Progress in Oceanography 137 (2015) 52–68

Contents lists available at ScienceDirect

Progress in Oceanography

journal homepage: www.elsevier.com/locate/pocean

Winter use of sea ice and ocean water mass habitat by southern elephant seals: The length and breadth of the mystery

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ARTICLE INFO

Article history:
Received 20 August 2014
Received in revised form 24 May 2015
Accepted 26 May 2015
Available online 3 June 2015

ABSTRACT

Understanding the responses of animals to the environment is crucial for identifying critical foraging habitat. Elephant seals (*Mirounga leonina*) from the Kerguelen Islands (49°20′S, 70°20′E) have several different foraging strategies. Why some individuals undertake long trips to the Antarctic continent while others utilize the relatively close frontal zones is poorly understood. Here, we investigate how physical properties within the sea ice zone are linked to foraging activities of southern elephant seals (SES). To do this, we first developed a new approach using indices of foraging derived from high temporal resolution dive and accelerometry data to predict foraging behaviour in an extensive, low resolution dataset from CTD-Satellite Relay Data Loggers (CTD-SRDLs). A sample of 37 post-breeding SES females were used to construct a predictive model applied to demersal and pelagic dive strategies relating prey encounter events (PEE) to dive parameters (dive duration, bottom duration, hunting-time, maximum depth, ascent speed, descent speed, sinuosity, and horizontal speed) for each strategy. We applied these models to a second sample of 35 seals, 20 males and 15 females, during the post-moult foraging trip to the Antarctic continental shelf between 2004 and 2013, which did not have fine-scale behavioural data. The females were widely distributed with important foraging activity south of the Southern Boundary Front, while males predominately travelled to the south-eastern part of the East Antarctica region. Combining our predictions of PEE with environmental features (sea ice concentration, water masses at the bottom phase of dives, bathymetry and slope index) we found higher foraging activity for females over shallower seabed depths and at the boundary between the overlying Antarctic Surface Water (AASW) and the underlying Modified Circumpolar Deep Water (MCDW). Increased biological activity associated with the upper boundary of MCDW, may provide overwintering areas for SES prey. Male foraging activity was strongly associated with pelagic dives within the Antarctic Slope Front where upwelling of nutrient rich Circumpolar Deep Water onto surface water may enhance and concentrate resources. A positive association between sea ice and foraging activity was found for both sexes where increased biological activity may sustain an under-ice ecosystem. Variability of the East Antarctic sea ice season duration is likely a crucial element to allow air-breathing predators to benefit from profitable prey patches within the pack ice habitat.

1. Introduction

The Southern Ocean is highly productive which influences the structure and dynamics of the Antarctic marine ecosystem at all trophic levels (Tynan, 1998; Nicol et al., 2000a, 2000b). Short and

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http://dx.doi.org/10.1016/j.pocean.2015.05.023
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intense phytoplankton blooms (Smetacek and Nicol, 2005) are dependent on spatio-temporal distribution of nutrients, themselves determined by interactions between topography of the seafloor, water mass properties and circulation, ocean currents and sea ice seasonality (Prézelin et al., 2000; Brierley and Thomas, 2002). The continental shelf, polynyas, sea ice edge and areas where the bathymetric profile allows intrusion of nutrient rich water masses onto the shelf (such as Circumpolar Deep Waters) stimulate primary productivity (Moore and Abott, 2000; Nicol et al., 2005) and the population growth of mid (Prézelin et al., 2000) and upper trophic levels (La Mesa et al., 2010) including top predators. The latter includes purely Antarctic species and also species breeding in the sub-Antarctic, such as southern elephant seals (SES, *Mirounga leonina*, Biuw et al., 2007, 2010), king penguins (*Aptenodytes patagonicus*, Bost et al., 2004) and Antarctic fur seals (*Arctocephalus gazella*). However, the nature of the linkages between environmental factors and higher trophic levels is unclear.

In this study, we investigated how physical environmental factors influence SES foraging strategies in the East Antarctic region of the Southern Ocean (0–150°E). This region is characterized by considerable intra- and inter-annual variation in sea ice and prominent ocean circulation features including the eastern end of the Weddell gyre, and an intense westward flowing current steered by the Antarctic continental shelf (the Antarctic Slope Current; ASC). Reported changes and variability in sea ice and ocean water masses in the East Antarctic region are possibly associated with changes in ocean circulation patterns (*e.g.* Rintoul, 2007; Nicol and Raymond, 2012; Massom et al., 2013). These changes can be rapid and complex with contrasting signals in close areas on regional to local scales. However, how these local changes of the environment would influence the dynamics of the entire ecosystem is poorly understood.

Several hypotheses have been proposed to link local environmental factors with apex predator foraging behaviour. One is that sea ice variability in East Antarctica may dictate the distribution of prey species, many of which are known to interact with sea ice. For example, krill (*Euphausia superba*) living within the seasonal pack ice zone depends on ice-algae to survive in winter (*e.g.* Daly, 1990; Atkinson et al., 2004; Meiners et al., 2012) and mesopelagic fish such as the Antarctic lanternfish (*Electrona antarctica*) feed on krill and other zooplankton under pack ice (Kaufmann et al., 1995). A second hypothesis is that discontinuities between nutrient-poor and nutrient-rich water masses may result in increased biological activity at these water masses boundaries (Rodhouse and Clarke, 1985; Prézelin et al., 2000), providing rich food sources that could be easily detected (Sticken and Dehnhardt, 2000) and exploited by predators (Boyd and Arnbom, 1991). A third hypothesis is that the complex regional circulation features such as the Antarctic Slope Front (ASF) may control the distributions of chlorophyll, krill and apex predators (Bindoff et al., 2000). This would be largely due to upwelling of nutrient rich circumpolar deep water, onto the eutrophic zone on the shelf, which would enhance productivity (Jacobs, 1991).

Elephant seals are deep-diving, wide-ranging (Hindell et al., 1991a, 1991b; McConnell et al., 1992) top predators of the Southern Ocean that utilize radically different marine habitats between different sexes, ages, breeding colonies and according to individual preferences (Biuw et al., 2007). The main populations are located in the South Atlantic, Southern Indian, and South Pacific oceans, and display contrasting demographic trends, presumably in response to environmental variability (McMahon et al., 2005). SES from Kerguelen show two-distinct foraging strategies: 75% of the females forage in frontal areas of the Antarctic Circumpolar Current (ACC) and 25% on the peri-Antarctic shelf. Males forage on the Kerguelen and peri-Antarctic shelf (Bailleul et al., 2010a). Our understanding of the foraging behaviour of SES and its interplay with environmental features such as hydrography, sea ice, bottom topography or dynamic environmental features such as eddies and fronts has increased in recent years (Bornemann et al., 2000; Bailleul et al., 2007a, 2007b, 2010a, 2010b; Biuw et al., 2007, 2010; Bestley et al., 2012; Guinet et al., 2014; Hindell et al., in press). However, no studies on Kerguelen SES have quantified the role of combined environmental factors that would make migrations of male and female within the East Antarctic sea ice zone during winter profitable and sustainable over years. Unique environmental features and important life history stages may hold the answer to the causes underpinning seal movements.

Understanding the effect of environmental variability on foraging behaviour requires knowledge of where and when animals feed and assimilate energetic reserves. A major challenge in marine ecology of top predators is the difficulty in obtaining appropriate foraging indices from simple behavioural data, particularly in the context of poorly known prey fields. Most studies use proxies for feeding such as changes in vertical or horizontal movements, or time spent in specific areas (Bailleul et al., 2007b, 2008; Biuw et al., 2007; Thums et al., 2011; Dragon et al., 2012a, 2012b; Hindell et al., in press). Although these proxies can indicate areas where foraging effort is focused, they do not necessarily quantify the foraging success of the animal. New approaches employing acquisition of high resolution data of seal body dynamics from accelerometers are now filling the gap (Guinet et al., 2014).

By simultaneously recording animal location, dive behaviour and hydrographic profiles *in situ* and in real time, we studied the foraging behaviour of Kerguelen elephant seals migrating during post-moult movements from the Kerguelen Islands to the Antarctic shelf. The aim of the study was to identify and quantify the role of environmental features involved in the acquisition of food resources for SES during winter trips in the Antarctic sea ice zone. We developed a new approach using indices of foraging derived from high resolution dive and accelerometry data (prey encounter events, PEE) to predict foraging behaviour in an extensive, low resolution dataset from CTD-Satellite Relay Data Loggers (CTD-SRDLs). Information on the properties of water masses, sea ice concentration and topography was combined and sexual differences were investigated.

2. Materials and methods

2.1. Animal handling and tag deployment

Two different datasets were used in this study; one as a training dataset to build a predictive model of foraging behaviour (hereafter, referred to as the training dataset), and a second on which that model was used to predict foraging in space and time and relate foraging activity to environmental features of the region (referred to as the study dataset). A summary of the different steps followed in this study is presented in Fig. 1.

The training dataset consisted of 37 post-breeding SES females captured on the Kerguelen Islands (49°20′S, 70°20′E) in October/November between 2008 and 2013 (Appendix A, Table A1). Twenty three seals were equipped with a head-mounted GPS capable of relaying data via satellite using Service Argos combined with an archival data logger (SPLASH10-Fast-Loc GPS, Wildlife Computers; WC). SPLASH10 devices transmitted Argos location data, collected GPS location data at 20 min intervals and recorded pressure at 1 or 2s intervals. In addition, 12 seals were equipped with a head-mounted conduc tivity–temperature–depth satellite-relay data loggers (CTD-SRDLs,

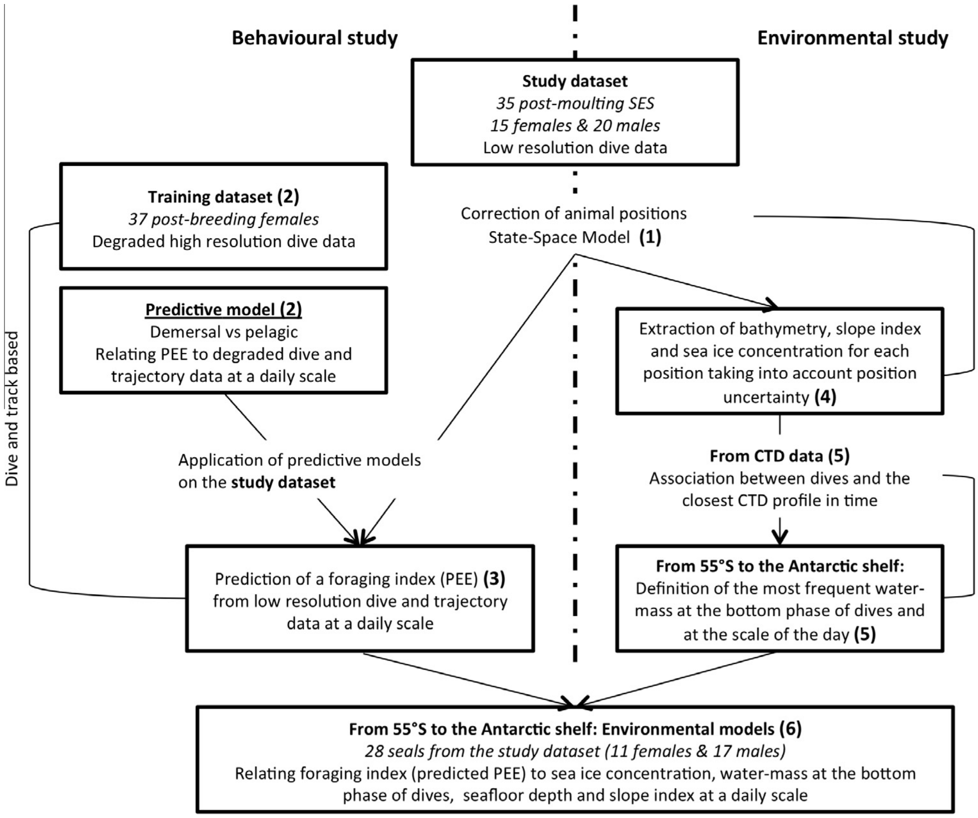

Fig. 1. Diagram summarizing the different steps of both behavioural and environmental studies. Numbers refer to the order in which these steps were realized.

