1992). Given the strong sexual dimorphism present in this species, it is expected that differences in diving and foraging behaviour are present for both sexes but also within sexes, as well as ontogenetic changes (Slip et al., 1994; McConnell et al., 2002; Field et al., 2004, 2007a, 2007b). Thus, information about the pelagic phase of their life cycle is crucial not only for a better understanding of their biology, ecology and physiology but also to help us understand about the influence that both small and large scale environmental changes might have over their populations.

Ocean habitat usage of female and under-yearling elephant seals from South Georgia and King George islands are generally in the area west of the Antarctic Peninsula (McConnell et al., 1992; McConnell and Fedak, 1996; Bornemann et al., 2000). Movements in relation to sea ice also vary, with juvenile elephant seals avoiding sea ice and adult females frequenting the outer ice fringe or venturing into thick pack ice (Bornemann et al., 2000). In contrast, there are indications that adult males would venture into steep continental slope areas south of the Weddell Sea and Marion Island (Tosh et al., 2009; McIntyre et al., 2010a, 2010b, 2011). Southern elephant seals from PV have been reported to show marked differences in diving/foraging behaviour (Campagna et al., 1995, 1998, 1999, 2000), foraging strategies and resource partitioning

between sexes and within a given sex (Campagna et al., 2000, 2006, 2007; Lewis M.N. et al., 1996, 2006; Eder et al., 2010). There are also marked differences in foraging strategies/locations for southern elephant seals from different colonies (Bornemann et al., 2000; Muelbert et al., 2004; Bradshaw et al., 2004b; Field et al., 2005a, 2005b; Lewis M.N. et al., 2006; Lewis R. et al., 2006; Biuw et al., 2007; Tosh et al., 2009; McIntyre et al., 2010a, 2010b) although SES seem to congregate in specific common foraging areas that have been defined herein as areas of ecological significance.

Although information on at-sea activities, dispersion and seasonal movements of most Southern elephant seal populations has become more and more frequent, there are virtually no records of the activities of southern elephant seals from Elephant Island, Antarctica. Until fairly recently, there were no reports of breeding activity occurring on the island and the presence of individuals year-round was questioned. Being at the northern tip of the Antarctic Peninsula, EI provides the southern elephant seals breeding there with potential access to foraging grounds in the Weddell Sea, the frontal zones of the South Atlantic Ocean, the Patagonian shelf and the Western Antarctic Peninsula (WAP). Quantifying where seals from EI forage will therefore provide insights into the types of important habitats available, and which are of particular importance to elephant seals. The objective of this study was therefore to describe the pelagic phase of the life cycle of southern elephant seals from Elephant Island (EI) (61°13'S, 55°23'W), Antarctica, to provide information about the at sea behaviour of these individuals. Specifically we aimed to (i) identify the environmental factors associated with important foraging habitats and (ii) quantify the intra-specific effects of sex, body size and phase of the annual cycle on fundamental foraging parameters.

2. Materials and methods

This study was conducted during the austral summers of 2007/2008, 2008/2009 and 2009/2010 at Stinker Point (61°13'S, 55°23'W), Elephant Island, South Shetlands, Antarctica, which lies off the northern tip of the Antarctic Peninsula (Fig. 1). The study area was approximately 1.45 km in length, featuring wide variation in topography, width, and types of substrate. The seals were chemically immobilised with *Zoletil* 100® which was administered by hand via intramuscular injection in the gluteal region (Baker et al., 1988, 1990; Campagna et al., 1995, 1998, 1999; Field et al., 2002). The tags were fixed to the animal's pelage using a 5-min setting epoxy resin (Muelbert et al., 2004). The individuals were closely monitored until full recovery.

Thirty-two southern elephant seals were randomly selected, captured, bled from the extradural vein, measured, weighed and equipped with telemetry equipment during the post-breeding (PB 2008, 2009) and post-moulting (PM 2007, 2008, 2009, 2010) trips to sea. Adult females (AF) were captured towards the end of the breeding season (mass range 392–532 kg at PB deployments, $n=4$) or towards the end of the moult (mass range 211–435 kg at PM deployments, $n=20$). Five PM sub-adult males (mass range 454–765 kg) were also captured near the end of their moult. As a result of tag malfunction there were tracks from twenty nine seals available for analysis. Each seal was instrumented with a conductivity, temperature and depth satellite relayed data logger (CTD-SRDs, Sea Mammal Research Unit, University of St Andrews). These devices provided Argos locations, diving behaviour, and high resolution CTD data (see Sections 2.1 and 2.2 for more details).

2.1. Area Restricted Searches (ARS)

Data analyses was performed using R-Programme version 2.10.1. R Development Core Team (2009). We used a hierarchical

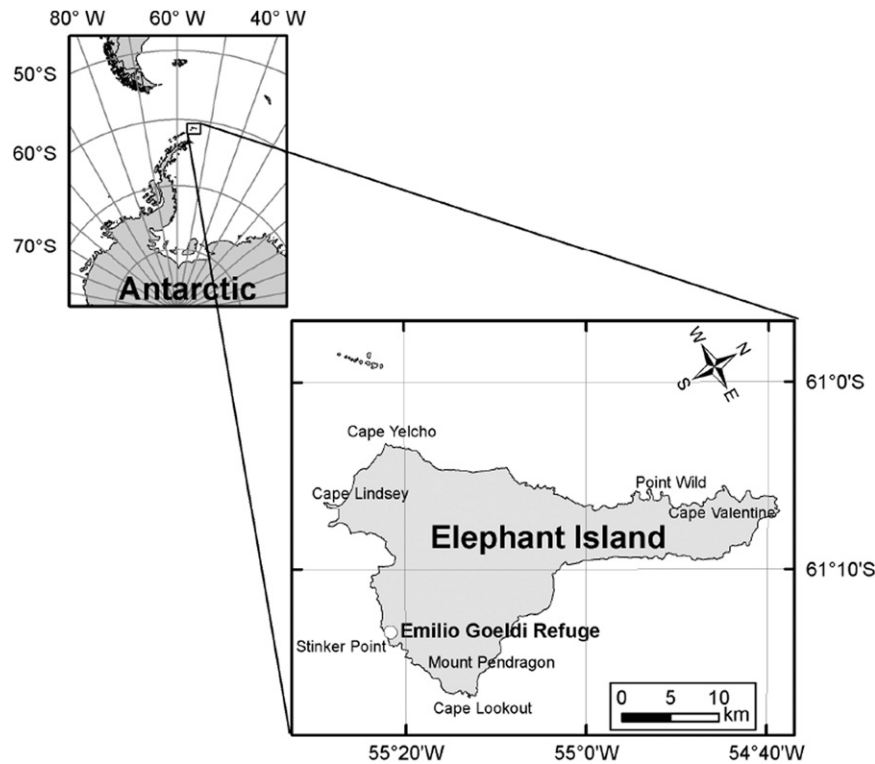


Fig. 1. The study site, Emilio Goeldi Refuge, Stinker Point (61°13'S, 55°23'W), Elephant Island in the regional context (left) where most of the displacements reported here took place and local context (right). El lies off the northern tip of the Antarctic Peninsula. Latitude expressed in °S, Longitude expressed in °W.

State Space Model (SSM) developed by Jonsen et al. (2006a, 2006b) to provide a best estimate of the path of each seal. This approach also provided (i) estimated locations (with their associated standard error) for regular time steps along the path (in our case every 12 h) and (ii) the likelihood of being in one of two behavioural states. These are “*transit*” when the seal made relatively linear and rapid progress, in contrast to “*search*” where the animal travelled slowly and made frequent changes in direction (also referred to as Area Restricted Search [ARS]). So, “*search*” areas were considered areas where foraging took place rather than migratory routes (“*transit*”).

Each dive made in “*search*” mode was allocated to one of two groups (i) benthic and (ii) pelagic. As this is a binary variable, all analyses of this variable used a GLMM with a binomial family and logit link function using seal as a random term (lme4 Package in R).

The behavioural mode data were subsequently used in two ways. The first was to contrast the environmental characteristics associated with “*transit*” and “*search*” modes to identify important habitat variables that influence foraging. The second was to compare the key foraging habitat characteristics (assuming that search mode locations were indicative of foraging activity) among phase of the annual cycle (post-breeding and post-moult), sex and size of seals.

