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

Cédric Cotté, Francesco d'Ovidio, Anne-Cécile Dragon, Christophe Guinet, Marina Lévy

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1 **Flexible preference of southern elephant seals for distinct**  
2 **mesoscale features within the Antarctic Circumpolar**  
3 **Current**

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7 Cédric Cotté<sup>a\*</sup>, Francesco d'Ovidio<sup>a</sup>, Anne-Cécile Dragon<sup>b</sup>, Christophe Guinet<sup>b</sup>, Marina Lévy<sup>a</sup>

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12 <sup>a</sup>Sorbonne Universités (UPMC, Univ Paris 06)-CNRS-IRD-MNHN, LOCEAN Laboratory, 4

13 place Jussieu, F-75005 Paris, France

14

15 <sup>b</sup>Centre d'Études Biologiques de Chizé, CEBC, CNRS, Villiers en Bois, France

16

17

18 \*Corresponding author: [cotte.cc@gmail.com](mailto:cotte.cc@gmail.com)

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21 Short title: Flexible mesoscale elephant seal preference

22 **Abstract**

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

## 45 **Introduction**

46           The seemingly homogeneous seascape is a patchy and highly variable physical-  
47 biological environment in space and time (Haury et al. 1978, Mann and Lazier 2006). An  
48 intense source of variability occurs through oceanic eddies (hereafter ‘mesoscale’ features,  
49 ~50-200 km and weeks to months) and filaments (hereafter ‘sub-mesoscale’ features 1-10 km  
50 and days to weeks), often referred to as the “internal weather systems of the ocean”  
51 (McGillicuddy 2001). This complex circulation shapes the distribution of waters and largely  
52 controls biogeochemical fluxes as well as the distribution, abundance and composition of the  
53 marine life (e.g., Angel and Fasham 1983, Strass et al. 2002, Godø et al. 2012). The biological  
54 responses of lower trophic levels, i.e. phytoplankton, to (sub-)mesoscale (terminology used to  
55 described both mesoscale and sub-mesoscale) physical processes are well documented (e.g.,  
56 Strass et al. 2002, Lévy 2008, d’Ovidio et al. 2010, Lévy et al. 2012). Numerous studies have  
57 shown the influence of eddies and sub-mesoscale structures on the distribution and the spatio-  
58 temporal dynamics of phytoplankton, mainly through vertical movements of water masses and  
59 enrichment of the surface layer (McGillicuddy et al. 1998, Oschiles and Garcon 1998, Strass et  
60 al. 2002, Levy 2008, Lehahn et al. 2007, Lévy et al. 2012). Recently, the concept of fluid  
61 dynamical niches has emerged, describing how transport properties, particularly physical fronts  
62 induced by horizontal stirring, drive the complex mesoscale distribution of phytoplankton  
63 communities (d’Ovidio et al. 2010). But is this dynamic structuring, previously identified at the  
64 lower trophic level, relevant for the whole ecosystem, i.e. across trophic webs and particularly  
65 for top predators? Indeed, while plankton species are passively advected, top predators are  
66 highly mobile and move actively. Their at-sea distribution is thus the result of behavioural  
67 choices (Le Boeuf et al. 2000, Biuw et al. 2010, Sharples et al. 2012, Wakefield et al. 2013).  
68 Recent studies proposed that eddies catalyse energy transfer across trophic levels and can be  
69 considered as oases for higher trophic marine life (i.e., Godø et al. 2012). We investigated here  
70 how horizontal properties associated with mesoscale circulation, as inferred from satellite-  
71 derived analyses, drive the distribution and behaviour of a top predator.

72           Advances in satellite tracking technology during the last two decades have provided  
73 important information on distribution and behaviour of several marine top predators. Large  
74 tagging programs described the large scale movements of oceanic predators, and their  
75 collection into multispecies hotspots provides the foundation for spatial management of large

76 marine ecosystems (Murphy et al. 2007, Bost et al. 2009, Block et al. 2011, Hindell et al. 2011,  
77 Fedak 2012). While tracking of predators was originally episodic, systematic remote  
78 monitoring now provides robust insights on their ecology and habitat at finer scales (e.g. Bost  
79 et al. 2009). In the meantime, remote satellite-derived measurements processed with  
80 appropriate analytical tools have improved the understanding of open ocean circulation (e.g.  
81 d'Ovidio et al. 2009, Chelton 2011). During the last decade, higher trophic levels, and  
82 especially top predators, were increasingly reported to be associated to the mesoscale and sub-  
83 mesoscale features. There is now evidences of the influence of eddies and associated fronts on  
84 the distribution and movements of various top predators such as turtles (Polovina et al. 2006,  
85 Lombardi et al. 2008), marine mammals (Bradshaw et al. 2004, Ream et al. 2005, Cotté et al.  
86 2011, Woodworth et al. 2011 Nordstrom et al. 2012), and seabirds (Nel et al. 2001,  
87 Weimerskirch et al. 2004, Cotté et al. 2007, Tew-Kai et al. 2009, De Monte et al. 2012).  
88 However, the relationships between both distribution and behaviour of animals and  
89 oceanographic processes at such scales remain unclear and largely under-investigated.

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

106 Using a multi-year satellite tracking database, we investigated the at-sea distribution

107 and behaviour of southern elephant seals (*Mirounga leonina*) in order to identify in which type  
108 of oceanographic structures they preferentially travelled and foraged within the intense eddy  
109 field of the Antarctic circumpolar Current (ACC). The database on elephants seals is unique  
110 among all predators within the Southern Ocean as the year-long tracking offers the opportunity  
111 to examine the flexible foraging preferences across seasons. Southern elephant seals spend  
112 90% of their lifetime at sea where they continuously dive to an average of 500m (Campagna et  
113 al. 1999, McIntyre et al. 2010). They feed predominantly on small pelagic fish in pelagic areas  
114 (Cherel et al. 2008). Their two long and distant trips per year last several months and cover the  
115 whole annual cycle, so that it is possible to study seal preferences for oceanographic (sub-  
116 )mesoscale structures under contrasted environmental conditions within the ACC. The ACC is  
117 the dominant physical feature of the Southern Ocean and a complex physical environment  
118 where elephant seals encounter numerous biophysical processes. They have to adjust their  
119 foraging behaviour while they encounter (sub-)mesoscale features on the timescale of their at-  
120 sea trip. Previous studies have identified eddies as favourable features for foraging elephant  
121 seals (Campagna et al. 2006, Simmons et al. 2007, Bailleul et al. 2010, Dragon et al. 2010). It  
122 is still unknown what are the physical characteristics of the few targeted structures per trip of  
123 seals in a dynamic field such as the ACC where numerous eddies occur (“dynamic” is used  
124 here and hereafter to refer to the intense mesoscale variability as described in Kostianoy et al.  
125 2003). Sub-mesoscale and mesoscale features with specific properties could have strong  
126 ecological implications because they could potentially generate high prey densities and  
127 favourable conditions for the development of food webs underpinning the presence of top  
128 predators. The purpose of this study was thus to propose a characterization of these  
129 oceanographic structures through the history of water parcels encountered by seals. To achieve  
130 a description of water dynamic history, we employed multisatellite Lagrangian diagnostics  
131 which measure properties of water parcels along seal trajectories, such as transport fronts,  
132 mesoscale temperature distribution and displacement rates of water parcels. We addressed this  
133 issue by examining seal preferences for distinctive (sub-)mesoscale features characterized by  
134 these specific transport or circulation properties within the ACC in relation to seasonal  
135 conditions and behavioral modes.

136 **Methods**137 ***Regional context: Circulation and biological activity in the southern Indian ocean***

138 - *Physical environment*: In the southern Indian Ocean, the circumpolar frontal system  
139 structures water masses latitudinally (depicted in Fig. 1). Going from north to south, the system  
140 includes the Subtropical front (STF), the Subantarctic Front (SAF), and the Polar Front (PF),  
141 the last two related to the jets of the ACC. The Kerguelen Plateau acts as a major physical  
142 barrier that breaks and deflects the strong eastward flow of the ACC (Park et al. 2008,  
143 McCartney and Donohue 2007, Roquet et al. 2009). In the eastern area of the plateau, the ACC  
144 flows southeastward, and associated fronts have the same orientation (Park et al. 2008, Roquet  
145 et al. 2009). Because of the intensity of the ACC along the entire length of the fronts, intensive  
146 meandering occurs and leads to important mesoscale and sub-mesoscale activity (Stammer  
147 1998, Moore and Abbott 2000, Park et al. 2002, Kostianoy et al. 2003, Sokolov and Rintoul  
148 2007). While the intrinsic zonal propagation of eddies is mainly westward in oceans, they  
149 propagate predominantly eastward within the ACC (Park et al. 2002, Fu 2009, Chelton et al.  
150 2011).