Sea Mammal Research Unit, University of St Andrews), and 2 others with Smart Position and Temperature Tags (SPOT, WC). All tags were combined with a TDR–accelerometer data logger (MK10-X, Wildlife Computers), sampling acceleration and pressure. Acceleration was measured at 16 Hz on 3 axes (longitudinal (surge), vertical (heave) and lateral (roll) axes) and the separation between dynamic and gravitational acceleration was done via post-processing of all 3 axes.

The study dataset consisted of 35 post-moulting SES, 20 males and 15 females, that were captured on the Kerguelen Islands between December/February from 2004 to 2013 (Appendix A, Table A2). For this analysis we used only post-moulting SES that used the sea ice zone. All animals were equipped with CTD-SRDLs (Sea Mammal Research Unit, University of St Andrews) measuring conductivity, temperature and pressure. An average of 2.8 ± 1 CTD profiles ($n = 29$) were transmitted daily (Boehme et al., 2009) and the tag positions were estimated by the Argos system. For all CTD-SRDLs (from Sea Mammal Research Unit, University of Saint Andrews), the datapoints transmitted for each profile (mean of 16 ± 6 (SD), $n = 29$) are a combination of T (temperature) and S (salinity) at a set of preselected standard depths, and at another set of depths chosen by a broken-stick algorithm that selects the important inflection points in T and S data (recorded every second during the ascent phase of the dives). All tags were initially calibrated at the laboratory and a part of them were also tested at sea against a ship based CTD before deployment. All tags were then post-calibrated using standardized procedures described in Roquet et al. (2011, 2014). The minimum accuracies of post processed data were estimated to be at ±0.03 °C in temperature and ±0.05 psu, increasing to ±0.01 °C and ±0.02 psu in the best cases (Roquet et al., 2014).

Individuals were anaesthetized using a 1:1 combination of tiletamine and zolazepam (Zoletil 100), which was injected intravenously (Field et al., 2002). Data loggers were glued to the head of the seals using quick-setting epoxy (Araldite AW 2101, Ciba; Field et al., 2012). Instruments were retrieved from post-breeding females upon returning from their foraging trip.

Females in the training dataset had an average weight of 288 ± 51 kg (mean ± standard deviation) and an average length of 243 ± 14 cm, similar to the weight and length of females from the study dataset of 324 ± 56 kg and 244 ± 16 cm respectively. However, males were heavier and longer than females (553 ± 256 kg and 292 ± 41 cm).

2.2. Behavioural data

2.2.1. Filtering trajectories

Of the 37 females in the training dataset, 23 individuals provided GPS positions, while 14 had only Argos locations. For both types, a simple speed filter similar to McConnell et al. (1992) was used.

For 35 individuals of the study dataset, Argos positions were filtered using State-Space-Model (SSM) (step 1, Fig. 1) with the package *bsam* following Jonsen et al. (2013). Locations of class Z (*i.e.* the lowest location quality index provided by Service Argos, and for which no stated position uncertainty is provided) were removed prior to analysis. Two Markov chains with a total of 100,000 simulations were computed, taking one in ten samples, with a burn in of 50,000 simulations. The analysis sets an interval of 6 h between each position and for each position we obtained 5000 samples per chain. The average of the 10,000 samples gave the estimated position of the animal as well as uncertainty estimate associated with this position. Confirmation of the convergence of the model was checked graphically. Two individuals were removed from analysis due to devices functioning for less than 30 days. Each dive's location was based on a time-based linear interpolation between corrected locations.

2.2.2. Dive data collected

For the training dataset, data from accelerometers were processed according to Viviant et al. (2009) and Gallon et al. (2013). Identification of prey encounter events (hereafter PEE) from the accelerometry data followed Guinet et al. (2014). A PEE does not mean that the seal was necessarily ingesting food, but should be considered as an index of prey encounters during the dive.

For the study dataset, tags were programmed to record dive depth and time every 4s, from which dive start time, dive end time, dive duration and post dive surface interval were determined. Only the four main inflection points of the time-depth time series, indicating a rapid change of the dive shape, were transmitted for each dive according to tag programming (Sea Mammal Research Unit).

For both datasets, a zero offset surface correction was set to 15 m (Guinet et al., 2014). Only dives deeper than 40 m and longer than 3 min were kept for analysis.

2.2.3. Predictive model of foraging behaviour

Following Viviant et al. (2014), we developed indices of foraging derived from high resolution dives, trajectory and PEE to estimate foraging behaviour from the lower temporal resolution dataset (CTD-SRDLs). The purpose of this step was to first use the high resolution training dataset to identify dive and trajectory parameters associated with high PEE (step 2 of Fig. 1). Using these results we then calculated PEE per day based on diving and movement patterns of the 35 individuals equipped with CTD-SRDLs (study dataset; step 3 of Fig. 1) for which no information on foraging success was available otherwise.

To obtain dive profiles with a similar resolution for both the training dataset used to construct the model (37 post-breeding SES) and the study dataset used to apply the prediction (35 post-moulting SES), we first computed a "broken-stick" algorithm (from Heerah et al., 2014) to degrade high resolution dive data into the four inflection time-depth points, *i.e.* identical to the dive data provided by the CTD-SRDLs. The variables (from degraded dive data) used to describe foraging behaviour were dive duration, bottom duration (time spent at 80% of the maximum depth), hunting-time (see Heerah et al., 2014), maximum depth, ascent speed, descent speed of the next dive, track turning angle (sinuosity) and horizontal speed (between two dives). These values were averaged for each day because the predictive abilities of similar models were low at the scale of a single dive and higher at a scale of a day containing multiple dives (Viviant et al., 2014). The daily PEE was calculated from the rate of PEE per hour multiplied by 24 h.

Southern elephant seals display either a demersal or pelagic foraging strategy (*i.e.* the dominant type of dive behaviour in a given day) depending on the habitat (Bailleul et al., 2007a, 2007b), which might influence patterns of foraging activity and dive behaviour. Therefore, to build the model, the training dataset was divided into pelagic and demersal dive strategies for locations on the Kerguelen shelf (Appendix B).

We then used a generalized linear mixed model (GLMM) to identify the most informative variables explaining daily PEE for each strategy based on the training dataset (Appendix C). A quasi-Poisson distribution was used for the error structure of the response variable and individuals were included as random factor. When applying the models to the study dataset, we distinguished between demersal and pelagic strategy over the peri-Antarctic shelf (rather than the Kerguelen Shelf) (Appendix B). The statistical model (averaged regression coefficients obtained from model averaging) was then applied to the variables of the study dataset for each strategy to predict PEE per day for the 35 post-moulting individuals (step 3 of Fig. 1; Appendix C).

2.3. In situ and remotely sensed oceanographic data

2.3.1. In situ salinity and temperature profiles

Among the 35 study individuals, 29 had usable CTD (Conductivity–Temperature–Depth) profiles. To obtain continuous T and S vertical profiles, a linear interpolation with a vertical resolution of 18 m was applied. The resolution of 18 m was chosen as the best compromise between high vertical resolution and avoiding addition of non-available data or loss of information (Heerah et al., 2013; the minimum of the mean intervals (for each individual) between two data points for all profiles was 18.3 m). CTD positions were corrected by interpolating SSM locations along the track based on the CTD date and time. Water masses sampled during the transit of seals along their trip from 55°S to the Antarctic continent were then determined from their temperature, salinity and neutral density γ_n (Jackett and McDougall, 1997). We distinguished between nine water masses (Bindoff et al., 2000; Meijers et al., 2010): (1) Intermediate Water (IW); (2) Antarctic Surface Water (AASW); (3 & 4) Modified and Circumpolar Deep Water (CDW, MCDW); (5) High Salinity Modified Circumpolar Deep Water (HSMCDW); (6) Mixed Shelf Water (MSW); (7) Antarctic Bottom Water (AABW); (8) High Salinity Shelf Water (HSSW); and (9) Ice Shelf Water (ISW). Criteria to define these water masses were adapted from Bindoff et al. (2000), Meijers et al. (2010), Lacarra et al. (2011) and Orsi et al. (1995), and are presented in Table 1.

To identify the water mass used when the seals were foraging, we used the water mass encountered during the bottom phase of each dive, as this is where most PEE are expected to occur (Guinet et al., 2014) (step 5 of Fig. 1). Each dive was then associated with the closest CTD profile in time collected by the same individual (step 5 of Fig. 1). A maximum time interval of 12 h between the CTD and the dive was set, leading to an average distance difference between the CTD and the dive of 9.1 ± 9.6 km. Following this procedure, 70.4% of dives were associated with a CTD profile.

Table 1
Definition criterions of water masses determined from CTD-SRDLs temperature, salinity, pressure collected by the 29 post-moulting seals at the bottom phase of dives from 2004 to 2013 along tracks from 55°S to the Antarctic continent and from 0 to 150°E.

Acronym	Type of water mass	Neutral density γ_n (kg m^{-3})	Potential temperature θ (°C)	Salinity S (psu)
AAIW	Antarctic Intermediate Water	$27.0 < \gamma_n < 27.5$		
AASW	Antarctic Surface Water	$27.5 < \gamma_n < 28.03$		
CDW	Circumpolar Deep Water	$28.03 < \gamma_n < 28.27$	$\theta > 1.5$	$S > 34.5$
MCDW	Modified Circumpolar Deep Water	$28.03 < \gamma_n < 28.27$	$\theta < 1.5$	$S < 34.7$
HSMCDW	High Salinity Modified Circumpolar Deep Water	$28.03 < \gamma_n < 28.27$	$\theta < 1.5$	$S >= 34.7$
MSW	Mixed Shelf Water	$\gamma_n > 28.27$	$\theta > -1.85$	
AABW	Antarctic Bottom Water	$\gamma_n > 28.27$	$\theta > -1.7$	$S > 34.6$
HSSW	High Salinity Shelf Water	$\gamma_n > 28.27$	$Tf < \theta < -1.85$	
ISW	Ice Shelf Water	$\gamma_n > 28.03$	$\theta < Tf$	

2.3.2. Extraction of ocean floor topography and sea ice concentrations at animal positions

This study focused on individuals using the Antarctic shelf and the sea ice zone. The maximum extension of sea ice was reached in September at latitudes close to 55°S. The area south of 55°S to the Antarctic continent was used as the spatial domain for the environmental study where hydrology, topography and sea ice data were linked to foraging behaviour.

