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Flexible preference of southern elephant seals for distinct mesoscale features within the Antarctic Circumpolar Current

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Short title: Flexible mesoscale elephant seal preference

Abstract

The open ocean is a highly variable environment where marine top predators are thought to require optimized foraging strategies to locate and capture prey. Mesoscale and sub-mesoscale features are known to effect planktonic organisms but the response of top predators to these features results from behavioural choices and is poorly understood. Here, we investigated a multi-year database of at-sea distribution and behaviour of female Southern elephant seals (*Mirounga leonina*) to identify their preference for specific structures within the intense eddy field of the dynamic Antarctic Circumpolar Current (ACC). We distinguished two behavioural modes, i.e. travelling and intensive foraging, using state-space modelling. We employed multisatellite Lagrangian diagnostics to describe properties of (sub-)mesoscale oceanic circulation. Statistical analyses (GAMMs and Student's *t*-tests) revealed relationships between elephant seal behaviour and (sub-)mesoscale features during the post-moulting period (Jan-Aug): travelling along thermal fronts and intensive foraging in cold and long-lived mesoscale water patches. A Lagrangian analysis suggests that these water patches – where the prey field likely developed and concentrated – corresponded to waters which have supported the bloom during spring. In contrast, no clear preference emerged at the (sub-)mesoscale during the post-breeding period (Oct-Dec), although seals were distributed within the Chlorophyll-rich water plume detaching from the plateau. We interpret this difference in terms of a seasonal change in the prey field. Our interdisciplinary approach contributes to elucidate the foraging strategies of top predators in a complex and dynamic environment. It also brings top down insights on prey distribution in remote areas where information on mid-trophic levels are strongly lacking and it identifies important physical-biological interactions relevant for ecosystem modelling and management.

Introduction

The seemingly homogeneous seascape is a patchy and highly variable physical-biological environment in space and time (Haury et al. 1978, Mann and Lazier 2006). An intense source of variability occurs through oceanic eddies (hereafter ‘mesoscale’ features, ~50-200 km and weeks to months) and filaments (hereafter ‘sub-mesoscale’ features 1-10 km and days to weeks), often referred to as the “internal weather systems of the ocean” (McGillicudy 2001). This complex circulation shapes the distribution of waters and largely controls biogeochemical fluxes as well as the distribution, abundance and composition of the marine life (e.g., Angel and Fasham 1983, Strass et al. 2002, Godø et al. 2012). The biological responses of lower trophic levels, i.e. phytoplankton, to (sub-)mesoscale (terminology used to described both mesoscale and sub-mesoscale) physical processes are well documented (e.g., Strass et al. 2002, Lévy 2008, d’Ovidio et al. 2010, Lévy at al. 2012). Numerous studies have shown the influence of eddies and sub-mesoscale structures on the distribution and the spatio-temporal dynamics of phytoplankton, mainly through vertical movements of water masses and enrichment of the surface layer (McGillicudy et al. 1998, Oschiles and Garcon 1998, Strass et al. 2002, Levy 2008, Lehahn et al. 2007, Lévy et al. 2012). Recently, the concept of fluid dynamical niches has emerged, describing how transport properties, particularly physical fronts induced by horizontal stirring, drive the complex mesoscale distribution of phytoplankton communities (d'Ovidio et al. 2010). But is this dynamic structuring, previously identified at the lower trophic level, relevant for the whole ecosystem, i.e. across trophic webs and particularly for top predators? Indeed, while plankton species are passively advected, top predators are highly mobile and move actively. Their at-sea distribution is thus the result of behavioural choices (Le Boeuf et al. 2000, Biuw et al. 2010, Sharples et al. 2012, Wakefield et al. 2013). Recent studies proposed that eddies catalyse energy transfer across trophic levels and can be considered as oases for higher trophic marine life (i.e., Godø et al. 2012). We investigated here how horizontal properties associated with mesoscale circulation, as inferred from satellite-derived analyses, drive the distribution and behaviour of a top predator.

Advances in satellite tracking technology during the last two decades have provided important information on distribution and behaviour of several marine top predators. Large tagging programs described the large scale movements of oceanic predators, and their collection into multispecies hotspots provides the foundation for spatial management of large marine ecosystems (Murphy et al. 2007, Bost et al. 2009, Block et al. 2011, Hindell et al. 2011, Fedak 2012). While tracking of predators was originally episodic, systematic remote monitoring now provides robust insights on their ecology and habitat at finer scales (e.g. Bost et al. 2009). In the meantime, remote satellite-derived measurements processed with appropriate analytical tools have improved the understanding of open ocean circulation (e.g. d'Ovidio et al. 2009, Chelton 2011). During the last decade, higher trophic levels, and especially top predators, were increasingly reported to be associated to the mesoscale and sub-mesoscale features. There is now evidences of the influence of eddies and associated fronts on the distribution and movements of various top predators such as turtles (Polovina et al. 2006, Lombardi et al. 2008), marine mammals (Bradshaw et al. 2004, Ream et al. 2005, Cotté et al. 2011, Woodworth et al. 2011 Nordstrom et al. 2012), and seabirds (Nel et al. 2001, Weimerskirch et al. 2004, Cotté et al. 2007, Tew-Kaï et al. 2009, De Monte et al. 2012). However, the relationships between both distribution and behaviour of animals and oceanographic processes at such scales remain unclear and largely under-investigated.

Oceanic top predators face a variable marine environment characterized by steep gradients of temperature, currents and food density at the mesoscale. They have to adjust their behavior at the spatio-temporal scales of the environmental heterogeneity that they detect (De Monte et al. 2012, Miramontes et al. 2012, Pelletier et al. 2012). Indeed, despite their ability to overcome ocean currents, some top predators have been shown to be associated with (sub-)mesoscale transport structures (Tew-Kaï et al. 2009, Cotté et al. 2011). Recent studies claimed that the observed co-location of predators with (sub-)mesoscale features could result from direct and/or indirect interactions. Direct influence of fronts was proposed for seabird behaviour, which take advantage of physical properties at the ocean-atmosphere interface for their flying movements (Tew-Kaï et al. 2009, De Monte et al. 2012). However, most studies reported that eddies and fronts affected top predators indirectly through cascading trophic (predator-prey) interactions and foraging opportunities (Bradshaw et al. 2004, Cotté et al. 2011, Nordstrom et al. 2012). These biophysical associations were observed during short periods as top predators were mostly studied during short breeding trips, when accessible from colonies. It is very likely that these biophysical associations are modulated in space and time by varying environmental conditions during extended journeys.

Using a multi-year satellite tracking database, we investigated the at-sea distribution and behaviour of southern elephant seals (*Mirounga leonina*) in order to identify in which type of oceanographic structures they preferentially travelled and foraged within the intense eddy field of the Antarctic circumpolar Current (ACC). The database on elephants seals is unique among all predators within the Southern Ocean as the year-long tracking offers the opportunity to examine the flexible foraging preferences across seasons. Southern elephant seals spend 90% of their lifetime at sea where they continuously dive to an average of 500m (Campagna et al. 1999, McIntyre et al. 2010). They feed predominantly on small pelagic fish in pelagic areas (Cherel et al. 2008). Their two long and distant trips per year last several months and cover the whole annual cycle, so that it is possible to study seal preferences for oceanographic (sub-)mesoscale strutures under contrasted environmental conditions within the ACC. The ACC is the dominant physical feature of the Southern Ocean and a complex physical environment where elephant seals encounter numerous biophysical processes. They have to adjust their foraging behaviour while they encounter (sub-)mesoscale features on the timescale of their at-sea trip. Previous studies have identified eddies as favourable features for foraging elephant seals (Campagna et al. 2006, Simmons et al. 2007, Bailleul et al. 2010, Dragon et al. 2010). It is still unknown what are the physical characteristics of the few targeted structures per trip of seals in a dynamic field such as the ACC where numerous eddies occur ("dynamic" is used here and hereafter to refer to the intense mesoscale variability as described in Kostianoy et al. 2003). Sub-mesoscale and mesoscale features with specific properties could have strong ecological implications because they could potentially generate high prey densities and favourable conditions for the development of food webs underpinning the presence of top predators. The purpose of this study was thus to propose a characterization of these oceanographic structures through the history of water parcels encountered by seals. To achieve a description of water dynamic history, we employed multisatellite Lagrangian diagnostics which measure properties of water parcels along seal trajectories, such as transport fronts, mesoscale temperature distribution and displacement rates of water parcels. We addressed this issue by examining seal preferences for distinctive (sub-)mesoscale features characterized by these specific transport or circulation properties within the ACC in relation to seasonal conditions and behavioral modes.

Methods

Regional context: Circulation and biological activity in the southern Indian ocean

- *Physical environment*: In the southern Indian Ocean, the circumpolar frontal system structures water masses latitudinally (depicted in Fig. 1). Going from north to south, the system includes the Subtropical front (STF), the Subantarctic Front (SAF), and the Polar Front (PF), the last two related to the jets of the ACC. The Kerguelen Plateau acts as a major physical barrier that breaks and deflects the strong eastward flow of the ACC (Park et al. 2008, McCartney and Donohue 2007, Roquet et al. 2009). In the eastern area of the plateau, the ACC flows southeastward, and associated fronts have the same orientation (Park et al. 2008, Roquet et al. 2009). Because of the intensity of the ACC along the entire length of the fronts, intensive meandering occurs and leads to important mesoscale and sub-mesoscale activity (Stammer 1998, Moore and Abbott 2000, Park et al. 2002, Kostianoy et al. 2003, Sokolov and Rintoul 2007). While the intrinsic zonal propagation of eddies is mainly westward in oceans, they propagate predominantly eastward within the ACC (Park et al. 2002, Fu 2009, Chelton et al. 2011).

