Deep-Sea Research II 113 (2015) 145–153

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Delineation of the southern elephant seal's main foraging environments defined by temperature and light conditions

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ARTICLE INFO

Available online 15 November 2014

Keywords:
Predator–prey interaction
Habitats
Prey capture attempts
Myctophidae
Elephants seals

ABSTRACT

Changes in marine environments, induced by the global warming, are likely to influence the prey field distribution and consequently the foraging behaviour and the distribution of top marine predators. Thanks to bio-logging, the simultaneous measurements of fine-scale foraging behaviors and oceanographic parameters by predators allow characterizing their foraging environments and provide insights into their prey distribution. In this context, we propose to delimit and to characterize the foraging environments of a marine predator, the Southern Elephant Seal (SES). To do so, the relationship between oceanographic factors and prey encounter events (PEE) was investigated in 12 females SES from Kerguelen Island simultaneously equipped with accelerometers and with a range of physical sensors (temperature, light and depth). PEEs were assessed from the accelerometer data at high spatio-temporal precision while the physical sensors allowed the continuous monitoring of environmental conditions encountered by the SES when diving. First, visited and foraging environments were distinguished according to the oceanographic conditions encountered in the absence and in presence of PEE. Then, a hierarchical classification of the physical parameters recorded during PEEs led to the distinction of five different foraging environments. These foraging environments were structured according to the main frontal systems of the SO. One was located north to the subantarctic front (SAF) and characterized by high temperature and depth, and low light levels. Another, characterized by intermediate levels of temperature, light and depth, was located between the SAF and the polar front (PF). And finally, the last three environments were all found south to the PF and, characterized by low temperature but highly variable depth and light levels. The large physical and/or spatial differences found between these environments suggest that, depending on the location, different prey communities are targeted by SES over a broad range of water temperature, light level and depth conditions. This result highlights the versatility of this marine predator. In addition, in most cases, PEEs were found deeper during the day than during the night, which is indicative of mesopelagic prey performing nycthemeral migration, a behaviour consistent with myctophids species thought to represent the bulk of Kerguelen SES female diets.

1. Introduction

Wildlife biologists are faced with the difficult task of properly establishing where and how species use their habitats. This is particularly difficult to achieve in marine environments which remain mostly cryptic and inaccessible for direct observation. However, characterizing the environmental factors which define the ecological niche of animal species is important to understand how changes in environmental conditions might impact their distribution.

Key physical parameters such as light, temperature, salinity and dissolved oxygen are known to control the three dimensional distribution of most pelagic ectotherms (Puvanendran and Brown, 1998; Rueda, 2001; Karna, 2003; Laurel and Blood, 2011) that evolved within the layers of the pelagic zone like the photic epipelagic layer (from the surface down to around 200 m), the intermediate mesopelagic layer (from 200 m down to around 500 m) or the deep mesopelagic layer (from 500 m down to around 1000 m). Air-breathing endotherms are less constrained by these environmental factors and their at-sea distribution is mostly controlled by the occurrence of their prey and by their physiological abilities (MacArthur and Pianka, 1966). In the past few years, an increasing number of studies have investigated the ecology of top marine pinnipeds such as Antarctic fur seals, gray

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http://dx.doi.org/10.1016/j.dsr2.2014.10.029

seals or elephant seals (Guinet et al., 2001; Thompson and Fedak, 2001; Lea and Dubroca, 2003; Austin et al., 2006; Biuw, 2007; Dragon et al., 2010). Using different types of bio-loggers, these studies provide concomitant measurements of predator's behaviour at sea and of a broad range of oceanographic parameters in their direct surroundings. According to the optimal foraging theory (MacArthur and Pianka, 1966) predators should concentrate their foraging activity in patches exhibiting marginally greater prey density compared to surrounding ones (Charnov, 1976). Thus, foraging activities of predators can be used to provide insights into the distribution of their prey which, for the most part, remain poorly understood (Verity et al., 2002; Weimerskirch et al., 2003).

Female southern elephant seals (SES) are major predators of the Southern Ocean and spend approximately 10 months at sea. It is generally admitted that they forage on a broad number of prey types ranging from squid to fish (Rodhouse et al., 1992; Slip, 1995). However an increasing and converging body of evidence challenged the general view that the diet of SES females, at least from Kerguelen Island, is dominated by squid. First nitrogen stable isotopes analyses revealed that none of the squid species identified in elephant seal stomach contents (accumulated squid beaks) represented a dominant component of the diet of Kerguelen SES (Cherel et al., 2008) but that the abundant and high energy content mesopelagic myctophids were the most likely prey candidates. Recently the fatty acid profiles of Kerguelen SES females were found to be far more consistent with a myctophid-dominated diet than a squid-dominated one (P. Nichols unpublished data). Last but not least, a recent study combining head-mounted cameras and a bio-energetic approach from prey encounter events/attempts (PEE) gathered by head-mounted accelerometers reveals that northern elephant seal feed mainly on small mesopelagic prey (10–20 g) including lantern fish (F. Myctophidae) (Naito et al., 2013). Furthermore, myctophid otoliths (from *Electrona antarctica*, *E. carlsbergi* and *Gymnoscopelus nicholsi*) have been found in stomachs of seals from the Kerguelen sector (Slip, 1995) and elsewhere (Daneri and Carlini, 2002).

