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2   Top marine predators track Lagrangian coherent structures

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26   **Abstract**

27   Meso- and submesoscales (fronts, eddies, filaments) in surface ocean flow have a crucial

28   influence on marine ecosystems. Their dynamics partly control the foraging behaviour and the

29   displacement of marine top predators (tuna, birds, turtles, and cetaceans). In this work we focus

30   on the role of submesoscale structures in the Mozambique Channel on the distribution of a

31   marine predator, the Great Frigatebird. Using a newly developed dynamical concept, namely the

32   Finite-Size Lyapunov Exponent (FSLE), we have identified Lagrangian coherent structures

33   (LCSs) present in the surface flow in the Channel over a 2-month observation period (August and

34   September 2003). By comparing seabirds' satellite positions with LCSs locations, we

35   demonstrate that frigatebirds track precisely these structures in the Mozambique Channel,

36   providing the first evidence that a top predator is able to track these FSLE ridges to locate food

37   patches. After comparing bird positions during long and short trips, and different parts of these

38   trips, we propose several hypotheses to understand how frigatebirds can follow these LCSs. The

39   birds might use visual and/or olfactory cues and/or atmospheric current changes over the

40   structures to move along these biological corridors. The birds being often associated to tuna

41   schools around foraging areas, a thorough comprehension of their foraging behaviour and

42   movement during the breeding season is crucial not only to seabirds' ecology but also to an

43   appropriate ecosystemic approach of fisheries in the Channel.

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In the oligotrophic open ocean mesoscale and submesoscale oceanic turbulence, which spans spatiotemporal scales from one to hundreds of kilometers and from hours to weeks, strongly modulates the structure, biomass and rates of marine pelagic ecosystems. Eddies can stimulate the primary productivity (1, 2), affect plankton community composition (3-5) or play a significant role in exchange processes in the transitional area between the coast and offshore by transporting organic matter and marine organisms from the coast to the open ocean and vice versa (6). In view of the strong influence of eddies on physical and biogeochemical properties, it is not surprising that higher level predators concentrate around them, where prey can be found. In fact, all investigations on the relationship between eddies and top predators communities, using satellite imagery observations, have evidenced strong ties between them (7, 8). Upper predators particularly used the boundary between two eddies (9 -12). The key point is that interactions between eddies generate strong dynamical interfaces (13) and make them a complex and energetic physical environment. In these interfaces the energy of the physical system is available to biological processes, increasing the trophic energy of the biological system (8). Eddies and associated structures have therefore a crucial ecological significance especially in tropical and sub-tropical regions, characterized by low mixing during winter inferring weak supply of nutrients to the photic zone (11).

Most previous works dealing with the influence of eddies on top-predator distribution show the necessity to concentrate on submesoscale (below 10 km) to fully appreciate the role of eddy-eddy interfaces on biological production (11). Many different studies confirm that submesoscale tracer patches and filaments are strongly related to interactions between mesoscale surface eddies (1, 14). Despite this, studies on top predators using remote sensing have only used Sea Surface Height (SSH) as an indicator

of eddy activity, which does not resolve sub-mesoscale structures such as filaments, where production should be concentrated. In addition, a fundamental question remains: how top predators can find these zones of higher productivity? This is particularly difficult to understand for central place foragers such as seabirds that breed on land but have to do continuous return trips between feeding zones and the colony where they care for their chick or egg. The additional difficulty in the case of eddies is that the location of production zones moves continuously.

In the West Indian Ocean, the Mozambique Channel (hereafter MC) can be considered as a natural laboratory to study the interactions between biological and physical processes at mesoscale in oligotrophic areas (sub-tropical region) due to the transient activity of eddies. Indeed mesoscale dynamics of the Mozambique Channel has been well described by previous works using remote sensing data, modelling and *in situ* observations (15-17). Mesoscale activity is dominant in two areas, the central part of the MC and south of Madagascar (17, 18). Weimerskirch et al. (10) have shown the main role of mesoscale eddies on the foraging strategy of the Great Frigatebirds. These birds fly hundreds or thousands of kilometres from the colony in a few days and spend their entire foraging trips in flight, being unable to sit on the water or enter the water column. Bird's pathways are preferentially associated with eddies in the MC during their long trips and especially with the edge of eddies, avoiding their core (10). However it is not clear where they exactly forage in the eddy system and whether and how they locate the zones of high production. The aim of our study here is first to describe the fine scale activity occurring at the edge of eddies and other submesoscale structures, and quantify the role of these on a top predator's foraging movements. Finally, we will try to understand how and why these predators might locate these structures.