- *Biological environment:* The phytoplankton distribution in the Southern Ocean is mainly assessed using ocean-colour satellite data (Moore and Abbott 2000). In contrast to the generally low phytoplankton biomass of the Southern Ocean referred to as “high nutrient low Chlorophyll” (HNLC, i.e. de Baar et al. 1995), the Kerguelen area is highly productive during the bloom period that extends from October to December (Fig. 2). During summer, High Chlorophyll concentrations are found on the plateau and a large plume of enhanced Chlorophyll concentration extends eastward (Mongin et al. 2008, Dragon et al. 2011). This productive area extends 1000s of km east of the plateau and is mediated by the eastward advection of the ACC and by mesoscale activity. In an east-west band, north of the Kerguelen Plateau and mainly upstream, a productive area corresponding to the region north of the SAF is also observed. Except for high biomasses of small pelagic fish (myctophids, main prey of elephant seal, Cherel et al. 2008) and zooplankton reported in circumpolar fronts (Pakhomov et al. 1994, Pakhomow and Froneman 2000, Labat et al. 2002), very little information is available on mid-trophic level distribution in the Southern Ocean. For highest trophic levels, large satellite tracking effort revealed that numerous predators (including seals and seabirds) prospected the circumpolar frontal system and intensively use the area east of Kerguelen to forage (see the review Bost et al. 2009).

Tracking and behaviour of elephant seals

At-sea distribution and behaviour of southern elephant seals from Kerguelen Island, south Indian Ocean, were monitored using satellite devices. Adult elephant seals performed two foraging trips during their year cycle. After breeding on land in September-October, seals performed a 2-3 months post-breed foraging trip and they return to land to moult in December-January. After the moult they remained at sea for an extended 7-8 month foraging trip building up their body reserves for the next breeding season. We consider thus two periods when at-sea: post-breeding, PB (October-December) and post-moult, PM (January-August). These two periods corresponded to different conditions of biological activity in the Kerguelen Plateau area, i.e. the phytoplankton bloom period for PB and the succeeding, more oligotrophic period during PM. Since males spent most of their trips on the Kerguelen/Antarctic shelves and did not exhibit pelagic foraging strategy (Bailleul et al. 2010), we excluded them from the following analyses. Consequently, only PB and PM females were taken into account in this study.

Animals were captured using a canvas head-bag and anaesthetized with a 1:1 combination of tiletamine and zolazepam (Zoletil 100) injected intra-venously (McMahon et al., 2000; Field et al., 2002). They were fitted with Conductivity Temperature Depth Data Loggers (CTD-SRDLs, dimensions:105 x 70 x 40 mm, 545g, cross-sectional area 28 cm²) designed and manufactured by the Sea Mammal Research Unit (SMRU, University of St Andrews, Boehme et al. 2009). The housings of devices were pressure-rated to 2000m and data were sampled every 5 seconds; however, since the limited throughput via the Argos satellite system does not allow all records to be transmitted, a pseudo-random method was used to schedule the transmission of an unbiased data sample of the stored records (Fedak 2004). The devices were glued on the heads of seals using quick-setting epoxy (Araldite AW 2101), once the hair had been cleaned with acetone. A total of 42 equipped female elephant seals travelled in the region of open ocean fronts of the Antarctic Circumpolar Current. Individuals were equipped before their departure for PB (N=18 individuals) or PM (N=24 individuals) foraging trip from 2005 to 2011. This study was approved by the ethics committee of the French Polar

Institute (IPEV).

In order to estimate seal behaviour at sea, the only available data are Argos tracking measurements. Tracking data consist of locations in a 3D-space (longitude, latitude, time) that are observed (i) with error and (ii) irregularly through time. The estimation of seal foraging behaviour relies on the concept of area restricted search (ARS) characterized by sinuous horizontal movements (Kareiva and Odell 1987). Hence, intensive foraging behaviour can be identify by slow displacement and ARS, and extensive behaviour corresponds to the travelling phases of seals' tracks (fast and directed movements). Previous studies have shown that improvements in body conditions occur after the display of ARS along the seals' tracks (Dragon et al. 2012). Even if foraging events are not exclusively restricted to ARS behaviour in elephant seals (Thums et al. 2011, Schick et al. 2013a), the identification of ARS allows to catch the most profitable foraging periods in a track (Dragon et al. 2012). We will use hereafter the terminology “intensive foraging” vs “travelling” to refer to the two distinct seal behavioural states. We used the Bayesian state-space framework developed by Jonsen et al. (2003, 2005) to simultaneously deal with the Argos measurement errors and the statistically sound estimation of seal behaviour. The switching state-space model relies on a transition equation and a measurement one (see details in Jonsen et al. 2005, Block et al. 2011). The transition equation relates the unobserved behavioural states from one time step to the next, given regular time steps every 6 hours. And the measurement equation links the behavioural states to the observed data, i.e. changes in move direction and speed inferred from the location data. For each individual seal, the state-space model was computed with freely available software WinBUGS (Bayesian Analysis Using Gibbs Sampler, Spiegelhalter et al. 1999) called from R (R Development Core Team 2009) with the package R2WinBUGS (Sturtz et al. 2005).

Dynamic environment of elephant seals

In order to describe the surface (sub-)mesoscale dynamic environment explored by seals and identify their habitat preference according behavioural modes, we used a multisatellite analysis of physical oceanic characteristics (similarly to De Monte et al. 2012).

- *Satellite data (A summary of satellite data used in this study is given in table 1)*:

Sea-surface currents were derived from satellite sea-surface altimetry data. We used the surface velocities computed from weekly merged products of absolute dynamic topography (ADT) at ⅓° resolution on a Mercator projection (Ssalto-Duacs) distributed by Archiving Validation and Interpretation of Satellite and Oceanographic data (AVISO, http://www.aviso.oceanobs.com). The absolute dynamic topography is obtained by satellite-derived anomalies to which the Rio et al. (2011) mean dynamic topography is added.

Sea surface temperature (SST) was derived from the Advanced Microwave Scanning Radiometer - Earth Observing System (AMSR-E) sensor on NASA's Aqua satellite (http://wwwghcc.msfc.nasa.gov/AMSR/). We used 25km resolution, 3 day composites gridded images. A key feature of AMSR-E is its detection capabilities through cloud cover (excluding precipitation events), thereby providing a practically uninterrupted view of the global SST field.

As single satellite products of Chlorophyll a (Chl *a*) concentration contain large spatial gaps because of the extensive cloud coverage in the Southern Ocean, we used weekly composite products at 9 km resolution provided by GlobColour (http://www.globcolour.info/), which merges data from SeaWiFS, Moderate Resolution Imaging Spectroradiometer (MODIS), and the Medium Resolution Imaging Spectrometer Instrument (MERIS). Climatologies of Chl *a* concentration for the bloom period from October to December (corresponding to the PB period of elephant seals), and the post-bloom period from January to August (corresponding to the PM period of seals) were then constructed.

- Lagrangian diagnostics of ocean dynamics

Since we focused on horizontal circulation properties to quantify the history of water parcels, we used Lagrangian diagnostics. This methodology is based on the construction of fluid particle trajectories from satellite-derived velocity field (see below).

1. At regional scale: Advection of waters which supported the bloom

Since southern elephant seals feed predominantly on small pelagic fish in the inter-frontal region (Cherel et al. 2008), it is essential to take into account the prey field. However, few information is available on mid-trophic organisms in this area. To cope with this lack of information on resources, we consider primary production as a proxy of regional biological richness together with the trophic lag between primary production and the intermediate trophic levels. Indeed, a lag time corresponding to the biomass flux through the trophic cascade needs to be considered for zooplankton and small pelagic fish. We attempted here to track biologically rich waters during the oligotrophic period after the spring bloom. During the post-bloom period, corresponding to homogeneously weak surface Chl *a* values in the whole study area, we built a diagnostic to distinguish water masses which had supported the bloom during spring from water masses which remained oligotrophic during the entire year. In order to achieve this we implemented a simple Lagrangian scheme by which the Chl *a*-rich pixels in spring-time GlobColour images are labelled as blooming waters and are then advected by altimetry-derived surface currents in the post-blooming months. More specifically, in order to define the patch of blooming waters which initialized the advection model (i.e., the situation at t_0) we built a climatology of mean Chl *a* concentration for December from 2005 to 2011 and we applied a threshold of 0.5 mg.m^{-3}. Then, these Chl *a*-rich waters were advected from January to August (i.e. during the PM period of elephant seals) by using Lagrangian trajectories computed from altimetry-based velocity fields.

2. Sub-mesoscale fronts

Our intention was to examine the preference of seals for sub-mesoscale transport fronts, often referred to as Lagrangian Coherent Structures (LCSs, see Haller and Yuan, 2000; details on biological implications in Tew-Kaï et al. 2009, De Monte et al. 2012, Cotté et al. 2011). To detect these fronts, acting as transport barriers for particle trajectories, we used a Lagrangian reanalysis of altimetry-derived surface currents: the finite-size Lyapunov exponent (FSLE) method (Boffetta et al. 2001, d'Ovidio et al. 2004, see also d'Ovidio et al. 2013, Sec. 2.1 for a review of the Lyapunov exponents applied to altimetry and for more details on the method). This method measures the rate of divergence of trajectories initialized for each point in space and time at small distances (in our case, in the range 1-10 km). The FSLE is simply defined as:

$$\lambda = \frac{1}{\tau}\log\frac{\delta_f}{\delta_0} \qquad (1)$$

where δ_0 is the separation of the initial positions of two trajectories, δ_f is their prescribed final separation, and τ is the first time at which a separation of δ_f is reached. Therefore, the Lyapunov exponent has the dimension of time^{-1}. When computed backward in time, its value corresponds to the timescale of the frontogenesis between the scale δ_0 and δ_f induced by horizontal stirring. Typical FSLE values along filament boundaries correspond to the range 0.1 - 1 day^{-1} (Lehahn et al. 2007). Altimetry-derived surface velocities are an approximation of the surface velocity field as they only detect the geostrophic component and have a limited spatio-temporal resolution. Therefore, mismatches in the order of a few km between altimetry-derived fronts and tracer fronts must be expected (d'Ovidio et al. 2009). For this reason, we used δ_0 = 10 km and chose δ_f = 40 km, which is smaller than eddy radii detected by altimetry (see Cotté et al. 2011 for details).