151

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

167 prospected the circumpolar frontal system and intensively use the area east of Kerguelen to  
168 forage (see the review Bost et al. 2009).

169

### 170 *Tracking and behaviour of elephant seals*

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

184 Animals were captured using a canvas head-bag and anaesthetized with a 1:1  
185 combination of tiletamine and zolazepam (Zoletil 100) injected intra-venously (McMahon et  
186 al., 2000; Field et al., 2002). They were fitted with Conductivity Temperature Depth Data  
187 Loggers (CTD-SRDs, dimensions: 105 x 70 x 40 mm, 545g, cross-sectional area 28 cm<sup>2</sup>)  
188 designed and manufactured by the Sea Mammal Research Unit (SMRU, University of St  
189 Andrews, Boehme et al. 2009). The housings of devices were pressure-rated to 2000m and data  
190 were sampled every 5 seconds; however, since the limited throughput via the Argos satellite  
191 system does not allow all records to be transmitted, a pseudo-random method was used to  
192 schedule the transmission of an unbiased data sample of the stored records (Fedak 2004). The  
193 devices were glued on the heads of seals using quick-setting epoxy (Araldite AW 2101), once  
194 the hair had been cleaned with acetone. A total of 42 equipped female elephant seals travelled  
195 in the region of open ocean fronts of the Antarctic Circumpolar Current. Individuals were  
196 equipped before their departure for PB (N=18 individuals) or PM (N=24 individuals) foraging  
197 trip from 2005 to 2011. This study was approved by the ethics committee of the French Polar



198 Institute (IPEV).

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

221

### 222 ***Dynamic environment of elephant seals***

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

226

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

228 Sea-surface currents were derived from satellite sea-surface altimetry data. We used the

229 surface velocities computed from weekly merged products of absolute dynamic topography  
230 (ADT) at  $\frac{1}{8}^\circ$  resolution on a Mercator projection (Ssalto-Duacs) distributed by Archiving  
231 Validation and Interpretation of Satellite and Oceanographic data (AVISO,  
232 <http://www.aviso.oceanobs.com>). The absolute dynamic topography is obtained by satellite-  
233 derived anomalies to which the Rio et al. (2011) mean dynamic topography is added.

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

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

248

249 - *Lagrangian diagnostics of ocean dynamics*

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

253

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

255 Since southern elephant seals feed predominantly on small pelagic fish in the inter-  
256 frontal region (Cherel et al. 2008), it is essential to take into account the prey field. However,  
257 few information is available on mid-trophic organisms in this area. To cope with this lack of  
258 information on resources, we consider primary production as a proxy of regional biological  
259 richness together with the trophic lag between primary production and the intermediate trophic

260 levels. Indeed, a lag time corresponding to the biomass flux through the trophic cascade needs  
 261 to be considered for zooplankton and small pelagic fish. We attempted here to track  
 262 biologically rich waters during the oligotrophic period after the spring bloom. During the post-  
 263 bloom period, corresponding to homogeneously weak surface Chl *a* values in the whole study  
 264 area, we built a diagnostic to distinguish water masses which had supported the bloom during  
 265 spring from water masses which remained oligotrophic during the entire year. In order to  
 266 achieve this we implemented a simple Lagrangian scheme by which the Chl *a*-rich pixels in  
 267 spring-time GlobColour images are labelled as blooming waters and are then advected by  
 268 altimetry-derived surface currents in the post-blooming months. More specifically, in order to  
 269 define the patch of blooming waters which initialized the advection model (i.e., the situation at  
 270  $t_0$ ) we built a climatology of mean Chl *a* concentration for December from 2005 to 2011 and  
 271 we applied a threshold of  $0.5 \text{ mg}\cdot\text{m}^{-3}$ . Then, these Chl *a*-rich waters were advected from  
 272 January to August (i.e. during the PM period of elephant seals) by using Lagrangian  
 273 trajectories computed from altimetry-based velocity fields.

274

## 275 2. Sub-mesoscale fronts

276 Our intention was to examine the preference of seals for sub-mesoscale transport  
 277 fronts, often referred to as Lagrangian Coherent Structures (LCSs, see Haller and Yuan, 2000;  
 278 details on biological implications in Tew-Kaï et al. 2009, De Monte et al. 2012, Cotté et al.  
 279 2011). To detect these fronts, acting as transport barriers for particle trajectories, we used a  
 280 Lagrangian reanalysis of altimetry-derived surface currents: the finite-size Lyapunov exponent  
 281 (FSLE) method (Boffetta et al. 2001, d'Ovidio et al. 2004, see also d'Ovidio et al. 2013, Sec.  
 282 2.1 for a review of the Lyapunov exponents applied to altimetry and for more details on the  
 283 method). This method measures the rate of divergence of trajectories initialized for each point  
 284 in space and time at small distances (in our case, in the range 1-10 km). The FSLE is simply  
 285 defined as:

$$286 \lambda = \frac{1}{\tau} \log \frac{\delta_f}{\delta_0} \quad (1)$$

287 where  $\delta_0$  is the separation of the initial positions of two trajectories,  $\delta_f$  is their  
 288 prescribed final separation, and  $\tau$  is the first time at which a separation of  $\delta_f$  is reached.  
 289 Therefore, the Lyapunov exponent has the dimension of  $\text{time}^{-1}$ . When computed backward in

290 time, its value corresponds to the timescale of the frontogenesis between the scale  $\delta_0$  and  $\delta_f$   
291 induced by horizontal stirring. Typical FSLE values along filament boundaries correspond to  
292 the range 0.1 - 1 day<sup>-1</sup> (Lehahn et al. 2007). Altimetry-derived surface velocities are an  
293 approximation of the surface velocity field as they only detect the geostrophic component and  
294 have a limited spatio-temporal resolution. Therefore, mismatches in the order of a few km  
295 between altimetry-derived fronts and tracer fronts must be expected (d'Ovidio et al. 2009). For  
296 this reason, we used  $\delta_0 = 10$  km and chose  $\delta_f = 40$  km, which is smaller than eddy radii  
297 detected by altimetry (see Cotté et al. 2011 for details).

298

### 299 3. Mesoscale distribution of Sea-Surface Temperature

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

309

### 310 4. Mesoscale water displacement by horizontal advection

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

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

321 2012).

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

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

338

### 339 *Statistical Analyses*

340 Using the multi-year large tracking dataset on elephant seal movements from  
341 Kerguelen, we were able to investigate the relationships between animal behaviour (travelling  
342 vs intense foraging) and physical environmental properties (transport fronts, mesoscale SST  
343 distribution and displacement of waters) for different periods of the elephant seal annual cycle  
344 (PB vs PM corresponding to bloom and oligotrophic conditions respectively). In practical  
345 terms, we extracted each satellite-derived physical environmental property at the seal location  
346 in space and accurate date in time, and compared it with the value in the surrounding  
347 mesoscale environment to highlight a possible difference. We interpreted observed differences  
348 as a preference for a given physical parameter characterizing environmental features of interest  
349 for seals. Before proceeding with statistical analyses, we normalized the data across individuals  
350 due to differing ranges of these physical parameters. Indeed seals explored large areas where  
351 SST presents an important latitudinal range over the different water masses, and dynamic

352 circulation parameters (transport fronts and displacement of water parcels) exhibited  
353 heterogeneous pattern accordingly ACC areas. Thus we applied a standardization by  
354 subtracting the mean of these physical parameters estimated over an animal trajectory from the  
355 measurements at each position and dividing by its standard deviation (SD) to obtain a mean of  
356 0 and an SD of 1 (Zuur et al. 2007).

