

Foraging behaviour of southern elephant seals over the Kerguelen Plateau

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ABSTRACT: A total of 79 (37 juvenile male, 42 adult female) southern elephant seals *Mirounga leonina* from the Kerguelen Islands were tracked between 2004 and 2009. Area-restricted search patterns and dive behaviour were established from location data gathered by CTD satellite-relayed data loggers. At-sea movements of the seals demonstrated that >40 % of the juvenile elephant seal population tagged use the Kerguelen Plateau during the austral winter. Search activity increased where temperature at 200 m depth was lower, when closer to the shelf break, and, to a lesser extent, where sea-surface height anomalies were higher. However, while this model explained the observed data ($F_{1,242} = 88.23$, $p < 0.0001$), bootstrap analysis revealed poor predictive capacity ($r^2 = 0.264$). There appears to be potential overlap between the seals and commercial fishing operations in the region. This study may therefore support ecosystem-based fisheries management of the region, with the aim of maintaining ecological integrity of the shelf.

KEY WORDS: Diving behaviour · 3-dimensional utilisation · Shelf break · Temperature · Sea-surface height · Fisheries management

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INTRODUCTION

Quantifying animal movement provides information on habitat requirements, which is fundamental to understanding the foraging ecology of a species (Ropert-Coudert & Wilson 2005). Because animal survival and reproduction depends on foraging success, marginal value theorem predicts that movement patterns will ultimately be determined by resource availability (Charnov 1976). In a heterogeneous environment, it is expected that predators should increase search effort following prey detection due to the high likelihood of other prey encounters (behaviour generally referred to as area-restricted search [ARS]; Kareiva & Odell 1987). Movement data can therefore provide information on turning angles and movement speeds which can be used to infer changes between behavioural states (Morales et al. 2004). For example, increased search effort is typi-

cally indicated by reduced transit speed and increased turning frequency within a given area and is often indicative of foraging activity (e.g. Hyrenbach et al. 2002, Bailleul et al. 2007b, Thums et al. 2011).

For animals with extensive spatio-temporal ranges, particularly in the marine environment, such movement studies have, historically, been difficult. However, the ongoing development of satellite telemetry and more recent track reconstruction methods have enabled movement and behavioural states to be mapped for a range of marine predators (Jonsen et al. 2005, Patterson et al. 2008, 2010, Sumner et al. 2009, Bestley et al. 2010, Pedersen et al. 2011, Jonsen et al. 2013).

The Southern Ocean is a highly dynamic and heterogeneous marine system where food resources are patchily distributed in time and space. Marine predators, therefore, rely on oceanographic features, such as frontal systems, upwelling and bathymetric fea-

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tures that help create prey patches, to find aggregated prey (Pinaud & Weimerskirch 2005, Crocker et al. 2006, Palacios et al. 2006, Bailleul et al. 2007b). Telemetry, coupled with remotely sensed ocean surface data, is commonly used to gain insight into a predator's associations with these features (Zainuddin et al. 2006). For example, green turtles *Chelonia mydas* are believed to use sea-surface temperature frontal zones and surface currents to locate aggregations of prey resources (Seminoff et al. 2008). However, many marine predators hunt well below the surface, so ocean properties on the surface may not adequately explain animal foraging behaviour (Bradshaw et al. 2004, Hindell 2008). Incorporating oceanographic sensors into telemetry devices can potentially overcome this shortcoming by collecting environmental data at more appropriate spatial and temporal scales, and, in particular, throughout the water column (Fedak 2004, Biuw et al. 2007).

Seasonal discontinuities in temperature and salinity conditions at the mixed layer depth (i.e. 150 to 200 m) are thought to be associated with patches of biological productivity (e.g. Sameoto 1984). Recent data, collected using elephant seals, have been used to characterise subsurface water masses (Bailleul et al. 2010a) and revealed the vertical thermal structure of cyclonic eddies (Bailleul et al. 2010b). Furthermore, bathymetric features such as sea mounts or shelf edges can also enhance prey concentrations (McConnell et al. 1992). These added 3-dimensional components can provide additional information for use in numerical models to explain foraging behaviour and habitat selection.

Like other southern elephant seals, those from the Kerguelen Islands population travel large distances to forage, e.g. up to 3000 km during a winter foraging trip (McMahon et al. 2005, Bailleul et al. 2007a,b). However, a proportion of the population remains on the Kerguelen Plateau (Bailleul et al. 2010a). This is significant for 2 reasons: (1) the unique oceanography of the region has the potential to influence the distribution of prey species and (2) a large Australian and French commercial fishery operates on the plateau, raising the possibility of operational or ecological interactions. The plateau encompasses approximately 1 200 000 km² of water less than 2000 m deep and is located in the northern part of the Antarctic Zone, in the vicinity of the Polar Frontal Zone (Park & Gamberoni 1997), making it 1 of only 2 bathymetric obstacles to the eastward flow of Antarctic waters (Orsi et al. 1995). The plateau, therefore, has considerable influence on both the distribution of water masses and the primary production in the area

via nutrient upwelling (Blain et al. 2001, Charrassin et al. 2002). Because of these biophysical attributes, the plateau is an important ecological area in the Southern Ocean, supporting many top predators including albatross (e.g. Lawton et al. 2008), penguins (e.g. Deagle et al. 2008) and fur seals (e.g. Lea et al. 2006). These attributes may also provide vital prey resources for elephant seals that remain on the plateau to forage.

Models based on ecosystem-based management often lack information regarding top predator ecology and produce unpredictable outcomes for the predator population concerned (Schmitz 2007, Heithaus et al. 2008). Studying the on-shelf foraging ecology of elephant seals from the Kerguelen Islands will provide valuable information for Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) ecosystem models, thereby improving the predicted outcome of anthropogenic impacts on local ecosystems.

The overall aim of this study was, therefore, to map and model the on-shelf use of the Kerguelen Plateau by southern elephant seals. The specific objectives were to: (1) use Argos satellite tracks to map the regional use of the plateau, (2) quantify their diving behaviour with respect to the seal's habitats, (3) develop habitat models based on multi-sensor satellite data and seal-borne telemetry data and (4) quantify environmental effects on habitat selection.