3. Mesoscale distribution of Sea-Surface Temperature

A latitudinal gradient of sea surface temperature (SST) characterizes the circumpolar waters of the Southern Ocean and particularly within the ACC. We used SST as a tracer of latitudinal movement of waters and describe seal thermal preference relative to the mesoscale surrounding area. Following De Monte et al. 2012, we computed downscaled (i.e. at a higher spatial resolution of 10 km) images of SST as a result of stirring with altimetry-based velocities AMSR-E images (resolution of 25 km) in analogy to what has been previously proposed with surface salinity (Despres et al. 2011). This method permits reconstruction of the SST field including the effects of the mesoscale turbulence by horizontal stirring and amplifies horizontal mesoscale gradients from low-resolution SST images.

4. Mesoscale water displacement by horizontal advection

The diagnostic using the horizontal advection (i.e. transport by currents) is based on the property of eddies to present transport properties relative to the global and strong flow of the ACC (Naveira Garabato et al. 2011). Since coherent eddies carry water along and across the fronts of the ACC, we estimated the longitudinal and latitudinal water displacement induced by horizontal stirring. Elephant seal were presumably affected by this mesoscale displacement of waters:

- Longitudinally (west-east axis), the aim is to segregate stable features from the global eastward jet of the ACC as an indicator of coherent and long-lived eddies (Chelton et al. 2011). This type of eddy is hypothesized to support local ecosystems where biological production cascades up through the food web attracting high trophic level organisms (e.g. Godø et al.

2012).

- Latitudinally (north-south axis), stable features can also be detected as the ACC eastward flow is deviated southeastward by the Kerguelen Plateau (Park et al. 2009). Intrusion of waters across fronts can also be detected through their southward or northward transport. This cross-front circulation can have a positive effect on biological distribution and production, especially by modifying the mixed-layer depth, but also because eddies trap and transport fluid parcels with different properties from those of the surrounding waters, creating strong mesoscale fronts (Strass et al. 2002). These physical processes are assumed to affect the vertical distribution and densities of prey and influence seal behaviour.

To characterize the origin of water parcels, we computed the trajectory and distance between particle locations at time t and their estimated origin at $t_0=t$-50 days (d). Because the displacement time of an eddy on the basis of its length scale is on average 1 month in the ACC (Park et al. 2002, Fu 2009), we chose a 50 d backward-in-time advection to avoid bias due to recirculation within eddies. Longitudinal and latitudinal displacements at a given location were interpreted as following: (*i*) positive and negative longitudinal displacements correspond respectively to water advected westward and eastward; (*ii*) positive and negative latitudinal displacements correspond respectively to poleward and equatorward horizontal transport.

Statistical Analyses

Using the multi-year large tracking dataset on elephant seal movements from Kerguelen, we were able to investigate the relationships between animal behaviour (travelling *vs* intense foraging) and physical environmental properties (transport fronts, mesoscale SST distribution and displacement of waters) for different periods of the elephant seal annual cycle (PB *vs* PM corresponding to bloom and oligotrophic conditions respectively). In practical terms, we extracted each satellite-derived physical environmental property at the seal location in space and accurate date in time, and compared it with the value in the surrounding mesoscale environment to highlight a possible difference. We interpreted observed differences as a preference for a given physical parameter characterizing environmental features of interest for seals. Before proceeding with statistical analyses, we normalized the data across individuals due to differing ranges of these physical parameters. Indeed seals explored large areas where SST presents an important latitudinal range over the different water masses, and dynamic circulation parameters (transport fronts and displacement of water parcels) exhibited heterogeneous pattern accordingly ACC areas. Thus we applied a standardization by subtracting the mean of these physical parameters estimated over an animal trajectory from the measurements at each position and dividing by its standard deviation (SD) to obtain a mean of 0 and an SD of 1 (Zuur et al. 2007).

Generalized additive models (GAMs, Hastie and Tibshirani 1990) were used to examine the response of seals to the standardized physical parameters. A GAM is a non-parametric regression technique useful for investigating non-linear relationships between response variables and covariates within the framework of studying species–habitat relationships (Guisan et al. 2002). It offers flexibility through smoothing terms applied to the explanatory variables to fit the model (Wood and Augustin 2002, Wood 2003). As we were interested in examining the preferences of seals, we inspected the relationship and functional form of each physical parameter according distance to seal locations. Smoothing splines were fitted using multiple generalized cross-validation (MGCV). The amount of flexibility given to a model term is determined in a maximum likelihood framework by minimizing the generalized cross-validation (GCV) score of models. Because we treated individuals as a random effect due to the variability among seals, we used generalized additive mixed models (GAMMs, Wood 2004). A GAMM inference relies upon independence between observations. However, this assumption is often violated because the conditions at each location of an animal's tracking are not independent to those at the previous location, which could result an underestimation of the uncertainty associated with model estimates. We have thus considered serial autocorrelation in the data for each physical parameter, and we incorporate an autocorrelation term in models. When data were not normally distributed (Shapiro-Wilks tests, $p<0.05$) the model was specified with a Poisson distribution and a logarithmic-link function (otherwise, a Gaussian distribution was used). Each physical parameter was averaged for 15 concentric annular sectors of 10km wide around each location, with distances ranging from 0 to 150km (i.e. 0-10 for the first band to 140-150km for the last band).

Because of the numerous results obtained from the combinations between periods, behaviours and physical parameters, we summarized them using the following methodology. As described in the Figure 3, the seal location was defined as the region within 30km of the Argos seal position in order to take into account errors of satellite-derived Lagrangian measures (derived from the [⅓]° resolution altimetry data). The surrounding region was defined as the region between 30km and 100km of the seal, which is the spatial dimension (radius) of eddies in this area (Park et al. 2002) and has been identified as a major scale for predator foraging activities (Fritz et al. 2003, Pinaud & Weimerskirch 2008, Weimerskirch et al. 2007). A mean of the physical parameters were estimated in these two regions at each seal location. In order to test the significance of the difference between the two areas, i.e. whether a seal preference can be inferred or not, we performed two-sample (Student) *t*-tests.

Finally, difference of Chl *a* at seal location *vs* Chl *a* within the whole area defined by animal longitudinal and latitudinal ranges were tested using two-sample Kolmogorov-Smirnov (KS) test. The analysis using the diagnostic of bloom waters advection differed from the other diagnostics explained previously: we estimated the proportion of seal locations in poor *vs* rich waters, i.e. advected waters with low and high Chlorophyll concentrations during the bloom, when travelling and foraging.

Results

Seal regional distribution and their seasonal environment

At regional scales, female elephant seals exhibited a clear preference in exploring waters east of Kerguelen, 15 individuals out of 18 during PB and 16 out of 24 during PM (Fig. 1a and 1b). Most animals travelled south of the SAF, however, several individuals, particularly those displaying intense foraging behaviour, were localized northerly in the area east of Kerguelen. The important difference between the PB and PM period was the maximum range, i.e. the distance from the colony, reached by seals. Animals were able to travel long distances (thousands of kms) and to reach very remote regions during both periods despite the duration of PM period being almost double that of PB period. Maximum distance from the colony was about twofold during PM compared to the PB period (3750km *vs* 1760km respectively). The mean swim speed of seals was 0.87 (± 0.49 std) $m.s^{-1}$ (~75 $km.day^{-1}$) during travelling and 0.50 (± 0.33 std) $m.s^{-1}$ (~43 $km.day^{-1}$) during foraging, although the speed is probably underestimated due to the distance computed along a theoretical straight line between two re-estimated locations of 6h interval.

Seals were located within the most productive areas (areas with high Chl-*a* values, i.e. higher than the value of $0.5mg.m^{-3}$ in the climatology) of the ACC during the PB period, which coincides with the seasonal spring bloom of phytoplankton (KS-test, $p>0.05$; Fig. 2a). Part of the trip or the whole trip of most individuals were located within the high Chl-*a* plume in the area just east of Kerguelen. Several individuals prospected outside the Kerguelen plume but still in other productive areas around the Kerguelen Plateau. However, during the PM period, the distribution of seals did not match the high Chl-*a* areas (KS-test, $p<0.001$; Fig. 2b) and their locations corresponded to lower Chl-*a* than during PB (Fig. 2c). Figure 4 shows the estimated position of waters which supported the bloom after 1 to 8 months from the bloom, together with positions and behaviour of seals during their PM trip. While the biologically rich waters moved eastward from January to August, seals tracked them over time especially for foraging purpose (Fig. 4, lower panel and small panels for travelling/foraging location proportions in rich/poor waters). A large proportion of seal locations is included in rich waters comparatively to poor waters, especially for foraging behaviour, whereas rich waters did not dominated the area. Seal locations were firstly closely associated with waters from the productive Kerguelen plume from January to March-April. From May, the northern region corresponding to upstream advected waters appears to be another favourable area for foraging of the seals. From January to April, animals travel more in rich waters (due to long distance migrations east of Kerguelen plateau) while they spend more time to forage in these waters from May to August. These results provided evidence that the origin of the waters where animals forage, particularly through an enrichment of the trophic chain from the bottom, appeared to be an important driver of seal foraging during PM migration corresponding to the post-bloom period.

Seal preferences at the (sub-)mesoscale

Since the distribution pattern differed according the periods of the year, we examined seal preferences for physical environmental properties (transport fronts, mesoscale SST distribution and displacement of water parcels) during PB and PM separately. The results detailed hereafter indicate a fundamental difference in the ecology of seals for the two periods (blooming/PB *vs* post-blooming/PM). From GAMMs and Student's *t*-tests analyses, significant seal preferences at the mesoscale were obtained only during the PM period (Fig. 5 and 6).