In general, an elephant seal diet dominated by myctophids make sense as they represent an abundant and high energy content (Lea et al., 2002a, 2002b) resource of the SO with an estimated total biomass of 70–200 million t (Tseitlin, 1982; Lubimova et al., 1987; Lancraft et al., 1989). This large myctophid stock is mainly dominated by 4 species: *Gymnoscopelus nicholsi*, *Electrona antarctica*, *Electrona calsbergi* and *Krefftichthys anderssoni* (Sabourenkov, 1991). All except *Krefftichthys anderssoni* have been reported in stomach contents of SES females. Furthermore SES are thought to rely, to a large extent, on their eye sight to locate their prey and they exhibit a maximum eye sensitivity to the wave length corresponding to bioluminesce produced by the most common myctophid species (Lythgoe and Dartnall, 1970). Elephant seals exhibit marked diurnal migration consistent with the nyctemeral migration undertaken by myctophids, according to ambient light levels, to avoid their predator and reach their copepod preys at night (Gjosaeter and Kawaguchi, 1980).

SES captures their prey over long foraging trips at depths up to 1500 m. Over the last few decades, our understanding of the at sea ecology of SES has dramatically progressed thanks to the development of biologging technologies (McConnell et al., 1992; Jonker and Bester, 1998; Bornemann et al., 2000; Biuw, 2007). The first generations of satellite relayed data loggers deployed on SES provided measurements of their horizontal movements and diving behaviors. The resulting dive and track datasets have been used to provide insights into the variations in their foraging behaviors (Bailleul et al., 2007; Biuw, 2007; Bailleul et al., 2008; Dragon et al., 2012). However, foraging activities of SES were estimated at meso-scales using these types of measurements (50–100 km). In addition, the prey density in the foraging areas of predators was estimated by indirect and qualitative indices.

The development of new devices such as esophagus temperature probes, Hall sensors and accelerometers can provide more direct indexes of PEE. Head mounted accelerometers have been successfully deployed to estimate occurrence of PEEs in elephant seals (Gallon et al., 2012; Naito et al., 2013; Guinet et al., 2014). This information combined with concomitant measurements of oceanographic factors such as temperature, light and pressure provide a unique opportunity to delimit and characterize the foraging environments of SES with a high degree of spatio-temporal accuracy. This fine scale identification and characterization of the foraging environments of SES provides valuable information on the foraging environment of SES and hence some insights into their prey distribution driven by oceanographic conditions.

The objective of this work was to use the foraging activity of SES to obtain insights into the distribution of their prey. We first differentiated locations where PEEs occurred within the water column. We then physically characterized the successful foraging environments of SES. Finally, we discussed our findings in light of our current understanding of the mesopelagic resources with a special emphasis on myctophids.

2. Materials and methods

2.1. Ethics statement

Our study on elephant seals was approved and authorized by the ethics committee of the French Polar Institute (Institut Paul Emile Victor – IPEV) in May 2008. This Institute does not provide any permit number or approval ID. However, animals were handled and cared for in accordance with the guidelines and recommendations of this committee (dirpol@ipev.fr).

2.2. Deployment of devices and data collected

In 2010 and 2011, 12 adult female SESs (more than 3 years old) were each equipped with a specific set of data loggers (Table 1). They were all equipped with either an Argos (CTD-SRDL Sea Mammal Research Unit – SMRU-, University of St Andrews Scotland) or a GPS (SPLASH10-Fast-Loc GPS, Wildlife Computers, Washington, USA) tag to provide location data and track the animals during their foraging trips. The devices were attached to the head of the seals. Each animal was also equipped with a MK10Acc (Wildlife Computers, Washington, USA) to measure movement acceleration and diving behaviors along with specific physical oceanography parameters. These devices were head or back-mounted (Table 1). The MK10Acc tags contained a depth sensor, a temperature sensor, a light sensor and a 3-axis acceleration sensor (i.e. accelerometer). The depth sensors provided highly accurate measurements of depth at 1 Hz with a 0.5 m resolution and a $\pm 1\%$ reading accuracy. The temperature sensors recorded at 1 Hz for temperatures ranging from -40 to $+60$ °C, with a 0.05 °C resolution and a ± 0.1 °C accuracy. The light sensors measured changes in light levels under very low light conditions at 1 Hz. It can detect raw light from 10 to 250 corresponding to 10^{-11}–10^{-1} W cm^{-2} in log

Table 1
Number of animals equipped and combination of tags for the 2010 and 2011 field sessions.

	CTD-SRDL		SPLASH Tag	
	MK10Acc head-mounted	MK10Acc back-mounted	MK10Acc head-mounted	MK10Acc back-mounted
2010	–	–	3 Individuals	–
2011	3 Individuals	–	4 Individuals	2 Individuals

transformed of light values. The acceleration sensors recorded tri-axial acceleration of animals at 16 Hz.

All the females were equipped during their reproductive period on land (October) on Kerguelen Island in the Indian Ocean (70°13E, 49°20S). Elephant seals were recaptured when coming back ashore to molt (January) to recover the data loggers. Animals were captured using a canvas head-bag and were anesthetized with a 1:1 combination of Tiletamine and Zolazepam (Zoletil 100) injected intravenously (~3 mL injected depending on the estimated weight and size of the animal) (McMahon et al., 2000; Field et al., 2002). Once anesthetized, each animal was weighted and equipped with data loggers or had previously deployed data loggers removed.