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

379 Because of the numerous results obtained from the combinations between periods,  
380 behaviours and physical parameters, we summarized them using the following methodology.  
381 As described in the Figure 3, the seal location was defined as the region within 30km of the  
382 Argos seal position in order to take into account errors of satellite-derived Lagrangian

383 measures (derived from the [ $\frac{1}{3}$ ] $^\circ$  resolution altimetry data). The surrounding region was defined  
384 as the region between 30km and 100km of the seal, which is the spatial dimension (radius) of  
385 eddies in this area (Park et al. 2002) and has been identified as a major scale for predator  
386 foraging activities (Fritz et al. 2003, Pinaud & Weimerskirch 2008, Weimerskirch et al. 2007).  
387 A mean of the physical parameters were estimated in these two regions at each seal location. In  
388 order to test the significance of the difference between the two areas, i.e. whether a seal  
389 preference can be inferred or not, we performed two-sample (Student) *t*-tests.

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



396 **Results**397 *Seal regional distribution and their seasonal environment*

398 At regional scales, female elephant seals exhibited a clear preference in exploring  
399 waters east of Kerguelen, 15 individuals out of 18 during PB and 16 out of 24 during PM (Fig.  
400 1a and 1b). Most animals travelled south of the SAF, however, several individuals, particularly  
401 those displaying intense foraging behaviour, were localized northerly in the area east of  
402 Kerguelen. The important difference between the PB and PM period was the maximum range,  
403 i.e. the distance from the colony, reached by seals. Animals were able to travel long distances  
404 (thousands of kms) and to reach very remote regions during both periods despite the duration  
405 of PM period being almost double that of PB period. Maximum distance from the colony was  
406 about twofold during PM compared to the PB period (3750km vs 1760km respectively). The  
407 mean swim speed of seals was  $0.87 (\pm 0.49 \text{ std}) \text{ m.s}^{-1}$  ( $\sim 75 \text{ km.day}^{-1}$ ) during travelling and  
408  $0.50 (\pm 0.33 \text{ std}) \text{ m.s}^{-1}$  ( $\sim 43 \text{ km.day}^{-1}$ ) during foraging, although the speed is probably  
409 underestimated due to the distance computed along a theoretical straight line between two re-  
410 estimated locations of 6h interval.

411 Seals were located within the most productive areas (areas with high Chl-*a* values, i.e.  
412 higher than the value of  $0.5 \text{ mg.m}^{-3}$  in the climatology) of the ACC during the PB period, which  
413 coincides with the seasonal spring bloom of phytoplankton (KS-test,  $p > 0.05$ ; Fig. 2a). Part of  
414 the trip or the whole trip of most individuals were located within the high Chl-*a* plume in the  
415 area just east of Kerguelen. Several individuals prospected outside the Kerguelen plume but  
416 still in other productive areas around the Kerguelen Plateau. However, during the PM period,  
417 the distribution of seals did not match the high Chl-*a* areas (KS-test,  $p < 0.001$ ; Fig. 2b) and  
418 their locations corresponded to lower Chl-*a* than during PB (Fig. 2c). Figure 4 shows the  
419 estimated position of waters which supported the bloom after 1 to 8 months from the bloom,  
420 together with positions and behaviour of seals during their PM trip. While the biologically rich  
421 waters moved eastward from January to August, seals tracked them over time especially for  
422 foraging purpose (Fig. 4, lower panel and small panels for travelling/foraging location  
423 proportions in rich/poor waters). A large proportion of seal locations is included in rich waters  
424 comparatively to poor waters, especially for foraging behaviour, whereas rich waters did not  
425 dominated the area. Seal locations were firstly closely associated with waters from the  
426 productive Kerguelen plume from January to March-April. From May, the northern region



427 corresponding to upstream advected waters appears to be another favourable area for foraging  
428 of the seals. From January to April, animals travel more in rich waters (due to long distance  
429 migrations east of Kerguelen plateau) while they spend more time to forage in these waters  
430 from May to August. These results provided evidence that the origin of the waters where  
431 animals forage, particularly through an enrichment of the trophic chain from the bottom,  
432 appeared to be an important driver of seal foraging during PM migration corresponding to the  
433 post-bloom period.

434

#### 435 *Seal preferences at the (sub-)mesoscale*

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

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

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

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468 **Discussion**

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

483

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

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

496 We hypothesized that the two contrasted trophic conditions, here in terms of primary  
497 production, during the bloom period and from the bloom onwards induced a fundamental  
498 difference in foraging strategies of elephant seals. The most evident seasonal environmental

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

517 We then found that PM elephant seals were still influenced by the spring bloom that had  
518 occurred upstream (i.e. the Kerguelen plume and the productive northern area) several months  
519 earlier and that had progressively drifted eastward. While mismatches between phytoplankton  
520 and higher trophic levels were often observed (Jacquet et al. 1996, Guinet et al. 2001, Suryan  
521 et al. 2012), elephant seals actively tracked post-bloom waters advected by the global flow of  
522 the ACC as the season progress. We argue that the marine ecosystem develops, matures and  
523 cascades up to higher trophic levels within these waters where fish congregate. As the time  
524 from the bloom elapsed, these productive waters were increasingly stirred by the mesoscale  
525 activity with other waters where lower biological activity occurs. This process was likely to  
526 induce an increasingly heterogenous pattern in the prey field. Such emerging patchiness  
527 occurring in the post-bloom season may lead to contrasted resource distribution differing from  
528 the spring-early summer, in agreement with the association between seals' behaviour and (sub-  
529 )mesoscale physical features occurring in the post-bloom season only. Interestingly, the process

530 we described here (development of ecosystems while they are transported by currents) is  
531 similar to what is simulated in high resolution trophic models which use the advective  
532 properties of the ocean to predict the location of secondary production and higher trophic level  
533 organisms (Sibert et al. 1999, Maury et al. 2007, Lehodey et al. 2008). These models could be  
534 utilized to assess our hypothesis of an increasing patchiness at (sub-)mesoscale of organisms at  
535 mid- and high trophic levels as the time from the spring bloom elapses.

536

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

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

550 PM seals were found to travel preferentially in transport fronts and colder surface  
551 waters. These properties defined cold filaments as physical features used by seals for moving  
552 between intensive foraging bouts and finding the most profitable areas. A strong mesoscale  
553 activity occurred in the eastern area of Kerguelen (Kostianoy et al. 2003, Langlais et al. 2011).  
554 Stirring creates a strong filamentary field induced by numerous eddy-eddy interactions. These  
555 filaments are elongated structures reaching hundreds of kilometres in length and widths of ~10  
556 km. Filaments may have water properties similar to those eddies from which they stem but are  
557 also associated to strong advection (Lapeyre et al. 1999, Lapeyre and Klein 2006, Legal et al.  
558 2007). Whereas most previous studies attributed such associations mainly for foraging  
559 purposes (Sims 1998, Tew Kai et al. 2009, Cotté et al. 2011, Nordstrom et al. 2012), we found  
560 that elephant seals were associated to sub-mesoscale fronts while travelling. Based on these

561 results, two hypotheses (not necessarily alternative) may be formulated: (i) seals may use these  
562 filaments of cold water as an environmental tracer to reach cold patches which may offer  
563 favourable foraging conditions; and/or (ii) seals' trajectories could be stretched by advection  
564 during their displacements along frontal structures when they swim in the vicinity of a  
565 filament. Concerning the first hypothesis, temperature appeared in our analysis as an important  
566 physical tracer of features of interest for seals (also reported by McIntyre et al. 2011, Bestley et  
567 al. 2012). A sharp change in water temperature associated to cold filaments could act as a local  
568 environmental cue and/or modulate prey distributional characteristics that can serve to reach  
569 favourable mesoscale features (Benoit-Bird et al. 2013). Beside the indirect effect of these sub-  
570 mesoscale physical features as cues, filaments were reported to carry high zooplankton  
571 densities (Labat et al. 2009, Perruche et al. 2011). Similarly, the fine-scale analysis of seabird  
572 behaviour recently suggested the use of fronts to both sustain movements of animals and locate  
573 prey-enriched filaments (De Monte et al. 2012). Seals may therefore temporally exploit rich  
574 filaments to reach the most profitable mesoscale features where higher prey densities occurred.  
575 The second hypothesis relies on the effect of transport fronts that are often areas of high  
576 current velocities likely to influence animal trajectories and estimated behaviours based on  
577 observed displacements (Gaspar et al. 2006, Fossette et al. 2012).