During the PM period, i.e. after the bloom, statistical analyses revealed several significant preferences (Fig. 5, 6b and 6d). The difference between SST at seal locations and the surrounding environment indicates that they travelled and foraged in colder surface waters (Fig. 5 and 6b). The behavioural distinction (travelling *vs* foraging) was crucial in the investigation of the following relationship with transport fronts and the displacement of water parcels relative to the flow of the ACC. When travelling, seals were strongly associated with transport fronts as the FSLEs on their trajectories were significantly larger than in the surrounding environment (Fig. 5 and 6b). While seal travelling was not linked to water displacement (Fig. 6b and low correlation in GAMM analysis in Fig. 5), the intensive foraging mode was associated to longitudinal positive transport anomalies and latitudinal negative transport anomalies indicative of stable (i.e. here slowly advected) and long-lived water patches relative to the global southeastward flow of the ACC (Fig. 5 and 6d). These waters could also be characterized by a southern origin corresponding to northward intrusion across circumpolar fronts of the ACC. This was coherent with the previous relationship on seal preference for low temperatures at mesoscale because northward intrusion across fronts advects cold water into warmer surrounding environment.

These significant preferences by seals for specific (sub-)mesoscale features highlighted during the PM period are illustrated in Fig. 7 for a seal trajectory in July 2005, where an individual reached an eddy located at the SAF. This part of the trip, lasting 3 weeks, is overlaid on daily sub-mesoscale fronts, SST and displacement of water parcels. The mesoscale eddy targeted by this seal to forage intensively was a long-lived (weeks to months) feature and propagated much slower than the surrounding waters which moved southeastward along the global flow of the ACC. The presence of cold waters in this feature can be explained by its southern origin. As an example of the link between daily seal travelling and corresponding transport fronts, an animation in the supplementary material shows simultaneously the trajectory, the behaviour and the transport fronts identified by large FSLEs.

Discussion

By analysing the long-term tracking dataset of southern elephant seals covering the whole annual cycle together with multi-satellite environmental data, we have provided new insights on the flexible foraging of predators relative to mesoscale and sub-mesoscale features. Several previous studies reported spatial co-location between various marine top predators and (sub-)mesoscale features, implying a generic influence of fronts and eddies (Sims 1998, Nel et al. 2001, Weimerskirch et al. 2004, Polovina 2006, Cotté et al. 2007, Tew-Kaï et al. 2009). Dissimilar distribution, foraging behaviour and flexible movements of marine predators were observed over time and especially between seasons suggesting different foraging strategies (Hays et al. 2006, Villegas-Amtmann et al. 2011). Thanks to the multi-year and homogeneous dataset we analysed here, our results suggest an elaborate picture. As illustrated by the preferences of elephant seals identified at the mesoscale, we inferred two seasonally-contrasted foraging strategies interpreted hereafter in the context of the highly dynamic ACC. They ultimately lead to building hypotheses on the circulation influences on ecosystems, and particularly for higher trophic levels.

1) Contrasted foraging strategies rely on seasonally-contrasted biological environment.

Our first finding highlights the contrasted seasonal difference in the relationship between the behaviour of elephant seals and (sub-)mesoscale circulation. This statement relies on the absence of clear preference by seals for (sub-)mesoscale features during the late spring – early summer period (i.e. PB trip) while significant relationships were identified during the late summer, fall and winter period (i.e. PM trip). We suggest that this seasonal change was indicative of a change in the prey field distribution relative to (sub-)mesoscale circulation, rather than a change in prey items consumed by southern elephant seals. Indeed, our results were consistent with the absence of changes in the trophic position of southern elephant seal females over the annual cycle, i.e. PB *vs* PM periods. Isotopic analyses reported a large predominance of mesopelagic fish, the myctophids, in the diet of female elephant seals during the two periods (Cherel et al. 2008, Chaigne et al. 2012).

We hypothesized that the two contrasted trophic conditions, here in terms of primary production, during the bloom period and from the bloom onwards induced a fundamental difference in foraging strategies of elephant seals. The most evident seasonal environmental signal was the increase in biological production occurring in late spring – early summer on the Kerguelen shelf and the eastward area (i.e. the so-called Kerguelen plume). When at-sea during the PB period, seal distribution coincided strikingly in time with the phytoplankton bloom and overlapped with the range of the large Kerguelen Chl-a plume (Mongin et al. 2008, Dragon et al. 2011). However, we failed to identify any relationship between the dynamic circulation from physical parameters and the foraging activity of the seals during this period. This result was consistent with independent findings showing that PB elephant seals females equipped with head-mounted accelerometers to detect prey capture attempts acquire resources at nearly constant rates during that period (Guinet et al. 2014); similar results were recently shown for northern elephant seals during the same period (Naito et al. 2013). Whereas primary production was under the influence of mesoscale motion (Strass et al. 2002), the time lag relative to phytoplankton development was probably too short to reach the highest trophic levels during the bloom period. Since we found no preference for the (sub-)mesoscale circulation during the PB period, we proposed that the distribution of marine biota including seal prey may be sufficiently concentrated at the scale of Kerguelen bloom (about 1500km) to ensure an efficient resource acquisition by the seals. Therefore we argue that during this period the prey field may be relatively homogeneous and dense within the plume and adjacent productive areas where resources presented a low spatial structure.

We then found that PM elephant seals were still influenced by the spring bloom that had occurred upstream (i.e. the Kerguelen plume and the productive northern area) several months earlier and that had progressively drifted eastward. While mismatches between phytoplankton and higher trophic levels were often observed (Jacquet et al. 1996, Guinet et al. 2001, Suryan et al. 2012), elephant seals actively tracked post-bloom waters advected by the global flow of the ACC as the season progress. We argue that the marine ecosystem develops, matures and cascades up to higher trophic levels within these waters where fish congregate. As the time from the bloom elapsed, these productive waters were increasingly stirred by the mesoscale activity with other waters where lower biological activity occurs. This process was likely to induce an increasingly heterogenous pattern in the prey field. Such emerging patchiness occurring in the post-bloom season may lead to contrasted resource distribution differing from the spring-early summer, in agreement with the association between seals' behaviour and (sub-)mesoscale physical features occurring in the post-bloom season only. Interestingly, the process we described here (development of ecosystems while they are transported by currents) is similar to what is simulated in high resolution trophic models which use the advective properties of the ocean to predict the location of secondary production and higher trophic level organisms (Sibert et al. 1999, Maury et al. 2007, Lehodey et al. 2008). These models could be utilized to assess our hypothesis of an increasing patchiness at (sub-)mesoscale of organisms at mid- and high trophic levels as the time from the spring bloom elapses.

2) The (sub-)mesoscale circulation affects the foraging strategy of post-moulting elephant seals

During the PM period seals exhibited clear (sub-)mesoscale preferences while either in travelling and intensive foraging modes. Within the ACC where seals searched for their prey, the little information available on mid-trophic levels reported that (*i*) the maximun densities of zooplankton and myctophids were encountered in the Polar Frontal Zone and (*ii*) that zooplankton is patchily distributed (Pakomov et al. 1994, Pakhomov and Froneman 2000, Labat et al. 2002). Within the favourable circumpolar frontal system (Biuw et al. 2007), previous works have already reported that elephant seals significantly selected eddies, with an apparent preference for the cold cyclonic structures (Campagna et al. 2006, Bailleul et al. 2010, Dragon et al. 2010). However all encountered eddies were not used intensively, suggesting that the preference for an eddy could be related to differences in the physical properties and/or "life history" of these eddies.

PM seals were found to travel preferentially in transport fronts and colder surface waters. These properties defined cold filaments as physical features used by seals for moving between intensive foraging bouts and finding the most profitable areas. A strong mesoscale activity occured in the eastern area of Kerguelen (Kostianoy et al. 2003, Langlais et al. 2011). Stirring creates a strong filamentary field induced by numerous eddy-eddy interactions. These filaments are elongated structures reaching hundreds of kilometres in length and widths of ~10 km. Filaments may have water properties similar to those eddies from which they stem but are also associated to strong advection (Lapeyre et al. 1999, Lapeyre and Klein 2006, Legal et al. 2007). Whereas most previous studies attributed such associations mainly for foraging purposes (Sims 1998, Tew Kaï et al. 2009, Cotté et al. 2011, Nordstrom et al. 2012), we found that elephant seals were associated to sub-mesoscale fronts while travelling. Based on these results, two hypotheses (not necessarely alternative) may be formulated: (*i*) seals may use these filaments of cold water as an environmental tracer to reach cold patches which may offer favourable foraging conditions; and/or (*ii*) seals' trajectories could be stretched by advection during their displacements along frontal structures when they swim in the vicinity of a filament. Concerning the first hypothesis, temperature appeared in our analysis as an important physical tracer of features of interest for seals (also reported by McIntyre et al. 2011, Bestley et al. 2012). A sharp change in water temperature associated to cold filaments could act as a local environmental cue and/or modulate prey distributional characteristics that can serve to reach favourable mesoscale features (Benoit-Bird et al. 2013). Beside the indirect effect of these sub-mesoscale physical features as cues, filaments were reported to carry high zooplankton densities (Labat et al. 2009, Perruche et al. 2011). Similarly, the fine-scale analysis of seabird behaviour recently suggested the use of fronts to both sustain movements of animals and locate prey-enriched filaments (De Monte et al. 2012). Seals may therefore temporally exploit rich filaments to reach the most profitable mesoscale features where higher prey densities occurred. The second hypothesis relies on the effect of transport fronts that are often areas of high current velocities likely to influence animal trajectories and estimated behaviours based on observed displacements (Gaspar et al. 2006, Fossette et al. 2012).