MATERIALS AND METHODS

Deployment of devices

Between 2003 and 2009 a total of 79 elephant seals *Mirounga leonina* (42 post-moult adult female and 37 post-moult juvenile males) from the Kerguelen Islands were equipped with conductivity-temperature-depth satellite-relayed data loggers (CTD-SRDLs, Sea Mammal Research Unit, University of St Andrews). Seals were caught with a canvas head-bag and then anaesthetized with a 1:1 combination of tiletamine and zolazepam (Zoletil 100 0.8 mg/100 kg) injected intravenously (McMahon et al. 2000). Data loggers were attached on the head of seals using a 2-component epoxy (Araldite AW 2110) after cleaning the hair with acetone (Bailleul et al. 2007a). All seals were captured between December and February, before their post-moult foraging trip, except for one animal that was equipped in September during a brief winter visit. Of these 79 seals, 19 (3 adult females and 16 juvenile males) spent some time forag-

ing on the Kerguelen Plateau (as opposed to passing over it to forage at more distant locations). Seals that remained on the plateau spent between 28 and 272 d in the region (Table S1 in the supplement at www.int-res.com/articles/suppl/m502p281_supp.pdf).

CTD-SRDL features

The CTD-SRDL devices provided Argos locations, diving behaviour and high resolution CTD data (see Fedak et al. 2001 for details). Between 4 and 14 locations per day were determined during satellite uplinks by the Argos system. Given the limited bandwidth available in Argos transmission, temperature sampled every 4 s was compressed into a single temperature-depth profile every 6 h by summarizing the dive into 12 inflections using a broken stick algorithm (see Fedak et al. 2001 for details). The temperature resolution was $\pm 0.01^\circ\text{C}$, and the dive data accuracy was ± 3 m at 100 m, decreasing to ± 24 m at >1400 m (for details see Fedak et al. 2001).

Depth was recorded on 5 channels (i.e. 5 levels of granularity); the first operated from 0 to 99 m with an accuracy of ± 3 m, the second operated from 99 to ~ 290 m with an accuracy of ± 6 m, the third operated from ~ 290 to 700 m with an accuracy of ± 12 m, the fourth operated from 700 to 1400 m with an accuracy of ± 24 m and the fifth operated from 1400 to 2000 m with an accuracy of ± 48 m. Water temperature was also recorded with a resolution of $\pm 0.001^\circ\text{C}$ and an accuracy of $\pm 0.01^\circ\text{C}$.

Path analysis

Raw Argos data contained locations of varying uncertainty. We fit first-difference correlated random walk switching state-space models (DCRWS SSM) to the raw location data (Jonsen et al. 2005) using the freely available software WinBUGS (www.mrc-bsu.cam.ac.uk/bugs/winbugs/contents.shtml) and the R package R2WinBUGS (Sturtz et al. 2005). Unlike ad hoc filters that remove uncertain locations (Austin et al. 2003), DCRWS SSM track estimations retain all locations, but account for the uncertainty in the data (Jonsen et al. 2005). Importantly, SSMs also fit multiple random walks to animal movement paths consisting of ordered sets of

step lengths and turning angles to infer switches between 2 behavioural states. Rapid and directional movement was interpreted as transit behaviour between haul-out sites and habitat patches, as well as between habitat patches. In contrast, comparatively slow and contorted movement was considered indicative of ARS behaviour (Morales et al. 2004). ARS behaviour (search) is considered a useful proxy for foraging behaviour and, consequently, was used to identify likely habitat patches along the seal's track (Biuw et al. 2003, Thums et al. 2008). Conversely, transit behaviour was provisionally regarded as movement between habitat patches. To fit the SSM to each individual seal location dataset, 2 Markov Chain Monte Carlo (MCMC) chains of 30000 iterations were run with a burn-in of 20000. Each chain was thinned so that 1 in every 5 samples was retained, for a final MCMC sample size of 4000. The model fit provided location points at 6 h intervals along the movement path.

At-sea movement at the population level

Most at-sea activity occurred on the northern plateau between the Kerguelen and Heard Islands (Fig. 1). We, therefore, defined the study site as corresponding to an area <2000 m deep and north of 56°S, hereafter referred to as the Kerguelen-Heard shelf (Fig. 1).

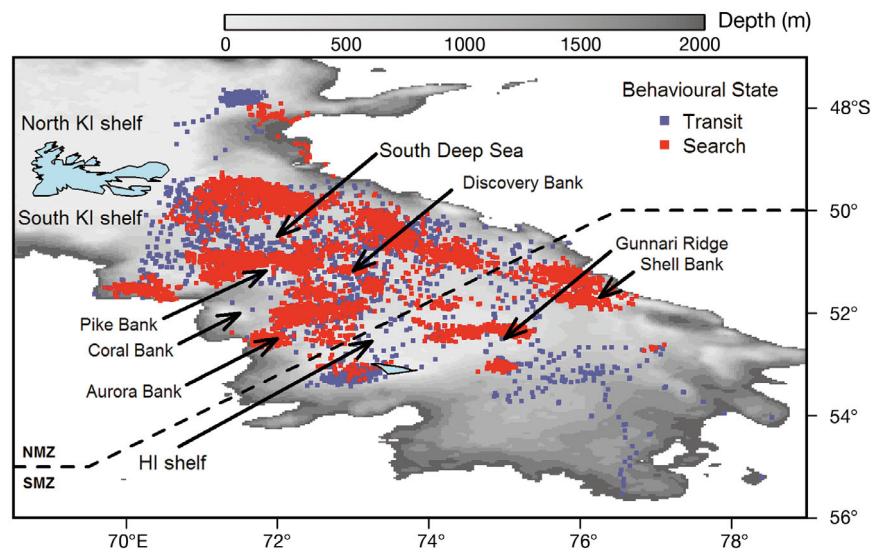


Fig. 1. Study site and spatial distribution of seals *Mirounga leonina* ($n = 19$) that occupy the Kerguelen-Heard Plateau. The outlined light blue areas show land: the Kerguelen Islands (KI, upper left) and Heard Island (HI, lower centre). Dashed line indicates the boundary between the northern (NMZ) and southern management zones (SMZ) on the shelf

Diving behaviour

Dive data returned from CTD-SRDLs and tracks (derived from SSM analysis) were aligned in time to assign a geographical position (longitude, latitude) to each dive. Bathymetry was extracted under each location and compared to the corresponding maximum dive depth to calculate the percentage of total bathymetric depth covered by the seal (%Bathymetry-Depth). We used bathymetry at 500 m resolution generated by Geosciences Australia to define the Kerguelen Plateau within 47° to 56°S, 68° to 80°E. The associated bathymetric depth of each interpolated dive location beyond the boundary of the high-resolution bathymetry data set (i.e. 48°S, 47°S, 68°E and 80°E) was derived from theETOPO2 bathymetry data set at 2' resolution.