2.3. Data processing

We only analyzed data during the diving time of the animals. We defined dives as periods of time spent at depths greater than 15 m, above which animals were considered to be at the surface. Dives were then divided into three separate phases: descent and ascent phases were characterized by a vertical speed of movements greater than 0.4 m/s from or towards the surface. The bottom phase was defined as a period between the descent and the ascent phases with a vertical speed lower than 0.4 m/s. Once identified, each dive was associated with corresponding longitudes and latitudes. Because the Argos or GPS tags did not record true locations for each individual, we estimated likely latitudes and longitudes of dives in between true locations using a linear interpolation between the closest locations before and after these dives. Each dive was also associated with a day, night, dawn or dusk period depending on its location and its starting date based on solar angles calculated using the r-package 'maptools'. Daytime is the period when solar angles were found positive and night time occurs when solar angles were lower than -6° below the horizon. Dawn and dusk were defined as the periods when solar angles were between -6° and 0° below the horizon.

2.4. Prey capture attempts analyses

Acceleration data were processed with methods from Viviant et al. (2010) and Gallon et al. (2012) using custom-written Matlab code. The position of the accelerometer (head or back) was not found to alter the detection of prey capture attempts (unpublished work from SES simultaneously equipped with head and back mounted accelerometers). Consequently, the method used was the same irrespective of the position of the accelerometer on the animal. We identified individual prey capture attempts by first filtering the 3-axis acceleration time series with a high pass filter of 3 Hz. This step filtered out the part of the signal that was due to swimming movements, while leaving the peaks in acceleration (rapid head/body movements) associated with prey capture events/attempts (Fig. 1A).

Second, we calculated the standard deviation over a fixed 1-sec window for each axis to get an average acceleration over 1 s (Fig. 1B). We then calculated the standard deviation over a 5-s moving window on the 3 previously averaged signals to extract high levels of standard deviations, and thus events of high acceleration (Fig. 1C). The thresholds separating those extreme events from baseline acceleration was determined using the *kmeans* function (Matlab, tool box statistics) and were thus unique for each seal and for each axis independently. Only events of high head/body movement detected simultaneously on the 3 axes were considered as a PEE (Fig. 2). Continuous values at 1-Hz above the threshold were considered as unique PEE. Events separated by more than 1 s (i.e. more than 1 s below the threshold acceleration value) were considered different PEEs. For the rest of the

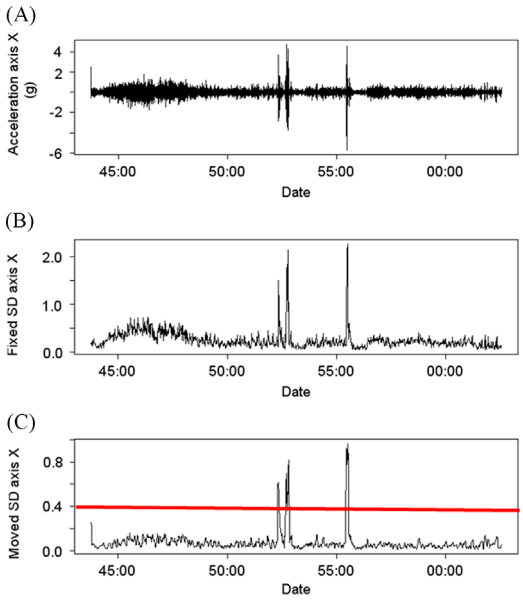

Fig. 1. Treatment applied on the time series of the 3 acceleration axes before detecting the prey capture events. (A) Raw acceleration data at 16 Hz of the *X* axis from one accelerometer. (B) The acceleration data at 1 Hz on graph B represent the standard deviation over fixed 1-s increment of the raw acceleration from graph A. (C) The acceleration data at 1 Hz on graph C represent the standard deviation over a moving 5-s window of the acceleration signal from graph B. Acceleration signals are in g (9.81 m s^{-2}).The red line represents the threshold for the *X* axis of this individual above which we detect significant accelerations.

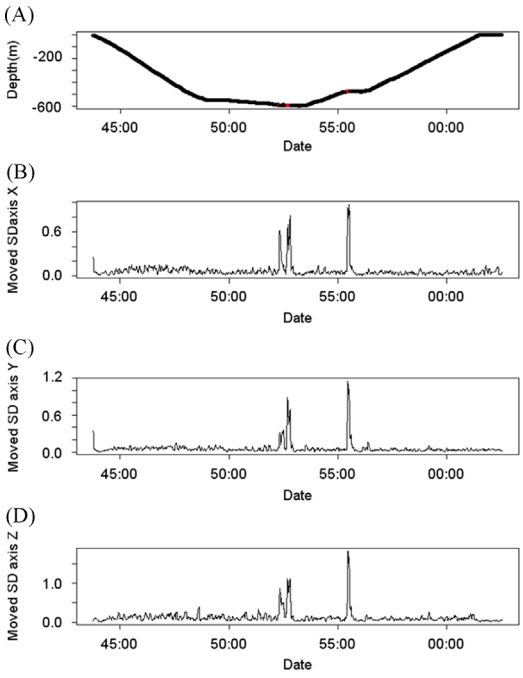

Fig. 2. Methodology to detect head movement events associated with prey capture attempts. (A) Depth profile for one dive. Red dots correspond to PEE detected for this dive. (B) Acceleration data at 1 Hz from a 5-s moving window standard deviation of the fixed 1-s standard deviation of the *X* axis corresponding to this dive. (C) Acceleration data at 1 Hz from a 5-s moving window standard deviation of the 1-s fixed standard deviation of the *Y* axis corresponding to this dive. (D) Acceleration data at 1 Hz from a 5-sec moving window standard deviation of the 1-s fixed standard deviation of the *Z* axis corresponding to this dive. The unit of the graphs B, C and D is *g* (9.81 m s^{-2}).