Favourable foraging eddies targeted by elephant seals were stable relative to the global eastward flow of the ACC. Eddy motion within the ACC propagates eastward considerably more slowly than the surface mean flow (Naveira Garabato et al. 2011). This horizontal transport property characterized coherent and long-lived eddies. Several studies have stressed the influence of long-lived mesoscale eddy history (age and pathway) together with seasons to explain the distribution and communities of zooplankton (Govoni et al. 2011) and small pelagic fish (Brandt 1983). The centre of cyclonic eddies and the edges of anticyclonic eddies were reported to be enriched in organisms of different trophic levels (Biggs 1992, Riandley et al. 2005, Landry et al. 2008, Benitez-Nelson and McGillicuddy 2008). Elephants seals could benefit from the enhanced local biological production and aggregation of prey created by stable mesoscale features that permit efficient resource acquisition influencing individual parameters and ultimately populations (New et al. 2014).

Recent investigations on circulation properties proposed retention as a possible physical parameter with ecological implication (d'Ovidio et al. 2013), involved in the so-called “ocean triad" enrichment–concentration–retention (Bakun 2006) that hypothetically increases the biological production from phytoplankton to higher trophic levels. Retention in particular allows the trophic development and the maintenance of spatially restricted marine ecosystems. All these findings suggested the importance of (sub-)mesoscale coherent features for the foraging strategy of top predators. Finally we have focused on both horizontal index of predator foraging strategy and horizontal properties of circulation. Future studies will examine the vertical dimension especially to better assess the foraging success of top predators through diving behaviour relative to their dynamic environment (Bailleul et al. 2008, Dragon et al. 2012, Thums et al. 2012, Schick et al. 2013b, Guinet et al. 2014).

Conclusion

Pelagic ecosystems can be fundamentally disrupted by multiple current threats (e.g. climate change, overfishing and pollution). Taking into account the spatio-temporal variability and dynamic nature of the marine environment in management planning is crucial and makes the conservation of the open ocean realm challenging (Game et al. 2009, Zydelis et al. 2011). This statement is especially relevant in remote areas such as the Southern Ocean where the consequences of environmental change have been already observed on at-sea behaviour of marine wildlife (e.g. response of foraging performances of albatrosses to the wind pattern, Weimerskirch et al. 2012). Because of their position in pelagic ecosystems, understanding how *marine top predators* exploit their complex environment and which oceanographic processes drive their foraging strategy is of primary importance to extrapolate to ecosystems (Boyd 2006). Due to a significant lack of data, very little information is available on mid-trophic levels in particular and there is a strong need to address this gap since it affects our understanding of ecosystem functioning (Handegard et al. 2012). Open ocean ecosystem understanding and predictions rely with growing importance on the development of ecosystem models that take into account the coupling between marine organisms and ocean dynamics. Results obtained on predators contribute significantly into identifying mechanistic processes of physical-biological interactions that could be included and improve ecosystem models.

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Table 1. Summary of the oceanographic remotely sensed data sets

Oceanographic parameter	Satellite	Spatial and temporal resolution	Link (URL)
Absolute dynamic topography	Topex-Poseidon - Jason - Envisat - GFO	Space: ⅓° (~30km) time: week	http://www.aviso.oceanobs.com
Sea surface temperature	AMSRE	space: 25 km time: 3-days	http://wwwghcc.msfc.nasa.gov/AMSR/
Chlorophyll *a* concentration	SeaWiFS - MODIS - MERIS	space: 9 km time: daily	http://www.globcolour.info/

Figure Captions

Fig. 1. Large-scale patterns of elephant seal distribution overlaid on bathymetry. Foraging trips of elephant seals equipped between 2005 and 2011 from Kerguelen during a) post-breeding period (September-December) and b) post-moulting period (January-August). Travelling (extensive behaviour) and foraging (intensive behaviour) bouts of trips are respectively in black and red. The main fronts of the Southern Ocean are indicated from the north to the south: Southern Sub-Tropical Front (STF), Sub-Antarctic Front (SAF), and Polar Front (PF).

Fig. 2. Large-scale patterns of elephant seal distribution and Chlorophyll concentration climatologies between 2005 and 2011. See caption of figure 2 for trajectories details. Climatologies of Chlorophyll concentration (from GlobColour products) are computed during (a) the bloom period (September-December) corresponding to post-breeding of seals and (b) the post-bloom period (January-August) corresponding to seal post-moulting. White lines display 1000m-bathymetric contours. c) Frequency distribution of Chlorophyll concentration extracted under seal locations from the climatologies during the bloom (continuous line) and post-bloom (dashed line) periods.

Fig. 3. Illustration of the areas defining seal location (distance from seal <30km) and mesoscale surrounding environment (30km< distance <100km) around each Argos location along seal trajectories used for physical parameters extraction.

Fig. 4. Multi-year (2005-2011) bi-monthly tracking of elephant seals overlaid on the distribution of waters which supported the phytoplankton bloom, in green (high Chlorophyll concentrations, i.e. > mean value of 0.5 mg.m^{-3}, from satellite data during the bloom period in December) in a forward-in-time advection. Travelling and foraging (intensive behaviour) locations are shown in black and red respectively. Histograms represent their proportion (same color) in low and high Chlorophyll concentrations. The lower graph shows the monthly evolution (y-axis) of the longitudinal range (x-axis) of both seals while foraging (gray dots) and waters which supported phytoplankton bloom (square is the bi-monthly longitudinal average and arrows are 10 and 90% quantiles) within the 50°S-55°S latitudinal band.

Fig. 5. Fitted GAMM results showing the functional form of each physical covariate (y-axis) according the distance for post-moulting female elephant seal locations (x-axis) during travelling and foraging behaviours. The solid lines are the smooth function estimates and the dashed lines represent 95% confidence intervals. Only significant relationships were displayed with resulting *F*-tests and *p*-values (*p<0.05, **p<0.01, ***p<0.001, N.S.: not significant).

Fig. 6. Preference of seals for sub-mesoscale fronts, temperature (SST), longitudinal (WD[lon]) and latitudinal (WD[lat]) displacement of water parcels during post-breeding (a,c) and post-moulting (b,d) when seals travelled (a, b) and when they foraged (c, d). Dark gray bars described mean properties of waters within 30 km of seal location while light gray bars represent the 30-100 km surrounding environment. Error bars are standard deviations and t-tests between seal location and surrounding areas are indicated when significant (*p<0.05, **p<0.01, ***p<0.001).

Fig. 7. Case study showing a part of an elephant seal trip (3weeks, from June 28 2005 to July 20 2005) overlaid on daily a) sub-mesoscale transport fronts (FSLEs in day^{-1}), b) SST (in °C), c) longitudinal, and d) latitudinal displacement of water parcels in a 50 d backward-in-time advection at halfway through the trip part (July 8 2005). Travelling (extensive behaviour) and foraging (intensive behaviour) bouts of trips are respectively in black and red.