100   For the physical environment, we have used horizontal velocity fields computed

101   from satellite altimetry products (19). We have applied to them a recently developed

102   Lagrangian technique, the Finite Size Lyapunov Exponent (FSLE), which allows

103   computing, from marine surface velocity field data, mixing activity and coherent

104   structures that control transport at specified scales (20). FSLEs measure how fast fluid

105   particles separate to a specified distance. Lagrangian coherent structures (LCSs), e.g.

106   transport barriers, filamental structures or vortex boundaries, are identified as ridges

107   (locations containing the maximum values) of Lyapunov exponent fields (21-24).

108   Dispersion rates of tracer particles can be calculated by integrating trajectories towards

109   the future (forward direction) or towards the past (backward), giving rise to two different

110   quantifiers, $FSLE_f$ and $FSLE_b$, respectively, containing complementary information (see

111   Methods section). Ridges of $FSLE_b$ attract neighboring trajectories whereas $FSLE_f$ repel

112   them. This is why we call them *attracting and repelling LCSs*, respectively. Sometimes,

113   especially for plotting, it is convenient to write $FSLE_b$ and $FSLE_f$ as having negative and

114   positive values, respectively, and expressions such as $\lvert FSLE \rvert$ refer simultaneously to

115   both types of exponents. For the marine top predators, we have used Argos positions of

116   Great Frigatebirds from the colony in Europa Island in the MC during August-September

117   2003. Additional details are given in the Material and Methods section.

118   In this paper, we test if seabirds' positions during their foraging trips are related to

119   dynamical structures. This is performed in different contexts: during short and long trips,

120   day and night, and during the outward part of their foraging trip and return part back to

121   the colony. We finally discuss which foraging strategy these top predators might use to

122   locate prey patches.

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127   **RESULTS**

128 **Seabirds' locations during trips and FSLE fields**

129 We compare here the locations of the LCSs identified as ridges in FSLE maps, and

130 measured bird positions during August-September 2003. We will see that the latter are

131 not random but correlated with the former.

132   First, Figure 1 shows Argos positions of Great Frigatebirds during long trips

133 (black points) and short trips (red points), between August 18 and September 30, 2003.

134 Locations of seabirds during long trips superimposed on FSLEs fields (September 24 to

135 October 6, 2003), are shown in Figure 2. During the week of September 24, bird 11377

136 (green circles) is located on high $FSLE_b$ values (the attracting LCSs), as well as location

137 of bird 16255 (blue circles). Positions of bird 8023 (red circles) seem to be linked with

138 fluid repelling structures (the ridges of $FSLE_f$) instead. For bird 8023, at the beginning

139 of the travel, the trajectory is rectilinear in the north-east direction and then follows the

140 repelling mushroom-like structures. Foraging patches (triangles), where birds reduce

141 flying speed, seem to exhibit the same distribution than the birds' moving positions.

142 During the week of October 6, movements of bird 8023 are mostly on repelling

143 structures (Fig.2, d) as during the week of September 24, and perhaps also on some

144 attracting structures. The important point is that any of both types of LCSs is more

145 visited than locations outside. Positions of bird 19827 (magenta circle) are well

146 superimposed on fluid attracting structures (ridges of $FSLE_b$) but not on repelling ones.

147 These two examples of the overlay of seabirds' moving and foraging positions on FSLE

148 fields during long trips show that the locations of birds tend to overlay on LCSs either

149 on attracting (Fig.2, a-c) or repelling ones (Fig.2, b-d).

