Linking foraging behaviour to physical oceanographic structures: Southern elephant seals and mesoscale eddies east of Kerguelen Islands

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\textbf{A B S T R A C T}

In the Southern Ocean, mesoscale features, such as fronts and eddies, have been shown to have a significant impact in structuring and enhancing primary productivity. They are therefore likely to influence the spatial structure of prey fields and play a key role in the creation of preferred foraging regions for oceanic top-predators. Optimal foraging theory predicts that predators should adjust their movement behaviour in relation to prey density. While crossing areas with sufficient prey density, we expect predators would change their behaviour by, for instance, decreasing their speed and increasing their turning frequency. Diving predators would as well increase the useful part of their dive i.e. increase bottom-time thereby increasing the fraction of time spent capturing prey. Southern elephant seals from the Kerguelen population have several foraging areas: in Antarctic waters, on the Kerguelen Plateau and in the interfrontal zone between the Subtropical and Polar Fronts. This study investigated how the movement and diving behaviour of 22 seals equipped with satellite-relayed data loggers changed in relation to mesoscale structures typical of the interfrontal zone. We studied the links between oceanographic variables including temperature and sea level anomalies, and diving and movement behaviour such as displacement speed, diving duration and bottom-time. Correlation coefficients between each of the time series were calculated and their significance tested with a parametric bootstrap. We focused on oceanographic changes, both temporal and spatial, occurring during behavioural transitions in order to clarify the connections between the behaviour and the marine environment of the animals. We showed that a majority of seals displayed a specific foraging behaviour related to the presence of both cyclonic and anticyclonic eddies. We characterized mesoscale oceanographic zones as either favourable or unfavourable based on the intensity of foraging activity as identified by the behavioural variables. Our findings highlight the importance of mesoscale features for top-predators’ behaviour and introduce a new approach for evaluating the importance to the seals of the origin and intensity of these features.

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1. Introduction

Environmental resources are often heterogeneously distributed both in time and space which results in dynamic, unpredictable and multiscale habitat structures. This is particularly the case in the fluid marine environment. Optimal foraging theory (MacArthur and Pianka, 1966; Pyke, 1984) predicts that foraging strategies maximising resource acquisition in an individual’s environment have been optimized through evolution. Predators should adjust their movement behaviour in relation to prey density (Charnov, 1976; Parker and Stuart, 1976; Parker and Sutherland, 1992). While crossing areas with sufficient prey density, we expect predators would change their behaviour by, for instance, decreasing their displacement speed, increasing their turning frequency and, for diving predators, increasing the time spent at the bottom of a dive. This behaviour, called area-restricted search (ARS, Kareiva and Odell, 1987), is frequently observed in free-ranging predators that undertake long migration in very heterogeneous environments (Laing, 1938; Tinbergen et al., 1967; Waugh and Weimerskirch, 2003; Morales et al., 2004, among others).

The identification and validation of ARS for marine predators is particularly challenging since no direct observation of their prey is generally available. Over the last 20 years, new technologies have revolutionised the way we observe fast swimming, wide ranging marine animals and their environment. Satellite measurements of surface oceanographic variables now provide information in previously poorly sampled areas such as polar zones. In addition, instrumenting marine predator species with electronic tags has greatly improved the knowledge of their distribution, migration behaviour and foraging movements (Jouventin and Weimerskirch,
Tracking data have highlighted the importance of both large-scale oceanographic features and seasonal and inter-annual oceanographic variation, and also changes in foraging behaviour of animals in relation to the oceanographic features encountered (Biuw et al., 2007). Studies combining remotely sensed oceanographic and animal tracking data have highlighted the importance of both large-scale and mesoscale (of the order of 100 km) oceanographic structures in providing favourable feeding conditions for top-predators (Atlantic: Brown and Gaskin, 1988; Pacific: Briggs et al., 1987). The physical structuring of the marine environment drives the heterogeneous spatial distribution of prey, both with temporal and spatial lags. For example, many albatross and penguin species target frontal structures and mesoscale eddies to forage (McConnell et al., 1992; Guinet et al., 1997; Weimerskirch, 1998; Le Boeuf et al., 2000; Campagna et al., 2006; Biuw et al., 2007; Cotté et al., 2007). These species rely on mesopelagic fish whose spatial distribution is much more predictable close to frontal structures (Bost et al., 2009).

Travelling thousands of kilometers per year in the circumpolar waters of the Southern Ocean (McConnell et al., 1992), southern elephant seals, Mirounga leonina, have been instrumented with Argos loggers since 1990 both to study the ecology of the species and increase our knowledge of the Southern Ocean. Within the Kerguelen population three key foraging habitats have been identified, targeted by animals of different age and gender (Fig. 1, Bailleul et al., 2007a), and focus on the links between species and its prey as well as their use of oceanographic features (Bailleul et al., 2008). Argos satellite-relayed data loggers (SRDL, Argos, 1996) deliver valuable four-dimensional oceanographic data (temperature and salinity) of a quality that makes it possible to enlist animals as part of the Global Ocean Observing System (http://ioc.unesco.org/goos, SCOR, 1996; Malone and Cole, 2000; Nowlin et al., 2001). These tools allow the assessment of seasonal and inter-annual oceanographic variation, and also changes in foraging behaviour of animals in relation to the oceanographic features encountered (Biuw et al., 2007).