We also used a Kalman filter which generated a statistical model for each seals' path (Johnson et al., 2008) to interpolate a position for every dive, based on its starting time. We then performed all subsequent analyses using individual dive as the fundamental experimental unit. This approach provides greater statistical power than alternatives, such as aggregating the data into longer (usually daily) time intervals.

2.2. Environmental data

We chose a suite of variables that encompassed both static and dynamic features of the environment drawn from a combination

of remotely sensed and in-situ data. The environmental covariates included in the analyses were: bathymetric depth under each dive, the bathymetric slope, the distance to the 1000 m bathymetric contour (as a measure of distance to the continental slope), the water temperature at the maximum depth of the dive, the salinity at the maximum depth of the dive and neutral density at the maximum depth of each dive and the weekly ice concentration at the dives location.

All in-situ CTD data were post calibrated using the approach of Roquet et al. (2009). The resulting in-situ temperature and salinity data were then expressed as neutral density (kg m^{-3}) and used to identify major water masses using the definitions in Sloyan and Rintoul (2001) and following Williams et al. (2011). These were

- Antarctic Intermediate Water (AAIW) < 26
- 26 < Subantarctic mode water (SAMW) < 27.1
- 27.1 < Antarctic Intermediate Water (AAIW) < 27.4
- 27.4 < Upper Circumpolar Deep Water (UCDW) < 28
- 28 < Lower Circumpolar Deep Water (LCDW) < 28.2
- 28.2 < Antarctic Bottom Water (AABW)

All bathymetric data came from the ETOPO1 1 arc-minute global relief model of Earth's surface from NOAA's National Geophysical Data Centre. Sea-ice extents and concentrations were from Aqua AMSR-E downloaded at a 7 day temporal resolution via Bloomwatch 360 (<http://coastwatch.pfeg.noaa.gov/coastwatch>).

2.3. Environmental characteristics associated with “*transit*” and “*search*” behaviour

In order to assess how environmental characteristics were associated with dive behaviour, we converted the dive-by-dive behavioural mode data to a binary variable by aggregating them

into 0.25° cells, and calculating the most common behavioural mode for all dives by each seal in each cell for this particular analysis. Cells with less than 5 locations for an individual were excluded from the analysis as these were considered to give unreliable estimates.

The mean value for each of the covariates was then also calculated for each 0.25° cell. The covariates were (i) distance (km) to the -1000 isobath, bathymetric contour ($d2s$), (ii) bathymetric depth (m) under the cell ($bathy$), (iii) bathymetric gradient ($slope$), (iv) ice concentration (%) (ice), (v) temperature at the maximum depth of the dives in that cell (tmp), (vi) salinity at the maximum depth of the dives in that cell (sal) and (vii) neutral density of water (kg m^{-3}) at the maximum depth of the dives in that cell (nde). Each covariate was log transformed where appropriate to ensure a normal distribution. The dominant behavioural mode (either “search” or transit) for each cell was compared to all the environmental variables using the generalised linear mixed-effects model (*lme4*) Package in R. The binary nature of the *mode* variable required logistic models, using a binomial family with a logit link. Model selection was conducted in accordance with Zuur et al. (2009). Firstly, we explored the optimal structure of the random effects, comparing random intercept models (*seal* or *cell* only) with random intercept and slope models (*seal* and *cell* and each environmental variable in turn). Next, retaining the slope terms that improved the models, we estimated the full additive model (*mode* ~ each environmental variable + random intercept + random slope terms). We then tested the individual fixed effects by sequentially removing the least influential fixed effects from the model. These were determined by comparison of the single fixed effect models with a *NULL*. In all cases, models were ranked via Akaike Information Criterion (AIC) (Burnham and Anderson, 2002), the most parsimonious model having the lowest AIC value. In addition, we used likelihood ratio tests to test between models. The final model was the one from this family of models with the lowest AIC, and which a likelihood ratio test indicated contained significantly more information than the next ranked model.

Dives were identified as being in sea-ice (defined here as $> 15\%$ ice cover), or not. We did not include *phase* in this analysis as ice was effectively absent during the post-breeding period of November to January. Further, as the data from the SAM seals was only from February to May in 4 of the 5 seals, we restricted the comparison of gender to those months for all seals. Again, as this is a binary variable, all analyses of this variable used a GLMM with a binomial family and logit link function using seal as a random term (LME4 Package in R).

The influence of water mass on diving behaviour was examined by (i) comparing the number of “search” and “transit” dives made in each water mass using a *g*-test and (ii) plotting depth/time profiles of neutral density, distinguishing the major water masses and overlaying the depth of daytime and night-time dives. The profiles were generated using thin plate splines of the full time and depth series of neutral density data for each individual (R package *Fields*).

2.4. Habitat characteristics of “search” dives by sex, size and phase

We then compared habitat characteristics (on or off the shelf, presence of sea-ice and sea-ice concentration) and dive behaviour (benthic or pelagic) made in “search” mode for seal sex, size and phase of the annual cycle (post-breeding and post moulting). In this case, we used a series of linear mixed effects model following the process outlined above.

3. Results

3.1. Movement data

Over the 3-year study five sub-adult males (SAM) and 24 adult females (AF) were tracked from 7 to 283 day yielding 167,699 dive locations and 12,940 CTD locations over the post breeding ($n=4$) and post moulting periods ($n=25$).

There were marked differences among the overall tracks exhibited by these seals over the years and between sexes (Fig. 2A). The 4 PB females provided location data for 58.5 ± 10.5 days and 1686 ± 661 dives (Table 1). The 20 PM adult females produced 227.9 ± 44.1 days and 7159 ± 1972 dives, compared to only 120.4 ± 73.2 days and 3554 ± 2352 dives for the PM sub-adult males. The AFs dispersed widely from Elephant Island during the post-moulting pelagic phase (Fig. 2A), some moving up to 3981 km to the west into the Pacific Ocean, others moving to the south of the West Antarctic Peninsula along Marguerite Bay, Wilkins Sound and the Bellingshausen Sea, while yet another group went towards the Weddell Sea (WS) and Scotia Sea (SS) regions. The region south of the WAP was particularly important to the PM adult females with 12 of the 20 AFs using the area and making a combined total of 90,461 dives (63.2% of all dives). In contrast, the PB adult females made much shorter trips; the majority staying in the immediate vicinity of Elephant Island. The only PB female that did not stay close to EI was

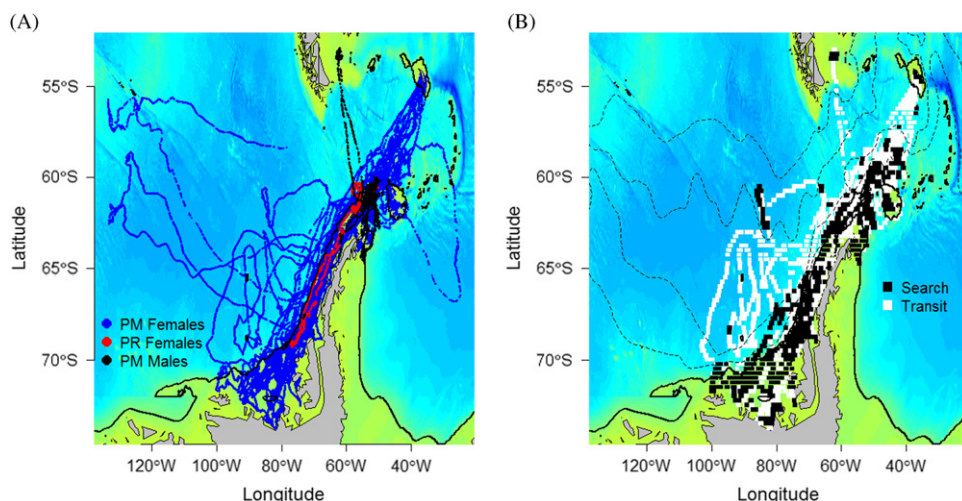


Fig. 2. Tracks of 29 southern elephant seals from Elephant Island. (A) The twice daily locations from the SSMs, overlaid on ocean bathymetry. (B) Map of gridded locations of seals from Elephant Island (0.25×0.25 degree cells with more than 5 locations per individual seal). “Search” mode locations are in black and “transit” are in white. The 1000 m bathymetric contour (bold black line), and the mean position primary oceanographic fronts (taken from Orsi et al., 1995).