150   To put the above observations in quantitative form, we defined a threshold

151   defining a significant presence of LCSs: $|\text{FSLE}| > 0.1 \, \text{d}^{-1}$. It corresponds to mixing times

152   smaller than one month. This value is chosen since it is a typical value for Lyapunov

153   exponents in different areas of the globe (14, 20) and because regions where the

154   Lyapunov exponents are larger already have the shape of one-dimensional lines (see Fig

155   2). The distributions of FSLEs in the whole MC and central part, and in areas crossed by

156   seabirds were tested for conformity to the normal distribution using the Kolmogorov–

157   Smirnov sample test and they all are clearly non-normal. Histograms of relative frequency

158   of FSLE in the whole MC, central part and on areas visited by seabirds are shown in

159   Figure 3. In the whole MC and central part, Lagrangian structures detected by |FSLE|>0.1

160   day^{-1} represent a minority of locations, occupying 30% or less of the total area. However

161   in areas crossed by frigatebirds more than 60% of the birds are on LCSs. Five

162   Kolmogorov-Smirnov 2-sample tests (KS2) comparing the distributions of FSLEs in the

163   whole MC and in the central part with the distribution of FSLEs on areas visited by

164   seabirds during long and short trips were performed. The tests confirmed that distributions

165   of FSLEs in areas crossed by seabirds are highly different from those found over the

166   whole area and central part (p<0.0001 for both long and short trips). Distribution patterns

167   provide clear evidence that Great Frigatebirds are not randomly distributed throughout the

168   FSLE range (both backward and forward) and that seabirds move over specific areas rich

169   in LCSs, despite the area occupied by LCSs is small. Close to 2/3 of the birds positions

170   are on LCSs, despite that only 30% or less of the whole area or of the central part (see

171   Fig. 3) contain high |FSLE| and are then occupied by LCSs. These numbers are further

172   checked by chi-square analyses using the one tailed G-test for Goodness of Fit (Log-

173   Likelihood ratio) which show clearly that there are significant differences between

174   positions of birds on LCSs and on other structures (Table 1) (G-test, p<0.001): this

175 confirms again that seabirds' positions are located more on LCSs ($|FSLE|>0.1$ day^{-1}) than

176 outside during long and short trips, despite the small area occupied by LCS (Fig. 3). An

177 additional test checking the relation between birds' positions at a given week t and the

178 LCSs computed for that week and for the following ones, t+1, t+2, ..., t+9, is described in

179 SI. The association of birds' tracks and LCSs, measured by the significance of a G-test, is

180 highest for the LCSs of the week t and decreases with the time lag to the other weeks

181 ($p_{t+1}=0.81 > p_{t+3}=0.19 > p_{t+5}=0.12$) (Supporting Information [SI], Table S1).

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183 **FSLE distributions over different types of flights**

184 We performed several statistical tests to see if there are statistically significant

185 differences among travel/foraging locations, outgoing/return trips, and day/night flights.

186 Boxplots of FSLEs on seabirds' positions during long and short trips are presented in

187 Figure 4. The range of variation of FSLE is clearly more dispersed during long trips

188 than short trips and the median between both kinds of trips is similar. Furthermore,

189 distributions are clearly different between long and short trips as confirmed by a KS-2

190 samples test ($p<<0.001$). Indeed, 65.9 % of seabirds' positions during long trips and 56

191 % during short trips are on LCSs (Table 1). During long trips, Great Frigatebirds forage

192 during a longer time, and so cover a larger range of variation of FSLE values than

193 during short trips. One tailed G-test for Goodness of Fit confirms that there is a

194 difference between the number of seabirds' locations on FSLE ridges and outside the

195 ridges (Table 1) (G=30.613; p=0.001; df (degrees of freedom)=10 for long trips and

196 G=32.057; p<<0.001; df=6 for short trips).

197 KS-2 tests show that the distribution of the birds between attracting and repelling

198 LCSs display no statistically significant difference during long trips (p>0.05) but differ

199 during short trips (p<0.01). During short trips birds follow more the attracting LCSs

than the repelling ones. The analyses clearly demonstrate that seabirds follow the FSLE

ridges during their foraging trips, but mostly during long trips than during short trips.

This result underlines the probable difference between the Great Frigatebirds behaviour

during long and short trips.

Boxplots of FSLE show that patterns of distribution of FSLE are not very different

between flying and foraging positions (SI, Fig. S1). Distributions of FSLEs are

statistically similar for foraging and crossed areas (KS-2 test, p=0.29 for long trips and

p=0.51 for short trips), but differ from FSLE distribution in the whole area (KS test

p<0.0001). During long trips 69.6% (resp. 61.8% during short trips) of seabirds' positions

during flying and 62% (resp. 66.7% during short trips) during foraging are on LCSs (SI

Fig.1). During flying and foraging seabirds split almost equally between repelling and

attracting structures (G-test p>0.05) (see SI, Table S2). All of this indicates that seabirds

seem to prefer being on ridges of FSLE both for travel and foraging.