Here, we extend recent work examining the influence of surface mesoscale structures on southern elephant seals’ foraging areas (Bailleul et al., 2010b), and focus on the links between behaviour and the vertical water column structure of eddies using in situ oceanographic data. Our primary objective is to examine whether the seals differed in their diving behaviour and foraging movement depending on their gender and on oceanographic conditions. Secondly, we focus on the observation of the oceanic mesoscale features specific to the interfrontal zone and characterise their influence on elephant seals’ at sea activity. Gaining a better understanding of the foraging behaviour of the seals, especially females, in this zone will improve the ecological knowledge of this species and its prey as well as their use of oceanographic features typical of the interfrontal zone.

2. Material and methods

2.1. Study species

Southern elephant seals are one of the important apex predators of the Southern Ocean ecosystem (Boyd and Arnbom, 1991). Kerguelen Island (49°20’S, 69°20’E), located on the boundary between Sub-Antarctic and Antarctic waters, hosts the second biggest sub-population of more than 120,000 individuals (Guinet et al., 1991). These animals travel large distances (McConnell et al., 1992) between semi-annual land residencies, which each lasts around 1 month during the austral spring (for reproduction) and late summer (for molting). They also display extraordinary diving abilities, achieving up to 2000-m depths (Stewart and Delong, 1990; Hindell et al., 1991). Taken together these factors make the animals exemplary broad-ranging samplers of the Southern Ocean (Biuw et al., 2007; Charrassin et al., 2008).

2.2. Tag deployment and data

Between 2003 and 2008, 55 southern elephant seals (31 females and 24 males) from the Kerguelen archipelago were tagged with conductivity – temperature – depth satellite – relayed data loggers (termed CTD-SRDLs). The devices collected and transmitted the locations of the seals as well as the pressure (dbar), temperature (°C), salinity (converted from conductivity) of the waters encountered by elephant seals. The loggers are designed and manufactured by the Sea Mammal Research Unit (University of St Andrews, Scotland). They were pressure-rated to 2000 m and a pseudo-random method was used to schedule the transmission of an unbiased data sample of the stored records (Fedak et al., 2002). Subadult males and adult females of similar mass (350–450 kg) were equipped. We focused our study on the interfrontal zone located between 0° and 125°E with latitudes ranging from 45° to 60°S. This area presents numerous oceanographic features, such as the Sub-Antarctic Front (SAF) and the Polar Front structures and covers a large part of the habitat range of the Kerguelen seal colony (Fig. 2a). Twenty-two seals went to the interfrontal zone among which 18 individuals were equipped before their post-moulting foraging trip, e.g. between December and March, and four others were equipped after a winter visit on land, e.g. in September during the austral spring (Table 1).

The diving behaviours derived from tags included: maximum depth, descent and ascent speeds, surface and diving durations, bottom-time (time spent below 80% of the maximum diving depth) as a proxy for the time spent hunting for prey (Chappell et al., 1993; Mitani et al., 2004) and bottom-time residuals (residuals of multiple regression of bottom-time vs. maximum dive depth + dive duration; calculated for each dive within a path, Bailleul et al., 2008). Argos locations were filtered using an Epanechnikov averaging filter based

![Fig. 1. Proportion of the subadult males and adult females in the three main habitats used as foraging areas.](Image)
on the assumption that southern elephant seals rarely travel at speeds higher than 3 m s$^{-1}$ (Gaspar et al., 2006). Three movement variables were then calculated: path length (distance travelled between two Argos locations), number of dives per km and displacement speed. In situ oceanographic measurements of temperature and salinity, collected along the dives, provided a detailed description of the dynamic three dimensional environment.

2.3. Remotely sensed oceanographic data

The objective of this study was to evaluate links between behavioural and oceanographic variables within the interfrontal zone. Considering that we did not know a priori what was affecting the animal behaviour in an eddy field, we decided to explore links with a large set of oceanographic variables. Weekly satellite maps of sea level anomalies (SLA), absolute dynamic topography (AbDynTopo) and geostrophic velocities, absolute and anomalies values (respectively AbGeoVel and GeoVelAn), were used. Chlorophyll a concentration (Chl) was used as a proxy for primary productivity (Table 2a) but due to cloud cover causing a large percentage of missing pixels, we used monthly data. Chlorophyll a anomalies about the monthly mean were also calculated for each pixel. The selected remotely sensed variables were extracted for each individual track location.