Table 1

Summary statistics for the 29 adult females and sub-adult males tagged in the study. The year of deployment is indicated by the last two digits on Seal ID.

Seal ID	Sex	Phase	Deploy. mass (kg)	Mean depth (m)	Mean duration (s)	No. of days	No. of dives	Max. dist. from EI (km)	% Search
ct22-11-08	F	PB	431	467.5	1350	67.37	1263	182.3	100.0
ct22-17-08	F	PB	347	332.5	1065	54.28	1127	182.2	96.3
ct56-M798-10	F	PB	532	523.8	1650	66.84	2587	1343.6 ^a	53.7
ct56-M665-10	F	PB	392	271.3	982	45.65	1767	179.5	91.1
ct39-40-08 ^b	F	PM	358	326.3	1545	233.17	8287	1331.94 ^a	67.6
ct39-41-08	F	PM	211	371.3	1650	277.36	9456	2323.8	30.0
ct39-42-08 ^b	F	PM	239	246.3	1485	230.15	7153	1369.1	43.4
ct39-43-08 ^b	F	PM	405	443.8	1980	243.24	7741	2231.7 ^a	57.8
ct39-44-08 ^b	F	PM	435	328.8	2205	230.82	6959	1316.5 ^a	52.5
ct39-45-08 ^b	F	PM	281	376.3	1590	244.95	9020	1650.5	50.4
ct39-46-08	F	PM	273	271.3	1440	283.20	8207	863.8	60.1
ct39-47-08 ^b	F	PM	385	371.3	2115	244.70	7706	1748.9 ^a	59.1
ct39-48-08	F	PM	404	291.3	1560	157.36	5549	1417.5 ^a	44.2
ct39-49-08 ^b	F	PM	383	396.3	2055	239.92	6395	1340.0 ^a	81.1
ct46-69041-09	F	PM	273	381.3	1560	225.88	8036	1977.6 ^a	50.1
ct46-69042-09	F	PM	N/A	449.4	1785	229.33	8814	1832.8 ^a	59.1
ct46-69044-09 ^b	F	PM	N/A	406.3	1995	243.65	8162	1502.2 ^a	59.7
ct46-69046-09 ^b	F	PM	423	413.8	1901	244.95	7272	1959.7 ^a	34.8
ct46-69049-09 ^b	F	PM	421	356.3	2055	235.62	7435	1380.5 ^a	68.3
ct56-M981-10	F	PM	290	351.3	1425	211.68	6756	3891.7 ^a	37.4
ct56-R021-10	F	PM	339	330	1920	206.70	2405	4312.9	34.2
ct56-R746-10	F	PM	352	343.8	1305	75.70	1693	1585.2	14.0
ct56-R760-10 ^b	F	PM	277	420.05	1110	243.61	8162	1991.2 ^a	16.3
ct56-R779-10 ^b	F	PM	423	361.3	1965	256.01	7979	1821.7 ^a	51.7
ct46-69040-09	M	PM	511	431.3	1350	92.78	2336	230.6	75.6
ct46-69043-09	M	PM	765	461.3	1710	90.82	2669	303.7	84.8
ct46-69045-09	M	PM	667	503.8	1635	75.67	2263	310.5	88.5
ct46-69047-09	M	PM	454	481.9	1290	92.10	2756	1011.7	58.1
ct46-69048-09	M	PM	675	553.8	1740	250.82	7744	395.6	87.1

PB: post-breeding; PM: post-moult.

^a Was tracked in the area of the southern WAP.

^b Observed to bred on South Georgia.

Table 2

Summary statistics for the 8 of the 14 seals tagged in 2008/09 that were recaptured the following phase or season.

Seal ID	Phase	Deployment mass (kg)	Recapture mass (kg)	Mass change (kg)	Time elapsed (approx., d)	% Body mass at recapt	No. of deploy. days	% of shelf dives	% of benthic dives	% of search dives
ct22-15-08 ^a	PB	350	492	142	90	28.8	–	–	–	–
ct22-17-08	PB	347	471	124	90	26.3	52,3	98.1	83.3	96.3
ct22-20-08 ^a	PB	268	383	115	90	30.0	–	–	–	–
ct39-43-08	PM	405	450	45	370	10.0	243,2	49.5	19.5	57.8
ct39-44-08	PM	435	430	–5	370	–1.2	230,8	93.2	39.5	52.5
ct39-47-08	PM	385	435	50	370	11.5	244,7	98.7	38.9	59.1
ct39-48-08	PM	404	445	41	370	9.21	157,4	94.0	86.2	44.2
ct39-49-08 ^b	PM	383	–	–	–	–	239,9	88.2	54.9	81.1

PB: post-breeding; PM: post-moult.

^a Only biological and biometric information available since CTD tag failed to transmit data.

^b Seal was not weighed the following season.

also one of our largest females (530 kg) and she went foraging in the region of the SW Pacific Ocean (SWPO), some 1000 km away. The PM sub-adult male displacements were similar to the PB adult females, remaining close to Elephant Island, albeit at different time of year (Feb–June for SAM compared to Nov–January for the PB AF). Ten of the twelve AFs (80%) using the south WAP area returned to South Georgia at the end of their foraging trip for the breeding season. Four additional females were heading towards SG at the time when the tags stopped transmitting. Therefore, 16 out of the 20 PM adult females can be regarded as belonging to the South Georgia population, and were merely hauled out on Elephant Island for their annual moult, while the remaining 4 PM adult females tracked over the winter period were considered as Elephant Island residents. On the other hand, all 4 of the PB adult females tracked had bred at EI and

were either captured or resighted in previous years as part of a different study.

3.2. Influence of body mass

Eight of the 14 adult females tagged at EI during the PB ($n=3$, 75%) and PM ($n=5$, 50%) periods in 2008/09 were recaptured and body mass measurements (BM) were collected from 7 of these (Table 2). Six adult females increased their BM (86.2 ± 45.7 kg) between recaptures while one PM adult female was 5% lighter upon recapture. PB female body mass was about 30% higher after approximately 2 months foraging while this increase represented about 11% for PM females after foraging for a whole year.

All of the seals demonstrated area restricted search (ARS) behaviour (Table 1), but the proportion of dives made while in

“search” mode varied considerably, ranging from 100% to 16% (overall mean = $58.9 \pm 22.7\%$). There were significant differences between the proportion of dives made while in “search” mode by the 3 groups of seals (post-breeding adult females PBAF, Post-moulting adult females PMAF, and post-moulting sub-adult males PMSAM) ($F_{2,26} = 11.8, p = 0.0002$), with PMAF spending less time diving in “search” mode (mean = 48.6%) than PMSAM or PBAF (79.0% and 85.3% respectively).

The vast majority of the “search” dives occurred over the continental shelf of the West Antarctic Peninsula (Fig. 2B), with 19 of the 29 seals making more than 60% of their foraging dives over the shelf (Table 3). There was no significant difference in the proportion of dives made over the shelf among the 3 sex/phase groups ($F_{2,26} = 0.85, p = 0.44$), with overall $67.3 \pm 36.7\%$ of “search” dives made on the shelf.

The mean dive depth of the individual seals ranged from 246.3 m to 553.8 m (mean = 388.4 ± 77.2). As so many of the individuals made the majority of their dives over the shelf, the ocean floor potentially constrained their dive depths (Fig. 3). We therefore defined any dive that had a maximum depth that was within 50 m of the ocean floor at that location as being a “benthic” dive, and all other dives were regarded as “pelagic”. Overall, $33.2 \pm 26.9\%$ of “search” dives were classified as “benthic”, and this did not vary among the sex/phase groups ($F_{2,26} = 1.59, p = 0.22$).