Two bathymetry datasets were used; the GEBCO One Minute Grid-database (1′ per cell grid) for graphical purpose, and GEBCO_08 Grid-database (30s per cell) for analysis (http://www.gebco.net/).

To take into account the spatial error associated with each location when extracting environmental variable under the seals' tracks, the mean and variance/covariance matrix of the 10,000 posterior samples available after the filtering process for each position estimate were computed. These were used to generate a random sample, from a bivariate Normal distribution, from which 200 random pairs of latitude/longitude coordinates were extracted for each position. Bathymetry associated with these 200 samples was then extracted and a mean bathymetry for each position was computed.

To define the shelf area and the continental slope, the inflection point in meridional bathymetric contours, which represents the shelf break, was identified for each half degree of longitude from 0 to 150°E. The boundary between the continental slope and the open ocean was defined as the region where the influence of the Antarctic Slope Front stops. We used pressure gradient on an isopycnal computed from historical Argo floats and ship observations of the region to dynamically define the influence of the slope front and associated it with, roughly, the 3500 m isobaths for our region. Each dive position of seals was attributed either to the shelf, slope or the open ocean area.

Sea ice concentration was extracted from AMSR-E daily sea ice concentration images for years 2004–2011 (http://www.iup.physik.uni-bremen.de:8084/amsr/amsre.html) and derived sea ice maps from SSMIS were used for the year 2012. Although AMSR-E resolution (6.25 km $*$ 6.25 km) is higher than SSMIS resolution (13.2 km $*$ 15.5 km), the same algorithm was applied and the grid spacing of 6.25 km was kept. The AMSR2 satellite was used for 2013. Each "grid cell" has an allocated sea ice concentration from 0% to 100%. Finally, we accounted for location uncertainty as described above (step 4). Ice concentrations were grouped into three categories based on their frequency distribution: class 1 ($[\text{ice}] \leqslant 5\%$), class 2 ($5\% < [\text{ice}] \leqslant 80\%$) and class 3 ($80\% < [\text{ice}]$).

2.4. Habitat use

We compared the proportion of time spent in several habitats: (a) different areas (*i.e.* shelf, continental slope, pelagic zone); (b) different water masses; (c) different sea ice concentrations; and (d) different seasons (*i.e.* summer defined by February, autumn by March–May, winter by June–August, and spring by September–November). We then tested if the time within each habitat type was significantly different between males and females by applying a Wilcoxon–Mann–Whitney test.

2.5. Statistical analysis of oceanographic conditions in foraging zones

The influence of hydrological features, sea ice concentration and sea floor topography on foraging behaviour (estimated PEE per day) was quantified using GLMMs (step 6 of Fig. 1; Appendix C). Bathymetry, slope and sea ice concentration values were averaged for each seal each day and the most frequent water masses encountered at the bottom phase of dives each day were used. Two models were built, one for each sex, based on 11 females and 17 males including trajectories from 55°S to the Antarctic continent. Explanatory co-variables included factor variables such as class of sea ice concentration, water masses at the bottom phase of dives and continuous variables such as the day of the year, the sea-bed depth and the slope index associated with topography features. The same process was followed for the 2 models; a negative binomial distribution was used for the error structure of the response variable and individuals were included as random factor.

3. Results

3.1. Trajectory and diving features

A total of 72,209 and 211,909 dives were recorded for the 37 post-breeding (training) and the 35 post-moulting (study) seals respectively, with an average track duration of 29 ± 17 days where accelerometry data were available (mean ± standard deviation) and 159 ± 75 days, respectively. Within each dataset (training and study), diving features are presented in Table 2 by separating demersal dives from pelagic ones.

Animals from the training dataset made 65.2 ± 12.1 dives per day and travelled 49.8 ± 30.1 km per day (Table A1), compared to 40.1 ± 17.5 dives per day and 38.7 ± 33.2 km per day for the study animals (Table A2). Some of the difference between the two datasets might arise from the non-transmission of some dives when the animal is surfacing for the Argos tags (study dataset). Demersal

Table 2
Summary of the dive and trajectory statistics for the study dataset (post-moulting SES) and for the training dataset (post-breeding SES) for each dive strategy (*i.e.* demersal or pelagic).

	Demersal			Pelagic		
	Quantile 25%	Median	Quantile 75%	Quantile 25%	Median	Quantile 75%
Study dataset (post-moulting)						
Maximum depth (m)	290	390	503.8	231.3	380	525
Dive duration (min)	16.1	21	27.1	17	23.5	31.3
Bottom time duration (min)	8.3	12.3	17.6	6.9	11.2	17.4
Speed descent (m s^{-1})	1.4	1.7	2.1	0.73	1.2	1.6
Speed ascent (m s^{-1})	0.88	1.2	1.4	0.65	0.97	1.2
Horizontal speed (m s^{-1})	0.18	0.32	0.51	0.32	0.60	0.98
Training dataset (post-breeding)						
Maximum depth (m)	460.9	545.5	591.4	356.5	491	674.8
Dive duration (min)	16	18.3	20.7	16	18.8	21.7
Bottom time duration (min)	7	9.5	11.9	6.1	8.6	11.1
Speed descent (m s^{-1})	1.1	1.7	2.3	1.1	1.5	1.8
Speed ascent (m s^{-1})	1.2	1.5	1.7	1.2	1.4	1.5
Horizontal speed (m s^{-1})	0.03	0.26	1.1	0.38	0.68	0.95

dives represented 5% of dives for the training dataset (only females) and 21% of the study dataset (8% of females' dives and 35% of males' dives).

Thirty one of the 35 study animals travelled to the Antarctic continent, remaining in the seasonal sea ice zone (Fig. 2). Some seals stayed exclusively within the sea ice zone while others had

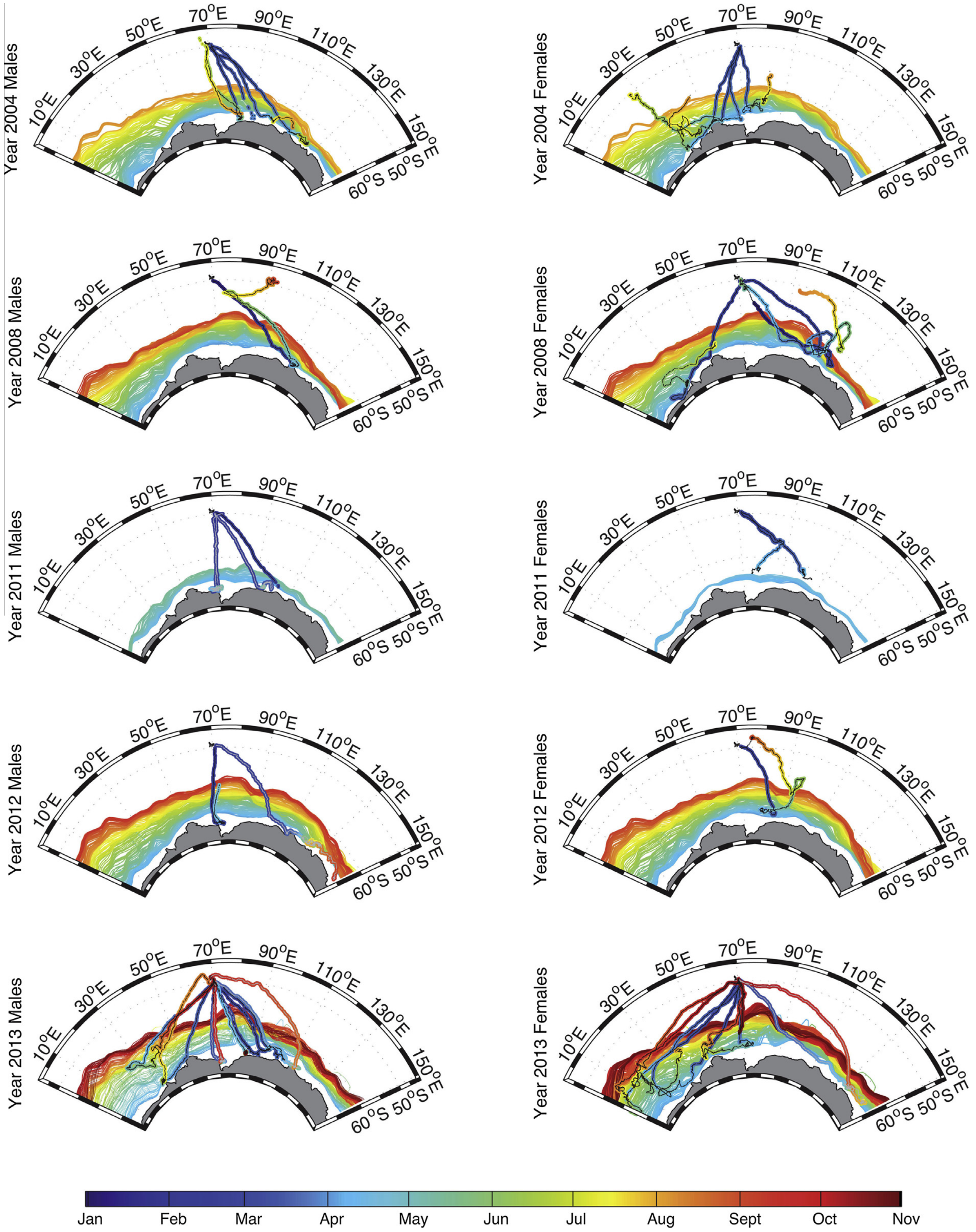

Fig. 2. Tracks per year of the 35 post-moulting SES equipped with CTD-SRDLs from 2004 to 2013 (study dataset), linked with the seasonality of the sea ice in the East Antarctic region. The colour scale represents the time expressed in month and the same scale is used for sea ice extent and tracks of animals; each sea ice line represents the maximum extent for a given day. Tracks of animal following the sea ice edge as sea ice extends are represented by a black line, while ones remaining in high sea ice concentration independently of the sea ice extension are represented by a grey line. Sea ice extent lines start from April for all years and were computed from AMSRE, SSMIS product and AMSR-2 satellite data. For each year, tracks of post-moulting animals are represented (left: males, right: females). The unique individual in 2009 was removed for visual purposes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

pelagic sorties out of the pack ice. Sex and individual differences were observed and are described in Section 3.3.1.2.

3.2. Foraging behaviour

3.2.1. Predictive model of foraging activity: diving predictors and performance

The training dataset was used to build the models of foraging behaviour relating observed PEE to dive and trajectory parameters. The demersal model was built with 60 days of observations from 8 different females. The pelagic model was built with 984 days of observations, using all 37 females.