Mesoscale features were identified from SLA (Fig. 3) and other oceanographic data such as temperatures and water densities. Two kinds of eddies can be distinguished according to their rotation direction: cyclonic (clockwise in the southern hemisphere) and anticyclonic (counter-clockwise) eddies. In cyclonic eddies, the Coriolis and centrifugal forces are directed radially outward and so the dynamic balance is maintained by a pressure force directed radially inward towards a local “low” situated at the eddy’s center (Bakun, 2006). Therefore, the cores of cyclonic eddies present negative sea level anomalies combined with a shallower thermocline and isopycnals tightening in the water column. Conversely anticyclonic eddies present positive sea level anomalies and deepening of the thermocline at their center (Mann and Lazier, 2006). As a cyclonic eddy is spinning up, the isopycnals on its flanks steepen, and denser water is raised upward in the center – usually a good indication of upwelling. Therefore negative sea level
anomalies, cold temperatures and high water density are generally
typical of spinning-up cyclonic eddies (Daniault and Ménard, 1985; 
Park and Gamborini, 1997). However
decaying cyclonic eddies, can sometimes present similar character-
istics (Bakun, 2006). In a downwelling process for instance, upward
vertical motions at the flanks of the eddy make the isopycnals tend
to mount back up to the levels that they were before the eddy span
up. This eddy's outer edges will present weak sea level anomalies
in situ 12 h Calculated from temperature and salinity
2.4. Significance of relationships between behaviour and oceanography

We focused on the pelagic part of the track, considering only the
zones with a bathymetry deeper than 1000 m and thereby exclud-
ing shelf areas where most of the seals forage benthically (Bailleul
et al., 2007b). We linked the behavioural, positional and oceano-
graphic data for the corresponding date with each filtered track
location (Fig. 4, Tables 2a and 2b). Several depth classes were cho-
sen on the basis of both biology and mesoscale ocean structure: the
surface layer, 50 m layer (±10%), 200 m layer (±10%, which charac-
terises the presence of oceanographic fronts, Park et al. (1998)),
and 500 m layer (±10%, which is the mean pelagic diving depth of
elephant seals, McConnell et al. (1992)). Density in each depth
class was then calculated from the in situ temperature and salinity.
Abbreviations of the oceanographic variables, defined according to
the previous depth classes mentioned, are presented in Table 2a.

2.4.1. Correlation coefficients

We worked with 16 oceanographic (Table 2a) and nine behav-
ioural (Table 2b) variables. For each of the 144 pairs of variables
per individual seal we calculated the pairwise Pearson correlation
coefficient $r_{pq}$ between the behavioural and oceanographic time
series (Pakhomov and McQuaid, 1996; R Development Core Team,
2005). We assumed a linear relationship between the behavioural
and the oceanographic variables.

2.4.2. Parametric bootstrap

In order to determine the strength of a linear link between the
pairwise variables, we tested the significance of the correlation
coefficients. When computing numerous correlation coefficients
from the same data set, care must be taken since chance alone
may result in spuriously significant correlations. Type I errors will
be increased with spatially and temporally dependant data points.
Therefore we used a bootstrap procedure (Gleason, 1988) to gener-
ate sampling distributions of the correlations for each data series
(Efron and Tibshirani, 1993). To account for the temporal depen-
dence within the time series we fitted, for each individual and each
behavioural time series, an autoregressive moving average model
(ARMA). The orders $p$ and $q$ of the ARMA (with $p$, for the AR part
of the model, belonging to $\{1, \ldots, 5\}$ and $q$, for the MA part, belong-
ing to $\{1, \ldots, 5\}$) were selected based on the smallest Akaike's
Information Criterion (AIC, Akaike, 1973; Burnham and Andersons,
1998). We then simulated an ARMA with estimated coefficients in
order to reproduce a series with the same characteristics as the ori-
ginal behavioural time series. Each series was simulated 1000
times, with the ARMA correlation model fitted on the behavioural
variable. We calculated the correlation coefficient between each

Table 2a
Oceanographic variables, abbreviation name, spatial resolution, temporal resolution and source.