There was however, clear spatial separation where the two types of dives were performed (Fig. 4), even when both were made over the shelf. For example, there were a total of 33,873 “search” dives made in the Marguerite Bay region over the course of the study, 56.7% of which were classified as “pelagic”. These dives were concentrated over, or immediately adjacent to, relatively deep water associated with a canyon extending inwards from the shelf break (Fig. 4B). In contrast, the “benthic” dives

were made either to north or south of this canyon, in regions of relatively shallow and flat bathymetry (Fig. 4A).

3.3. Environmental characteristics associated with “transit” and “search” behaviour

The model with the best fit describing behavioural mode in a grid cell included 5 environmental variables, ice concentration, bathymetric depth, distance to the –1000 m contour, mean water temperature at the maximum depth of the dive and bathymetric slope. Model parameters and results are detailed in supplementary materials (Tables A1 and A2). It should be noted that the model which included all variables was ranked only slightly lower than this one and that a likelihood ratio test suggested no difference between the two in terms of information content. Thus we chose this as our final model on the basis of parsimony, given that it contained 5, compared to 7 fixed effect terms.

Cells in which “search” behavioural mode was predominant were associated with higher ice concentrations, shallower bathymetric depths and were closer to the shelf edge (Fig. A1). To a lesser extent, these cells were also associated with gentler bathymetric gradients and higher water temperatures at the maximum depths of the dives.

The influence of water mass on diving behaviour was assessed by plotting depth/time profiles of neutral density, distinguishing the major water masses and overlaying the depth of daytime and night-time dives (Fig. 5). There were no clear associations between dive depth and water mass for any of the seals, despite the seals moving through several water masses along their trips. However, there was a tendency of PM females to forage in close proximity to the Circumpolar Deep Water. There was also a tendency for night dives to occur in close association with the SAMW boundary layer (27.15 kg m^{-3}).

Table 3

Summary statistics of “search” dive variables used in the statistical models for the 29 seals used in the study.

Ref	Sex	Phase	Bathymetry \pm s.e. (m)	No. of dives		Mean ice Conc. \pm s.e.	% Diurnal migration	Per cent (%)	
				Benthic	In ice			Shelf	Benthic
ct22-11-08	F	PB	-2576 ± 42	121	0	0 ± 0	14.9	16.4	4.5
ct22-17-08	F	PB	-323 ± 4	909	0	0 ± 0	0.0	98.1	83.3
ct56-M798-10	F	PB	-505 ± 2	930	1148	72.34 ± 1.01	23.1	100.0	59.0
ct56-M665-10	F	PB	-293 ± 2	1083	0	0 ± 0	20.5	100.0	63.6
ct39-40-08	F	PM	-422 ± 2	2423	1614	22.72 ± 0.49	27.7	99.4	30.7
ct39-41-08	F	PM	-603 ± 16	1382	187	4.38 ± 0.29	12.6	93.1	42.5
ct39-42-08	F	PM	-1839 ± 25	441	496	8.57 ± 0.38	40.6	30.2	8.5
ct39-43-08	F	PM	-1461 ± 17	898	3559	70.84 ± 0.59	9.5	49.5	19.5
ct39-44-08	F	PM	-471 ± 8	1794	1576	33.17 ± 0.69	11.3	93.2	39.5
ct39-45-08	F	PM	-2661 ± 24	393	519	7.7 ± 0.33	22.7	24.8	5.0
ct39-46-08	F	PM	-1750 ± 22	1164	1682	25.22 ± 0.52	30.7	51.7	13.6
ct39-47-08	F	PM	-405 ± 3	2262	3564	65.32 ± 0.60	18.5	98.7	38.9
ct39-48-08	F	PM	-186 ± 10	2140	722	23.12 ± 0.76	17.2	94.0	86.2
ct39-49-08	F	PM	-581 ± 11	2976	300	3.8 ± 0.22	14.9	88.2	54.9
ct46-69041-09	F	PM	-1011 ± 17	1174	1100	22.43 ± 0.60	28.7	78.3	22.6
ct46-69042-09	F	PM	-370 ± 3	3531	3962	70.95 ± 0.59	3.2	98.1	64.6
ct46-69044-09	F	PM	-195 ± 2	4131	2577	44.04 ± 0.63	20.3	99.3	81.7
ct46-69046-09	F	PM	-438 ± 11	1593	2168	78.8 ± 0.70	14.4	88.9	52.2
ct46-69049-09	F	PM	-450 ± 2	2294	2170	35.59 ± 0.60	13.0	100.0	37.3
ct56-M981-10	F	PM	-3623 ± 35	313	0	0 ± 0	22.2	18.5	7.4
ct56-R021-10	F	PM	-3688 ± 17	0	0	0 ± 0	2.9	0.0	0.0
ct56-R746-10	F	PM	-4917 ± 9	0	0	0 ± 0	20.0	10.0	0.0
ct56-R760-10	F	PM	-549 ± 3	269	474	29.32 ± 1.11	25.0	100.0	18.8
ct56-R779-10	F	PM	-725 ± 8	1366	3331	72.29 ± 0.60	28.8	79.5	21.2
ct46-69040-09	M	PM	-1027 ± 15	400	159	5.98 ± 0.47	26.0	60.3	19.2
ct46-69043-09	M	PM	-1482 ± 13	0	0	0 ± 0	18.5	1.2	1.2
ct46-69045-09	M	PM	-1579 ± 11	1	0	0 ± 0	14.5	8.7	1.4
ct46-69047-09	M	PM	-564 ± 5	842	0	0 ± 0	25.9	96.6	56.9
ct46-69048-09	M	PM	-1079 ± 11	2651	3193	43.04	17.4	78.3	28.7

PB: post-breeding; PM: post-moult.

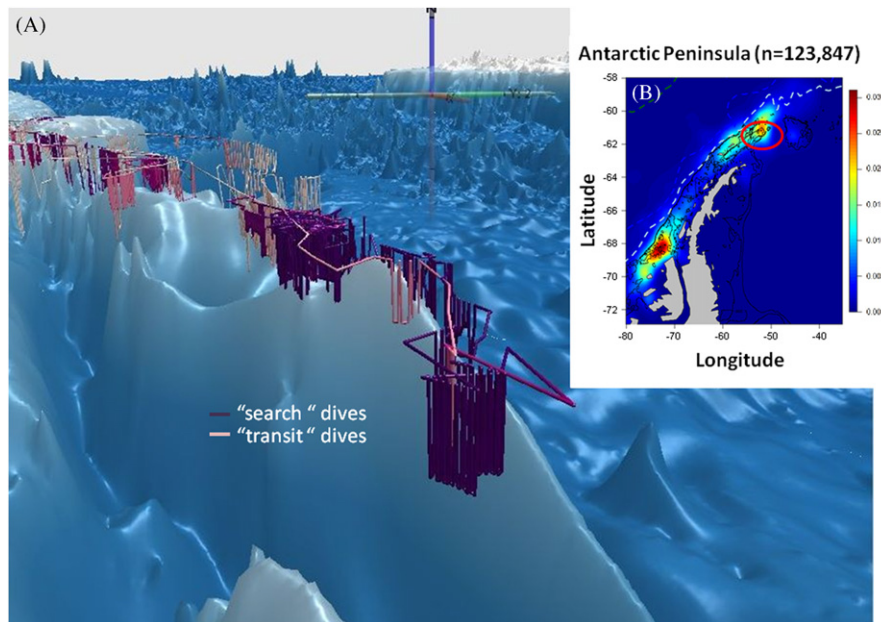


Fig. 3. Track of two southern elephant seals foraging on the north Antarctic Peninsula. Profile data from the CTD-SLDs provide a continuous trace of depth and time in three dimensions. The lines are colour coded to indicate the behavioural mode, also derived from the SSMs. Inset: a kernel density representation of all dive locations derived in the study. The red circle indicates the region illustrated in the main figure. Latitude expressed in °S, Longitude expressed in °W. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