For the demersal model, retained variables after checking colinearity were ascent speed, maximum depth of the dive, dive duration and turning angle, but only ascent speed and dive duration were retained as significant after the stepwise procedure. In the full model, 79% of variance was explained by fixed effects (marginal R^2) and 82% by both fixed and random effects (conditional R^2) (Table 3). Regression coefficients computed using leave-one-out cross-validation (CV) (see Appendix C) (Table 3) indicate low individual variability and increased PEE with increasing ascent speed and dive duration. Ascent speed had the largest predictive value of the model. The predictive ability of the model was assessed using CV, and explained 53% of the deviance.

Table 3
Summary of regression coefficients and goodness-of-fit indices from the two generalized linear mixed effects models of Prey Encounter Events (PEE, based on high-frequency sampled activity data) as a function of various summary dive parameters, based on 37 post-breeding females (training dataset). Separate models were fitted for demersal and pelagic type dives.

Quasi-Poisson distribution Explanatory variables	Pelagic Model (n = 984, 37 females) Coef ± SE	Demersal Model (n = 60, 8 females) Coef ± SE
Intercept	6.20 ± 0.02	5.47 ± 0.11
Maximum depth	−0.28 ± 0.01	/
Dive duration	/	0.44 ± 0.05
Bottom-time	0.09 ± 0.02	/
Speed ascent	0.28 ± 0.01	0.31 ± 0.12
Horizontal speed	−0.21 ± 0.01	/
Goodness-of-fit		
Deviance explained$_{CV}$	30.36%	52.68%
$R^2_{LMM/GLMM(m)\text{-}full}$	38.58%	79.21%
$R^2_{LMM/GLMM(c)\text{-}full}$	67.45%	81.97%

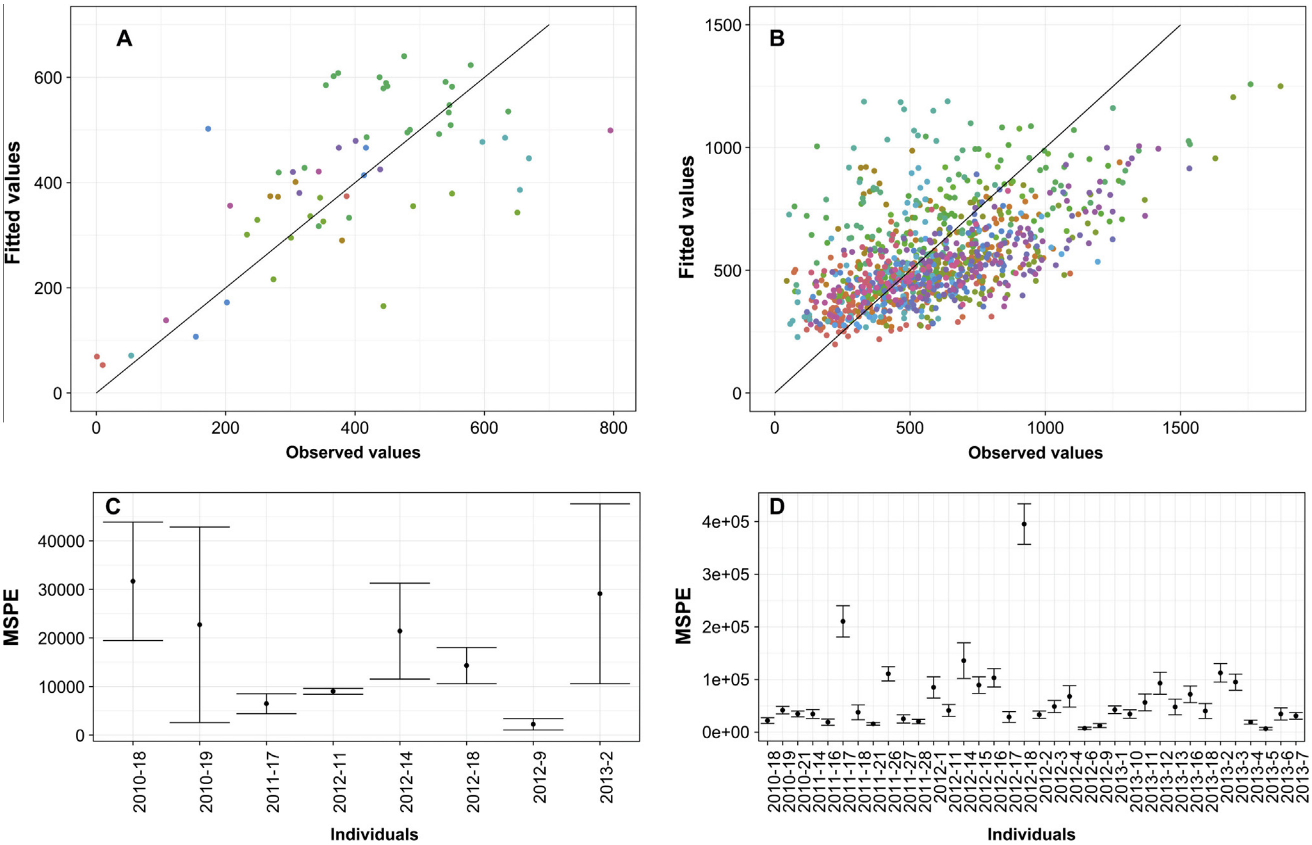

Fig. 3. Predictive ability of behavioural models based on the training dataset of 37 post-breeding females. For A and B, observed versus predicted values obtained after the leave-one-out cross-validation (CV) process are represented for the demersal model (A) and the pelagic model (B). For C and D, MSPE and standard error computed for each individual along the CV process are represented for the demersal model (C) and the pelagic model (D). Colour scale on A and B represents each individual and the line 1:1 is shown, each dot corresponds to one daily observation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

For the pelagic model, the use were ascent speed, maximum depth of the dive, bottom time duration, horizontal speed and turning angle, of which four were retained after the stepwise procedure (turning angle was removed). Based on this model, 39% of the variance was explained by fixed effects (marginal R^2), and 67% by both fixed and random effects (conditional R^2) (Table 3). Regression coefficients indicate that PEE increased with increasing bottom phase duration and ascent speed, and decreasing maximum depth and horizontal speed. Maximum depth and ascent speed represented the most important contributors of the model. About 30% of deviance was explained by the model. Fig. 3A and C show the predictive ability for the demersal model determined by the CV and Fig. 3B and D the predictive ability for the pelagic model. In the pelagic model, three individuals had some predicted values over-estimated relative to their observed values (Fig. 3B), and a deviation is also observed on MSPE (Fig. 3D). Tracks of these three individuals are mostly composed of demersal daily observations that could explain why they differed from the 33 animals left when they are involved in a pelagic strategy. Moreover, for high PEE between 1000 and 1870 PEE (maximum observed in the training dataset), the model tended to under-estimate the values.

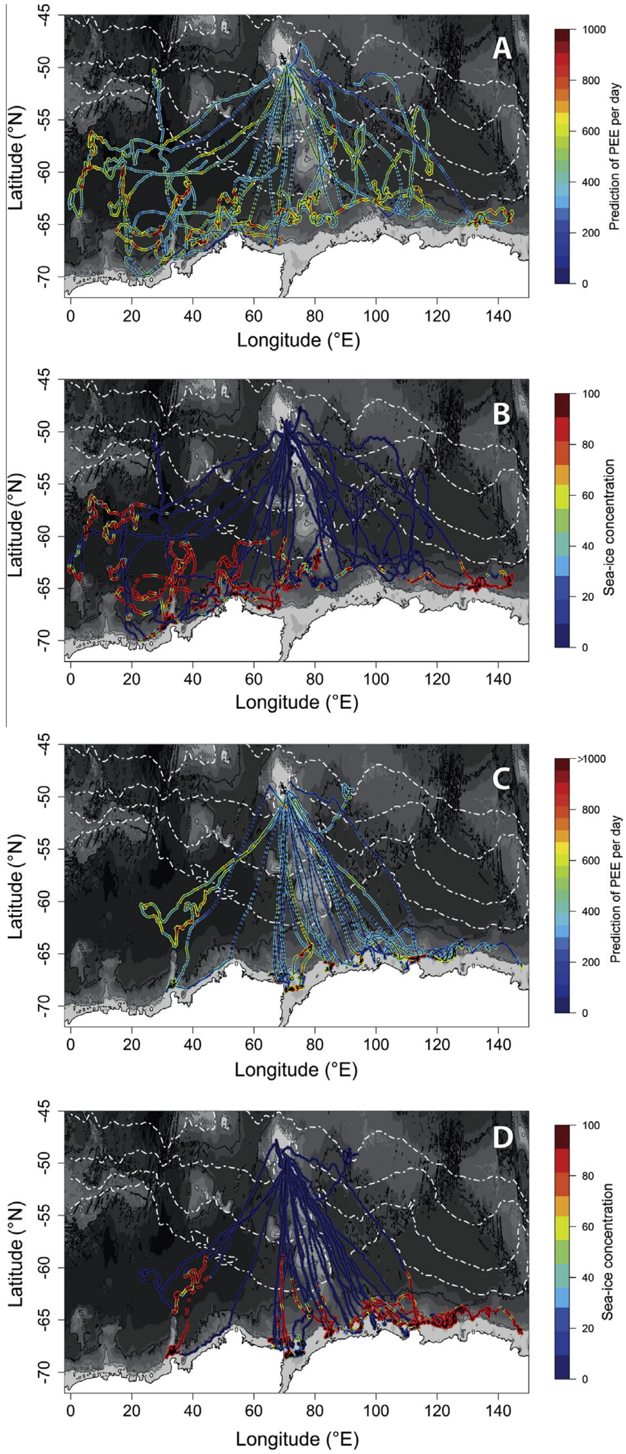

Fig. 4. Tracks of the 35 post-moulting individuals equipped with CTD-SRDLs from 2004 to 2013 (study dataset). For A and C, colour indicates prediction of PEE/day along the track for females (A) and males (C). An interpolation every 12 h was applied for visual purpose. For B and D, colour indicates sea ice concentration associated with females (B) and males (D) filtered positions. A position every 6 h is shown. Oceanic fronts from Roquet et al. (2013) are represented in white dot-dashed lines, from North to South: Subantarctic Front (SAF), Polar Front (PF), Southern Antarctic Circumpolar Current Front (SACCF) and Southern Boundary of the Antarctic Circumpolar Current (SB). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2.2. Application and prediction of the foraging activity on the study dataset

Within the study dataset, 19% of daily observations represented the demersal strategy (Fig. D1), of which 15% were from females (6 individuals) and 85% were from males (19 individuals). The pelagic strategy represented 81% of the dataset (Fig. D1), with 58% and 42% of female and male observations respectively, made by 15 females and 20 males.

Mean predicted values obtained from the demersal model were 251 ± 106 PEE/day, less than the mean of observed values from the training dataset of 394 ± 165 PEE/day. For the pelagic model, the mean of the predicted values from the study dataset was of 510 ± 231 PEE/day, similar to the mean of observed values from the training dataset of 585 ± 278 PEE/day. For subsequent analyses, predicted values with PEE/day above 1000 and dive depths $\leqslant$250 m were removed due to the predictive range of the model. It represented 88 daily observations on a total of 3889 (*i.e.* 2.3% of the study dataset) from 5 individuals, all of which were males.