The %BathymetryDepth data were placed into 4 categories based on where in the water column the seal was diving: %BathymetryDepth <20% = shallow dive, %BathymetryDepth 20 to 50% = mesopelagic dive, %BathymetryDepth 50 to 80% = demersal dive and %BathymetryDepth >80% = benthic dive. All dives that exceeded the bathymetric depth were taken to represent benthic diving activity rather than removing these values from the data set. We then computed dissimilarity indices based on the Euclidean distance of dive type proportion exhibited by each seal and used to perform a hierarchical cluster analysis by the 'average' method (R Development Core Team, functions: *vegdist*, *hclust*; Oksanen et al. 2013). Clusters were cut into 4 groups of dive strategies (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m502p281_supp.pdf). We tested the significance of these dive strategy groups using analysis of similarities (R Development Core Team, function *anosim*; Oksanen et al. 2013).

Modelled utilisation distributions (UDs) of dive data were investigated qualitatively by calculating horizontal kernel density maps at 10 equally spaced depth intervals. The maximum depth for each dive was merged to each individual's track data using linear interpolation between the SSM-derived 6 h location estimates and combined for all individuals. The resulting 3-dimensional cloud of points was then divided into 10 equally spaced horizontal slices, and a kernel density was calculated for each slice. Finally, we calculated two 3-dimensional iso-surfaces (density envelopes) that enclosed the 50 and 90 percentile components for these kernels. Data manipulations and visualisations were performed using Eonfusion software (www.myriax.com).

Use of the Kerguelen Plateau—fisheries management boundaries

We calculated the time that the seals spent within 4 management boundaries—including the Kerguelen (France) and Heard (Australia) Exclusive Economic Zones (EEZs)—and CCAMLR Divisions 58.5.1 and 58.5.2—using shape files from <http://data.aad.gov.au>. From here on CCAMLR Division 58.5.1 and the Kerguelen EEZ are referred to as the Northern Management Zone (NMZ) and CCAMLR Division 58.5.2 and the Heard EEZ are referred to as the Southern Management Zone (SMZ) (Fig. 1).

Environmental influences

Data were collected from 3 different aspects of the ocean environment: sea-surface, subsurface and bathymetric variables (Table 1).

Sea-surface variables

We used sea-surface temperature (SST, °C), sea-surface height anomalies (SSH_a, cm) and sea-surface chlorophyll *a* concentration (chl *a*, mg m⁻³). The SST was derived from OI-Daily v2 data (Reynolds et al. 2007), obtained from www.ncdc.noaa.gov; SSH_a was derived from AVISO weekly composites, with a spatial resolution of 0.25° (www.aviso.oceanobs.com); and chl *a* was derived from MODIS monthly composites, with a nominal resolution of 0.05 mg m⁻³ and a spatial resolution of 0.25° (Feldman & McClain 2006), obtained from <http://oceancolor.gsfc.nasa.gov/cgi/l3>. The mean monthly chl *a* dataset was used specifically because of the patchy nature of chlorophyll data at higher temporal resolutions due to cloud cover.

Subsurface variables

Temperature data collected by the CTD-SRDLs were used to create vertical and horizontal temperature profiles across the Kerguelen-Heard shelf. We used a 24 h temporal resolution for these analyses to maximize temperature-depth coverage. Firstly, COnstrained B-Splines (COBS) using nonparametric regression quantiles (Ng & Maechler 2011) were fitted to the combined daily depth and temperature profile data for each seal, to derive interpolated temperature records at 25 m intervals from 0 to 500 m, providing a single temperature-depth profile per

Table 1. Details of each environmental variable from each aspect of ocean habitat: sea-surface, subsurface and bathymetric conditions. SI: remotely sensed satellite images; SB: seal-borne data; SS: ship survey; CTD-SRDL: conductivity-temperature-depth satellite-relayed data loggers

Aspect of seal habitat	Environmental variable	Unit	Temporal scale	Data type	Source
Sea surface	Sea-surface temperature (SST)	°C	Daily	SI	OI-Daily v2 (Reynolds et al. 2007) (www.ncdc.noaa.gov)
	Sea-surface height anomaly (SSHa)	cm	Weekly	SI	AVISO (0.25°) (www.aviso.oceanobs.com)
	Sea-surface chlorophyll (chl a)	mg m ⁻³	Monthly	SI	MODIS ($\pm 0.005 \text{ mg m}^{-3}$) (http://modis.gsfc.nasa.gov/data)
Subsurface	Mixed layer (ML)	°C	Daily	SB	On-board CTD SRDLs
	Temperature minimum (T_{\min})	°C	Daily	SB	On-board CTD SRDLs
	Temperature at depth (T_{depth})	°C	Daily	SB	On-board CTD SRDLs
Bathymetry	Bathymetric depth (ocean depth)	m	–	SS	GEBCO (30' arc) (www.bodc.ac.uk/data/)
	Distance from the shelf break (ShB)	m	–	SS	GEBCO (30' arc) calculated using Eonfusion (v1.2, www.myriax.com)
	Bathymetric slope (BSl)	°	–	SS	GEBCO (30' arc) calculated using Eonfusion (v1.2)

day. This was then combined with the mean daily locations for that seal. The spline tended to not fit points deeper than 500 m very well due to the relative scarcity of points at these deeper depths. All temperature profiles were applied to hierarchical cluster analysis based on Euclidean distance to investigate spatial patterns (Bestley et al. 2009) and to reveal common temperature inflection points in the water profile. We used average clustering and cut the dendrogram based visually on height into 4 clusters. The most common temperature inflection points in the water profile were selected visually (see Fig. S2 in the Supplement). Temperatures at 75, 200 and 400 m were therefore considered potentially important parts of the water column, and hereafter are termed the mixed layer (ML), temperature minimum (T_{\min}) and temperature at depth (T_{depth}), respectively.

Bathymetric variables

We calculated the associated bathymetric depth (ocean depth) and bathymetric slope (BSl, defined as the 1000 m contour line) of each interpolated seal location within 48° to 56° S, 68° to 80° E using bathymetry data derived from the ETOPO2 bathymetry data set at 2' resolution. We also calculated the distance of each location to the shelf break (ShB),

defined as the 1000 m contour line, because it represents where the bathymetric gradient is the steepest between the shelf and the ocean abyss.

Statistical analysis

We converted the binary dive-by-dive behavioural mode data into a continuous variable by aggregating them into 0.25° cells and calculating the mean behavioural mode for all dives by each seal in each cell. Cells with <3 locations for an individual were excluded from the analysis, as these were considered to give unreliable estimates of the mean. The resulting mean behavioural mode per cell was a continuous variable reflecting the relative importance to the amount of time spent in search behavioural mode, but retained the important individual seal information. The resulting cell values were arcsine transformed before analysis. The mean value for each of the covariates was then calculated for each 0.25° cell. Each covariate was log transformed, where appropriate, to ensure a normal distribution.