578 Favourable foraging eddies targeted by elephant seals were stable relative to the global  
579 eastward flow of the ACC. Eddy motion within the ACC propagates eastward considerably  
580 more slowly than the surface mean flow (Naveira Garabato et al. 2011). This horizontal  
581 transport property characterized coherent and long-lived eddies. Several studies have stressed  
582 the influence of long-lived mesoscale eddy history (age and pathway) together with seasons to  
583 explain the distribution and communities of zooplankton (Govoni et al. 2011) and small pelagic  
584 fish (Brandt 1983). The centre of cyclonic eddies and the edges of anticyclonic eddies were  
585 reported to be enriched in organisms of different trophic levels (Biggs 1992, Riandley et al.  
586 2005, Landry et al. 2008, Benitez-Nelson and McGillicuddy 2008). Elephants seals could  
587 benefit from the enhanced local biological production and aggregation of prey created by stable  
588 mesoscale features that permit efficient resource acquisition influencing individual parameters  
589 and ultimately populations (New et al. 2014).

590 Recent investigations on circulation properties proposed retention as a possible physical  
591 parameter with ecological implication (d'Ovidio et al. 2013), involved in the so-called "ocean

592 triad” enrichment–concentration–retention (Bakun 2006) that hypothetically increases the  
593 biological production from phytoplankton to higher trophic levels. Retention in particular  
594 allows the trophic development and the maintenance of spatially restricted marine ecosystems.  
595 All these findings suggested the importance of (sub-)mesoscale coherent features for the  
596 foraging strategy of top predators. Finally we have focused on both horizontal index of  
597 predator foraging strategy and horizontal properties of circulation. Future studies will examine  
598 the vertical dimension especially to better assess the foraging success of top predators through  
599 diving behaviour relative to their dynamic environment (Bailleul et al. 2008, Dragon et al.  
600 2012, Thums et al. 2012, Schick et al. 2013b, Guinet et al. 2014).

601

## 602 **Conclusion**

603 Pelagic ecosystems can be fundamentally disrupted by multiple current threats (e.g.  
604 climate change, overfishing and pollution). Taking into account the spatio-temporal variability  
605 and dynamic nature of the marine environment in management planning is crucial and makes  
606 the conservation of the open ocean realm challenging (Game et al. 2009, Zydalis et al. 2011).  
607 This statement is especially relevant in remote areas such as the Southern Ocean where the  
608 consequences of environmental change have been already observed on at-sea behaviour of  
609 marine wildlife (e.g. response of foraging performances of albatrosses to the wind pattern,  
610 Weimerskirch et al. 2012). Because of their position in pelagic ecosystems, understanding how  
611 *marine top predators* exploit their complex environment and which oceanographic processes  
612 drive their foraging strategy is of primary importance to extrapolate to ecosystems (Boyd  
613 2006). Due to a significant lack of data, very little information is available on mid-trophic  
614 levels in particular and there is a strong need to address this gap since it affects our  
615 understanding of ecosystem functioning (Handegard et al. 2012). Open ocean ecosystem  
616 understanding and predictions rely with growing importance on the development of ecosystem  
617 models that take into account the coupling between marine organisms and ocean dynamics.  
618 Results obtained on predators contribute significantly into identifying mechanistic processes of  
619 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: $\frac{1}{3}^{\circ}$ (~30km) time: week	<a href="http://www.aviso.oceanobs.com">http://www.aviso.oceanobs.com</a>
Sea surface temperature	AMSRE	space: 25 km time: 3-days	<a href="http://www.ghcc.msfc.nasa.gov/AMSR/">http://www.ghcc.msfc.nasa.gov/AMSR/</a>
Chlorophyll <i>a</i> concentration	SeaWiFS - MODIS - MERIS	space: 9 km time: daily	<a href="http://www.globcolour.info/">http://www.globcolour.info/</a>

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982 **Figure Captions**

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

989

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

998

999 Fig. 3. Illustration of the areas defining seal location (distance from seal <30km) and  
1000 mesoscale surrounding environment (30km< distance <100km) around each Argos location  
1001 along seal trajectories used for physical parameters extraction.

1002

1003 Fig. 4. Multi-year (2005-2011) bi-monthly tracking of elephant seals overlaid on the  
1004 distribution of waters which supported the phytoplankton bloom, in green (high Chlorophyll  
1005 concentrations, i.e. > mean value of  $0.5 \text{ mg.m}^{-3}$ , from satellite data during the bloom period in  
1006 December) in a forward-in-time advection. Travelling and foraging (intensive behaviour)  
1007 locations are shown in black and red respectively. Histograms represent their proportion (same  
1008 color) in low and high Chlorophyll concentrations. The lower graph shows the monthly  
1009 evolution (y-axis) of the longitudinal range (x-axis) of both seals while foraging (gray dots)  
1010 and waters which supported phytoplankton bloom (square is the bi-monthly longitudinal  
1011 average and arrows are 10 and 90% quantiles) within the 50°S-55°S latitudinal band.

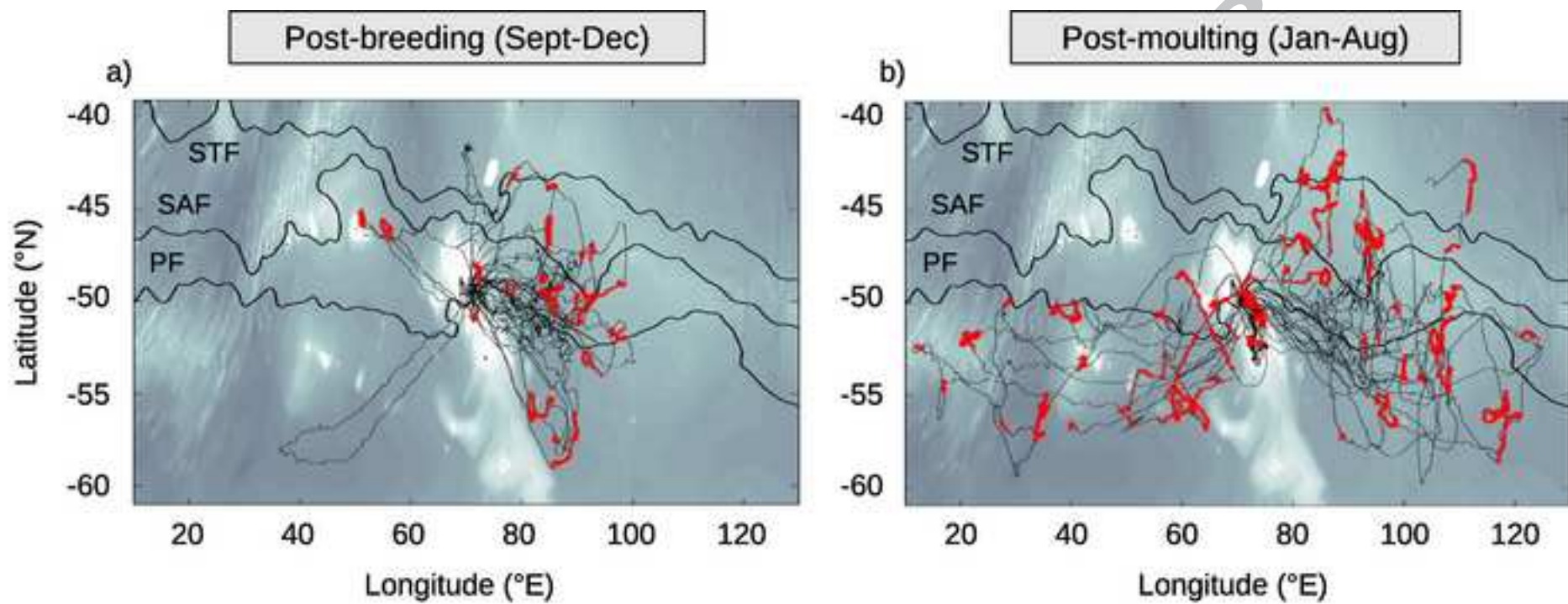
1012

1013 Fig. 5. Fitted GAMM results showing the functional form of each physical covariate (y-axis)  
1014 according the distance for post-moulting female elephant seal locations (x-axis) during  
1015 travelling and foraging behaviours. The solid lines are the smooth function estimates and the  
1016 dashed lines represent 95% confidence intervals. Only significant relationships were displayed  
1017 with resulting  $F$ -tests and  $p$ -values ( $*p<0.05$ ,  $**p<0.01$ ,  $***p<0.001$ , N.S.: not significant).  
1018