Figure1

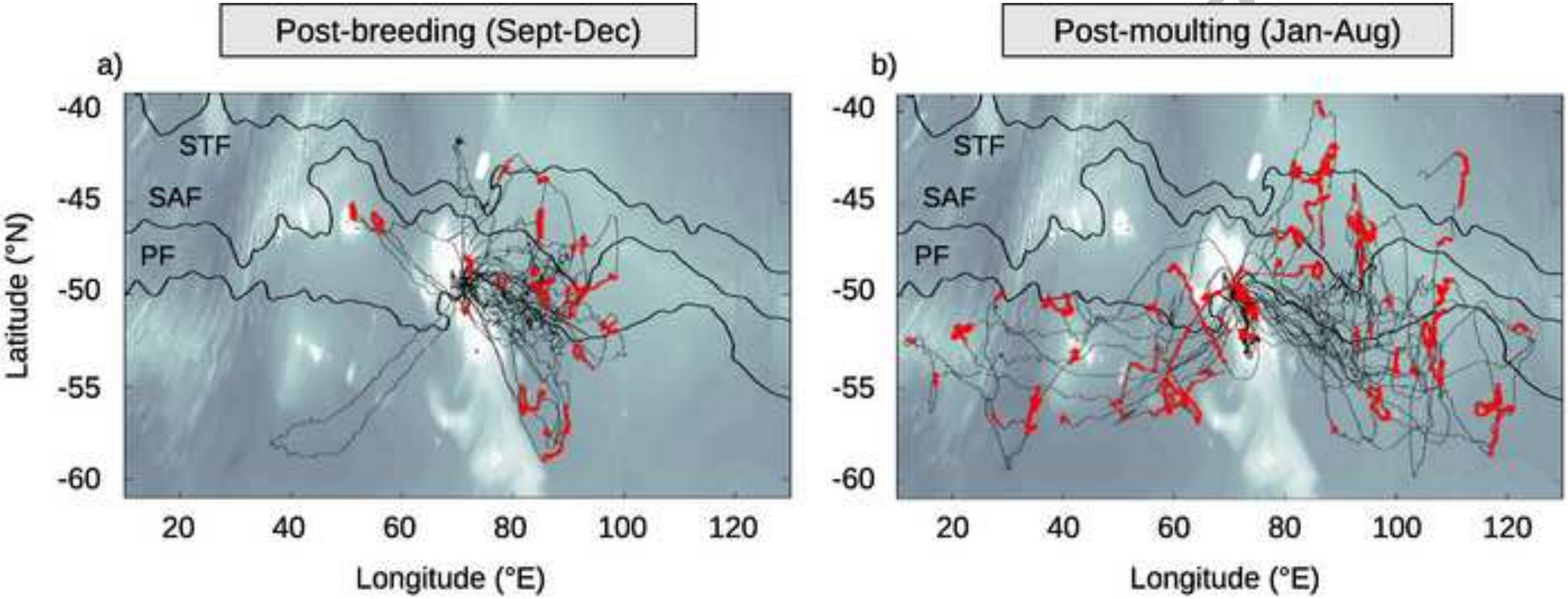
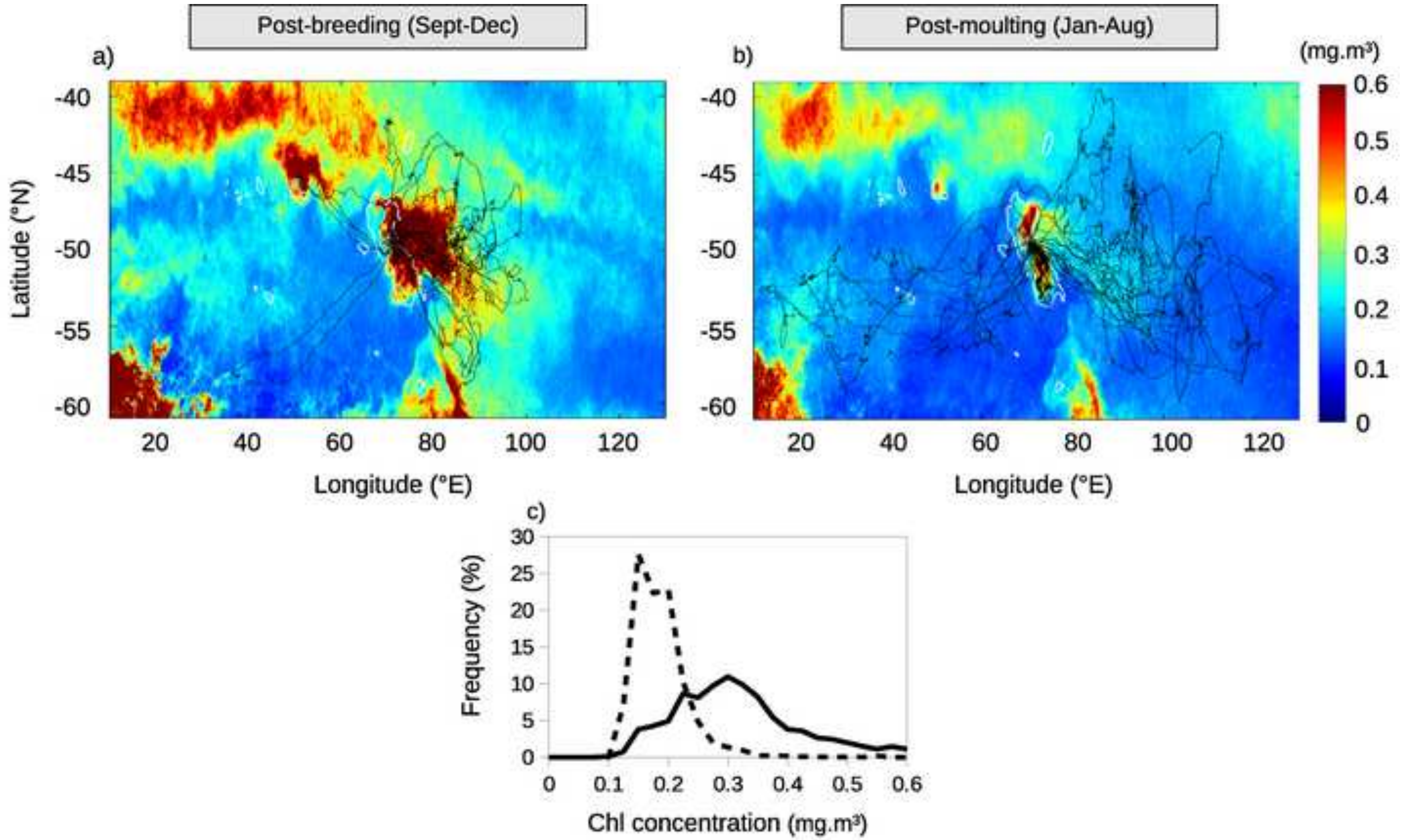

Post-breeding (Sept-Dec)
Post-moulting (Jan-Aug)
a)
b)
STF
SAF
PF
Latitude (°N)
-40
-45
-50
-55
-60
20
40
60
80
100
120
Longitude (°E)

Figure2


Post-breeding (Sept-Dec)

Post-moulting (Jan-Aug)

Figure3

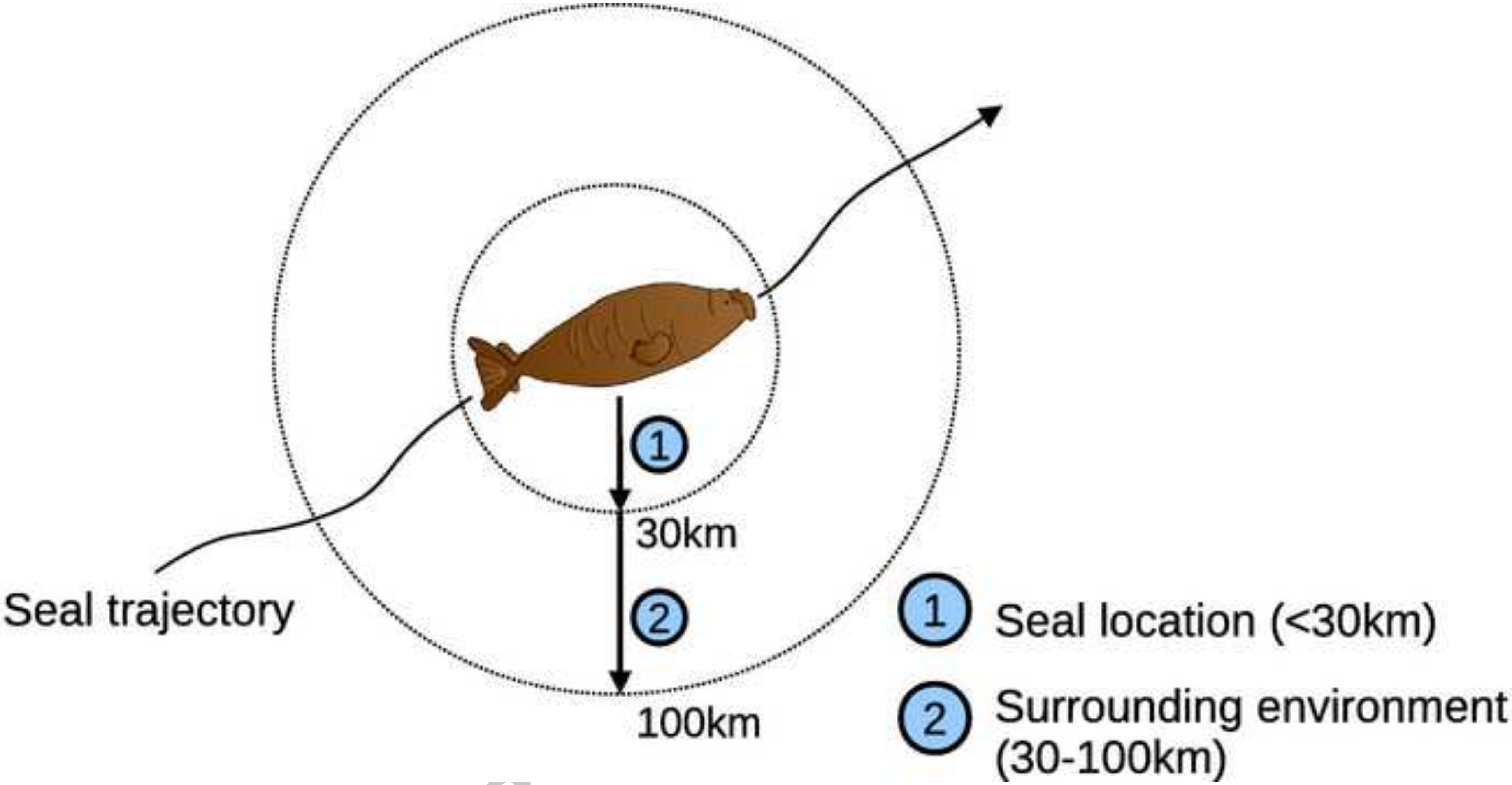

1
30km
2
100km
Seal trajectory
1 Seal location (<30km)
2 Surrounding environment (30-100km)