<table>
<thead>
<tr>
<th>Variable name</th>
<th>Abbreviation name</th>
<th>Spatial resolution</th>
<th>Temporal resolution</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sea level anomalies</td>
<td>SLA</td>
<td>1/3°</td>
<td>Week</td>
<td><a href="http://atoll-motu.aviso.oceanobs.com/">http://atoll-motu.aviso.oceanobs.com/</a></td>
</tr>
<tr>
<td>Absolute dynamic topography</td>
<td>AbDynTopo</td>
<td>1/3°</td>
<td>Week</td>
<td><a href="http://atoll-motu.aviso.oceanobs.com/">http://atoll-motu.aviso.oceanobs.com/</a></td>
</tr>
<tr>
<td>Absolute geostrophic velocities</td>
<td>AbGeoVel</td>
<td>1/3°</td>
<td>Week</td>
<td><a href="http://atoll-motu.aviso.oceanobs.com/">http://atoll-motu.aviso.oceanobs.com/</a></td>
</tr>
<tr>
<td>Geostrophic velocities anomalies</td>
<td>GeoVelAn</td>
<td>1/3°</td>
<td>Week</td>
<td><a href="http://atoll-motu.aviso.oceanobs.com/">http://atoll-motu.aviso.oceanobs.com/</a></td>
</tr>
<tr>
<td>Chlorophyll</td>
<td>Chl</td>
<td>9 km</td>
<td>Month</td>
<td><a href="http://www.oceancolor.gsfc.nasa.gov/cgi.html">http://www.oceancolor.gsfc.nasa.gov/cgi.html</a></td>
</tr>
<tr>
<td>Chlorophyll anomalies</td>
<td>AnomChl</td>
<td>9 km</td>
<td>Month</td>
<td>Calculated from Chl</td>
</tr>
<tr>
<td>Surface temperature</td>
<td>Temp.Surf</td>
<td>In situ</td>
<td>12 h</td>
<td>Recorded in situ by CTD tag</td>
</tr>
<tr>
<td>50 m deep temperature</td>
<td>Temp.50</td>
<td>In situ</td>
<td>12 h</td>
<td>Recorded in situ by CTD tag</td>
</tr>
<tr>
<td>100 m deep temperature</td>
<td>Temp.100</td>
<td>In situ</td>
<td>12 h</td>
<td>Recorded in situ by CTD tag</td>
</tr>
<tr>
<td>200 m deep temperature</td>
<td>Temp.200</td>
<td>In situ</td>
<td>12 h</td>
<td>Recorded in situ by CTD tag</td>
</tr>
<tr>
<td>500 m deep temperature</td>
<td>Temp.500</td>
<td>In situ</td>
<td>12 h</td>
<td>Recorded in situ by CTD tag</td>
</tr>
<tr>
<td>Surface salinity</td>
<td>Sal.Surf</td>
<td>In situ</td>
<td>12 h</td>
<td>Recorded in situ by CTD tag</td>
</tr>
<tr>
<td>50 m deep salinity</td>
<td>Sal.50</td>
<td>In situ</td>
<td>12 h</td>
<td>Recorded in situ by CTD tag</td>
</tr>
<tr>
<td>100 m deep salinity</td>
<td>Sal.100</td>
<td>In situ</td>
<td>12 h</td>
<td>Recorded in situ by CTD tag</td>
</tr>
<tr>
<td>200 m deep salinity</td>
<td>Sal.200</td>
<td>In situ</td>
<td>12 h</td>
<td>Recorded in situ by CTD tag</td>
</tr>
<tr>
<td>500 m deep salinity</td>
<td>Sal.500</td>
<td>In situ</td>
<td>12 h</td>
<td>Recorded in situ by CTD tag</td>
</tr>
<tr>
<td>Surface density</td>
<td>Dens.Surf</td>
<td>In situ</td>
<td>12 h</td>
<td>Calculated from temperature and salinity</td>
</tr>
<tr>
<td>50 m deep density</td>
<td>Dens.50</td>
<td>In situ</td>
<td>12 h</td>
<td>Calculated from temperature and salinity</td>
</tr>
<tr>
<td>100 m deep density</td>
<td>Dens.100</td>
<td>In situ</td>
<td>12 h</td>
<td>Calculated from temperature and salinity</td>
</tr>
<tr>
<td>200 m deep density</td>
<td>Dens.200</td>
<td>In situ</td>
<td>12 h</td>
<td>Calculated from temperature and salinity</td>
</tr>
<tr>
<td>500 m deep density</td>
<td>Dens.500</td>
<td>In situ</td>
<td>12 h</td>
<td>Calculated from temperature and salinity</td>
</tr>
</tbody>
</table>
simulated behavioural (i) and the oceanographic (j) time series, thereby obtaining a distribution of the coefficient values. The significance of each correlation coefficient $q_0$ was then determined at risk $\alpha = 0.05$ i.e. through comparison with the 95%-confidence interval of this simulated distribution (Buckland and Garthwaite, 1991).

### 2.5. Detecting homogeneous behavioural subsets among the individuals

Among the individuals studied, gender, deployment date (post-breeding vs. post-moulting) and deployment year could be factors biasing the bootstrap results. To detect the existence of coherent subsets, a cluster analysis was conducted. Thereupon we deter-