document, it is important to consider that PEEs do not obligatorily represent successful feeding events but should rather be taken as a relative proxy of prey encounter. Each of these detected PEEs was

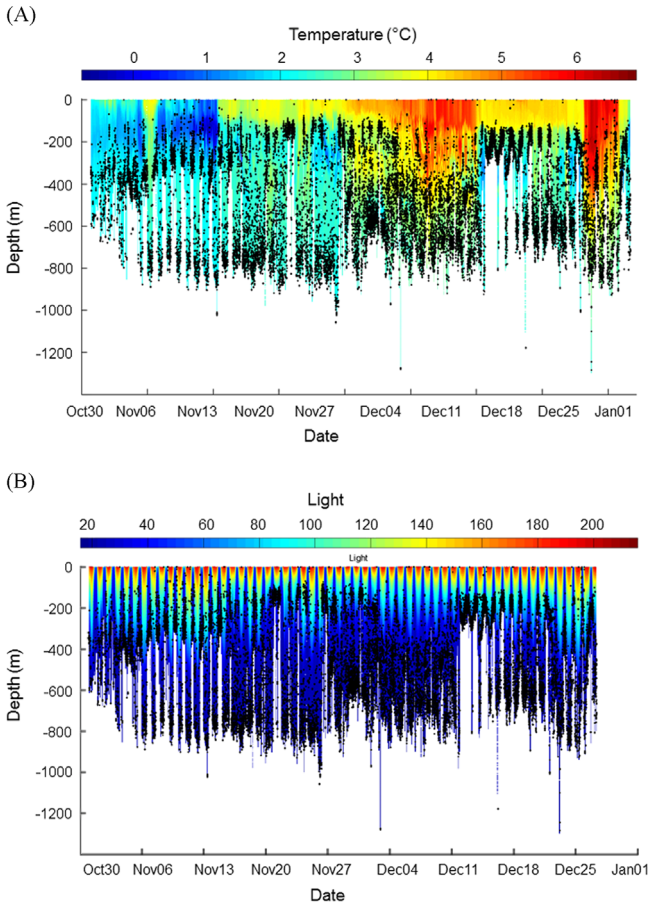

Fig. 3. Temperature and light profiles obtained for a two-month foraging trip of one SES. (A) Light profile in raw data. (B) Temperature profile in °C. Each black dot corresponds to a prey capture attempt obtained from the corresponding acceleration data.

finally associated with a corresponding time of day and dive phase (descent, bottom or ascent).

2.5. Delimitation and characterization of 3-dimensional SES foraging environments

Different types of SES foraging environments were delimited using specific combinations of light, temperature and depth parameters when PEEs occurred. To do so, all the PEEs were first associated with the corresponding values of light, temperature and depth that were recorded at the exact time that PEEs occurred (Fig. 3). To avoid any collinearity problem between these variables, we first conducted a principal component analysis. We then used a mixed classification method on the three resulting principal components (Lebart et al., 1997) based both on a k-means and on a hierarchical clustering analysis. The k-means step partitioned all observations into k clusters of the nearest mean. The number of cluster k was arbitrarily fixed to 20 in our study. The 20 clusters were then grouped and classified hierarchically in different classes according to the distances between them. These statistically different classes of environmental conditions corresponded to separate foraging environments of SES. Once identified and characterized by a set of specific light, depth and temperature levels, distinct foraging environments were spatially located on a map.

For all the environments combined, we first calculated the proportions of PEEs occurring at each day period and each dive phase. Then, using Wilcoxon tests, the mean depths at which PEEs occurred and the number of PEE per unit of time passed in each period were compared between time periods mentioned earlier (daytime, nighttime, dawn and dusk time).

For each foraging environment individually, we first calculated the proportions of PEEs occurring at each day period. Then, using Wilcoxon tests, the mean depths at which PEEs occurred were compared between time periods.

3. Results

3.1. Diving and foraging characteristics of the SES

The 12 female elephant seals spent on average 71 ± 23 days at sea traveling large distances. Six out of the 12 accelerometers failed after 10 ± 4 days, i.e. before the end of their trip. Nevertheless, the data recorded by these devices were retained in the analyses. During their foraging trips animals gained 75.4 ± 45.8 kg. When at sea, individuals dove to a maximum depth of 1032 ± 253 m ($N=12$). They recorded surrounding temperatures ranging from -0.21 ± 1.42 °C to 11.02 ± 3.82 °C ($N=12$) and raw light values from 15.92 ± 3.53 to 226.92 ± 9.47 ($N=12$).