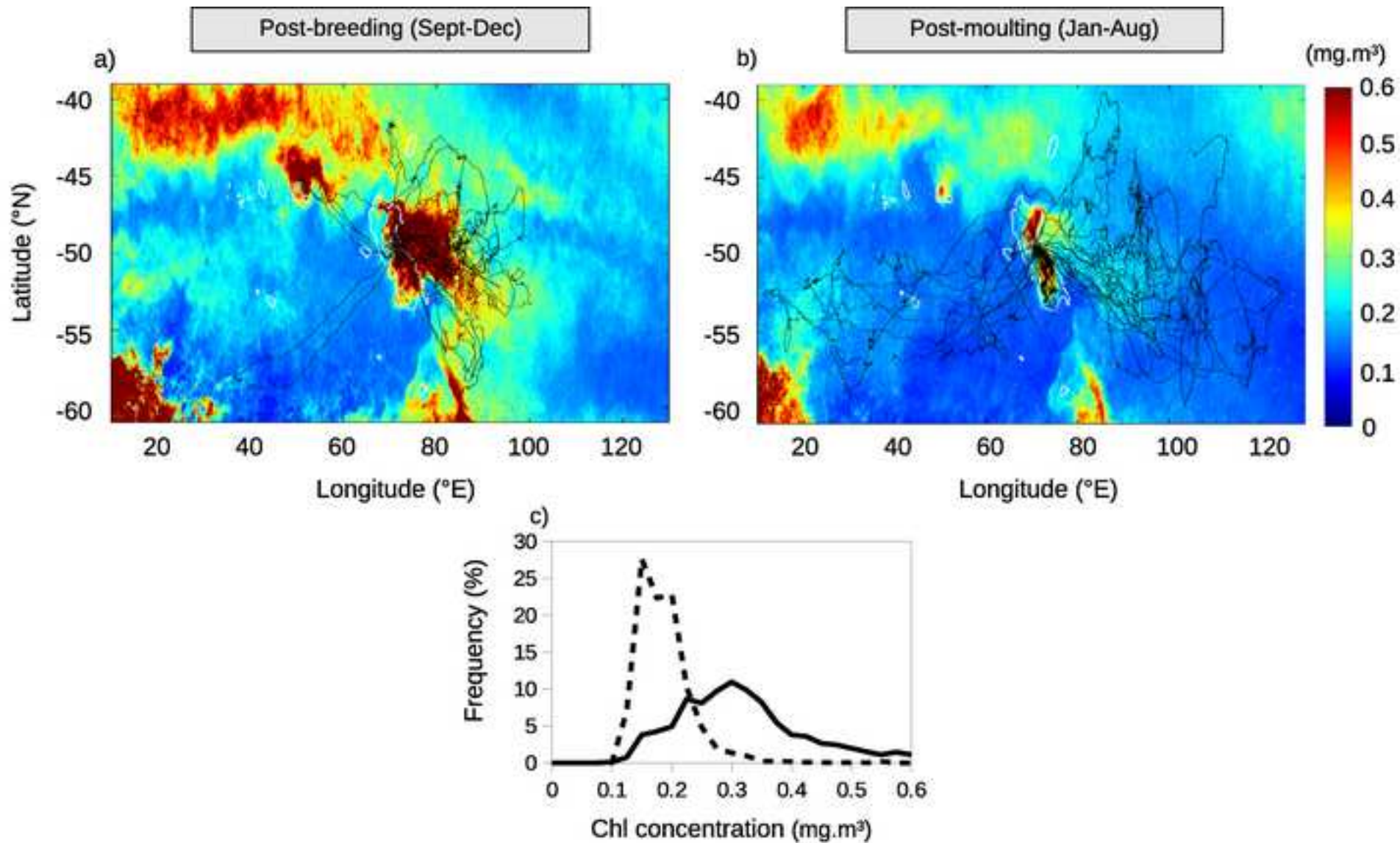
1019 Fig. 6. Preference of seals for sub-mesoscale fronts, temperature (SST), longitudinal (WD[lon])  
1020 and latitudinal (WD[lat]) displacement of water parcels during post-breeding (a,c) and post-  
1021 moulting (b,d) when seals travelled (a, b) and when they foraged (c, d). Dark gray bars  
1022 described mean properties of waters within 30 km of seal location while light gray bars  
1023 represent the 30-100 km surrounding environment. Error bars are standard deviations and  $t$ -  
1024 tests between seal location and surrounding areas are indicated when significant ( $*p<0.05$ ,  
1025  $**p<0.01$ ,  $***p<0.001$ ).

1026  
1027 Fig. 7. Case study showing a part of an elephant seal trip (3weeks, from June 28 2005 to July  
1028 20 2005) overlaid on daily a) sub-mesoscale transport fronts (FSLEs in  $\text{day}^{-1}$ ), b) SST (in  $^{\circ}\text{C}$ ),  
1029 c) longitudinal, and d) latitudinal displacement of water parcels in a 50 d backward-in-time  
1030 advection at halfway through the trip part (July 8 2005). Travelling (extensive behaviour) and  
1031 foraging (intensive behaviour) bouts of trips are respectively in black and red.  
1032