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**Table 2b**

<table>
<thead>
<tr>
<th>Variable name</th>
<th>Abbreviation name</th>
<th>Unit</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Travelling speed</td>
<td>Trav.Spd</td>
<td>km/ day</td>
<td>Calculated from Argos track</td>
</tr>
<tr>
<td>Path length</td>
<td>PathLgth</td>
<td>m</td>
<td>Calculated from Argos track</td>
</tr>
<tr>
<td>Number of dives per km</td>
<td>Nb.Dive.</td>
<td>km</td>
<td>Calculated from Argos track</td>
</tr>
<tr>
<td>Descent speed</td>
<td>Des.Spd</td>
<td>m/s</td>
<td>TDR</td>
</tr>
<tr>
<td>Ascent speed</td>
<td>Asc.Spd</td>
<td>m/s</td>
<td>TDR</td>
</tr>
<tr>
<td>Dive duration</td>
<td>Dive.Dur</td>
<td>s</td>
<td>TDR</td>
</tr>
<tr>
<td>Maximum diving depth</td>
<td>Max.Depth</td>
<td>m</td>
<td>TDR</td>
</tr>
<tr>
<td>Bottom-time</td>
<td>Bott.Time</td>
<td>s</td>
<td>Calculated from TDR data</td>
</tr>
<tr>
<td>Bottom-time residuals</td>
<td>resBT</td>
<td>s</td>
<td>Calculated from TDR data</td>
</tr>
</tbody>
</table>
mined whether the origin of these subsets stemmed from experimental bias. The distance matrix between individuals was calculated, with Euclidian distance, from the significant correlation coefficients matrix.

2.6. Behavioural transition analysis and associated oceanographic transitions

We focused the last part of the analysis on “behavioural transitions,” when the animals exhibited a sharp switch from extensive to intensive foraging behaviour. These were identified using bottom-time residuals (Bailleul et al., 2007b). Large positive residuals should indicate a longer than expected time at the bottom of the dive, presumably due to favourable foraging. The three broadest and longest transitions per track were identified using the 90% percentiles of the distribution of the residuals from an individual seals (Fig. 5). We then focused on the in situ and remotely sensed oceanographic data during the 48 h before and after each transition. A 2 day scale ensured a conservative approach to avoid artifacts related to local measurement errors. To corroborate the bootstrap results, we applied pairwise t-tests to the mean samples obtained 48 h before and 48 h after the behavioural transitions to evaluate which oceanographic variable showed significant variation during this time.

3. Results

3.1. Descriptive statistics of the tracks

Among the 22 animals equipped that went to the interfrontal zone, four presented either very poor quality locations or a track shorter than a month and were not used for the analyses (Fig. 2a and b). The 18 animals equipped for this study covered an average of 11,790 ± 6089 km, including 10,116 ± 5687 km in pelagic waters. They spent an average of 5.4 months at sea (162 ± 68 days) with 4.2 months in the pelagic area (126 ± 67 days). In our data, individual seals dived on average 67 times per day which is consistent with the literature (Boyd and Arnbom, 1991). This provided about 10,854 ± 4556 dives while at sea, of which 8442 ± 4489 were in pelagic waters.

3.2. Detection of homogeneous behavioural subsets among individuals

The subsets identified by the cluster analyses are presented in Fig. 6. The biggest subset of 13 pooled individuals which were not homogeneous in gender or deployment year. This supports the hypothesis of similarity in their foraging behaviour. However, of the remaining five individuals, no significant correlation for any pairwise test was obtained for two individuals, while the last three presented few significant correlations and these differed between individuals. The subsequent analysis therefore focused on the homogeneous subset of 13 individuals.

3.3. Links between behavioural and oceanographic variables

3.3.1. Sea level and geostrophic velocities

For these 13 individuals, sea level anomalies showed a significant negative correlation with several behavioural variables such as number of dives per km, bottom-time and bottom-time residuals (correlation coefficients ± standard deviation respectively −0.1643 ± 0.1145; −0.1627 ± 0.0919 and −0.1472 ± 0.0429). Absolute dynamic topography (AbDynTopo) was negatively correlated to both travel speed and the bottom-time residuals (resp. −0.1759 ± 0.0416 and −0.1539 ± 0.0462) and positively correlated with both path length (0.2835 ± 0.0207) and dive duration (0.1183 ± 0.0451). With respect to geostrophic velocities, absolute values were positively correlated with the maximum diving depth (AbGeoVel: 0.2529 ± 0.1223) when both absolute values and anomalies were positively correlated with descent speed (AbGeoVel: 0.3243 ± 0.3163; GeoVelAn: 0.2515 ± 0.0973). Both geostrophic variables appeared negatively correlated with bottom-time (AbGeoVel: −0.1215 ± 0.0587; GeoVelAn: −0.1729 ± 0.1416).

3.3.2. Chlorophyll

Maximum diving depth (Chl: −0.3778 ± 0.1631; AnomChl: −0.2645 ± 0.0894), dive duration (Chl: −0.2639 ± 0.0201) and path length (AnomChl: −0.1586 ± 0.028) were negatively correlated with chlorophyll a concentration and its anomalies. However the bottom-time residuals (AnomChl: 0.1702 ± 0.1167), number of dives per km (Chl: 0.2644 ± 0.0201), displacement speed (Chl:

![Fig. 5. Representation of a behavioural transition detection: dashed line corresponds to the 90% quantile value of the bottom-time residuals distribution. Highly positive bottom-time residuals indicate an intense foraging effort.](image-url)
Conversely, in situ transition were lower than during the 48 h before the transition. Differences, i.e. averaged values from the 48 h after the behavioural lies as well as absolute dynamic topography both showed negative fore-transition and 48 h after-transition samples. Sea level anomalies showed positive correlations with these two variables.