A total of 25,593 dives, lasting on average 20.3 ± 4.7 min were analyzed. Eighty-seven percent of these dives (22,478) were associated with at least one PEE which means an average of 5.93 ± 6.01 (0–46) PEEs per dive. A total of 227,707 PEEs were detected over all 12 individuals. Nearly 14% of these PEEs were detected in the descent phase, 74% in the bottom phase and 12% in the ascent phase of the dives. More than 60% of the PEEs occurred during the day, 27% at night and 12% at dawn or dusk. The mean depth of PEEs occurring during the day was significantly greater than at night, dawn or dusk (p-value < 0.001). However the larger number of PEEs during the day corresponded to the longer daylight hours compared to night periods as the data were collected during the austral summer. When considering the PEE occurring per unit of time in each period, seals were found to be significantly more efficient during dawn or dusk compared with at night (0.59 ± 0.45 PEE/min during dawn and dusk and 0.47 ± 0.38 PEE/min at night; $p < 0.001$) or during the day (0.38 ± 0.34 PEE/min during the day; $p < 0.001$). They were also more efficient during the night compared with during the day ($p < 0.001$).

3.2. Delimitation and characterization of 3-dimensional SES foraging environments

The range of environmental conditions where the seals caught their prey was more limited than the range of conditions visited by seals (i.e. obtained using all the temperature, light and depth values measured by seals) (Fig. 4a and b). We identified five different foraging environments from the 227,707 PEEs using the mixed classification method. The 5 foraging environments are coded in different colors (Fig. 5) and their characteristics are synthesized in Table 2. The yellow-, orange- and red-coded foraging environments are characterized by cold temperatures. However, the red-coded environment occurs at greater depth compared to the yellow and orange ones that occured at shallow depths. The yellow- and orange-coded foraging environments seem to differ from one another mainly based on their light levels, i.e. low and high light levels associated with the orange-coded and yellow-coded environments respectively. The green-coded environment is characterized by great depths and warm temperatures, and the blue-coded foraging environment by intermediate depths and temperatures.

The yellow-coded and the red-coded foraging environments were defined by PEEs occurring mainly during the daytime (99.8% and 92.3% respectively) (Fig. 6). The other environments were

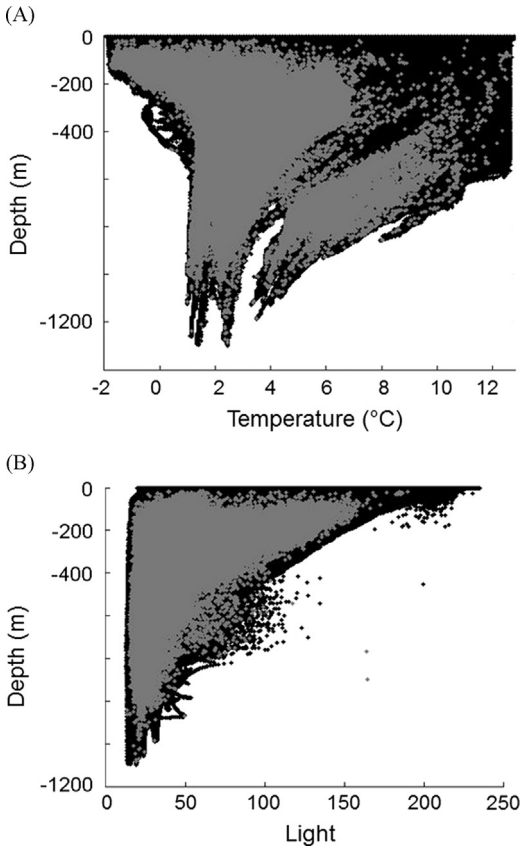

Fig. 4. Environments visited vs used during foraging by the twelve southern elephant seals. (A) Depths visited by elephant seals as a function of temperatures. (B) Depths visited by elephant seals as a function of light levels. Black dots represent the environment visited by elephant seals (i.e. measure by sensors) and gray dots (i.e. prey capture attempts) represent the environment used by elephant seals while foraging.

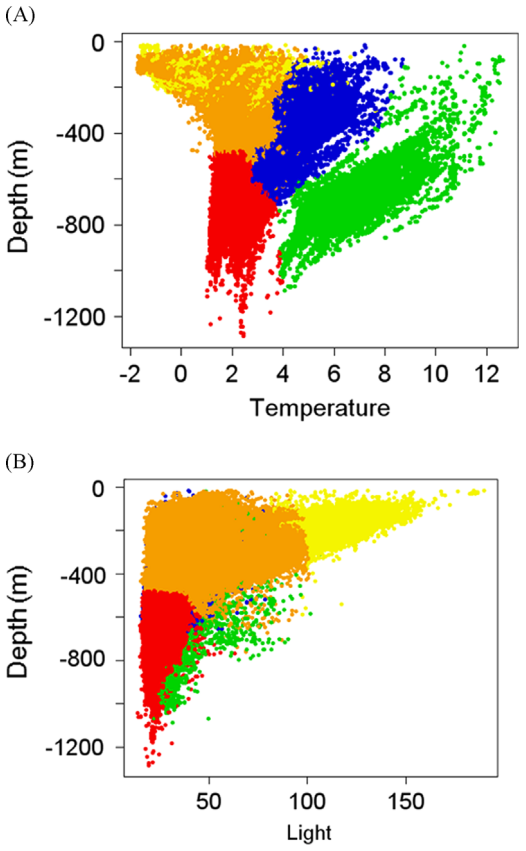

Fig. 5. Characterization of the five different foraging environments using temperature, depth and light measurements during prey capture attempts. (A) Depth at which prey capture attempts occurred as a function of temperature. (B) Depth at which prey capture attempts occurred as a function of light levels. Each dot corresponds to a prey capture attempt and each color corresponds to a specific foraging environment. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

defined by PEEs occurring both during day and night times ($47 \pm 8\%$ and $34 \pm 7\%$ respectively) (Fig. 6), with those occurring during daytime being significantly deeper than those occurring at night (p value < 0.001 for each test) (Fig. 7). The characteristics of the 3 foraging environments composed by PEEs occurring during day and night are synthesized by period in Table 3.