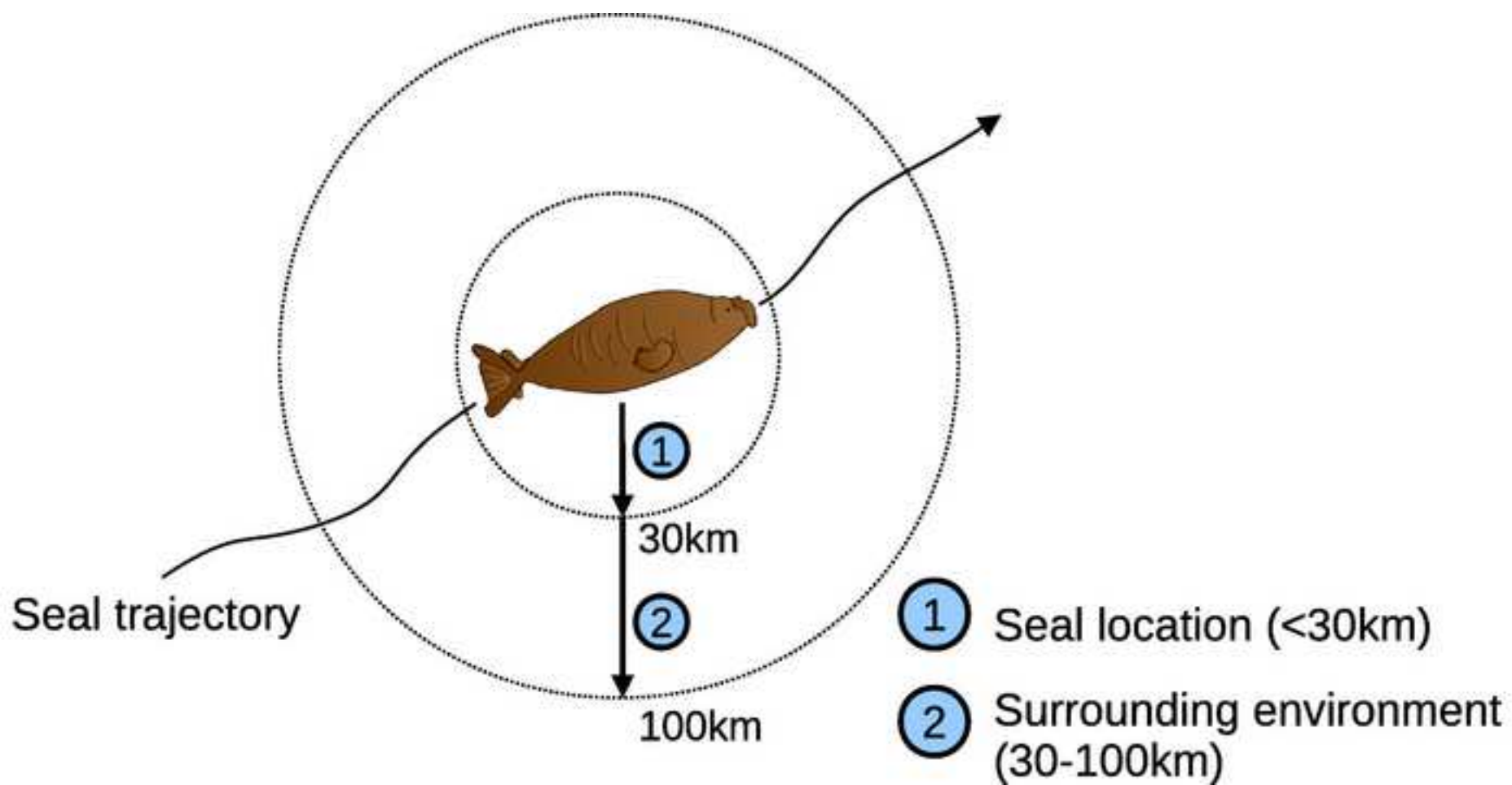
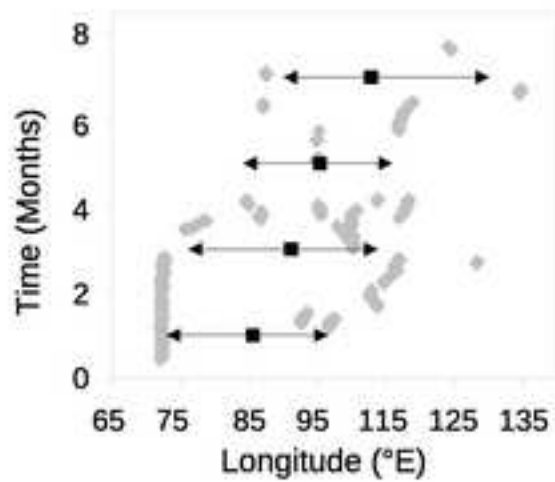
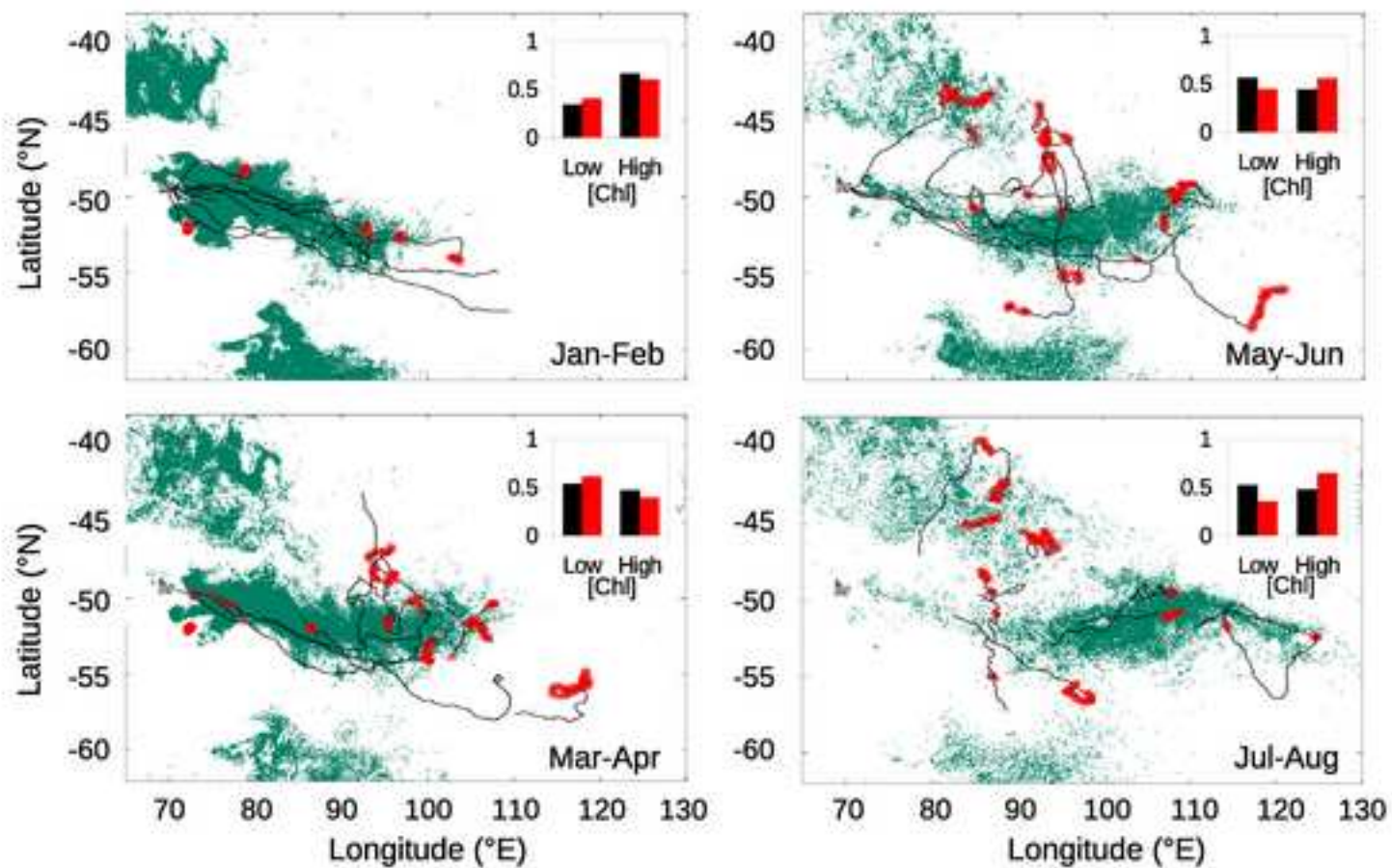