3.3.3. In situ temperature and density

Surface temperatures were positively correlated with descent (0.3663 ± 0.1656) and ascent (0.1336 ± 0.0342) speeds whilst negatively correlated with dive duration (−0.3718 ± 0.1476). Strong links, negative and positive, were also observed between the temperature of the bottom layers of the water column (depth > 50 m) and a number of behavioural variables. Ascent speed and dive duration were positively correlated with Temp.50 (resp. 0.3846 ± 0.0907 and 0.4239 ± 0.319), Temp.100 (resp. 0.1186 ± 0.0261 and 0.3241 ± 0.1727) and Temp.200 (resp. 0.1184 ± 0.0258 and 0.3156 ± 0.2413). Maximum diving depth was also positively correlated with Temp.50 (0.5248 ± 0.1883) and Temp.200 (0.1608 ± 0.0355). Descent speed, dive duration and path length appeared positively correlated with Temp.500 (respectively: 0.3338 ± 0.1672; 0.2511 ± 0.1187; 0.2717 ± 0.1349). However, few correlations with the water column temperature variables showed coefficients higher than 0.3.

With respect to the density variables, between 50 m and 500 m depth, the number of dives per km (Dens.200: 0.1214 ± 0.0265), bottom-time (Dens.100: 0.2039 ± 0.1665; Dens.200: 0.1668 ± 0.0265 and Dens.500: 0.1249 ± 0.0827), ascent (Dens.50: 0.3026 ± 0.1074) and descent speeds (Dens.200: 0.3858 ± 0.1525 and Dens.500: 0.3048 ± 0.0528) all showed positive correlations. Maximum diving depth (−0.2789 ± 0.2379) and dive duration (−0.11 ± 0.047) were negatively correlated with Dens.100. Considering the density at the surface, correlations with the same order of magnitude were observed for all the density variables mentioned above but with a sign inversion (Dens.Spd: −0.2962 ± 0.216; Dive.Dur: −0.2553 ± 0.0641; Bott.Time: 0.1117 ± 0.0399 and resBT: 0.2042 ± 0.1208).

3.4. Behavioural transition analysis

Table 3 contains the significant (p value <0.05) or marginally significant (p value <0.1) paired t-tests realised on the 48 h before-transition and 48 h after-transition samples. Sea level anomalies as well as absolute dynamic topography both showed negative differences, i.e. averaged values from the 48 h after the behavioural transition were lower than during the 48 h before the transition. Conversely, in situ surface density and salinity showed positive differences (Fig. 7), i.e. values before were higher than after the behavioural transition.

<table>
<thead>
<tr>
<th>Variable</th>
<th>t-Value</th>
<th>Mean</th>
<th>p-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>SLA</td>
<td>2.1876</td>
<td>−3.107</td>
<td>0.023</td>
</tr>
<tr>
<td>AbDynTopo</td>
<td>2.5897</td>
<td>−3.975</td>
<td>0.012</td>
</tr>
<tr>
<td>Dens.Surf</td>
<td>2.0299</td>
<td>2.978</td>
<td>0.048</td>
</tr>
<tr>
<td>Sal.Surf</td>
<td>2.0153</td>
<td>3.553</td>
<td>0.05</td>
</tr>
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</table>

4. Discussion

In this study, we found evidence of significant correlations between southern elephant seal behaviour and their oceanographic environment in the interfrontal zone. Previous studies have shown that a variety of foraging strategies existing among the Kerguelen seal population. While some individuals target the Antarctic zone, others prospect in the interfrontal zone or the Kerguelen shelf. Considering the Antarctic foraging strategies, the influence of sea temperature and sea ice on elephant seal foraging behaviour has been studied in detail by Bailleul et al. (2007a). Our results suggest that the most favourable foraging habitats of elephant seals, in the interfrontal zone, are associated with cyclonic and anticyclonic eddies. Our study also highlights that, even within the polar interfrontal zone, relationships between the foraging behaviour and oceanographic conditions do vary between individuals.