To compare the relative degree of foraging per cell with all the environmental variables we fitted a series of generalised linear mixed-effect models (GLMMs) using the R software package *nlme* (R Development Core Team, function *lme*; Pinheiro et al. 2013), following model selection procedures in accordance

with Zuur et al. (2009). Firstly, we assessed using the 'full' (most complex) model, with and without the random intercept term, to ensure that individual seals were contributing to the model fit. Next, we explored the optimal structure of the random effects comparing random intercept models (seal only) with random intercept and slope models (seal and each environmental variable in turn), retaining the slope terms that improved the models. Next, we assessed the effect of inclusion of an autocorrelation term in the resulting optimal model. We then tested the individual fixed effects by sequentially removing non-significant terms from the model. In all cases, models were ranked via Akaike Information Criterion (AIC) (Burnham & Anderson 2002), the most parsimonious model having the lowest AIC value. In addition, we used likelihood ratio tests to test between models with different random effect structures, and *F* and *t* statistics to examine the significance of individual fixed effects. The final model is presented using restricted maximum likelihood (REML) methods.

Explanatory variables that encompassed surface, subsurface and bathymetric conditions were included: SST, SSHa, chl *a*, ML, T_{\min} , T_{depth} , ocean depth, ShB and BSI. These variables encompassed each of the 3 different aspects of the ocean environment including surface, subsurface and bathymetric conditions (Table 1).

RESULTS

Path overview

Of the 79 seals tagged in the study, 24 % spent some time foraging on the Kerguelen Plateau. The average duration of the deployments for these 19 seals (16 juvenile males and 3 adult females) was 94

± 60 d (range: 28 to 272 d) (Table S1 in the Supplement), of which 83 ± 56 d (91 % of the total time at sea) was spent on the Kerguelen-Heard shelf, and all seals exhibited search behaviour in that region. In all but 2 cases transit and search behaviour were quite distinct (Fig. S3 in the Supplement). Search behaviour of 12 seals was at a single site, while search behaviour of 7 others was in several patches (Fig. S3). However, only 7 seals had complete foraging trips (101 ± 50 d) recorded, while the 12 other seals had foraging trips that were incomplete due to tag failure (90 ± 66 d). Despite known differences in foraging behaviour of males and females (Hindell et al. 1991b), our sample size was too small to investigate sex differences.

While on the Kerguelen Plateau the seals spent 71 ± 41 d, or 88 % of their total time at sea in search mode; 18 ± 14 d (12 %) were spent in transit.

Diving behaviour

Diving data described how seals used the water column on the Kerguelen-Heard shelf when in search mode. A total of 29 688 dives made were identified as searches: 19 865 (67 %) of these dives were benthic, 5730 (19 %) were demersal, 2884 (10 %) were meso-pelagic, while only 1209 (4 %) were shallow dives. Fewer dives were made in transit ($n = 4081$), although a similar pattern existed, with most dives being benthic ($n = 2840$; 70 %), followed by demersal ($n = 642$; 16 %), meso-pelagic ($n = 427$; 11 %), and the least were shallow dives ($n = 172$; 4 %).

Of the shallow search dives 83 % were in the top 100 m of the water column, and approximately 70 % of the meso-pelagic search dives were between 100 and 400 m depth, nearly half of which were between the 200 and 300 m depth layers (Fig. 2). Most demer-

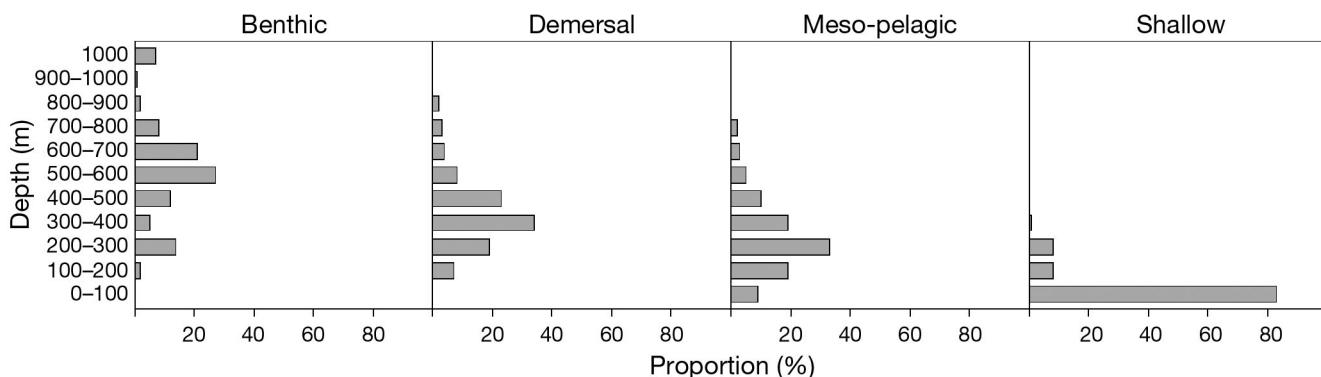


Fig. 2. *Mirounga leonina*. Proportion of dive depth intervals for each area-restricted search dive type (i.e. shallow, meso-pelagic, demersal and benthic dives)

sal search dives were within the 200 to 500 m depth layer (76 %), and most benthic search dives were 400 to 700 m deep (61 %), although the benthic search dive depth ranged between 200 and 900 m and greater (Fig. 2). Benthic and demersal search dives were predominately in the south deep sea or in deep water (500 to 1000 m) at major adjacent seamounts (i.e. Shell Bank, Pike Bank, Aurora Bank and/or Discovery Bank) and were carried out to a depth of ~400–700 m (Fig. 3). However, 2 seals travelled to the shallow shelves at either the Gunnari Ridge or Aurora Bank and exhibited shallower benthic search dives (~250 m deep). Meso-pelagic and shallow search dives were often along either the western or eastern shelf break (Fig. 3).