Figure4



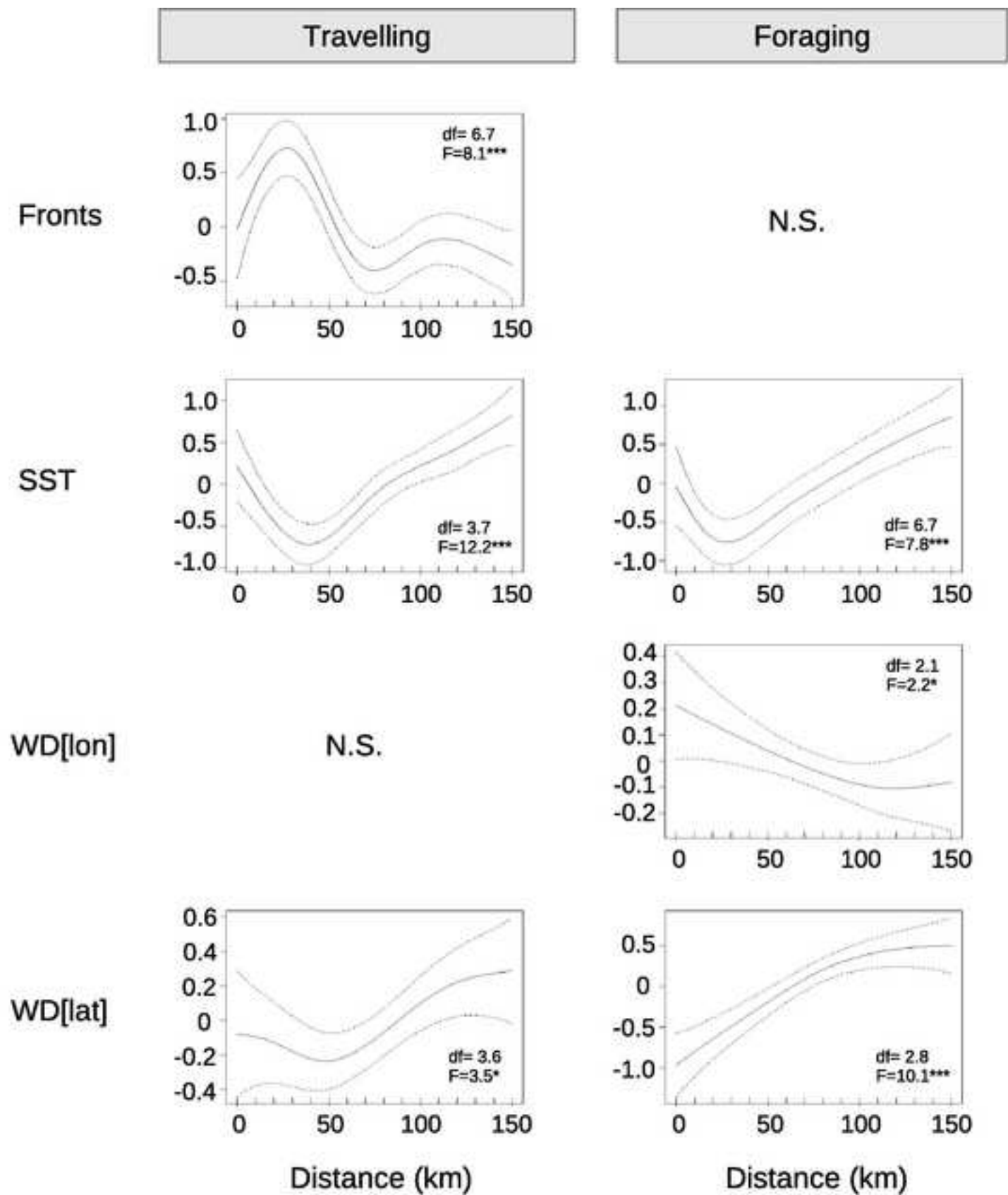
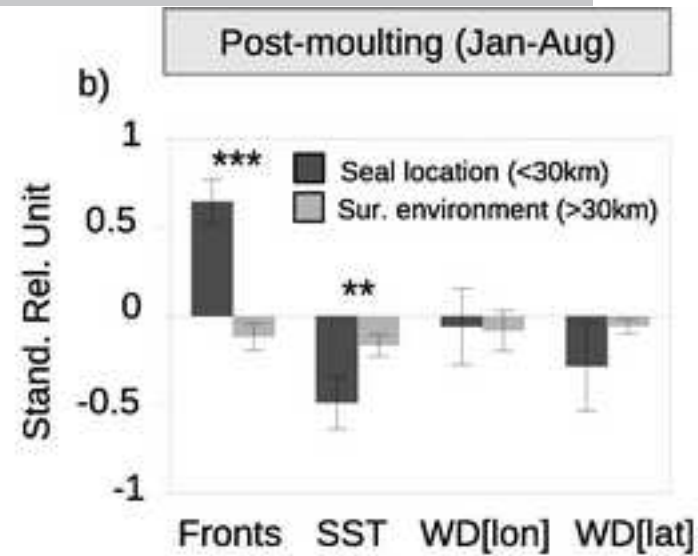
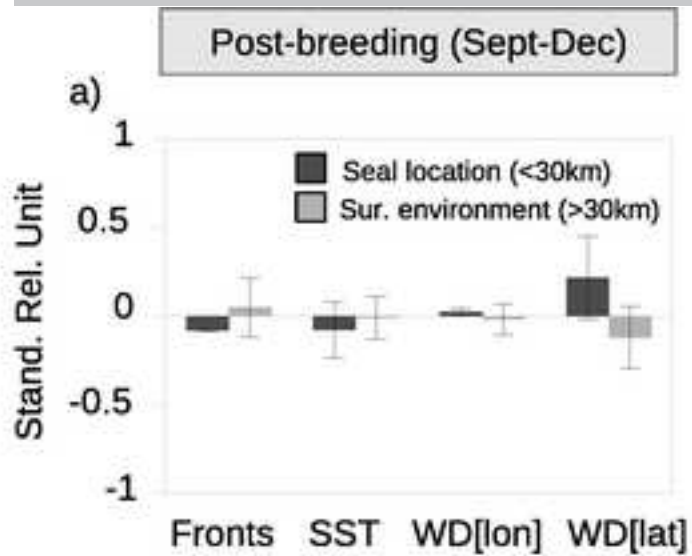


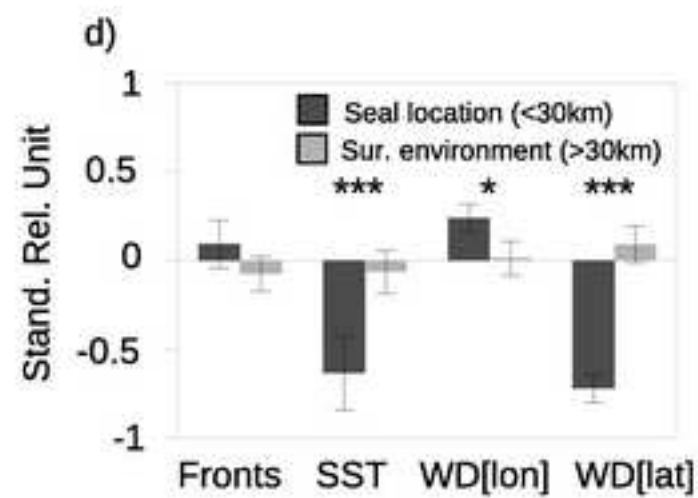
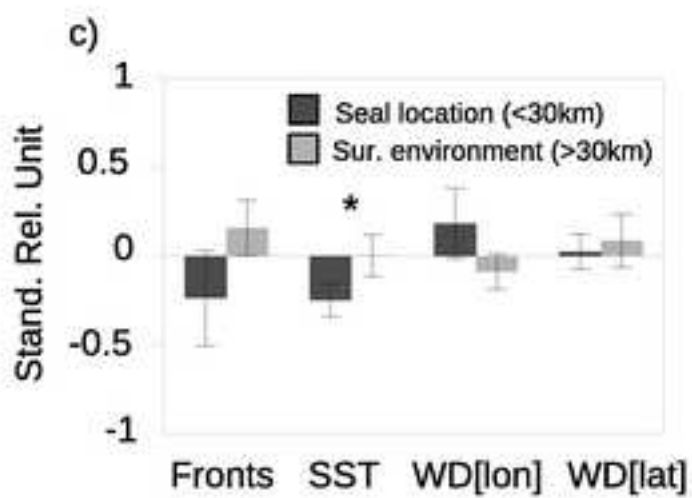