Males had on average 418 ± 226 PEE/day and females 494 ± 170 PEE/day. For illustration purposes, we used a threshold of 500 PEE/day, slightly above the average values, to define areas of high foraging activity ("hotspots"). On the shelf, 402 ± 265 PEE/day were observed, 459 ± 180 PEE/day within the continental slope and 481 ± 161 PEE/day for the pelagic area.

Post-moult females had a wide distribution in the East Antarctic region with dominant movements within pelagic areas and the continental slope for some individuals (Fig. 4A). Conversely, male movements were mostly on the south-eastern part of the region within the Antarctic shelf and slope zone (Fig. 4C). Only two males did not exhibit such behaviour; one of which was foraging on the south part of the Gunnerus Ridge along the continental slope and over the shelf (Ind. 2013-4), while the other remained within the pelagic area (Ind. 2013-12).

For females, high foraging activity was mostly localized south of the 4000 m isobaths, within the continental slope/shelf and in pelagic area (Fig. 4A). Conversely, male foraging activity was concentrated principally over the Antarctic shelf and continental slope with hotspots in the region of Cape Darnley within the Amery Ice shelf and in the region close to 110–115°E within the shelf and shelf break (Fig. 4C). One region around 30°E within the shelf break represented a hotspot used by both males and females (Fig. 4A and C). Foraging areas tended to be located in area of high sea ice concentration along the trip of both males and females (Fig. 4).

3.3. Linking behaviour to oceanographic conditions

From the 35 total individuals, only 28 seals were used; 11 females and 17 males. One individual with short tracks and 6 seals with incomplete hydrological data were removed prior to analysis.

3.3.1. Qualitative approach: Description of seals movements within the habitat

3.3.1.1. Topographic features. The twenty-eight seals spent 36.4%, 16.6% and 50% of their time within the shelf, the continental slope and the pelagic area respectively (Fig. 5A).

Over the shelf, the pelagic strategy represented 32% of observations (of which 9% were performed by females and 91% by males) and the demersal strategy 68% (of which 13% were performed by females and 87% by males). Over the continental slope, the pelagic strategy represented 83% of observations (with 48% and 52% for females and males respectively), while the demersal strategy represented 17% (with 18% and 82% for females and males respectively). Deep dives in canyons within the shelf and slope area (previously defined by criteria for demersal strategy; see Appendix B) represented 1.7% of total dives of which 21% female dives and 79% male dives.

3.3.1.2. Movements within sea ice. The seals spent 38% of their time within sea ice concentration of class 1, 28% within class 2 and 34% within class 3 (Fig. 5B).

Sex-specific differences were observed in the movements of animals in relation to the seasonality of the sea ice (Fig. 2). Most females in 2004, 2008, 2012 and 2013 remained in high sea ice concentration inside pack ice, but tended to track the sea ice edge (Fig. 2). In contrast, one female in 2013 travelled to the West along the Antarctic continent despite increased sea ice extent before going back to Kerguelen (Fig. 2). Among males, two different behaviours were exhibited by different individuals throughout the ice covered season: one group of males in 2004, 2012 and 2013 remained within the peri-Antarctic shelf independently of the sea ice extent (Fig. 2); while another group (1 individual each time in 2004, 2008, 2009, 2012, and 4 individuals in 2013) exhibited patterns similar to females (Fig. 2). The latter group arrived on the Antarctic shelf earlier in the season than the other individuals.

Fig. 6 shows the monthly animals' track versus the monthly sea ice extent variability for the specific year 2013. Females (red tracks on Fig. 6) exploited mostly areas where sea ice concentration was highly variable (except the female travelling to the West) a pattern not observed for males (black tracks on Fig. 6).

3.3.1.3. Hydrographic properties. A total of 9 water masses were used by the seals during their bottom phase of dives (Figs. 5C and 7). Females only rarely visited shelf-associated water masses (*i.e.* HSSW and ISW). Males and females clearly targeted different water masses for hunting (Fig. 8). While both males and females tended to use hunting hotspots in AASW and MCDW, they used very distinct temperature/salinity classes within these water masses. The largest hotpot for females was in the warmer part of MCDW and AASW, while males favoured mainly the coldest part of AASW. Males also used hotspots of foraging activity in the warmer part of AASW, but to a lesser extent than those in the colder AASW. These distinct TS classes were characteristic of distinct geographic regions. The coldest part of AASW lies over the shelf and over the continental slope (Bindoff et al., 2000), while the warmer AASW is observed further north, in the open ocean, and shallower than the warmer part of MCDW (Bindoff et al., 2000).

3.3.2. Quantitative approach: Environmental conditions and foraging behaviour

For males, the most parsimonious model describing PEE/day included all variables except bathymetry (Table 4): PEE/day was higher for high slope indices, in class 2 of sea ice concentration and in AASW relative to other water masses. However, male PEE/day was significantly lower within the MSW relative to other water masses and with advance of the year. Both AASW and high slope indices correspond to the continental slope area where the Antarctic slope current is observed. High slope indices could be found within canyons as well. For females, the most parsimonious model included all variables (Table 4). Female foraging activity (predicted PEE/day) was higher for shallower seabed depths, high slope indices, class 3 of sea ice concentration, and within the MCDW. Note that while foraging activity was higher for shallower seabed depths, these shallower depths refer to relatively deep water, north of the continental shelf (females stay mostly north of the continental shelf; see Fig. 4A). Female foraging behaviour (predicted PEE/day) was significantly lower within the AAIW relative to other water masses and with advance of the year.

4. Discussion

4.1. From dives to prey: new approach, limits and perspectives

A key objective of this study was to assess if PEE in SES could be predicted from low-resolution dive parameters at the scale of one day. PEE represent a proxy of foraging activity (Viviant et al., 2009; Gallon et al., 2013) and provide indirect information on the distribution and relative abundance of prey (Naito et al., 2013; Guinet et al., 2014). The objective was not to predict the exact number of PEE/day but to obtain a relative index of foraging activity for a large number of individuals foraging in Antarctic waters.

4.1.1. Predictive ability, population inference and limitations

Our method has a number of limitations with respect to sample size, foraging area, life stage and sex ratio. Despite these factors, patterns of dive behaviour and path trajectory linked to foraging activity were nonetheless identified. Moreover, predictive models provided important information on foraging activity for low-resolution datasets for which no information on foraging activity was otherwise available. Indeed, most studies on low-resolution datasets of SES used proxies of feeding activity associated with specific vertical movements (*e.g.* Bailleul et al., 2007a), horizontal movements (*e.g.* Dragon et al., 2012b) or both (Dragon et al., 2012a; Bestley et al., 2012, 2015) without direct evidence with a foraging metric. Studies using body condition (*e.g.* Biuw et al., 2007) as a proxy of feeding success are complicated by the temporal lag between feeding areas and detectable responses in body condition (Thums et al., 2008; Dragon et al., 2012a).

The limited number of individuals in the training dataset for the demersal model (*i.e.* 8 out of 37 individuals) reduces confidence in predictions at the population level. However, in view of the behavioural differences observed between the demersal and pelagic dives, a specific model for each foraging strategy was probably still better than considering a global model.

No post-moulting animals feeding close to the Antarctic continent have been equipped with accelerometers due to technical (high memory need of accelerometer data) and field logistics (recapture of the animal) limitations. Thus, both pelagic and demersal predictive models were built on individuals using the frontal zones around the Kerguelen Islands, but subsequently applied to individuals in the Antarctic region. However the animals in the training dataset encounter a sufficient range of environmental

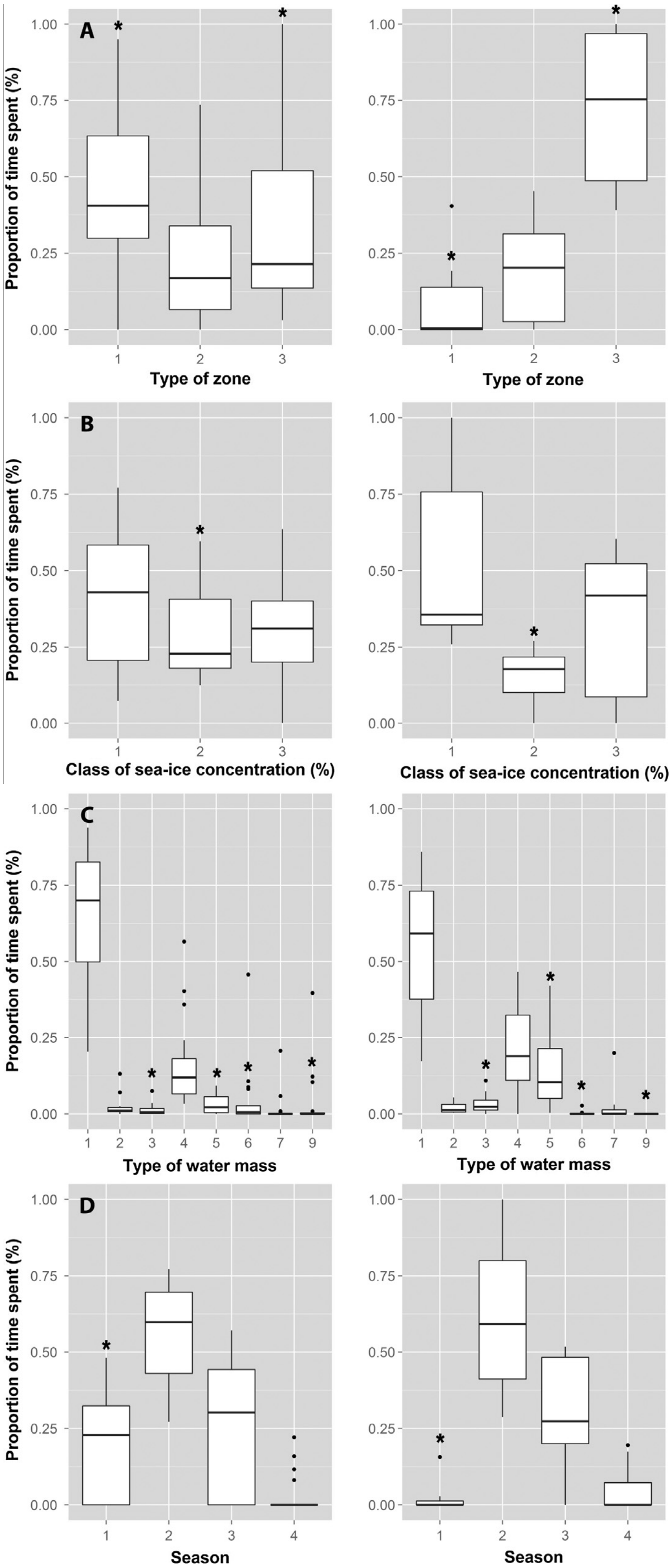

Fig. 5. Boxplots representing the proportion of time spent in each type of environment for the 28 post-moulting animals equipped with CTD-SRDLs from 2004 to 2013 and including tracks from 55°S to the Antarctic continent. Statistics are presented separately for males (left panels) and females (right panels). Part A indicates the time spent in different type of zone, (1) the Antarctic shelf, (2) the continental slope, (3) the pelagic area. Part B indicates the time spent in different type of sea ice concentration, (1) from 0% to 5%, (2) from 5% to 80%, (3) from 80% to 100%. Part C indicates the time spent in different water masses (1) AASW, (2) AAIW, (3) CDW, (4) MCDW, (5) HSMCDW, (6) MSW, (7) AABW, (8) HSSW, (9) ISW. Part D indicates the time spent in different seasons (1) Summer, (2) Autumn, (3) Winter, (4) Spring. Significant differences of time spent in each type of environment between males and females are indicated by a star.