Based on our cluster analysis of proportion of dive types, we showed 4 significantly distinct search dive strategies between individuals ($p < 0.001$; Table 2, Table S2 in the Supplement). Dive Strategy 1 (DiveStgy1) involved diving predominately in the meso-pelagic zone (65 %), dives using Strategy 2 (DiveStgy2) were in both the shallow (29 %) and benthic zones (47 %), seals using Strategy 3 (DiveStgy3) dived mainly in the benthic zone (80 %) and Strategy 4 (DiveStgy4) had dives in both the demersal (29 %) and benthic zones (56 %). Most seals adopted either

Table 2. *Mirounga leonina*. Dive strategies adopted by seals based on cluster analysis of dive type proportions: Dive Strategy 1 (DiveStgy1) involves diving predominately in the meso-pelagic zone, Dive Strategy 2 (DiveStgy2) involves diving in both the upper (meso-pelagic and shallow) and benthic zones, Dive Strategy 3 (DiveStgy3) involves diving predominately in the benthic zone and Dive Strategy 4 (DiveStgy4) involves diving both in the demersal and benthic zones

Dive strategy	Proportion (%)			
	Shallow	Upper	Lower	Benthic
1	8.1	65.1	21.1	5.7
2	29.3	9.1	14.7	46.8
3	1.4	6.4	12.4	79.9
4	2.7	13.1	28.7	55.5

DiveStgy3 ($n = 9$) or DiveStgy4 ($n = 8$) and were significantly distinct from each other ($p < 0.001$). Only 1 seal adopted either DiveStgy1 or DiveStgy2 (Table S2). The maximum depths of DiveStgy3 dives (589 ± 315 m) were deeper than those of other strategies, followed by DiveStgy1 dives (464 ± 190 m), DiveStgy4 dives (427 ± 208 m) and DiveStgy2 dives (243 ± 349 m) ($F_{3,29684} = 1384$, $p < 0.0001$). The only seal to adopt DiveStgy1 (ct11-10097-05) dived off the northwest shelf break in water up to ~1800 m deep

(1167 ± 526 m), the only seal to adopt DiveStgy2 (ct16-174-06) dived in comparatively shallow waters on Gunnari Ridge (251 ± 73 m), seals that adopted DiveStgy3 generally dived in deep-sea shelf areas (575 ± 214 m) and seals that adopted DiveStgy4 dived near the shelf break at a greater range of water depths (578 ± 328 m) (Fig. 4).

Depth (m)

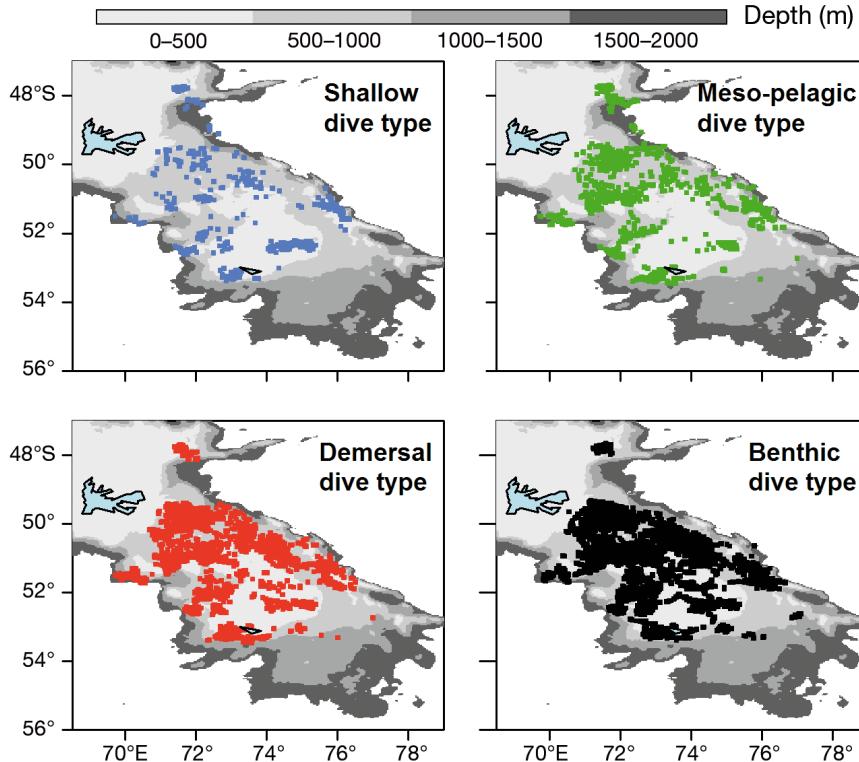


Fig. 3. *Mirounga leonina*. Spatial distribution of search dives with associated dive types: shallow, meso-pelagic, demersal and benthic. See Fig. 1 for details

Three-dimensional utilisation

The utilisation distributions for search dives show that seal activity aggregated in specific areas and at different depth intervals, particularly in association with the shelf edge (Fig. 5). At the surface (i.e. 0 to 50 m depth) search activity was relatively uniform across the shelf, but there was little activity between 50 and 350 m. Search activity between 350 to 450 m and 450 to 550 m depth was mainly across the south deep-sea region, but also on the shelf break southwest of

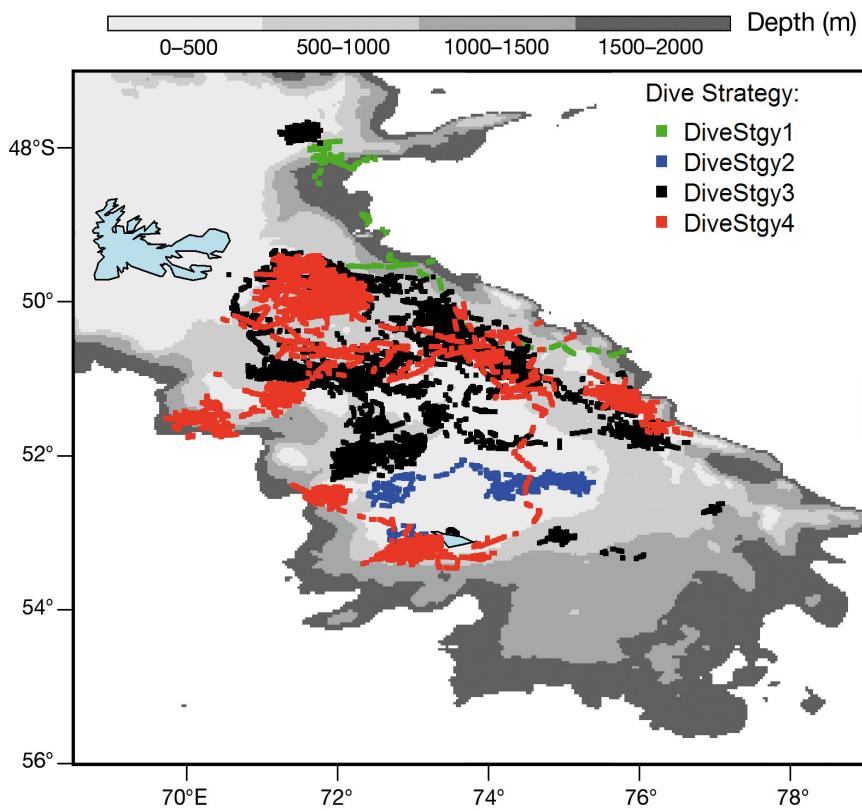


Fig. 4. *Mirounga leonina*. Spatial distribution of seals associated with the adopted dive strategy: Dive Strategy 1 (DiveStgy1) involves diving predominately in the meso-pelagic zone, Dive Strategy 2 (DiveStgy2) involves diving in both the upper (meso-pelagic and shallow) and benthic zones, Dive Strategy 3 (DiveStgy3) involves diving predominately in the benthic zone and Dive Strategy 4 (DiveStgy4) involves diving both in the demersal and benthic zones. See Fig. 1 for details