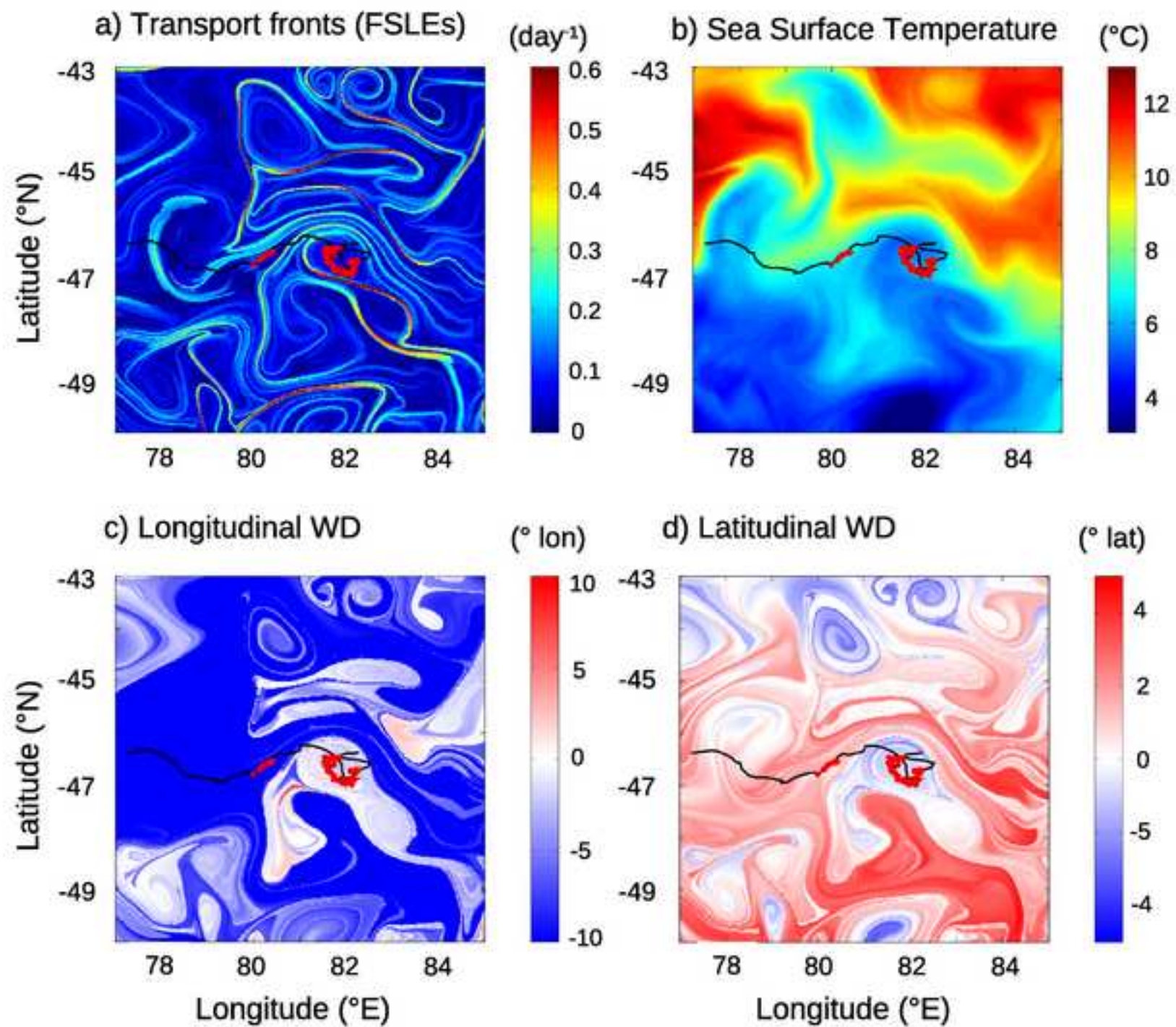
Figure6

Travelling

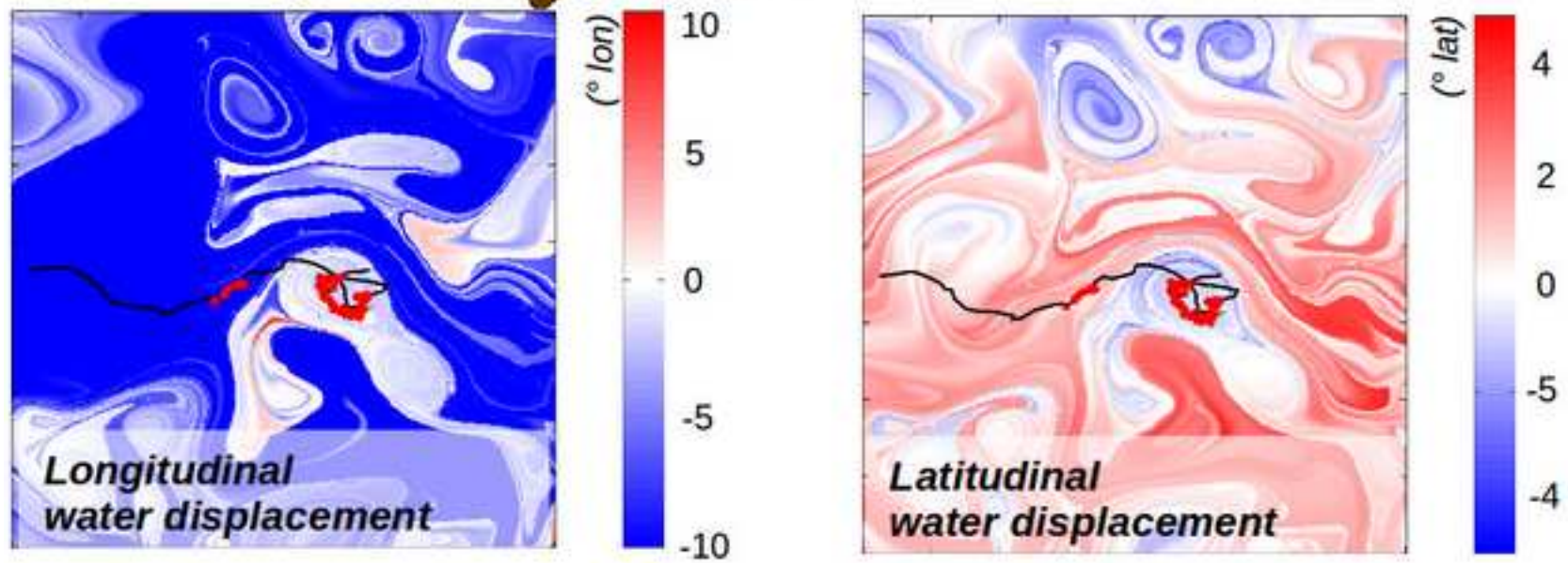
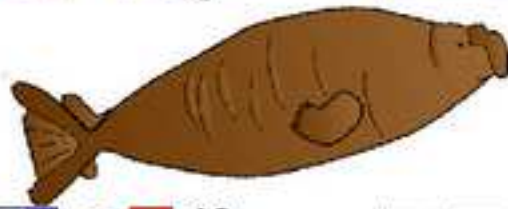
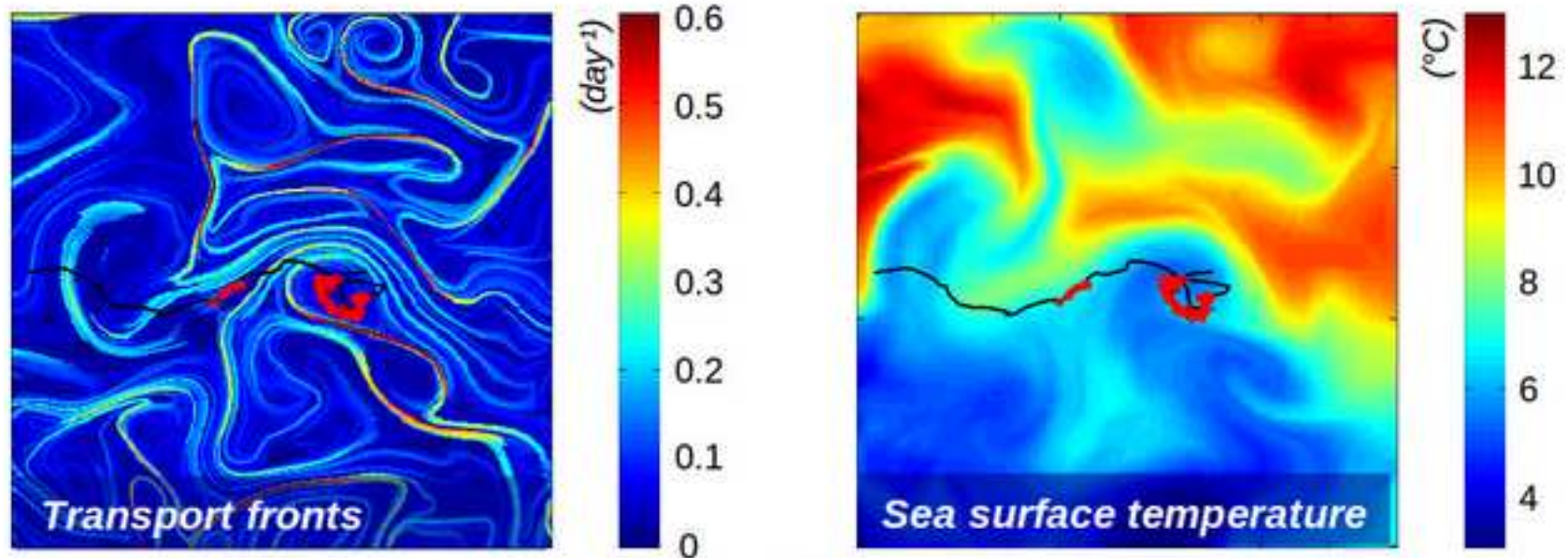


Foraging











## 1033 Highlights

- 1034 1. The mesoscale behavioural preferences of female southern elephant seals are seasonally  
1035 flexible
- 1036 2. No environmental preference emerged when postbreeding seals distributed in blooming  
1037 waters
- 1038 3. Postmoult seals travelled along thermal fronts and foraged in stable mesoscale waters
- 1039 4. Favorable patches correspond to waters which have supported the bloom during spring
- 1040 5. Dynamic circulation of the ACC influenced the foraging strategies of top predators
- 1041
- 1042
- 1043
- 1044

ACCEPTED MANUSCRIPT