The green-coded environment was located north of the sub-Antarctic front (SAF) and was clearly spatially segregated from the others that were located south of the SAF (Fig. 8). The yellow-, orange- and red-coded environments showed a strong spatial mixing with each other but not as strikingly with the blue-coded environment (Fig. 8).

4. Discussion

Pelagic marine ecosystems are difficult to access. Therefore the combination of multiple data sources can be extremely useful to improve our understanding of how marine resources are structured in space and time. However, each method presents its own bias. For instance, some mesopelagic species could be more successful than others in avoiding sampling trawl nets. Bioacoustic sampling is generally biased toward fish with a swim bladder. Oceanographic vessels are also costly to operate and the Southern Ocean remains poorly understood due to its remoteness and harsh weather conditions. Predators themselves are also biased samplers of ocean resources. For example, the range of SES prey could exceed the range accessible to SES. Moreover predators can select prey according to their energy content and availability.

Nevertheless, studying the relationships involving top marine predators, recording information on the bio-physical environment (e.g., temperature, salinity, phytoplankton concentration) they forage in (Bailleul et al., 2007; Charrassin et al., 2008; Jaud et al., 2012) contribute to a better understanding of the relationship linking the different components of the marine ecosystem. We can expect very fruitful output by comparing and synthesizing the knowledge emerging from these different approaches. Indeed, despite inherent bias linked to the use of top marine predators, they can complement other approaches, especially because they sample areas and seasons that vessels rarely do. In that aspect SES are particularly interesting due to their extensive foraging grounds and deep diving capabilities which exceed the water column that is most commonly sampled using conventional approaches. Using recent advances in biologging technologies, this study provides insight into the environmental conditions in which SES forage, and thus on the largely ignored distribution of elephant seals prey.

First, it is worth noting that SES females encounter very different foraging environments illustrated by the broad range of temperature and light conditions associated with PEEs. Nevertheless their foraging environment is more restricted than the oceanographic conditions they encounter. Our analyses suggested that this foraging environment is likely to result from the combination of several distinct ones. For instance there is a clear division between two environments which are blue and green-coded (see Figs. 5 and 8). These two foraging environments were clearly physically segregated as they showed no overlap in terms of depths, temperatures or light levels. Moreover, these two foraging

Table 2
Characteristics of the five different foraging environments.

Foraging environments	Yellow-coded	Orange-coded	Blue-coded	Red-coded	Green-coded
Temperature (°C)	[−1.7–9.5] 1.5 ± 1.4	[−1.7–5.9] 1.9 ± 0.9	[3.4–8.9] 4.9 ± 0.8	[0.4–4.7] 2.4 ± 0.6	[4.3–12.6] 7.0 ± 1.6
Depth (m)	[16.5–587.6] 166.6 ± 55.1	[15.8–707.5] 274.8 ± 105.3	[17.1–635.7] 356.2 ± 106.6	[438.6–1285.0] 623.6 ± 110.7	[19.4–1071.0] 662.5 ± 131.8
Light (raw data)	[75.2–189.7] 110.2 ± 15.9	[15.2–92.2] 38.9 ± 12.4	[16.5–90.2] 30.0 ± 7.1	[13.5–68.7] 25.9 ± 5.6	[20.5–133.5] 30.5 ± 8.5

Numbers in square brackets are minimum and maximum values and below are the mean and standard deviation of each variable.

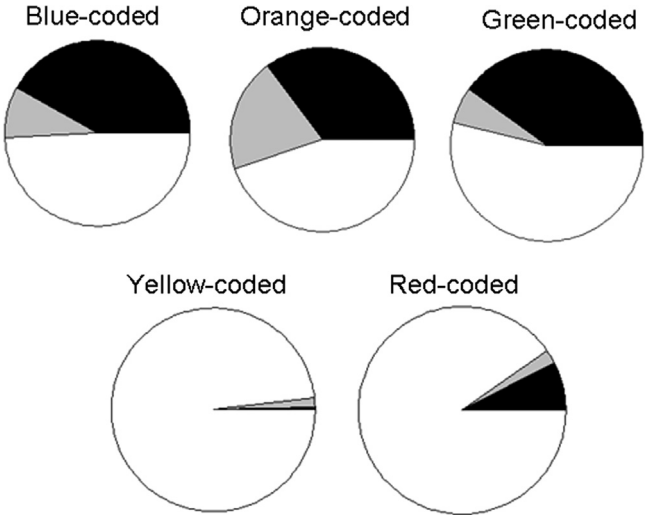

Fig. 6. Proportions of PEE occurring during the day, at night or at dawn/dusk for each type of foraging environments. The pie charts show the proportion of PEE occurring during the day, at night or at dawn/dusk for the blue-coded, orange-coded, green-coded, yellow-coded and red-coded foraging environments respectively. For each type of foraging environments, the daytime is represented in light color, the dawn and dusk period in intermediate color and the night period in dark color.

environments are also spatially segregated as they are separated by the sharp SAF–STF transition zone observed north of Kerguelen Islands: the green-coded environment was found north of the SAF–STF transition while the blue- one was south of the SAF. The SO is characterized by broad concentric bands of water masses around the Antarctic continent, with each zone maintaining its unique physical properties (e.g. Orsi et al., 1995; Belkin and Gordon, 1996). The concentric nature of the current and water masses of the SO ensures circumpolar continuity of its ecosystems and zooplankton and fish species (Baker, 1954). Therefore, our findings regarding the vertical distribution of the foraging depth of SES is likely to be extrapolated to other parts of the SO.