Heard Island and on the eastern side of the south deep-sea region, respectively (Fig. 5a,b). At 550 to 650 m and 650 to 750 m there were also higher aggregations of diving activity between Pike Bank and Discovery Bank, and on the northwest edge of the Heard Island shelf, respectively (Fig. 5c,d). Very little search activity occurred below 750 m.

Temporal use of the Kerguelen Plateau

The Kerguelen-Heard shelf was used primarily in the austral summer and autumn (January, 20%; February, 24%; March, 19%; April, 12%; May, 10%), and very little in winter, spring, or early summer (June, 5%; July, 3%; August, 3%; September, 3%; October, 0.5%; November, 1%; December, 1%) (Fig. 6).

The seals occupied different fisheries management zones: 46% (687 d) of their time was spent within the NMZ and 54% (809 d) was spent within the SMZ.

Specifically, 9 seals spent >70% of their time within the NMZ, 9 spent 70% of their time within the SMZ and 1 spent an equal amount of time in all fisheries management zones (Table S3 in the Supplement). The NMZ and SMZ were occupied equally by seals adopting DiveStgy3 and DiveStgy4, but seals adopting DiveStgy1 and DiveStgy2 spent the majority of their time within the NMZ and SMZ, respectively; Table S3). The seals spent ~20% of their time in either the NMZ or the SMZ during mid- to late austral summer, but during the autumn and early to mid-winter months they spent more time in the SMZ (29%) compared to the time spent in the NMZ (20%). However, during spring and early summer seals spent 3% of their time in the NMZ, but no time was spent in the SMZ.

Environmental influence on habitat selection

The best model relating search behavior to environmental factors included the random intercept term (seal), as well as the random slope term (ShB), an autocorrelation term and the fixed effects ShB, SSHa and

T_{\min} (Table 3). In each case there was a negative relationship between the mean proportion of searching locations per cell and the covariate. Cells with the highest proportion of search locations were those with the lowest T_{\min} , particularly below 2°C (Fig. 7a) which were closest to ShB (Fig. 7b) and, to lesser extent, those with higher SSHa (Fig. 7c). The highest proportions of search locations were in waters 0.25°C cooler than surrounding waters where the proportions of search locations were low; however, both ShB and SSHa effects, although significant, were biologically negligible (4.00×10^{-6} m closer and 0.02 cm lower, respectively) (Table 3).

We performed a cross-validation analysis, based on removing 1 cell at random from the data, re-running the model on the remaining data and comparing the resulting predicted values with the observed value data. This was repeated 244 times ($n - 1$). A regression of the observed against the predicted values was positively significant ($F_{1,242} = 88.23$, $p < 0.0001$;

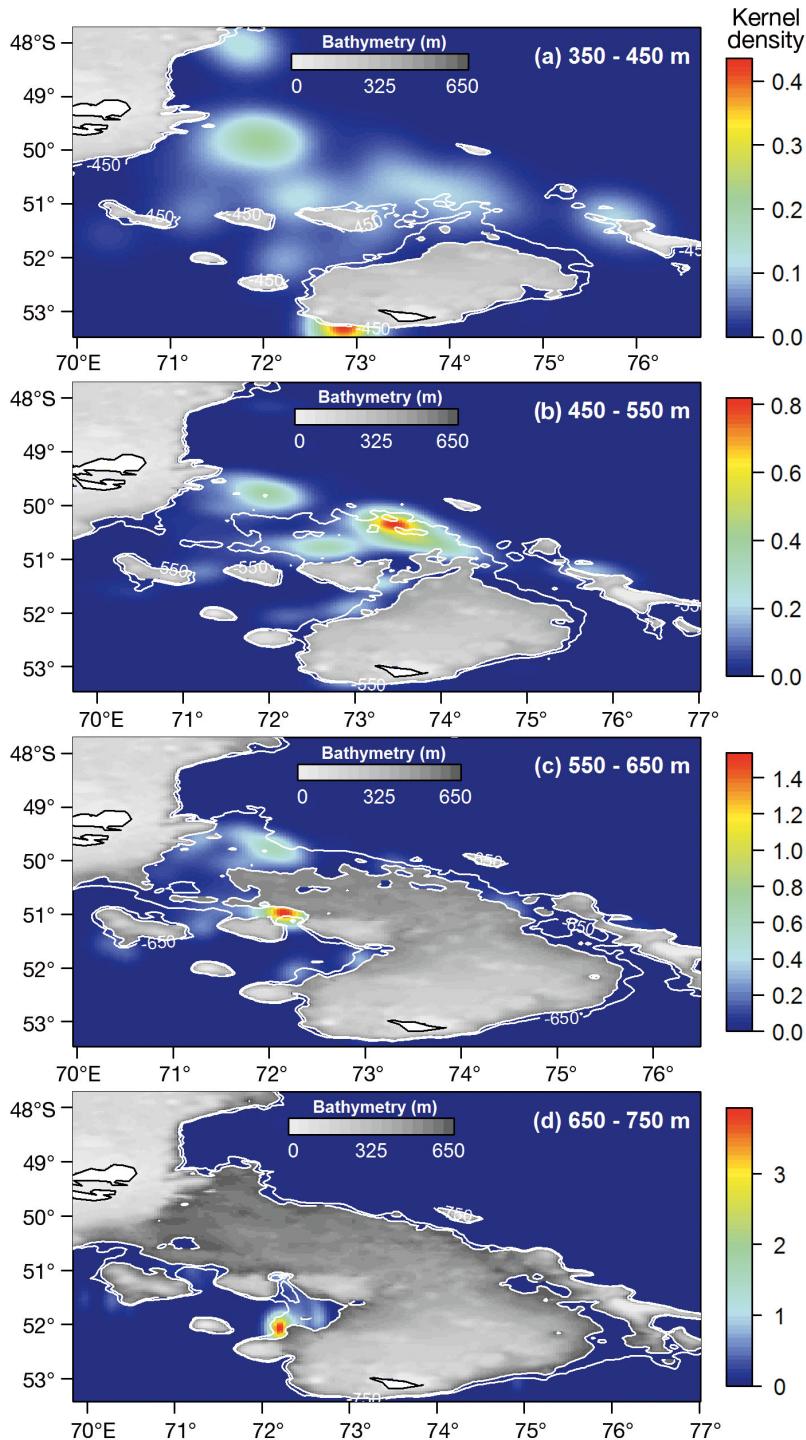


Fig. 5. *Mirounga leonina*. Kernel density estimates for all the search locations, based on the 6-hourly time step locations derived from state space models. There are 4 horizontal kernel density estimates at: (a) 350 to 450 m, (b) 450 to 550 m, (c) 550 to 650 m and (d) 650 to 750 m depth based on the number of locations in each of those depth bands

Fig. 7d), but had a relatively low r^2 of 0.264, indicating that, while the final model explained the observed data, it had a poor predictive capacity.