Figure4

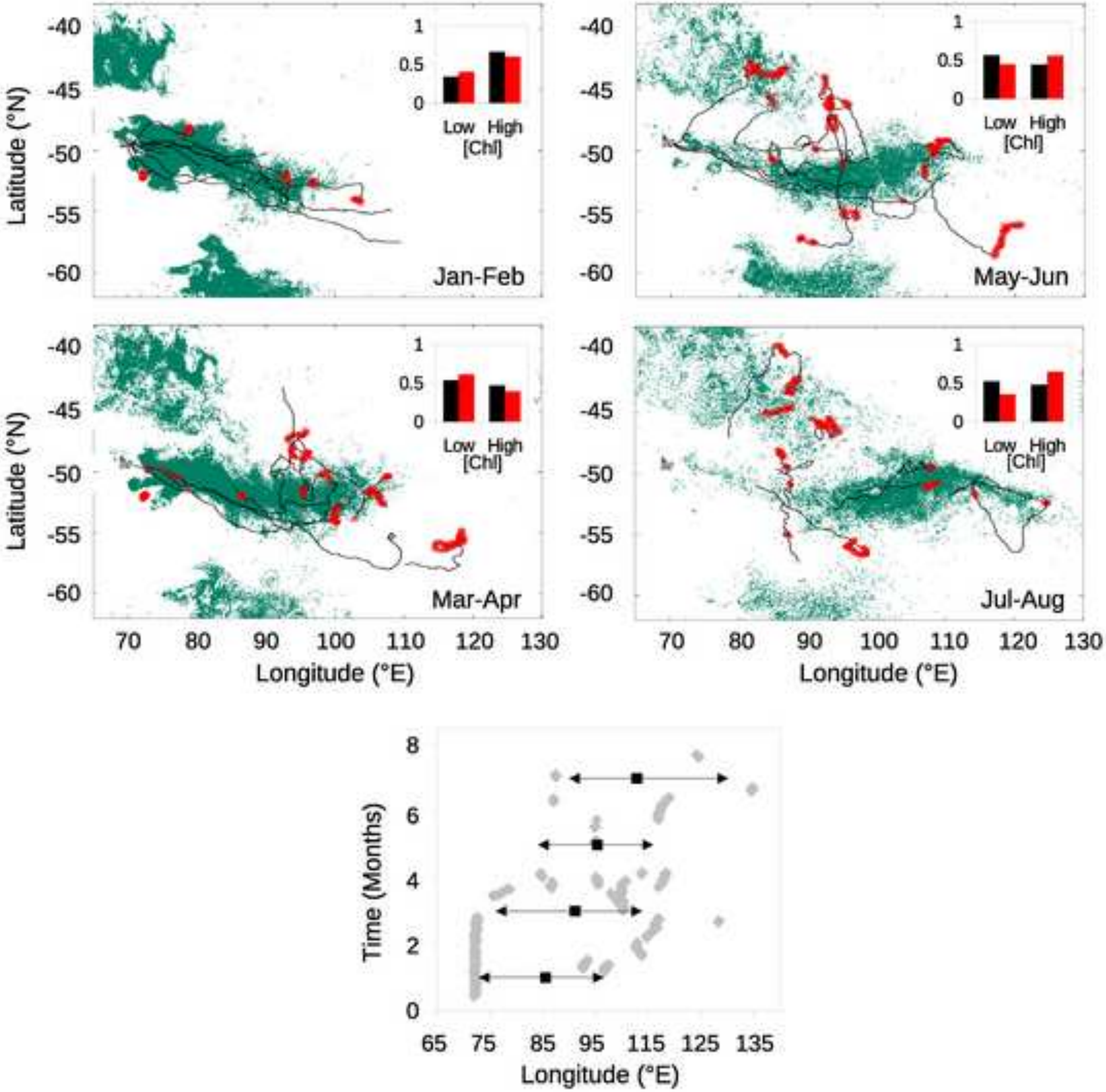

Latitude (°N)
-40
-45
-50
-55
-60
1
0.5
0
Low
High
[Chl]
Jan-Feb
May-Jun
Mar-Apr
Jul-Aug
70
80
90
100
110
120
130
Longitude (°E)
Time (Months)
0
2
4
6
8
65
75
85
95
115
125
135
Longitude (°E)

Figure5

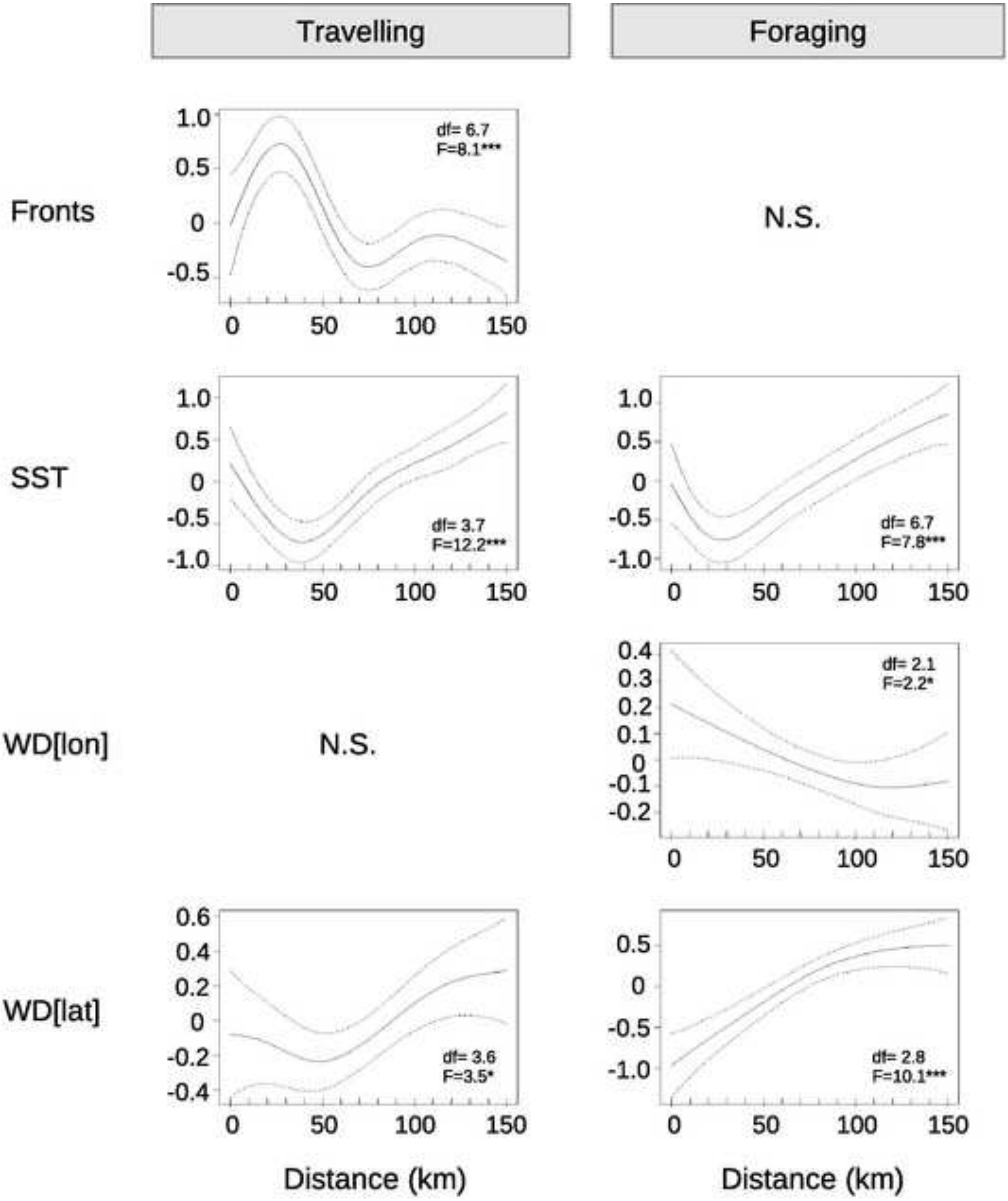

Travelling
Foraging
Fronts
df= 6.7
F=8.1***
1.0
0.5
0
-0.5
0
50
100
150
N.S.
SST
1.0
0.5
0
-0.5
-1.0
df= 3.7
F=12.2***
0
50
100
150
1.0
0.5
0
-0.5
-1.0
df= 6.7
F=7.8***
0
50
100
150
WD[lon]
N.S.
0.4
0.3
0.2
0.1
0
-0.1
-0.2
df= 2.1
F=2.2*
0
50
100
150
WD[lat]
0.6
0.4
0.2
0
-0.2
-0.4
df= 3.6
F=3.5*
0
50
100
150
0.5
0
-0.5
-1.0
df= 2.8
F=10.1***
0
50
100
150
Distance (km)
Distance (km)