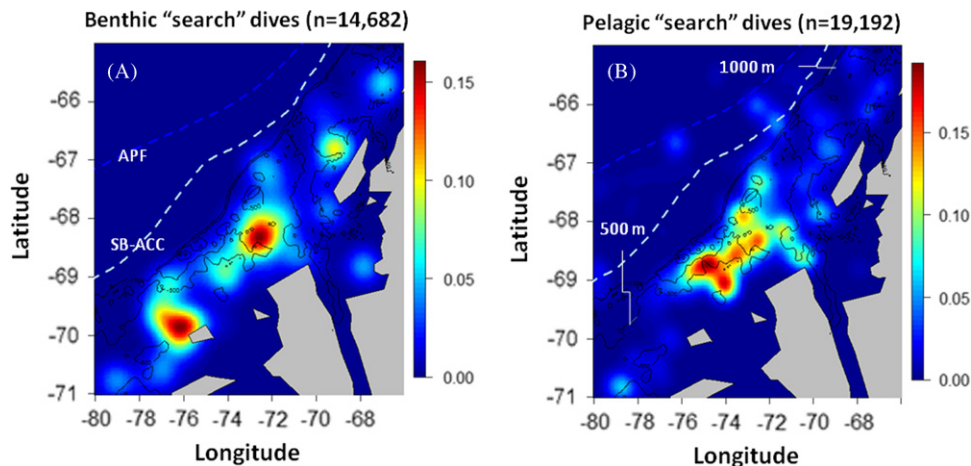


Fig. 4. Kernel density plots of (A) the 14681 benthic “search” dives and (B) the 19192 pelagic “search” dives made in the Marguerite Bay region. The –1000 m and –500 m bathymetric contours are also shown. Latitude expressed in °S, Longitude expressed in °W.

Overall, the vast majority of dives were made in LCDW and UCDW (Fig. 6). A g -test indicated that there was difference in the number of “transit” and “search” dives made in the different water masses (Log likelihood ratio statistic (G)=3787.8, $X^2df=4$, $p < 0.001$), with the largest difference being that the LCDW was more common in “search” dives than “transit” dives. Generally, both LCDW and UCDW were present in the water column (Fig. 6), and the seals utilised both bodies of water in the course of a day, accessing the LCDW during the deeper dives made during the day when making pelagic dives, or when making benthic dives.

3.4. Habitat differences in “search” dive behaviour between sex, phase and seal mass

3.4.1. Bathymetry

Having established the environmental influences on behaviour mode (“transit” vs. “search”), we then focused on the “search” dives to test for differences in the foraging habitat characteristics

between sex, phase and seal mass. We tested 4 habitat variables (i) bathymetric depth under the dive (ii) position in the water column, (iii) the presence of sea-ice and (iv) the concentration of sea-ice. When initially running the models, the fixed terms failed to converge, probably due to the unbalanced nature of the deployments. So specific tests were made on subsets of the data. Firstly *sex* was compared only for the post-moult period, then *phase* was compared for the adult females. Analysis of mass used all the female data combined, as there was no difference in the mass of females tagged in either phase.

The influence of sex, and phase on the bathymetry under “search” mode dives was tested using linear mixed models (LMMs) with seal as a random term. There was no difference in the ocean depth under the “search” dives made by sub-adult male or female seals (Table A2) despite their foraging having occurred in very different regions, with the females diving about 1300 km southwest of Elephant Island, while the SAMs foraging primarily in the region adjacent to Elephant Island (Fig. 2A). In both

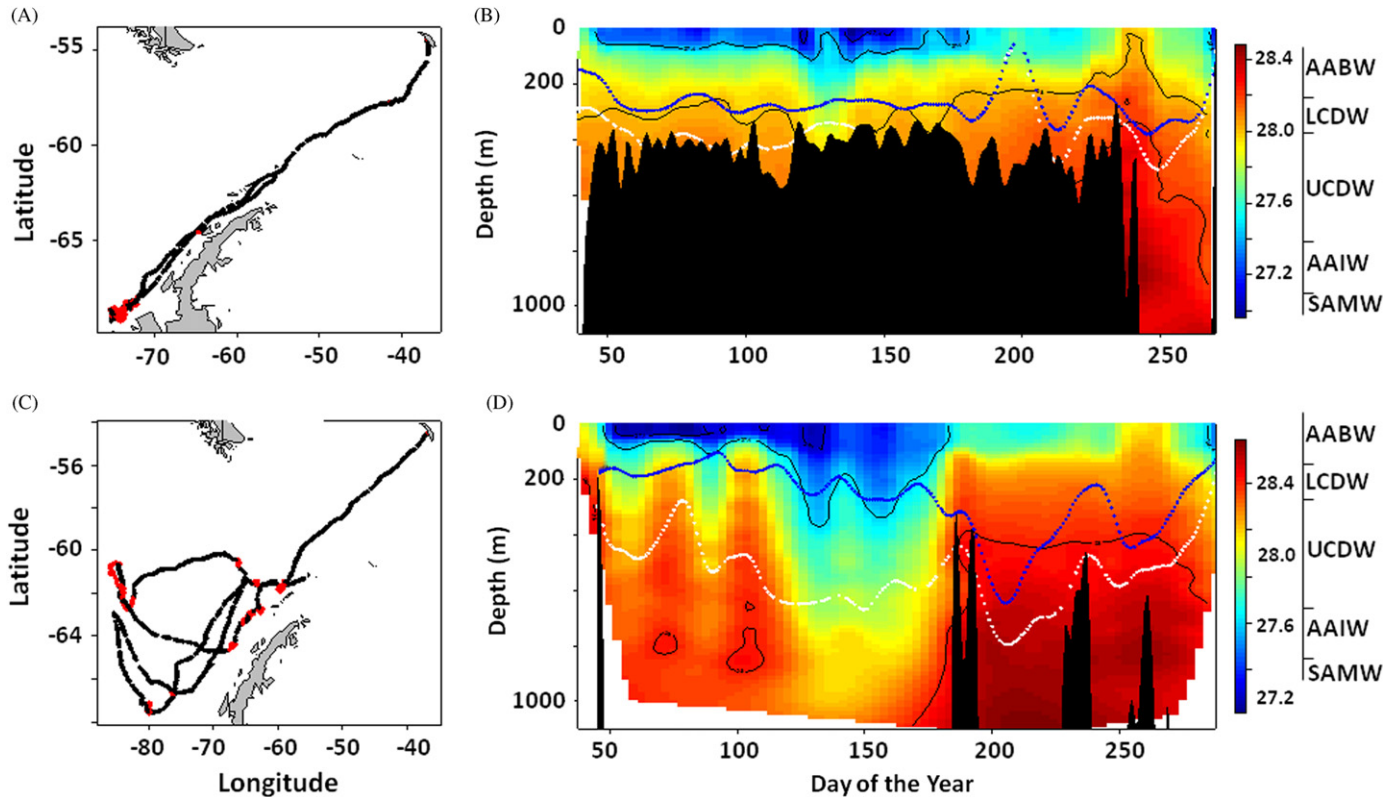


Fig. 5. Example of a vertical water mass profile for two adult females, ct39–40–08 (A, B) and ct39–45–08 (C, D). A map of the seals track (A, C), with red dots indicating “search” mode; and, the neutral density of the water column (kg m^{-3}) for each day of the foraging trip (B, D). Black represents the mean depth of the ocean floor on each day, the blue dots are the mean nighttime dive depths and the grey dots the mean daytime dive depths (all smoothed using a cubic smoothing spline). The black lines are boundaries between the water mass, using the definition of Sloyan and Rintoul (2001). Latitude expressed in °S, Longitude expressed in °W, Date expressed in days after Jan. 1st. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

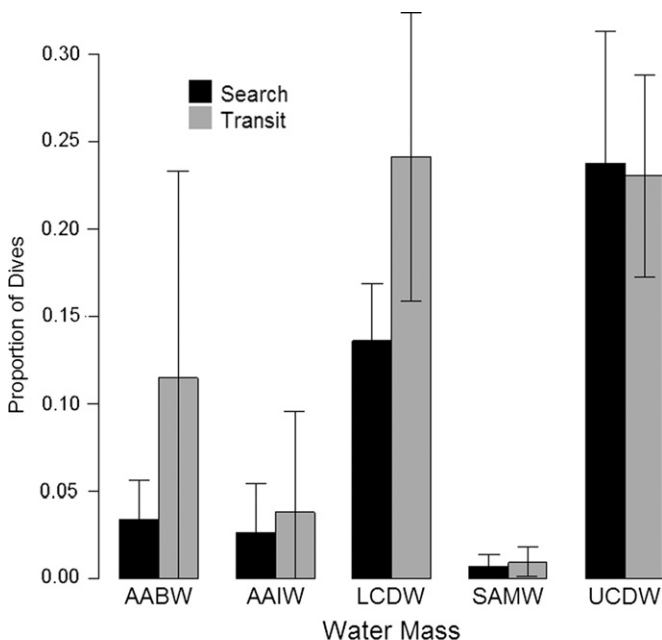


Fig. 6. The mean proportion ($\pm 95\%$ confidence interval) of total dives made per individual in each of 5 water masses with respect to the behavioural mode identified by the State Space models (“transit”, “search”). AABW=Antarctic Bottom Water, AAIW=Antarctic Intermediate Water, LCDW=Lower Circumpolar Deep Water, UCDW=Upper Circumpolar Deep Water, SAMW=sub-Antarctic mode water.

cases, the majority of “search” dives occurred over the Antarctic Continental Shelf, which accounts for the similarity in bathymetric depth between the sexes.