DISCUSSION

This study revealed that a large component of the southern elephant seal population from the Kerguelen Islands utilised the Kerguelen Plateau as a foraging area. Individual seals had a range of dive strategies, but the majority specialised in either benthic or demersal search behaviour in habitat patches. The benthic specialists utilised the relatively shallow waters on the plateaus, while the demersal specialists used the shelf slope.

The physical oceanography associated with the plateau provides ideal conditions for seasonal phytoplankton proliferation on the shelf (for details see Park et al. 2008a), providing food for prey species that, in turn, are used by top marine predators such as the elephant seal. Indeed, our results show that focal seals occupy the shelf predominately in the late summer and throughout autumn (during peak phytoplankton blooms). It is, however, important to remember that these data are biased because few seals were studied during winter; many trips ending early-to-late autumn (see trip end dates in Table S1 in the Supplement). Nonetheless, stable isotope analyses suggest that the majority of males that use the shelf use it year round (Authier et al. 2012).

For most seals SSM results clearly distinguished between locations displaying transit and search behaviour. Indeed, seals from Macquarie Island often transit directly to distinct pelagic foraging areas (Thums et al. 2011). We acknowledge, however, that seals will also feed during transit phases as they encounter prey opportunistically (Thums et al. 2011). This is perhaps why we found that dive types did not differ between transit and search locations. With this in mind, our aim was to identify and quantify environmental conditions of

habitat areas important to seals foraging on the Kerguelen-Heard shelf. For instance, many focal seals displayed direct transit to distinct patches of search

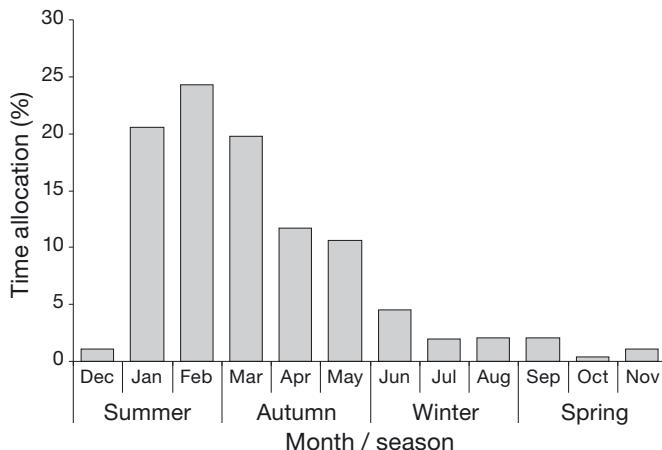


Fig. 6. *Mirounga leonina*. Temporal allocation of time (%) seals spent at sea on the Kerguelen-Heard shelf over 5 yr between 2004 and 2009

Table 3. *Mirounga leonina*. The final model including each significant fixed and random effect (see 'Materials and methods' for details on model selection). T_{\min} : temperature at 200 m ($^{\circ}\text{C}$); SSHa: sea-surface height anomalies (cm); ShB: distance from the shelf break at the 1000 m contour boundary (m)

Effect	Value	SE	df	t	p
Intercept	1.99	0.19	225	10.61	<0.0001
T_{\min}	-0.25	0.08	225	-3.23	0.0014
SSHa	-0.02	0.01	225	-2.26	0.0250
ShB	-4.00×10^{-6}	1.48×10^{-6}	225	-2.69	0.0076

on the shelf. We, therefore, assume that these patches are areas where seals are likely to perform most of their foraging activity. The similarity in the depths of transit and search dives and the adoption of specific dive strategies in particular regions suggest that seal dive depth is not solely related to behavioural mode (as defined by the SSMs). Instead it may be due to searching the water column and opportunistic feeding (e.g. Thums et al. 2011).

Both squid (Cherel et al. 2004) and fish (Cherel et al. 2000) are important trophic linkages in the Kerguelen Plateau food web and are also known prey of elephant seals (Green & Burton 1993, van den Hoff 2004). Surveys of CCAMLR Divisions 58.5.1 (i.e. NMZ) (Duhamel 2009) and 58.5.2 (i.e. SMZ) (Williams & De La Mare 1995) indicate that *Dissostichus eleginoides* (Patagonian toothfish) are the most common species on the shelf, found at similar depths to those frequented by the seals in our study. Indeed, *D. eleginoides* is a known component of the elephant seal diet elsewhere (Burton & van den Hoff 2002, Field et al. 2007) and is, therefore, a possible prey for seals on the Kerguelen Plateau shelf. These surveys also found significant biomass of a benthopelagic species, *Lepidonotothen squamifrons* (grey rockcod), in the south deep sea (Duhamel 2009) and at moderate densities on several banks in the SMZ (Williams & De La Mare 1995). Even pelagic species *Channichthys rhinoceratus* (unicorn icefish) and *Champscephalus gunnari* (mackerel icefish) on Gunnari Ridge (Williams & De La Mare 1995) coincide with