Figure6

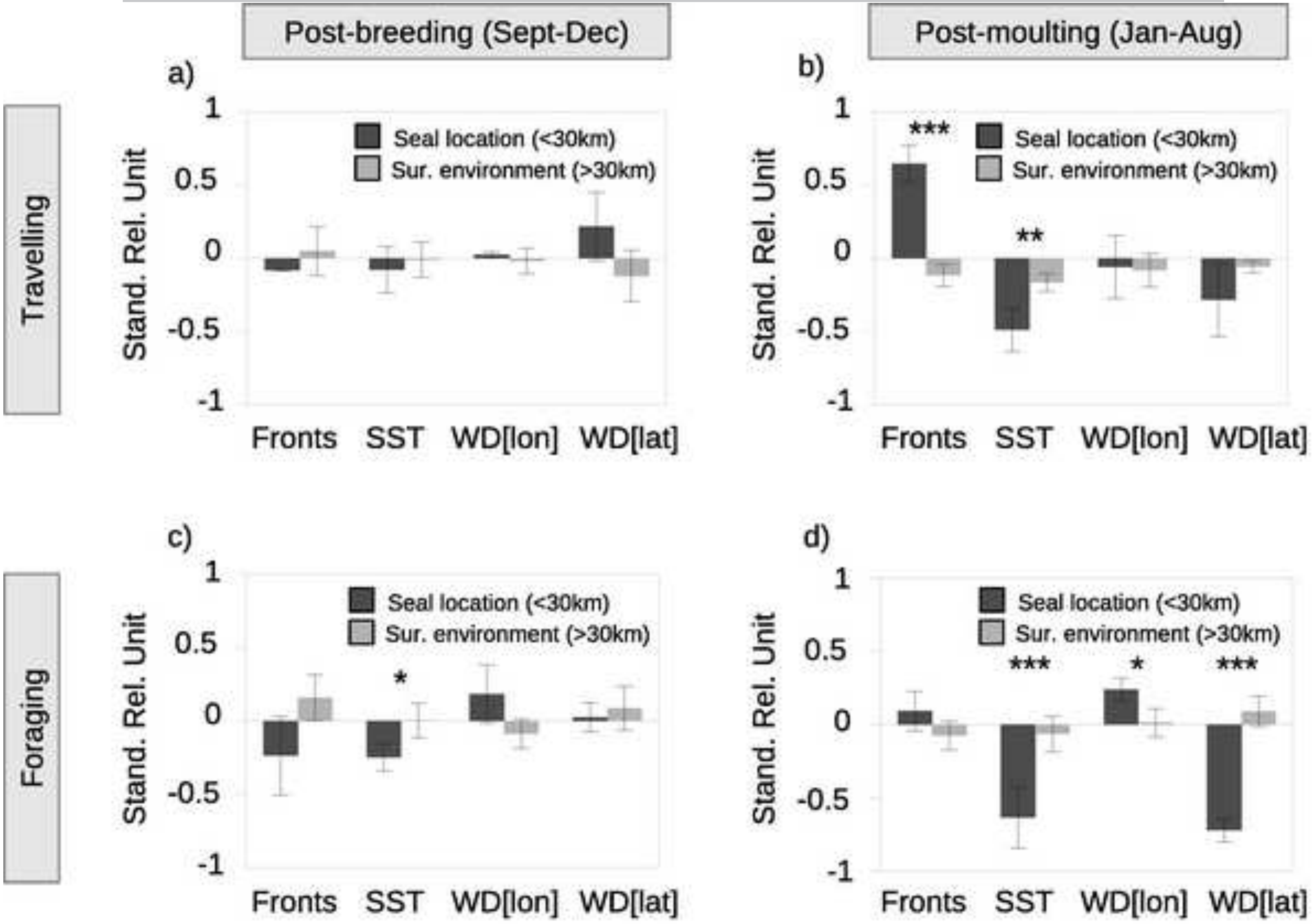
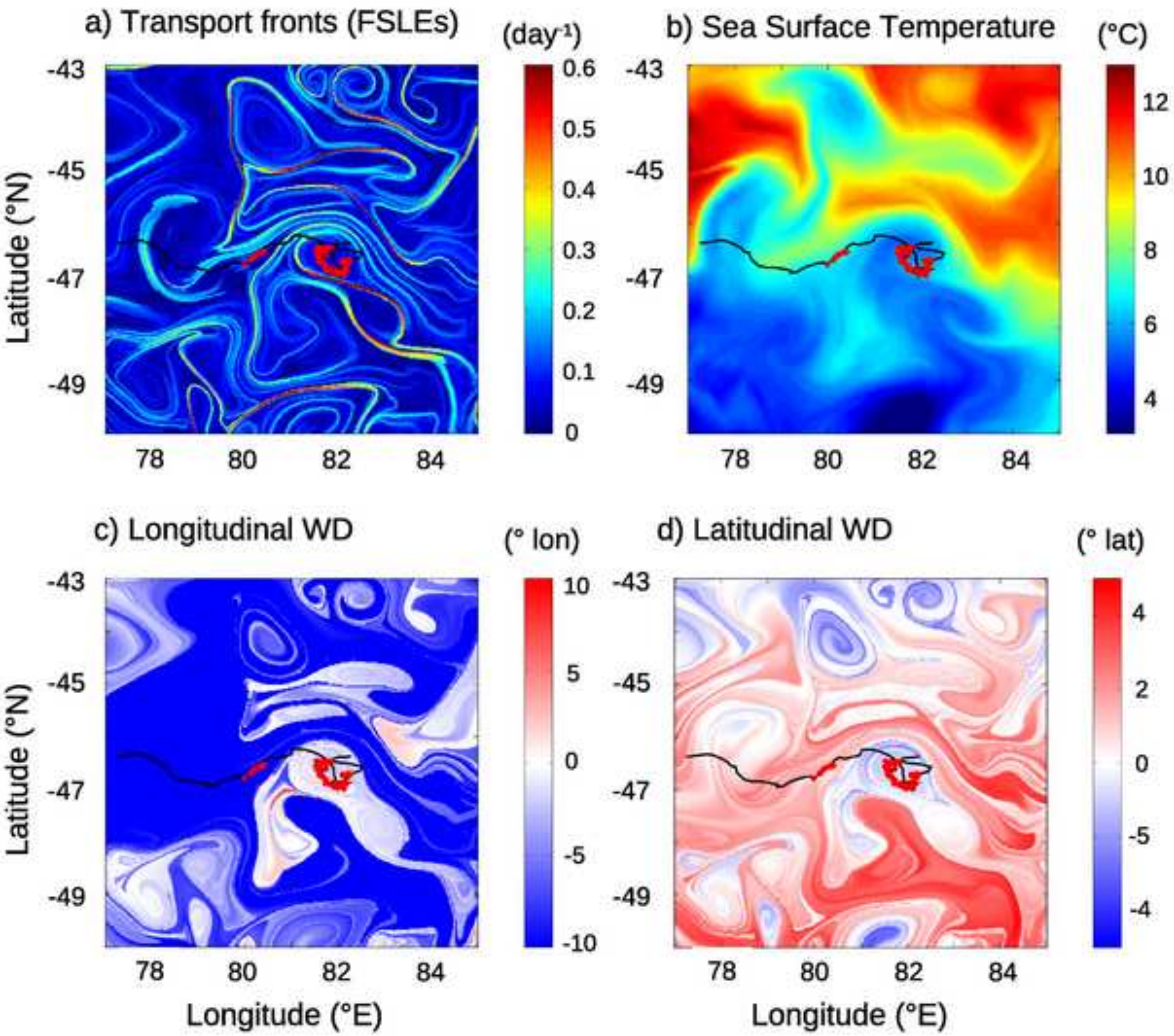
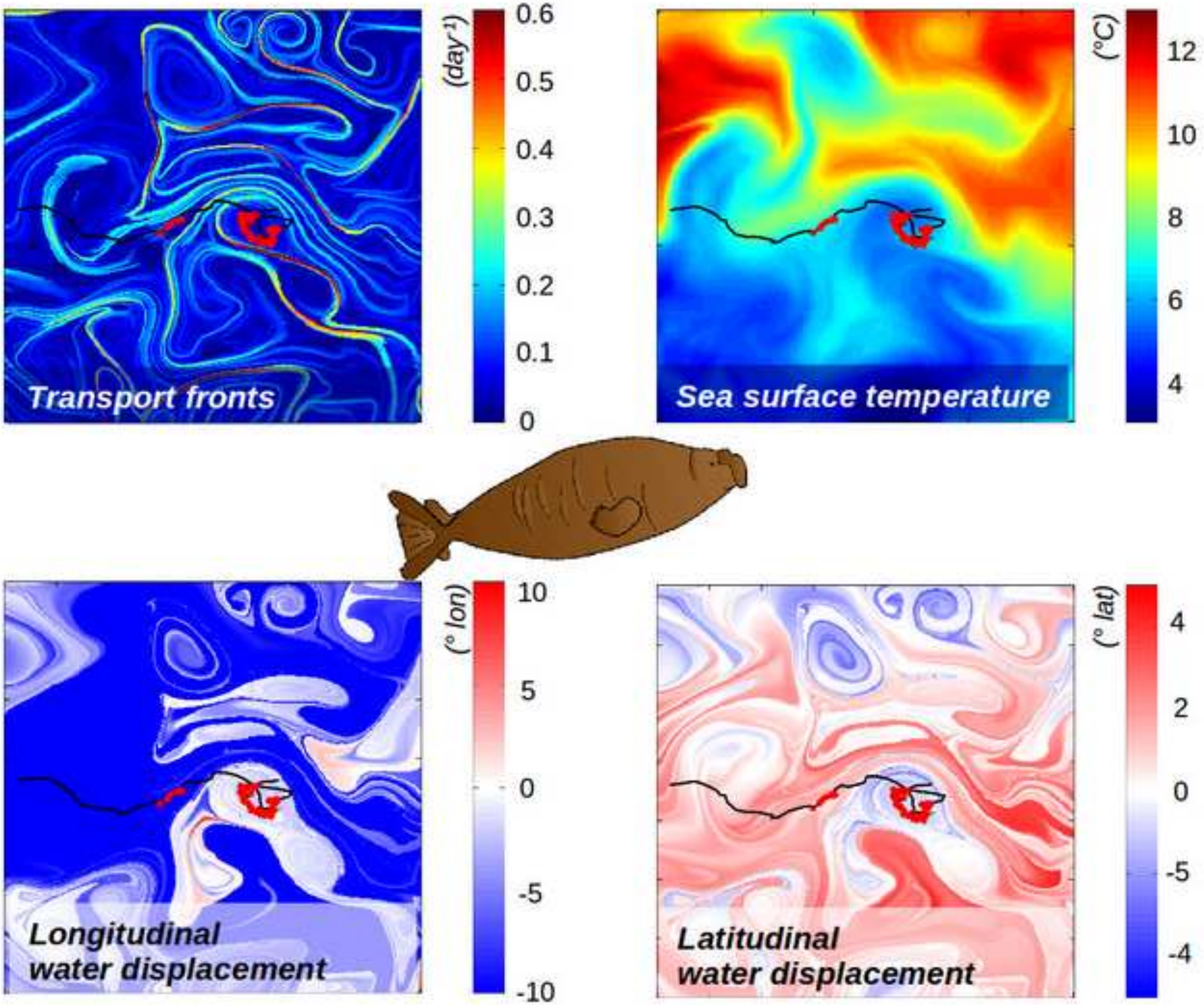

Post-breeding (Sept-Dec)
Post-moulting (Jan-Aug)
Travelling
Foraging
a)
b)
c)
d)
Stand. Rel. Unit
1
0.5
0
-0.5
-1
Seal location (<30km)
Sur. environment (>30km)
***
**
*
***
*
***
Fronts
SST
WD[lon]
WD[lat]

Figure7


a) Transport fronts (FSLEs)
(day-1)
0.6
0.5
0.4
0.3
0.2
0.1
0
b) Sea Surface Temperature
(°C)
12
10
8
6
4
c) Longitudinal WD
(° lon)
10
5
0
-5
-10
d) Latitudinal WD
(° lat)
4
2
0
-5
-4
Latitude (°N)
-43
-45
-47
-49
78
80
82
84
Longitude (°E)


Transport fronts
(day⁻¹)
0.6
0.5
0.4
0.3
0.2
0.1
0
Sea surface temperature
(°C)
12
10
8
6
4
Longitudinal water displacement
(° lon)
10
5
0
-5
-10
Latitudinal water displacement
(° lat)
4
2
0
-5
-4

Highlights

1. The mesoscale behavioural preferences of female southern elephant seals are seasonally flexible
2. No environmental preference emerged when postbreeding seals distributed in blooming waters
3. Postmoult seals travelled along thermal fronts and foraged in stable mesoscale waters
4. Favorable patches correspond to waters which have supported the bloom during spring
5. Dynamic circulation of the ACC influenced the foraging strategies of top predators