Assuming that myctophids represent the bulk of Kerguelen SES female diets, our results suggest that SES may target different communities of myctophids at different depths north of the SAF-STF zone. The SAF front represents a major bio-geographical boundary for marine organisms (Pakhomov and McQuaid, 1996; Pakhomov et al., 2000) that can be physically restricted to one side of the front (e.g. *Electrona antarctica* has an upper temperature tolerance of about 3 °C – Andriashev, 1965; Hulley, 1990). According to Hulley (1981) the myctophids community in this zone is likely to be dominated by *Electrona calsbergi*, *Electrona subaspera*, *Gymnoscopelus piabilis*, *Gymnoscopelus fraseri* and *Gymnoscopelus bolini*, which deepen with increasing temperature north of the SAF. Analyses of the number of PEEs provide more indirect evidence of a prey switch north and south of the SAF–STF zone. Indeed despite lower numbers of PEEs per day and higher foraging cost due to greater diving depth, SES females foraging north of the SAF–STF zone were found to improve their body condition as quickly as females foraging south of the SAF–STF zone and which perform nearly twice as much PEEs per day and at shallower depth. This result indicates that, north of the SAF–STF zone, SESs were foraging on larger and/or bigger energy content prey (Guinet et al., 2014).

The three other foraging environments (yellow-, orange- and red-coded) (see Fig. 5) were all encountered south of the SAF and did not exhibit any spatial patterns. Instead, they were randomly mixed along the tracks of several individuals. The segregation of these environments was only physical and mainly defined by different depth and light levels. Very few PEEs occurred at night in the yellow- and the red-coded environments (see Fig. 5). This result suggests that the community of prey targeted by SES might be different. Indeed, the yellow coded environment was representative of prey targeted during the day relatively close to the surface as emphasized by the relatively moderate depth and high light level while the red-coded environment was representative of prey targeted at great depth and very low light level during the day. Both yellow- and red-coded environments (see Fig. 5) exhibit a major vertical segregation. Certainly, the yellow-coded foraging environment could be housing an epipelagic prey assemblage. Interestingly, in Antarctic waters, *Electrona carlsbergi*, a schooling species, is commonly encountered close to the surface during the day (Fielding et al., 2012). Krill is also observed within the top 100 m of the water column (Fielding et al., 2012) and could be targeted by some seals feeding close to the surface during the day. Indeed krill is suspected to be preyed upon by some seals exhibiting an unusually low nitrogen signature and combined with carbon signatures representative of Antarctic waters (Y. Cherel pers. comm.).

During daylight hours the red, orange and yellow-coded foraging environments may represent the vertical stratification of the different prey communities targeted by SES ranging from deep mesopelagic, intermediate depth mesopelagic to epipelagic resources. The decision of the SES to target different layers is likely to depend on their local occurrence and profitability. While yellow and red-coded environments were almost exclusively identified during daylight hours (see Fig. 7), the orange-coded environment is detected during both day and night but at different depths (see Figs. 5 and 7). At night, we are currently unable to determine if the orange-coded environment represents or not a mixture between on one hand the day red-coded environment representative of a deep mesopelagic prey assemblage migrating closer to the surface at night and on the other hand the intermediate depth mesopelagic one which extend its distribution to epipelagic waters and possibly mix with the yellow-coded epipelagic resources observed during the day.

Oceanographic parameters other than the ones considered in our analyses are also likely to affect prey distribution and foraging habitat, such as chlorophyll density, which is linked to primary production (Moore and Abbott, 2000), salinity, a key physical

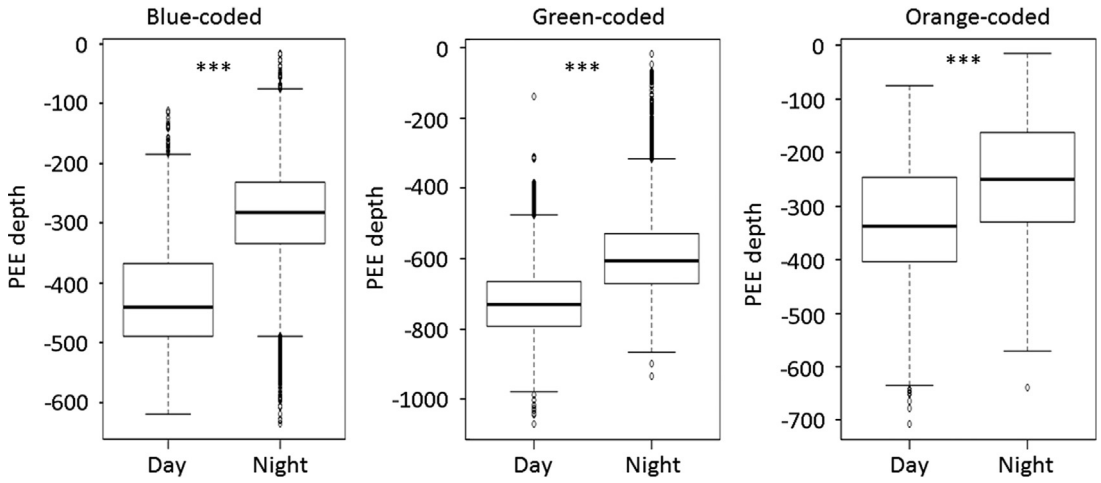

Fig. 7. Depth composition of the foraging environments determined by PEE occurring both during day and at night. The boxplots show the distribution of depths at which PEE occurred for the blue-coded, green-coded and orange-coded foraging environments respectively, during day and night periods.