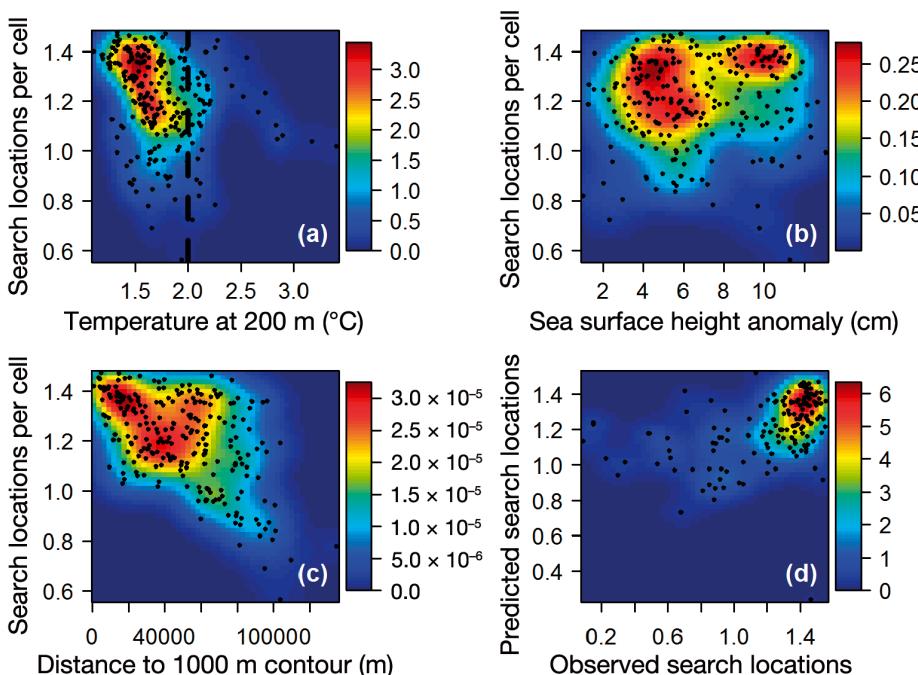


Fig. 7. *Mirounga leonina*. Kernel density plots (colour scale) illustrating the relationship between the model-fitted proportion of search locations per cell and each of the 3 important environmental covariates: (a) temperature at 200 m (the vertical dashed line indicates waters associated with the Antarctic Polar Front), (b) sea-surface height anomaly and (c) distance to 1000 m bathymetric contour. (d) Results of cross-validation analysis, relating the observed and predicted proportions of search locations per cell from the best model (see Table 3)

seal dive activity. Furthermore, seals that exhibited meso-pelagic dives along the western and eastern shelf breaks may be targeting diverse cephalopod communities (Cherel et al. 2004). We expect changes in dive depth and dive strategy between individuals are largely influenced by the type of prey encountered for that particular individual. Stable isotope analysis of seals foraging exclusively on the shelf could help confirm target prey species on the plateau (e.g. Bailleul et al. 2010a).

Foraging behaviour and environmental variables

SST is the most frequently studied physical parameter in relation to behaviour (e.g. Field et al. 2001, McConnell et al. 2002, Bradshaw et al. 2004), but may be inappropriate for deep-diving species. Concentrations of search behaviour occurred well below the surface (up to 750 m) across the plateau. The seals are, therefore, likely to be responding more directly to factors other than SST.

Water profile data collected using animal-mounted sensors are increasingly being used to characterise foraging areas of southern elephant seals by identifying differences in water masses (Hindell et al. 1991a, Biuw et al. 2007, Dragon et al. 2010). Our study demonstrates that information from the vertical dimension of the water column is important in explaining foraging behaviour. Specifically, temperature at 200 m depth (i.e. ML) was an important habitat descriptor, with increased search activity occurring at lower temperatures, particularly below 2°C. Results suggested that likely habitat patches were up to 0.25°C colder than surrounding waters. Bailleul et al. (2007b) has already argued that seals may use these changes in temperature to target prey patches. It is likely that colder water at 200 m is related to the temperature maxima, which Biuw et al. (2010) demonstrated to be a key limiting factor in the depth of night-time dives. This represents a boundary between water masses and perhaps prevents the upward migration of zooplankton during the night. Furthermore, the Antarctic Polar Front (APF) can be defined by a sharp decrease in water temperature at 200 m down to 2°C (Roquet et al. 2009). Elephant seal populations from Marion Island and Macquarie Island have been associated with this frontal boundary (Jonker & Bester 1998, van den Hoff et al. 2002, Field et al. 2004), which is an area of elevated productivity (Pakhomov & McQuaid 1996). Our analysis shows that increased search activity occurred, at, or south of the APF. This is one of the few times ocean

profiles have been used in this way and confirms that, at least for deep-diving animals, 3-dimensional water profiles can improve the understanding of foraging habitats.

Though search behaviour was statistically closer to the 1000 m bathymetric contour (i.e. ShB), its effect was biologically irrelevant. Individual track variability showed some seals transited either partially ($n = 4$) or entirely ($n = 6$) to the south deep-sea region rather than to the shelf edge. Nonetheless, Martin et al. (2011) has shown that larger males move closer to the shelf edge, where they are likely to encounter larger fish. The northwestward flow of the Fawn Trough Current and its influence on shelf bathymetry generate nutrient-enriched, deep-water upwelling sites associated with the eastern shelf break (Park et al. 2008b). Furthermore, the complex arrangements of seamounts and troughs over the shelf provide ideal conditions for seasonal blooms of primary production (Park et al. 2008a). However, the nature of connectivity between the surface and demersal habitats is unclear and likely to be complex in both space and time (Cornejo-Donoso & Antezana 2008). Nevertheless, large, diverse communities of the potential prey of elephant seals from both shelf and pelagic habitats occur at the shelf break, including *Dissostichus eleginoides*, *Lepidonotothen squamifrons* (Williams & De La Mare 1995, Duhamel 2009), a myriad of cephalopod species (Cherel et al. 2004) and myctophids (Loots et al. 2007). The shelf break is also the region targeted by commercial fisheries, confirming the abundance of potential prey in that area.

Implications for ecosystem-based management

Both *Dissostichus eleginoides* and *Champscephalus guanari* commercial fisheries operate within the Kerguelen-Heard shelf CCAMLR and EEZs (i.e. NMZ and SMZ) (Constable 2002), where seals in this study forage. Indeed, our study suggests a potential overlap between seals and these fisheries, supported by studies citing either direct (e.g. McMahon et al. 2000, van den Hoff et al. 2002, G. Duhamel pers. comm.) or indirect (e.g. van den Hoff et al. 2002) interaction. Interaction may be particularly pronounced in areas where temperatures at 200 m are relatively low. These features, which attract high aggregations of seal foraging activity, are also likely to attract high levels of other fish predators.

The Kerguelen Islands elephant seal population is currently stable (Guinet et al. 1999). However, the effects of climate change on environmental factors,

such as the water temperature profile (Jaud et al. 2012), coupled with the potential impact of fisheries, could result in decreased foraging and demographic performance. Indeed, it has been well documented that climatic perturbations influence species' distributions (Walther et al. 2002, Parmesan 2006). Investigations into predator use of the shelf and the *in situ* environment will help understand these changes and perhaps help mitigate negative impacts. Specifically, larger sample sizes and further dietary analyses are needed for a more objective and predictive analysis of future datasets.

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