4.1. Foraging patterns associated with mesoscale oceanographic structures

Within our subset of homogeneous foraging individuals, seals were found to modify their foraging behaviour, i.e. decrease the distance travelled, increase the numbers of dives performed per km and increase the relative time spent at the bottom of dives, in response to specific oceanographic conditions. All these behaviours were related to variations in sea level. A consistent increase of the foraging-searching effort of these seals was concordant with decreasing sea level anomalies, absolute dynamic topography and geostrophic velocities. The seals were also found to increase their descent speed and their dive duration with decreasing temperature.
and increasing water density at 500 m. They were also found to increase their path length (e.g. travelling speed) with increasing temperature and decreasing density at the depth of 500 m. These results suggest an increase in foraging-searching effort in high density and cold waters. Within the 2 days following a transition from extensive to intensive foraging-searching behaviour, elephant seals were consistently observed in waters that were significantly denser and with lower sea level anomalies, i.e. lower sea level in height, than the two previous days. All these results suggest that the most favourable foraging zones are associated with cyclonic eddies. However a bouncing effect on isopycnals at an anticyclonic eddy’s outer edge can also induce weak SLA and relatively cold temperatures compared to the adjacent waters (Bakun, 2006). Therefore mesoscale structures targeted by the seals can either be the cores of cyclonic structures or the edges of anticyclonic structures. Inspection of the eddies present at the transition times (from mapped SLA and geostrophic velocities) confirm the importance of both structures: cores and outer edges in the opposite shear zone (Bakun, 2006).

Southern elephant seals in colder and denser waters, potentially upwelled mid-waters, were also found to increase their diving frequency and bottom-time, while decreasing their path length and maximum diving depth in regions of high chlorophyll concentrations. This finding suggests that these elephant seals may favour or target the most productive areas of the interfrontal zone. However no significant change in chlorophyll was found in the vicinity of behavioural transitions, suggesting rather an indirect causal link between foraging and chlorophyll. Surface chlorophyll-a concentration could simply be a bio-marker of these mesoscale features and of the local biological richness (Park et al., 2002) rather than a direct indicator of elephant seals’ prey density. Oceanographic studies have actually shown that there is generally a spatial and temporal decorrelation, through advection processes associated with currents, between the distribution of phytoplankton and the distribution of secondary and tertiary production (Vinogradov, 1981; Jacques, 1988; Lévy, 1996; Jaquet and Whitehead, 1996; Wheeler et al., 2003). This low correlation can perhaps be explained by the time-lag and likely spatial-lag between primary, secondary and tertiary production (Frontier and Pichod Viale, 1998; Guinet et al., 2001).

Mesoscale processes such as eddies are known to be important for nutrient fluxes in the open ocean (McGillicuddy and Robinson, 1997). Eddies have different dynamical properties between the inner and outer part of their structure. While the interior part of the eddy, or core, transports particles within it, the outer produces intense stirring of the ambient environment (Olson, 1991). These physical processes can lead both to enhanced productivity due to the upwelling of deep nutrient rich waters and/or the spatial structuring and trapping of biological particles. Therefore nutrient injection in the surface layers due to upwelling processes can allow eddies to exhibit elevated primary productivity relative to the adjacent waters of the Southern Ocean (Ainley and DeMaster, 1990; Polovina et al., 2004). The increase in marine productivity associated with eddies can induce prey aggregation which can ultimately benefit top-predators. Isopycnal shoaling induced by vertical movement of water masses associated with eddies is likely to influence prey behaviour, driving upward migrations to remain at preferred densities and temperatures (Wiebe, 1982). Myctophid fish, principal prey for females and young males (Ducatez et al., 2008; Cherel et al., 2008), and euphausiids have been shown to aggregate in the periphery of downwelling structures where high biomass of micronekton and zooplankton is found (Rodhouse et al., 1996; Pakhomov and Frohman, 2000). Cold water and high biomass in the surface layers may cause a decrease of luminosity contributing to the presence of cryptic myctophids species at shallower depths (Flierl and McGillicuddy, 2002). To avoid predators which can detect bioluminescent prey, the optimal habitat of these fishes depends on temperature, density and especially light level at depth (Widder, 2010).

Our results are consistent with those obtained by Campagna et al. (2006) for a single individual elephant seal, and by Bailleul
et al. (2010b) who used the Okubo–Weiss criterion to identify eddies. However, our findings further understanding of the relationships and processes linking the foraging-searching behaviour of elephant seals to mesoscale features within the interfrontal zone.

While a majority of seals target cyclonic eddies, where they probably find denser prey biomass, some individuals differ in their foraging behaviour in relation to mesoscale features. These differences are not understood but might be the consequences of each individual's past experiences (Bradshaw et al., 2004). Variations in foraging-searching behaviour and/or differences in prey selection (Field et al., 2004, 2007a) could explain this inter-individual variability that generates the observed population plasticity. Fitness variability is likely to be related to inter-individual strategies (Hindell et al., 1999; Field et al., 2007b). This could be directly measured through biometrics (pre- and post-track weights), changes in drift rate of dives along the track (Biuw et al., 2003) and ultimately through demographic monitoring, e.g. of reproduction success, pup weight, etc. (McMahon and Burton, 2005).