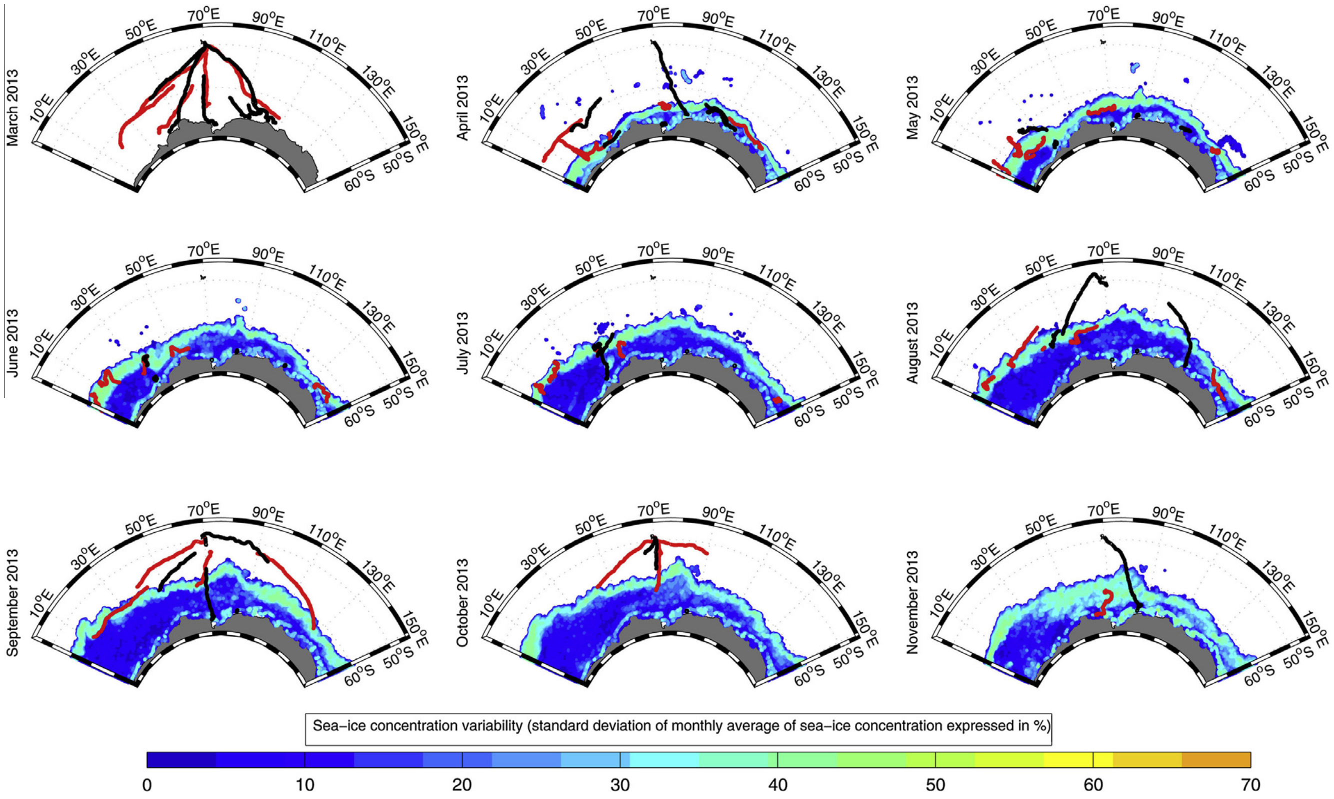

Fig. 6. Tracks per month of the 13 individuals equipped with CTD-SRDLs in 2013 (5 females, 8 males) linked with sea ice variability. The variability is expressed as the standard deviation of the monthly average of sea ice concentration (expressed in %) from AMSR-2 satellite data. Tracks in red correspond to females, while the black ones are for males. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

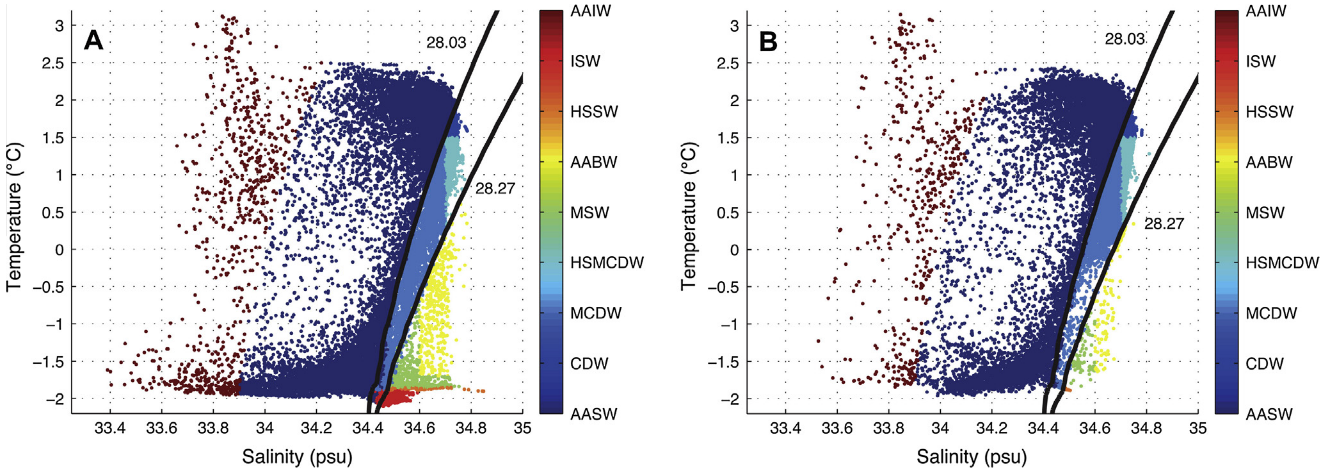

Fig. 7. Temperature salinity diagrams representing all water masses sampled at the bottom phase of dives of the 17 males (A) and 11 females (B) equipped with CTD-SRDLs from 2004 to 2013. Acronyms and definitions of water mass classes can be found in Table 1.

conditions to capture a range of behaviours so we assumed that any bias associated with differences in foraging areas is limited.

Furthermore, the models were developed on post-breeding animals and then applied to post-moulting animals, which have different energy requirements and prey abundance. Shallower and longer dives were observed for post-moulting seals compared to post-breeding for both strategies (*i.e.* demersal and pelagic), leading to a potential overestimation of foraging activity when applying regression coefficients from the training dataset on the study dataset (cf. Table 3).

Males were not represented in the training dataset. Bailleul et al. (2010a) described marked differences in behaviour according to sex and age, most likely due to different mass and previous investigations highlighted a positive correlation between body size and maximum dive durations (Hindell et al., 2000; Irvine et al., 2000; McIntyre et al., 2010a) while the physical size of animals did not govern the depths utilized (McIntyre et al., 2010a). Differences in body condition between males and females could also be expected with implications on dive behaviour: for example, juvenile males allocate relatively more energy to lean tissue than

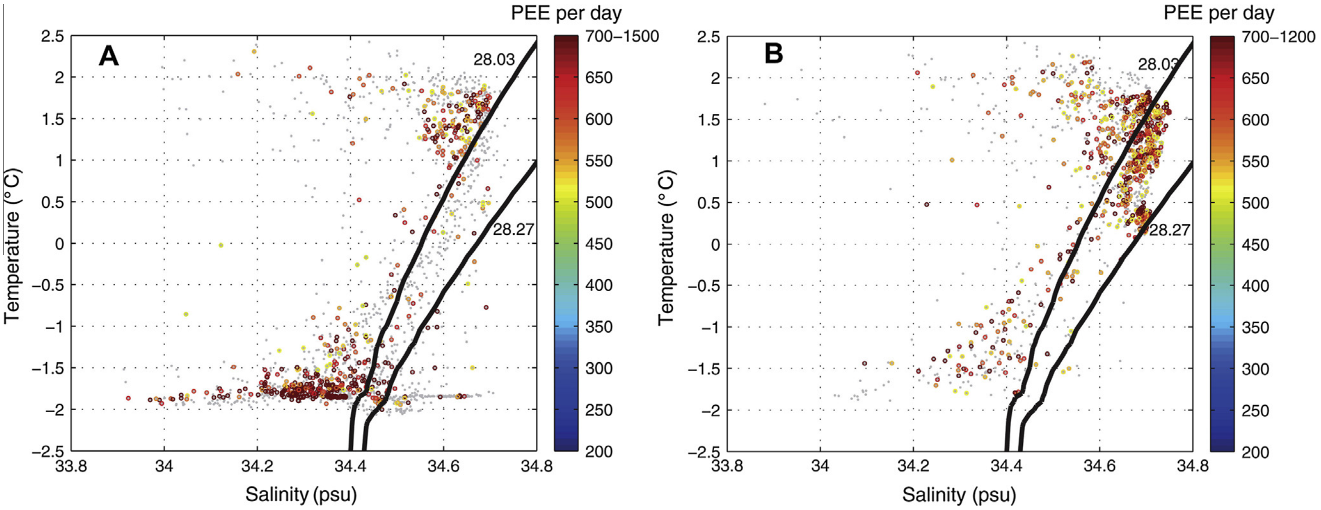

Fig. 8. Temperature salinity diagrams representing hydrologic properties sampled at the bottom phase of dives averaged at the scale of the day of the 17 males (A) and 11 females (B) equipped with CTD-SRDLs from 2004 to 2013. Colour scale represents predicted prey encounter events from behavioural models. PEE per day below 500 is shown in grey as an attempt to highlight foraging hotspots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Summary of regression coefficients from the two most parsimonious models (GLMMs) relating predicted PEE/day to environmental parameters for the 28 post-moulting SES equipped with CTD-SRDLs from 2004 to 2013. Coefficients are presented ± SE with their *p*-value associated. Significant parameters are denoted by bold characters. For factor variables (*i.e.* class of sea ice concentration and type of water mass) coefficients are given relative to the class 1 of sea ice concentrations and AASW for water masses.