Bathymetric depth and life history phase of adult females (post-moult vs. post-breeding) had no effect on dive behaviour such that most “search” dives occurred on the Antarctic continental Shelf of the West Antarctic Peninsula even though the two groups of AFs used very different regions. Once again PBAF remained close to Elephant Island, in a very similar region used by the SAM during the winter months. Furthermore, PM female body size had no effect on the bathymetric depth attained during “search” dives (Table A2).

3.4.2. Position in the water column

The GLMM indicated moderate support for a sex effect (Table A2), with sub-adult males having less dives in the benthic group and females less dives in the pelagic group (Fig. 7A). However, foraging habitat did not differ with phase of the annual cycle among adult females, nor did it vary with the size of adult females.

3.4.3. Presence and concentration of sea-ice

During the post-moult phase, sub-adult males were less likely to make dives in the presence of sea ice than females (Table A1). Within the females, larger seals were more likely to make dives in the presence of sea-ice than smaller animals (Fig. 7B and D).

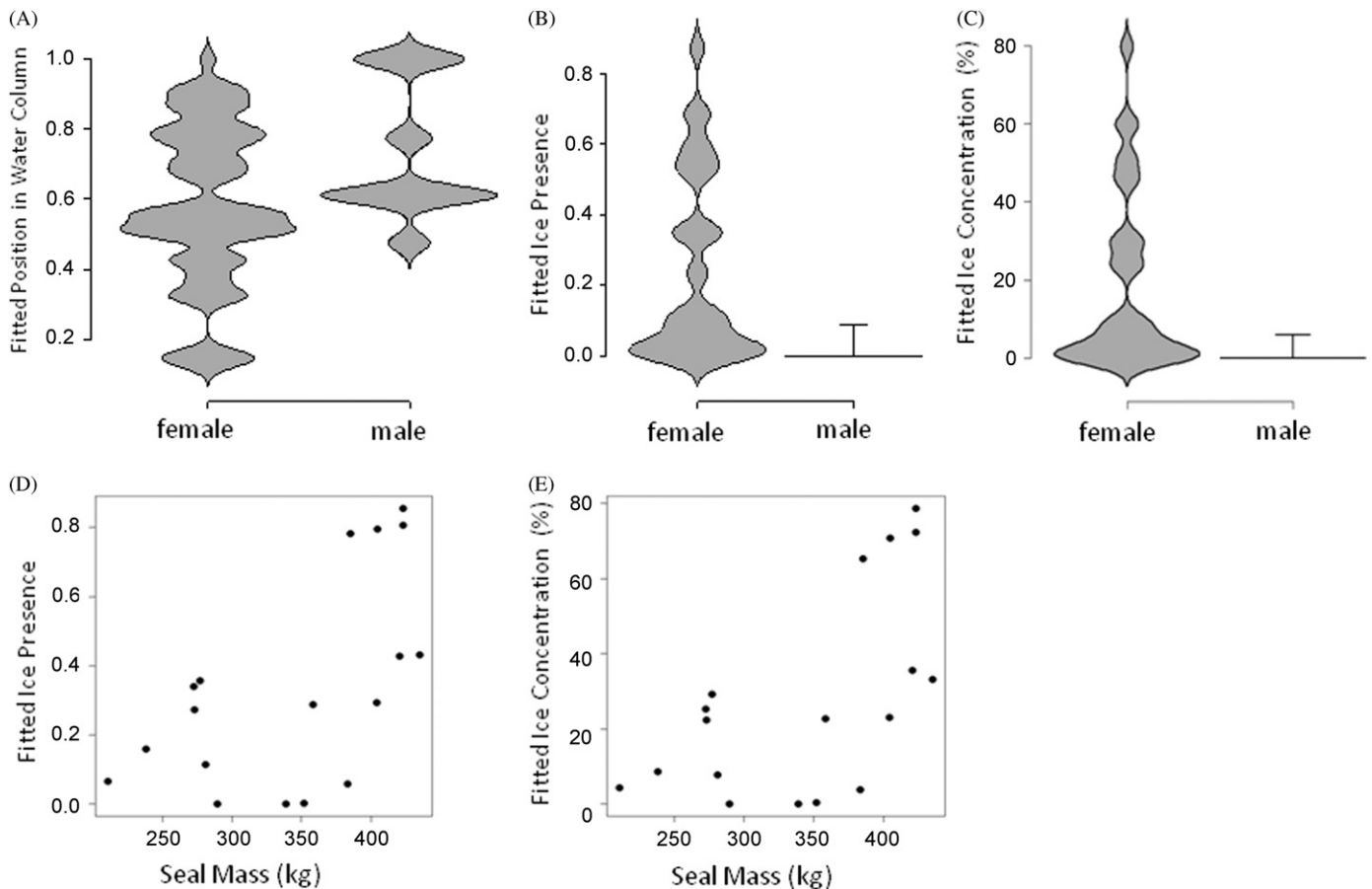


Fig. 7. Habitat differences in “search” dive behaviour between sex, phase and seal mass. (A) Violin plot of sex and fitted position in the water column, (B) violin plot of sex and fitted ice presence, (C) violin plot of sex and fitted ice concentration, (D) seal mass and fitted probability of ice presence and (E) seal mass and fitted ice concentration.

Sub-adult males also performed dives in lower ice concentrations than adult females (Table A2), and large females made dives in higher concentrations than smaller females (Fig. 7C and E).

4. Discussion

The southern elephant seals from Elephant Island used a diversity of habitats, but some were more important than others. Over the three years of study, the spatial displacement of southern elephant seals tagged at EI was wide and far reaching but foraging activity, defined as a suite of behaviours displayed by the seal while in “search” mode, was restricted to a few important areas in the South Atlantic and Bellingshausen/Amundsen Sea Sectors of the Southern Ocean. While travelling across the Southern Ocean, or when diving through the water column, southern elephant seals traversed several water masses and experienced critical changes in the marine environment that reflected the oceanographic conditions encountered west and north of the Antarctic Peninsula where subtle changes in thermocline depth suggest the presence of meso-scale structures along the shelf-break. The presence of cold core eddies is also suggested by its typical signature: upwelling of the thermocline depth accompanied by the rising of intermediate water masses towards the upper layers of the ocean. At about day 75 and day 110 seal ct-39-45 may have crossed and interacted with cold core eddies. In contrast, warm core eddies were also found along the tracks. The clear signature of the southern Antarctic Circumpolar Current Front (sACCF) is evidenced at the end of both seal tracks between days 240–260, just before their arrival at South Georgia Island. Important water

masses such as Antarctic Intermediate Water (AAIW), Subantarctic Mode Water (SAMW), Antarctic Intermediate Water (AAIW), Antarctic Bottom Water (AABW), Circumpolar Deep Water (CDW) and its derivations (UCDW, LCDW and mCDW), as well as important oceanographic fronts like the Antarctic Circumpolar Current (ACC), Southern Antarctic Circumpolar Current Front (sACCF), Polar Front (PF), Sub-Antarctic Front (SAF), the Southern Boundary of the ACC (SB), and the Winter Front (WF) were also encountered along the tracks.