Table 3
Characteristics of the different foraging environments composed by PEE occuring during day and night by periods.

Foraging environments	Orange-coded		Blue-coded		Green-coded	
Periods	Day	Night	Day	Night	Day	Night
Temperature (°C)	[−0.6–5.9] 2.1 ± 0.6	[-1.7–5.4] 2.1 ± 1.1	[3.4–7.5] 4.7 ± 0.7	[3.4–8.9] 5.0 ± 0.9	[4.3–12.4] 6.4 ± 1.4	[4.5–12.6] 7.8 ± 1.7
Depth (m)	[75.6–707.5] 324.4 ± 95.4	[15.5–639.4] 247.4 ± 100.4	[112.0–620.1] 425.7 ± 79.8	[17.1–635.7] 292.5 ± 90.6	[140.7–1071.0] 723.8 ± 100.1	[19.0–933.5] 587.0 ± 129.4
Light (raw data)	[16.2–92.2] 43.8 ± 13.0	[16.2–88.0] 31.8 ± 8.2	[16.5–90.2] 29.8 ± 7.2	[16.5–86.2] 29.7 ± 6.5	[20.5–133.5] 30.9 ± 8.9	[21.0–106.0] 29.9 ± 8.0

Numbers in square brackets are minimum and maximum values and below are the mean and standard deviation of each variable.

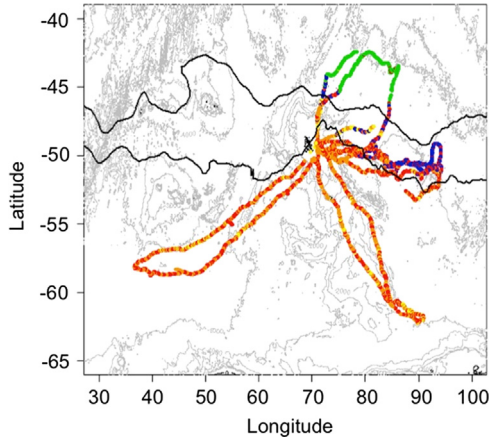

Fig. 8. Spatial distribution of the five highlighted foraging environments. Each dot represents a prey capture attempt and each color corresponds to a foraging environment. The black lines correspond to the SAF (on the top) and PF (on the bottom). These fronts were represented using Park et al. (1993) but it is known that these structures are dynamic. (For interpretation of the references to color in this figure, the reader is referred to the web version of this article.)

parameter of oceans (Caldwell, 1974), or dissolved oxygen, a major biogeochemical component for marine ectotherms (Karna, 2003). Including them in our habitat models could refine our analysis improve the distinction between different habitat environments.

Investigating species distribution in association with their surrounding environmental conditions is essential for improving our understanding of the marine ecosystem, particularly within the context of climate change (Chen-Tung, 2008; Ishizaka, 2010; Doney et al., 2012). These changes are expected to have substantial biological consequences on marine ecosystems by impacting both the horizontal and vertical distribution of food resources (Cantin et al., 2011) and consequently the foraging efficiency of their natural predators. Currently, these biological consequences remain poorly understood. The results in this study provide a better understanding of the delimitation and the characterization of foraging environments of a top predator, but also emphasize how eclectic SESs are in their foraging environments. This suggests that this species, according to its horizontal and vertical range, is likely to adapt to future climatic perturbations. Indeed, this study provides insight into the horizontal and vertical variability of mesopelagic resource distribution targeted by a deep diving predator. However, we would like to stress that it would be highly beneficial to combine these results to data obtained from acoustic survey and trawl net sampling (MyctO-3D -MAP project; Fielding et al., 2012) to improve our assessment of prey distribution, and compare them with other CLIOTOP approaches such as the Seapodym model (Lehodey et al., 2010).

Acknowledgment

The authors would like to thank all the colleagues and volunteers involved in the field work on southern elephant seals at Kerguelen Island, with the special acknowledgment of the invaluable field contribution of N. El Ksaby, G. Bessigneul and

A. Chaigne. This work was supported by the ANR Topp-Patches, ANR Mycto- 3D-Map, the CNES-TOSCA and the Total Foundation. We are indebted to IPEV (Institut Polaire Français), for financial and logistical support of Antarctic research program 109 (Seabirds and Marine Mammal Ecology lead by H. Weimerskirch). Special thanks also go to Pascal Monestiez (INRA Avignon), Kevin Le Rest and David Pinaud (CEBC CNRS) for their helpful advice at the different stages of the manuscript. Finally authors also thank Tiphaine Jeanniard Du Dot, Samantha Patrick and Malcolm O'Toole for their help with English editing.

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