Southern elephant seals are predators that prospect continually within and between prey patches (Bailleul et al., 2007b). From the perspective of an individual seal, interfrontal zones are characterized by eddies: (1) that are random and unpredictable; (2) are sufficiently numerous, (3) and occur in spatially structured patterns, e.g. the interfrontal zone can be conceived as a moving three dimensional eddy field (Knox, 2006). Therefore, during any long range migration there may be a high probability of encountering a number of these structures en route, even without any previous experience. It is currently still unclear if elephant seals are searching for certain oceanographic conditions to find their prey or simply responding to changes in prey densities which are themselves related to oceanographic features. Relatively little is known about the distribution of prey in the interfrontal zone, particularly in the remote areas frequented by the seals. To investigate this point we need further information such as a direct measurement of prey intake or prey density within the habitats visited by southern elephant seals.

4.2. Methodological perspectives

Statistical procedures were purposely chosen to be conservative, in order to identify the strongest and most significant relationships between seals behaviour and their environment. Another approach, such as integrative modeling (Box and Pierce, 1970), might also be appropriate but can often yield confusing interaction terms that are difficult to interpret. In this approach, it is also difficult to identify the individual process involved. We therefore preferred an inferential approach that allowed testing our hypothesis. The oceanographic variables we chose focused on describing the direct physical surroundings and their gradients. Composite variables, such as Eddy Kinetic Energy, Okubo–Weiss Criterion or Lyapunov Exponents, were therefore excluded because of their redundancy with the other variables, although their use for the detection of eddies and sub-mesoscale structures is common (Tew et al., 2009). Few studies have directly demonstrated the sensitivity of top-predator movements to their physical environment (Cotté et al., 2007), although it appears that swimming directions of elephant seals are not influenced by ocean currents (Bailleul et al., 2010b). As we identified all the individual significant relationships between behaviour and oceanographic variables, we were able to focus on the variables detected by the animal that significantly influenced their behaviour and those, (for instance those related to SLA), that are strong indicators of mesoscale features.

Identifying areas of intensive foraging is necessary to explain distribution with respect to habitat features, and the underlying behavioural mechanisms that predators use to capitalise on such habitats (Mangel and Clark, 1989; Patterson et al., 2008). Animal behaviour can be modeled as a dynamic variable changing in relation to the animal’s internal state and/or its environment (Morales et al., 2004; Jonsen et al., 2007). Search modes along the track can also directly depend on a behavioural variable such as the bottom-time or the time spent in the vicinity of successive path locations (Bailleul et al., 2008; Barraquand and Benhamou, 2008). The combination of change point analysis, trajectory segmentation and bout, e.g. segment of track, identification could be an interesting next step (Patterson et al., 2008). This could be used to systematically detect behavioural transitions along the tracks and associate them with the animal's surroundings. It is our intention to examine this in future work.

Finally new technological devices are very promising, such as fluorometers combined with the CTD-loggers and GPS technology added to high resolution temperature depth recorders. Fluorescence detection in situ within the upper 200 m of the water column can be used as a proxy for chlorophyll a. It will indicate the richness of the local biological productivity in the mesoscale and sub-mesoscale structures. Foraging behaviour and oceanographic features will be able to be simultaneously investigated at small spatial and temporal scales. Direct information on prey distribution remains very scarce in the Southern Ocean. Therefore the combination of fine scale foraging studies with in situ oceanographic measurements appears to be the most practical and cost effective way to improve knowledge on prey distribution and the feeding ecology of apex predators.

5. Conclusion

Previous studies have shown that fronts and sea-ice play a key role in the foraging activity of elephant seals in other geographic areas (Bradshaw et al., 2004; Biuw et al., 2007). Here we have shown that the majority of the Kerguelen southern elephant seals that travel through the interfrontal zone forage preferentially within characteristic oceanographic mesoscale features. Frontal zones are major components of the Southern Ocean in terms of biological production and are frequently populated with intense mesoscale eddies. Upward cold water masses, from cyclonic eddies’ cores and anticyclonic eddies’ edges, appeared to be preferential foraging structures where the animals clearly intensified their diving effort. It is probable that by going to the interfrontal zone where resources are both spatially and temporally highly variable, elephant seals can concentrate their foraging searching activity in the most productive parts of the zone to maximise feeding success. Because of restricted ship deployments, relatively little is known about the distribution of prey in the interfrontal zone particularly in the remote areas frequented by the seals. Monitoring the diving behaviour of this species and the in situ oceanographic conditions with high resolution data, is an interesting further step in research on the foraging activity of elephant seals in relation to mesoscale structures and prey distribution in the Southern Ocean. It has been suggested that winds over the Southern Ocean have strongly increased over the past few decades (Meredith and Hogg, 2006) causing increased eddy activity and number. This could have significant impacts on primary productivity (Le Quéré et al., 2007) and hence prey opportunities for top-predators. However, the way in which these important mesoscale features, and the ecological communities they support, will vary on short and longer term time scales remains to be determined.

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