4.1. Breeding of southern elephant seals in the South Shetland Islands and its proximity to WAP foraging grounds

The Bellingshausen Sea and the WAP are important foraging areas for southern elephant seals, and are used by seals from several breeding populations including South Georgia, the largest breeding aggregation for the species, and the only site with a stable population. The number of seals that remain in these areas year round is however relatively small, and in particular the number of females that breed in the South Shetlands is less than 2300, compared to approximately 113,000 females at South Georgia (Boyd et al., 1996). Sixteen PM females tagged at EI (80%) returned to South Georgia to breed, and eight of these (40%) were resighted at Elephant Island the following moulting period. Carlini et al. (1997) have shown that southern elephant seals breeding in the South Shetlands (KGI) are heavier than South Georgia individuals, a finding that was attributed to better foraging conditions found at WAP than those found around SG (McConnell and Fedak, 1996; Bornemann et al., 2000). This suggests that the SSI and particularly EI may play an important

role during the post breeding/foraging activities of some seals of a much larger population such as SG which forage elsewhere.

Unlike southern elephant seals from other populations, most PB female and sub-adult male PM dispersal from EI was restricted to a few hundred kilometres from the breeding beaches, while female post-moult dispersal was wide and far reaching. Most PB females and SAMs stayed in the vicinity of EI and in the Weddell Sea/Scotia Sea region. Some PM females spent time in open waters of the Pacific Ocean close to the region known as the De Guerlache Seamounts. Most PM females from EI, however, travelled down to the WAP towards Marguerite Bay and the Bellingshausen Sea as do females from SG (McConnell et al., 1992), KGI (Bornemann et al., 2000) and Livingston Island (Costa et al., 2008). Nevertheless, in all other non-WAP populations post-reproductive dispersals are much greater, indicating the remoteness of foraging grounds to those animals.

4.2. The importance of the Continental Shelf to southern elephant seal foraging

This study has identified three major areas where southern elephant seals tagged at EI concentrated their foraging: (a) the region in the southern WAP around Marguerite Bay (radiating from about 68S 74W) which is common foraging ground for several breeding colonies of southern elephant seals and other Antarctic predators (Burns et al., 2004 and references therein); (b) the region around the Antarctic Polar Front in the Bellingshausen Sea; and (c) the area around the NAP and Elephant Island itself (61S 51W). This latter area represents the region in the northern Weddell Sea which is quite close to where Tosh et al. (2009) identified important foraging activity of adult southern elephant seals males from KGI. Despite the wide geographic distribution of these areas (Filchner Trough, De Guerlache Seamounts, Burbwood Bank, Drake Passage, Cristal Sound, Alexander Island) they represent specific regions bathymetric features such as underwater canyons, seamounts, banks and troughs. These features are found in close association with the distribution of several pinniped species, including southern elephant seals, likely as a result of changes in hydrographic conditions favouring the local enhancement of food availability.

Crabeater seals are ice-breeding phocids with circumpolar distribution that live in close association with fast and pack ice and the Antarctic Continental shelf year round (Testa 1994; Burns et al., 2004, 2008) unlike southern elephant seals that breed in close association with land. Nevertheless, crabeater seals share the shelf foraging habitat on the WAP region with southern elephant seals over the winter months, with considerable overlap in the southern part of the WAP. When diving, crabeater seals from east Antarctic make predominantly shallow dives (Wall et al., 2007), unlike the seals on the WAP which make deep dives to the ocean floor often associated with bathymetric depressions, which may concentrate vertically migrating prey during the day time (Burns et al., 2008). Although southern elephant seals and crabeater seals are unlikely to be targeting the same prey, this overlap of foraging habitat in the WAP highlights the fact that the shelf region is an important habitat for a range of predators, and their prey (Padman et al., 2012; Costa et al., 2010).

4.3. Environmental characteristics associated with foraging behaviour

Marine mammals typically exhibit a predominant foraging strategy often associated with a given age class, sex, or geographical region (Villegas-Amtmann et al., 2008) but it is not uncommon for these groups to exhibit a combination of foraging strategies. Male southern elephant seals have been described as

benthic shelf foragers while females forage on the benthos switching to pelagic foraging in proximity to the ice edge (Bailleul et al., 2007a). Other studies have reported female SES foraging predominantly in the pelagic zone while males foraged mostly in the benthic zone while over the continental shelf, but mixing these two zones elsewhere (Hindell et al., 1991, 1999).

The movements of southern elephant seals from EI stress the important influence of the continental shelf habitat on where and how SES spend their time foraging, despite their apparent widespread pelagic distribution. Area restricted search behaviour was more likely to occur than “transit” behaviour in higher concentrations of sea ice, over shelf waters, and close to the continental slope. All of these have been identified as important habitats before, but rarely for such a high proportion of the population. For example, seals from both Isles Kerguelen and Macquarie Island utilise the continental shelf, but in those circumstances seals must travel over 1000 km to reach it, which imposes a considerable energetic cost. Only 8% of foraging by PM adult females from Macquarie Island used the continental shelf of Adelie Land and the Ross Sea, but those that did demonstrated higher foraging success than seals using other habitats (Thums et al., 2011). In both of those populations shelf areas were more commonly used by males which had different energetic and breeding constraints (Bailleul et al., 2007a, 2007b).

When on the shelf, the seals from EI used a range of habitats and exhibited a suite of behaviours, which is a reflection of the complexity of these local habitats. The waters over the shelf are complex and dynamic with different water masses occurring at different locations and depths depending on factors such as ice formation, on-shelf current flow, proximity to the continental slope and the presence of canyons and seamounts (Hofmann et al., 2004). Overall, UCDW and LCDW were more commonly used than other water masses while diving, which is consistent with the location of the seals in southern WAP during the winter time. In particular LCDW had more “search” than “transit” dives. However, it is difficult to infer causality between the seal distribution and behaviour and water mass, as seals will ultimately be responding to the distribution and abundance of prey which in turn will be influenced by environmental variables such as light attenuation, temperature and oxygen concentration (Hofmann and Klinck, 1998; Hofmann et al., 1996, 2004). Recent studies have shown that southern elephant seals have the ability to adjust their behaviour and foraging strategies to local oceanographic conditions (Biuw et al., 2007a), ocean surface properties (Bradshaw et al., 2004a, 2004b) eddies (Campagna et al., 2006, 2007; Dragon et al., 2010), ice coverage (Bailleul et al., 2007a) and differing oceanic regimes (Boehme et al., 2008a, 2008b; Meredith et al., 2011) and prey availability (Burns et al., 2004, 2008; Bornemann et al., 2000). This is also reflected in the diving behaviour with pelagic search dives over deeper, more complex shelf regions. Areas in which “search” behavioural mode was predominant were associated with higher ice concentrations, shallower bathymetric depths and were closer to the shelf edge (Fig. 4). To a lesser extent, these cells were also associated with gentler bathymetric gradients and higher water temperatures at the maximum depths of the dives.

Seal ct-39-40 represents a good example of a PM shelf foraging seal while seal ct-39-45 represents a PM open ocean foraging seal with an interesting tendency to perform deeper dives towards the end of its tracking period in closer association with CDW. Both seals also periodically show correspondence between their night dives and the limit for the SAMW. This water mass “sinks” to an intermediate depth when it meets lighter/less dense water masses at about the Drake Passage area. In these strong density gradients primary and secondary production are trapped in each stratus, making it difficult for plankton to move up or down since

the boundary acts like a real “cap” (Biuw et al., 2010; Hofmann and Klinck, 1998; Hofmann et al., 1996).

Also in contrast with other studies, adult females from EI spent more time on benthic dives than males. Typically, southern elephant seal males make predominantly benthic dives while over the continental shelf, and females perform a mix of benthic and pelagic dives (Bailleul et al., 2007a). The reasons for this are unclear, but may be related to different nature of the bathymetry on the WAP compared to east Antarctica, where the other studies have been conducted. Also, males and females are likely to be exploiting different prey, due to their size differences, although direct quantities descriptions of the diets of the seals on their foraging grounds are presently lacking. A study comparing fatty acids in the blubber of adult females from Macquarie Island indicated that animals feeding on the shelf consumed more fish than animals feeding offshore which ate more squid (Bradshaw et al., 2003). Size based resource partitioning among seals feeding on the WAP shelf is possible, but awaits studies of stable isotopes or fatty acids to be confirmed.

