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

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3 **Current**

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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.

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

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-Kaï 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-Kaï 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-Kaï 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 strutures 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.

5

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, Pakhomow 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-SRDLs, dimensions:105 x 70 x 40 mm, 545g, cross-sectional area 28 cm²)

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

8

229 surface velocities computed from weekly merged products of absolute dynamic topography

230 (ADT) at ⅓° 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://wwwghcc.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

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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 mg.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:

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

286   (1)

287   where δ_0 is the separation of the initial positions of two trajectories, δ_f is their

288   prescribed final separation, and τ is the first time at which a separation of δ_f is reached.

289   Therefore, the Lyapunov exponent has the dimension of time^{-1}. When computed backward in

                                                                                                      10

290   time, its value corresponds to the timescale of the frontogenesis between the scale δ_0 and δ_f

291   induced by horizontal stirring. Typical FSLE values along filament boundaries correspond to

292   the range 0.1 - 1 day^{-1} (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 δ_0 = 10 km and chose δ_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.

11

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 [⅓]° 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 std) m.s^{-1} (~75 km.day^{-1}) during travelling and

408 0.50 ($\pm$ 0.33 std) m.s^{-1} (~43 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 0.5mg.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.

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-Kaï 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

18

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

19

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 maximun 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 occured 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 Kaï 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, Zydelis 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.

23

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981

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/

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 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 day^{-1}), b) SST (in °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

Figure1

a) Post-breeding (Sept-Dec)

b) Post-moulting (Jan-Aug)

Figure2

a) Post-breeding (Sept-Dec)

b) Post-moulting (Jan-Aug)

c)

Figure3

Seal trajectory

30km

100km

① Seal location (<30km)

② Surrounding environment (30-100km)

Figure4

Figure5

Figure6

Figure7

a) Transport fronts (FSLEs)   (day⁻¹)

b) Sea Surface Temperature   (°C)

c) Longitudinal WD   (° lon)

d) Latitudinal WD   (° lat)

Latitude (°N)

Longitude (°E)

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
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