Negative binomial distribution	Male Model (n = 1774, 17 males)		Female Model (n = 1419, 11females)	
Explanatory variables	Coefficient ± SE	*p*-value	Coefficient ± SE	*p*-value
Intercept	**5.85 ± 0.08**	**$<2.0 \cdot 10^{-16}$*****	**6 ± 0.04**	**$<2.0 \cdot 10^{-16}$*****
Topographic parameters				
Bathymetry	/	/	**−0.18 ± 0.02**	**$<2.0 \cdot 10^{-16}$*****
Slope	**0.07 ± 0.01**	**$1.4 \cdot 10^{-8}$*****	**0.07 ± 0.01**	**$3.2 \cdot 10^{-12}$*****
Sea ice (relative to Class 1)				
Class 2 of sea ice concentration	**0.19 ± 0.03**	**$1.2 \cdot 10^{-9}$*****	0.02 ± 0.03	0.4
Class 3 of sea ice concentration	**0.11 ± 0.03**	**0.0008*****	**0.14 ± 0.03**	**$3.6 \cdot 10^{-8}$*****
Water masses (relative to AASW)				
CDW	−0.14 ± 0.22	0.54	0.08 ± 0.05	0.1
MCDW	−0.02 ± 0.03	0.54	**0.05 ± 0.02**	**0.038***
HSMCDW	−0.07 ± 0.07	0.29	−0.01 ± 0.03	0.62
MSW	**−0.25 ± 0.05**	**$6.4 \cdot 10^{-6}$*****	0.20 ± 0.15	0.16
AABW	−0.03 ± 0.1	0.78	0.03 ± 0.06	0.56
HSSW	−0.13 ± 0.1	0.16	0.18 ± 0.32	0.59
ISW	−0.08 ± 0.06	0.17	/	/
AAIW	−0.14 ± 0.10	0.16	**−0.31 ± 11**	**0.0035****
Time				
Day of the year	**−0.05 ± 0.02**	**0.0025****	**−0.06 ± 0.01**	**$6.1 \cdot 10^{-6}$*****

Signif. codes: 0 '***' 0.001 '**' 0.01 '*'.

juvenile females storing greater proportions as fat (Field et al., 2007a). The training dataset only composed by females did not allow us to test the gender difference in the relation between dive patterns and PEE. However, only two males in our study had a mass above 1000 kg suggesting most of males were sub-adult males with mass similar to females (Table A2). We then expected the same sign in the relation for males and females with differences in the strength of the relation depending of the sex.

4.1.2. Dive and trajectory parameters: predictors of foraging activity

The study shows that dive behaviour and path trajectory parameters can be used to predict PEE of SES. Only two variables (dive duration and ascent speed) were needed to predict foraging activity adequately for the demersal model, while four variables (ascent speed, horizontal speed, maximum diving depth and bottom phase duration) were required in the pelagic model.

The metrics for dive time differed between pelagic and demersal strategies, with an important positive contribution of dive duration in the demersal model while only bottom duration was retained for the pelagic model and made a poor contribution to the prediction. The number of PEE/day was lower in the demersal strategy compared to pelagic strategy, and on the shelf compared to the continental slope and pelagic area. Small, schooling prey (*e.g.* Myctophids; Koz, 1995; Cherel et al., 2008) were likely to be targeted by seals foraging in pelagic waters, while larger prey items such as Notothenids and Morids (Bradshaw et al., 2003; Banks et al., 2014) are probably more dominant prey items for seals foraging demersaly on the shelf. Foraging theory predicts that animals exploiting clumped or ephemeral prey such as schooling fish need to invest less time in foraging activities than animals feeding on solitary prey (Perry and Pianka, 1997; Thums et al., 2013; Bestley et al., 2015). In a demersal dive strategy, longer dives would increase the probability of encountering prey (Mori and Boyd, 2004; Austin et al., 2006). Between the pelagic and demersal strategies, the differences in selection and contribution of dive time variables and number of PEE/day suggest that optimal dive parameters of elephant seals vary significantly depending on habitat, prey size, quality and distribution (Costa, 1991; Thompson and Fedak, 2001). Regarding the negative relationship between foraging activity and dive depth for the pelagic strategy, we suggested that seals are likely to obtain a prey items sooner in a high-quality patch (*i.e.* high average rate of resources acquisition) than in a low-quality patch, thus reducing diving depth as reported by Bestley et al. (2015).

Finally, we observed that predators reduced their horizontal speed, increasing their search and encounter rate with prey as suggested by Fauchald and Tveraa (2003), Thums et al. (2011) and Dragon et al. (2012a) when engaged in a pelagic dive strategy and in areas of high prey density (based on high PEE). Vertical transit rate (ascent speed) was an important predictor of foraging activity for both pelagic and demersal model as previously observed for Antarctic fur seals and SES which adopt higher ascent and descent rates in high-quality patches (Thums et al., 2013; Viviant et al., 2014) probably to optimize the energy gained from prey relative to the energy expended during a dive, but also presumably to quickly relocate the favourable prey patch (Gallon et al., 2013).

4.2. Long migration within a remote and constrained environment: linking oceanographic conditions to foraging efforts

We identified the foraging behaviour of elephant seals in relation to oceanographic processes that might influence nutrient availability and resource abundance. We described different strategies adopted by males and females and linked our results with inference about the diet, life-history traits and predictability of foraging grounds.

4.2.1. Female patterns

The distribution of female foraging activity broadly matched the southern extent of the Southern Boundary Front, an important region of high primary production supporting a rich marine ecosystem (*e.g.* Tynan, 1998).

Sea ice played also an important role in terms of the seal distribution patterns. Females mostly exploited coastal regions west of 70°E where short duration of seasonal ice cover is observed in coastal and marginal ice regions west of 85°E (Massom et al., 2013). Further east (from 70°E to 145°E), females remained over deep waters between 4000 m and 2000 m isobaths again coinciding with the short duration of seasonal ice cover largely confined to the marginal ice zone for the eastern sector (Massom et al., 2013). Females from Kerguelen may overcome the constraints of sea ice by using areas where sea ice is highly variable or the outer part of the pack ice, enabling them to avoid the risk of getting trapped by sea ice (Bornemann et al., 2000; Bailleul et al., 2007a; Thums et al., 2011; Hindell et al., in press). A recent study demonstrated a negative influence of increased sea ice duration on female abundance in breeding colonies at Macquarie Island between 1988 and 2011 with a lag of three years, probably by preventing them from accessing profitable prey patch areas close to the continental shelf or within the pack ice (van den Hoff et al., 2014). Observed changes and variability of East Antarctic sea ice season duration from 1979/80 to 2009/10 highlights that in this region sea ice patterns are considerably more complex than the well-documented trends in the western Ross Sea sectors showing extensive increased ice season duration over the past three decades (Massom et al., 2013). It is then likely that areas of more variable sea ice conditions allow females to benefit from profitable prey patch areas within the pack ice in East Antarctica while minimizing the risk of getting trapped compared to the western Ross Sea.

A key finding of our study was that predicted foraging activity was higher within high sea ice concentration, which is consistent with the seasonal sea ice zone being one of the most dynamic and productive marine ecosystems on Earth (Brierley and Thomas, 2002; Clarke et al., 2008). During formation, sea ice incorporates particulate matter, so its algal biomass is considerably greater than in the underlying upper water column (Quetin and Ross, 2009) during autumn through early spring (reviewed by Massom and Stammerjohn, 2010), providing a readily accessible food source for pelagic herbivores such as krill (Meiners et al., 2012). Extended and high sea ice concentration is usually linked with elevated ice-algal productivity and a higher krill biomass (Loeb et al., 1997; Atkinson et al., 2004). Krill represents a keystone organism in the Antarctic food chain that could sustain higher predators including SES foraging within the pack ice (Nicol, 2006; Schofield et al., 2010; Walters et al., 2014).

The hydrographic properties of hotspots of foraging activity suggested that female SES feeding south of the 4000 m isobaths within the pack ice and over middle basins dived through the cold AASW to target discontinuities such as the transition between the AASW and the MCDW. The MCDW may represent important overwintering areas for mesopelagic fauna such as zooplankton, fish and squid (Schnack-Schiel, 2001; Lawson et al., 2004; Biuw et al., 2007). Females were also foraging in areas close to the Antarctic shelf and within the continental slope where intrusion of MCDW brings relatively warm and nutrient rich water onto the continental shelf stimulating primary and secondary production in the region (Prézelin et al., 2000). These results are clearly illustrated in Fig. 9B, where TS classes of Fig. 8 recorded by females SES were projected on a high resolution meridional oceanographic section (along 60°E; Meijers et al., 2010) similar to the study of Biuw et al. (2007). The figure shows an important area of foraging activity along the upper boundary of MCDW and close to the shelf as previously observed by Biuw et al. (2007) and Hindell et al. (in press). Interestingly, females also spent an important proportion of time within HSMCDW (the saltiest part of MCDW), which could be used to locate prey patches as it is known that seals may employ high salinity chemo-olfaction for prey location (Sticken and Dehnhardt, 2000). Foraging activity was significantly lower within AAIW confirming that the area encompassed between the PF and the SACCF is less profitable to SES (Biuw et al., 2007; Guinet et al., 2014).

The ocean properties of areas of high foraging activity can be explained by the presence of potential prey of female SES. For example, the Antarctic silverfish (*Pleuragramma antarcticum*), which is the most abundant pelagic fish in Antarctic shelf water (La Mesa et al., 2010), generally spawns at the sea ice edge (Koubbi et al., 2009) and juveniles are often associated with intrusion of MCDW onto the Antarctic shelf/slope (La Mesa et al., 2010). Similarly, mesopelagic fish such as the Antarctic lanternfish (*Electrona antarctica*), which usually inhabit deep waters and are found under pack ice feeding on zooplankton (Kaufmann et al., 1995), may also be consumed by SES. A recent study coupling tracking data with fatty acid signature analysis (FASA) on female SES from Macquarie Island, reported that females foraging in the pack ice habitat were likely to have a multi-species diet, *i.e.* an evenly mixed diet of fish and squid (Banks et al., 2014). Females may therefore consume various types of prey associated with the sharp discontinuity and intrusion on the shelf of the MCDW and inhabiting the pack ice.