Post-moulting females that foraged on WAP spent less time in “search” mode than PM sub-adult males and PB females. It is likely that females foraging at the WAP spent less time diving in “search” mode due to the longer trips that they make, which is a consequence of their more distant foraging sites.

4.4. Sea ice and foraging behaviour

A greater proportion of the diving activity during “search” mode occurred in heavier sea-ice conditions, a finding in contrast with observations of PM AF from other locations (Bornemann et al., 2000; Thums et al., 2011). This could be partly due to animals spending much of their time in the southern WAP (where ice is also densest), again reinforcing the notion that this region is a very good foraging habitat. Sub-adult males from Kerguelen Island remain over the continental shelf longer than females, perhaps because the females cannot risk being trapped by sea-ice and thus be prevented from returning to KI to breed (Bailleul et al., 2008). This could suggest behavioural differences between male and female SES in relation to ice concentration. In contrast, EI PM females remained in sea-ice throughout the winter, where the median ice concentration was 95%, similar to the concentrations reported for KGI males (Tosh et al., 2009).

An alternative explanation is that body size, or age, rather than gender may influence the ability of a seal to deal with sea-ice. There was a clear relationship between body size and ice concentration in PM females from EI, with larger seals occupying much denser ice than smaller ones. If the shelf habitat is the best available, but becomes obscured by sea-ice during the winter months, it may be that only the larger, older females are able to exploit this better habitat. There may also be an ontogenetic progression of diving behaviour from open water foraging focusing on frontal systems and eddies (Bailleul et al., 2010), to over the shelf and into ice-covered areas (this study). Certainly, juvenile elephant seals from Macquarie Island demonstrated a southward expansion of their foraging range (Field et al. 2007a, 2007b), but breeding age animals were not included in that study.

Although EI PM sub-adult males were larger than PM females (614.4 ± 128.0 kg vs. 342.9 ± 71.8 kg, respectively), they rarely used high concentrations of sea ice which could suggest that experience/ontogenetic development of dive behaviour would play a more significant role than body size. Elephant Island PM sub-adult males were nonetheless larger than our PB and PM females but SAM did not remain in ice rich waters. SAM in our study were also smaller than some of the males reported in other studies (Tosh et al., 2009; McIntyre et al., 2010a, 2010b; Muelbert et al., 2004) but larger than Bornemann's et al. (2000) weaners. Nevertheless, they exhibited

similar ice-avoidance behaviour but tended to associate themselves with specific hydrographic and/or bathymetric features such as the 1000 m isobath, Burbwood Bank and Scotia Ridge.

In 2008/09 we were able to recapture and weigh 7 of 14 females that were tagged at EI during the PB ($n=3$) and PM ($n=4$) periods. PB female body mass at recapture was about 30% higher than body mass at tag deployment (3 out of 3 PB females) after approximately 2 months and about 11% higher for PM females (3 out of 4) after a whole year during which time they have likely bred at SG. The largest PB female (532 kg) was able to travel to and return to the South Shetlands in less than three months while the other smaller females (268–431 kg) tended to stay around Elephant Island for the PB period. Yet small PB females still recovered about 25% of their body mass (Tables 1 and 2) over the post-breeding foraging period. If the large PB female recovered a similar proportion of her body mass, she was likely to weigh about 665 kg upon her arrival on the beach to moult. It is possible that large body size influences the distance travelled to foraging grounds thus representing an advantage to larger females. On the other hand, one PM female that stayed around the NAP during winter foraging and then went to SG to breed was 5% lighter at recapture than it was during tag deployment the previous year. This suggests poor foraging performance during the post moulting period what would agree with McConnell et al. (1992) and McConnell and Fedak (1996) who have suggested that the area situated around SG contained insufficient prey resources to sustain southern elephant seals breeding there. Although we do not have recapture weights for the other Weddell Sea/Scotia Sea females it is likely that foraging in the WAP confers better body condition than at NAP as we can see from the other females in Table 2.

4.5. Ecological implications of spatial separation between breeding and foraging grounds

There were clear differences in spatial use between phase and sex classes. PM females from EI have a migratory component (e.g. moving to the southern WAP) to their life cycle but this displacement is not as large as for other populations. Even so, EI seals seem to “prefer” the shelf habitat but within the shelf some regions are targeted and others are not. This is likely a reflection of complex interplay of competition, individual energetic demands and costs and benefits associated with the location/distance between breeding and foraging sites. Such relationships are better understood and explained in central place foragers like Antarctic fur seals (Lea and Dubroca, 2003; Lea et al., 2006, 2008) which need to find food for their metabolic needs and for their offspring over the lactation period and return to their breeding grounds after each foraging trip to nurse their young. This restricts the foraging areas chosen in different years according to environmental conditions such as ice density and prey availability. Southern elephant seals are, as most phocids, capital breeders faced with the spatial and temporal separation of breeding/moulting grounds and foraging sites such that they require the storage of energy as fat reserves during both the breeding and moulting periods. As a result, they have to obtain enough energy to sustain basic energy requirements but also to replenish the energy spent during breeding or moulting as well as energy storage for their gestation and the next breeding season.

The spatial separation between breeding and foraging is less of a problem for ice-breeding species such as crabeater and leopard seals that use the ice as breeding and nursing substrate what makes the actual distance between breeding grounds and foraging places shorter. On the other hand land breeding seals like southern elephant seals have to offset the cost of sometimes lengthy displacements between suitable foraging habitat like the continental shelf of the WAP and their breeding grounds in subantarctic islands like the South Shetlands and South Georgia.

4.6. Ice breeding vs. land breeding strategies: influence of breeding habitat

Unlike most other southern elephant seal populations studied to date, EI is a relatively southerly breeding colony located on the Antarctic continental shelf with an estimated breeding population of about 2300 individuals which seems to be increasing (Ciotti, 2007). Although there is evidence that southern elephant seal stocks on the Atlantic side of their distribution are stable in recent years, McMahon et al. (2005a, 2005b), SCAR (2000) and Tosh et al. (2009) (and information therein) have suggested that there may have been a decline in the southern elephant seal population at KGI in recent years. The decline in stocks from other populations has been attributed to reductions in either juvenile survival or adult female survival or both possibly as a result of limited food availability (Pistorius et al., 2004, 2008a, 2008b; McMahon et al., 2005a, 2005b). This might not be the case at EI since seals breeding there are in closer proximity to shelf and the shelf break, their preferred foraging habitat.

During the second year deployment (2008/09), ice conditions at the breeding site were not as harsh as during the first and third years (2007/08 and 2009/10, respectively) when the breeding beach was covered in snow and blocked with ice up until early December. These conditions at the breeding site made access to the beach more difficult than other years. Further, there were less pups weaned at Stinker Pt. in 2009/10 than in 2008/09 (96 vs. 117) likely as a result of difficult beach access. There was also higher pup mortality as a result of pup entrapment in ice puddles on the beach (Muelbert unpublished info). Furthermore, like KGI females (Burton et al., 1997; Carlini et al., 1997) both PB and PM females from EI seem to be heavier than SG individuals and wean heavier pups (Muelbert, unpubl. info). Thus higher latitude breeding sites may confer the advantage of proximity to better/richer foraging grounds such as the WAP but could also mean unpredictable and harsher breeding substrate and increased pup mortality in heavy ice/snow years.

5. Conclusion

Elephant Island (EI) being situated close to the Antarctic Continental Shelf offers clear advantages for foraging southern elephant seals (“prime habitat”). However, this advantage is not reflected in the demography since most of the seals still breed on South Georgia. It is possible that there are important trade-offs at play in that the advantages for breeding at SG are not just foraging: higher latitude sites may confer disadvantages in terms of access to breeding habitat in years of heavy snow and ice, and/or reduced pup survival in heavy snow years. Nevertheless, if the Northern Antarctic Peninsula (NAP) continues to warm up as a result of climate change EI may become more suitable habitat for southern elephant seals.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2012.07.009>.

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