Females foraging in the inter-frontal zone weaned smaller pups than females foraging in Antarctic waters (Authier et al., 2012b). Thus, Antarctic trips associated with ocean features with predictable enriched resources (such as the MCDW and pack ice

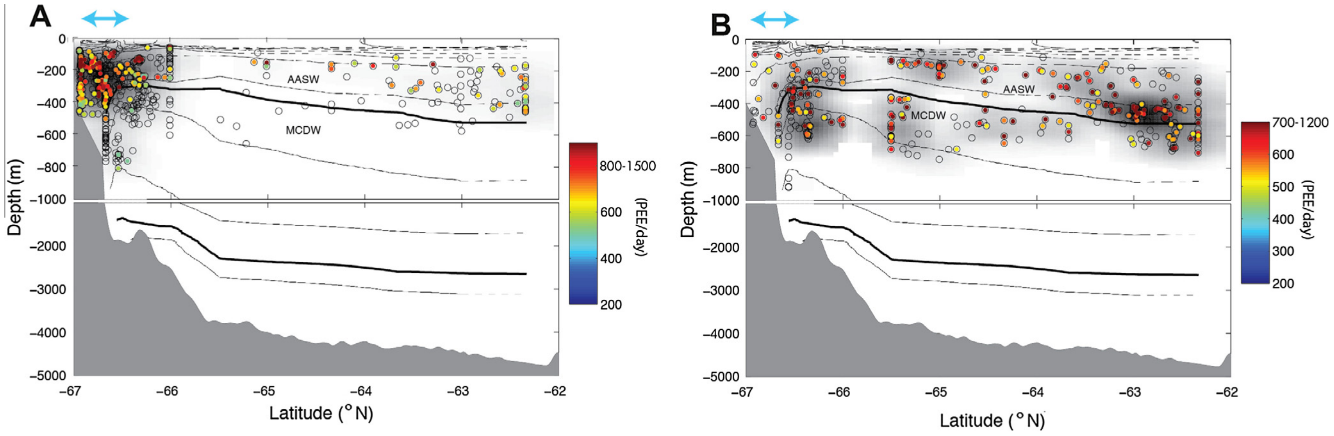

Fig. 9. Projection of the foraging activity in temperature–salinity classes (shown in Fig. 8) onto a high-resolution meridional oceanographic section (along 60°E; Meijers et al., 2010). Colour scale represents predicted prey encounter events from the behavioural models for males (A) and females (B). PEE per day below 500 are not colour-coded as an attempt to highlight foraging hotspots. The grey shading in the background corresponds to the sum of PEE per day per grid points: darker areas are associated with a concentration of high foraging events. Bold lines represent the 28.03 kg m^{-3} (upper) and the 28.27 kg m^{-3} (lower) neutral surfaces, while dashed lines represent intermediate neutral surfaces every 0.1 kg m^{-3}. Blue arrows represent the horizontal extent of the Antarctic Slope Front defined by the maximum LADCP zonal velocities observed along the meridional section (from Meijers et al., 2010). Bottom bathymetry along the section is shown in grey. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

habitat), adopted by 25% of females from Kerguelen (Bailleul et al., 2010a), may explain the apparent benefit in terms of pup survival observed in the study of Authier et al. (2012b).

4.2.2. Male patterns

Our study revealed that sub-adult males mainly travelled and foraged within the south-eastern part of the study area: east of ~70°E and in the Antarctic shelf and continental slope regions.

One prominent feature of the male foraging strategy was the number of pelagic dives performed on the Antarctic shelf. Males spent 51% of their time on the shelf where pelagic dives represented 33% of all dives, which resulted in a higher rate of foraging when feeding pelagically. This result contrasts with previous studies assuming that seals within the peri-Antarctic shelf region mostly foraged benthically (Bailleul et al., 2007a, 2007b; Biuw et al., 2007, 2010; Costa et al., 2010; James et al., 2012; McIntyre et al., 2014). Individuals using a pelagic strategy likely target pelagic fish prey (*e.g. P. antarcticum*) or squid, while those using a demersal strategy likely take deep species such as Antarctic toothfish (*Dissostichus mawsoni*). However, adult toothfish also use the water column and are potentially more common at depths shallower than 200 m than previously thought (Fuiman et al., 2002). The pelagic dive strategy displayed by males over the shelf/slope region could be a response to a large biomass of prey in the water column, and is an important supplement to the demersal dives (*e.g.* Bailleul et al., 2007a, 2007b). The lack of influence of seafloor depth on the foraging behaviour of males and the importance of pelagic dives within the ASF can possibly be attributed to sub-adult males exploiting the seafloor itself less often, compared to adult males (*e.g.* McIntyre et al., 2014). Interestingly, the deep dives within canyons were mainly performed by males with above average weight (*i.e.* 664 ± 177 kg; average male weight 553 ± 256 kg), perhaps the only ones physiologically capable of foraging deeper (McIntyre et al., 2010b) and catching bigger prey items such as large squid (Field et al., 2007b) thereby increasing the range of prey sizes and their foraging niche. Another explanation may lie in greater energy requirements of large males forcing them to hunt for larger and/or more energetically rewarding prey in these deep canyons. Further, a few males continuously dived for short periods to depths shallower than 250 m with high PEE (above 1000) on the shelf mostly during winter season when sea ice cover is important. Male SES from King George Island displayed similar behaviour with shallower dives when in high sea ice concentrations (McIntyre et al., 2014). This new observation could reflect SES foraging on prey close to the surface in response to reduced surface light intensity during winter, such as the Antarctic silverfish (*Pleuragramma antarcticum*) (Fuiman et al., 2002) or even krill associated with sea ice habitat (Walters et al., 2014).

Foraging activity was higher within the continental slope in AASW relative to other regions and water masses. The influence of the AASW is from the coldest class (<−1.6 °C; Bindoff et al., 2000; Fig. 8A) and TS characteristics show typical waters of the Antarctic Slope Front and shelf waters. High foraging activity was clearly associated with TS classes corresponding on the meridional oceanographic section to a deepening of isopycnals and high horizontal velocity (Fig. 9A). This strongly suggests that the TS classes in which males actively foraged were tightly associated with Antarctic Slope Current jet (ASC) and Antarctic Slope Front (ASF). The ASF corresponds to the strong subsurface horizontal temperature and salinity gradient separating the lighter AASW from the denser MCDW (Meijers et al., 2010). The significance of the continental slope region to biological productivity in the Antarctic is evident from the potential of upwelling deep water to elevate the early larval stages of krill (*Euphausia superba*) onto the continental shelf (Marr, 1962). Jacobs (1991) observed a regionally higher biological productivity along the ASF, which plays an important role in the distribution of sea ice, chlorophyll, krill and cetaceans (Nicol et al., 2000a, 2000b). This cold, dynamic and topographically constrained structure, might constitute a deep ocean source region for nutrients (Jacobs, 1991), resulting in higher productivity and enhanced and concentrated resources, which could be detectable in terms of prey availability for SES. Meijers et al. (2010) found the ASF extends from the surface to the bottom over the maximum gradient in the shelf break (*i.e.* depths ~500 dbar to 1000 dbar) that could be reached by SES. Two important hotspots of foraging activity were identified for males associated with the ASF. One was situated in the region of Cape Darnley known for the particular "V" shape of the Antarctic Slope Front at 70°E (Meijers et al., 2010). The second is situated in the region close to 110–115°E within the shelf and shelf break, and matches with observations from Bindoff et al. (2000) who described a very pronounced horizontal temperature, salinity and density gradient of the ASF at 112°E. Connection between important physical oceanographic features and SES foraging behaviour has been also reported by McIntyre et al. (2012) for males from Marion Island with increased foraging efforts along the South West Indian Ridge due to higher productivity in mid-water depth layers associated with upwelling (Sokolov and Rintoul, 2007). Similarly, males from King George Island travelled to the region of the Filchner Trough outflow in the Weddell Sea that supports intensive mixing (Tosh et al., 2009).

The pattern of males remaining on the shelf irrespective of sea ice extent is consistent with results of Bailleul et al. (2007a) and Hindell et al. (in press). However, one group of males did move north with the ice to pelagic foraging grounds similar to the females. This group was mostly composed of smaller seals, probably corresponding to juvenile animals and of two heavier sub-adult animals. Younger and less experienced seals may not take the risk of being trapped by sea ice probably due to mid-year haulouts for these age classes, which agrees with the observed ontogenetic change in foraging ground selection from oceanic to neritic in males (Bailleul et al., 2010a; Chaigne et al., 2012). As the seals age, they perform longer trips to sea, travelling farther and spending more time closer to Antarctica (Field et al., 2004). In contrast, the two larger males may have moved north to avoid getting trapped by sea ice, since they are approaching or reached sexual maturity and therefore may prioritize returning to breeding colonies (as suggested by Biuw et al., 2010).

Different individuals tended to forage in the same zones (both within and between years) suggesting that the distribution of many prey species associated with some meso-scale features may be predictable to some degree (Field et al., 2001; Bradshaw et al., 2004; Weimerskirch, 2007). While opportunistic foraging was observed during transit, most males maintained their trajectory towards the Antarctic continent supporting the hypothesis that elephant seals possess a “memory map” of expected foraging gains in different regions, based on experience from previous years (Thums et al., 2011). Finally, Authier et al. (2012a) revealed how a stable foraging strategy developed early in life positively covaried with longevity in male SES. This could explain why similar movements and foraging patterns are observed for males in our study over multiple years.

5. Conclusion

The present study shows that low-resolution dive data can be used to predict the foraging behaviour of apex predators, allowing older datasets to be re-visited.

Over years, females showed a wide distribution with area of high foraging activity mainly south of the 4000 m isobaths, within the pack ice and over mid-depth basins. They targeted the upper boundary of MCDW which may represent important overwintering areas for mesopelagic fauna and avoided being trapped by sea ice by remaining in areas of high sea ice variability. Males predominately travelled to the south-eastern part of the East Antarctica region where they were found to be associated, at a large scale, with the ASF known to play an important role in the concentration of potential prey species of SES. Unexpectedly, hotspots of high foraging activity were associated with pelagic dives within the ASF and not to demersal behaviour on the shelf probably due to their diving capacities associated with their age. High foraging activity was associated with intermediate sea ice concentration that could be explained by an early arrival in the season on the Antarctic region, restricted trajectories to the Eastern part where sea ice extent is lower or a potential use of coastal polynyas.

Sea ice is an ecological double-edged sword: it can impede access to marine food resources while enhancing biological productivity. However, the precise contribution of sea ice to utilization of the peri-Antarctic region in winter by SES remains unknown. Further work is needed to identify the type of sea ice used by seals (compact or diffuse sea ice edge, flaw leads, fast ice, polynyas) and how they rely on these features in terms of cost and benefit. Optimal sea ice zones in terms of SES foraging activity probably constitutes an important information source regarding the under sea ice physical and biological habitat, a current “blind spot” that we can investigate using instrumented vertebrates. The complex responses of organisms to sea ice requires to investigate the complete linkage between SES and sea ice and how apex predators and their related resources could be influenced by changes in sea ice in the East Antarctic region.

Acknowledgements

This study is part of a French Polar Institute (Institut Paul Emile Victor, IPEV) research project IPEV # 109, PI H. Weimerskirch, and of an Australian collaborative research structure “The Integrated Marine Observing System” (IMOS). This work was funded by a CNES-TOSCA project (“Elephants de mer océanographes”) and IMOS, supported by the Australian Government through the National Collaborative Research Infrastructure Strategy and the Super Science Initiative. Special thanks go to J.O. Irisson, A.C. Dragon, M. Lacarra, J. Jouma’a, J.C. McKnight and M.A. Lea for very useful comments. Finally we would like to thank N. El Skaby and all colleagues, volunteers involved in the research on southern elephant seals in Kerguelen. All animals in this study were treated in accordance with the IPEV ethical and Polar Environment Committees guidelines. We are extremely grateful to the 4 anonymous referees for their constructive suggestions and the detailed comments provided.

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.pocean.2015.05.023.

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