We have also investigated for differences in seabirds' distributions in relation to FSLEs

between the outward and return part of the trip (see SI, Fig. S2a, c). KS-2 test shows

that there is no significant difference of seabirds' distribution during long trips (KS-2

p>0.01) and during short trips (p>0.05), between the outward and return parts of the

trip. For all types of trips (short and long), there is no significant difference of seabirds'

positions, either on repelling or attracting flow structures, during the outward and return

parts of the trip (G-tests p > 0.05) (see SI, Table S3).

Great Frigatebirds feed mainly during daytime (10). We therefore examined

whether we could identify differences between day-time and night-time distribution of

seabirds. Boxplots of seabirds' distribution on FSLE between day and night show that

patterns of distribution of FSLEs are similar during day and night during short (SI, Fig.

S2b) and long trips (SI, Fig. S2d). The range of variation of FSLE during long trips is

225   however more dispersed at night than during short trips. KS-2 test shows that there is no

226   significant difference between FSLE distributions visited by birds during day and night

227   (p>0.05 during long or short trips). The probability for the frigatebirds to fly over

228   attracting or repelling structures during day and night is statistically similar (G-tests

229   p>0.05) for long trips but may be different for short trips (G-test p=0.025) (SI, Table

230   S3). During daytime short trips, seabirds may follow more the attracting structures than

231   the repelling ones.

232

233   **DISCUSSION**

234   As eddies affect all stages of the marine ecosystem, they are determinant for the

235   triad "enhancement-concentration-retention" identified by Bakun (25, 8). From

236   upwelling-driven processes at the centre of cyclonic eddies (1, 2), or from other processes

237   at the boundaries between eddies (13), local enrichment and new production have been

238   observed. The cyclic circulation in vortices produces also retention of larvae and other

239   planktonic organisms in their core, whereas concentration occurs in the convergence

240   zones located at the boundary between them, which are detected by FSLEs.

241   Transport barriers and filament generation by interaction between eddies induce

242   horizontal and vertical biogeochemical and biological enhancement (13). Finite Size

243   Lyapunov Exponents seem very well-suited to detect such transport barriers, vortex

244   boundaries, and filaments at meso- and submesoscale (20, 26) and to study the link with

245   the ecological behaviour of marine top predators. However, a word of caution is required

246   about the spatial resolution we used. Indeed, the FSLEs are computed from satellite

247   altimetry products (19) with a spatial resolution of 1/4 of a degree interpolated here onto a

248   1/40 of a degree grid. This interpolation might induce some bias in the data. However

249   FSLEs, because of the averaging effect produced by computing them by integrating over

250   trajectories which extend in time and space, are rather robust against noise and

251   uncertainties in velocity data (26, 27) (see also SI). The velocity field used here has been

252   validated and the correlation with velocities from Lagrangian drifting buoy data in the

253   MC was satisfactory (see SI). Furthermore, Argos positioning of birds is not of equivalent

254   quality. Some positions have a margin of error of a few hundred metres, while others have

255   an error margin of more than one kilometre. Definite improvements would be to reduce

256   interpolation by using an original higher resolution velocity field and to obtain more

257   precise birds' locations.

258   In the central part of the Mozambique Channel, it is known that the boundary of

259   eddies is very energetic and allows the aggregation of top predators foraging, especially

260   Great Frigatebirds (10), which preferentially stay in this part of the channel. So far it was

261   believed that Great Frigatebirds used edges of eddies mainly for food because these areas

262   are rich in forage species and associated top predators (especially tuna and dolphins,

263   (28)). Superimposing Great Frigatebirds's positions on FSLE fields shows that their

264   spatial distribution is linked to eddies, and more generally to the different types of LCSs.

265   And not only for foraging but also for travelling. Observations are in agreement with the

266   histograms and Kolmogorov-Smirnov tests, which demonstrate that seabirds are not

267   randomly distributed in relation to attracting and repelling LCSs.

268   However, analysis of location of seabirds during long and short trips shows that

269   the percentage of positions on LCSs is different between both kinds of trips (Table 1).

270   During long trips, birds seem to take full measure of the LCSs while on short trips they do

271   not take full advantage of them. This difference between long and short trips is probably

272   due to the behaviour of seabirds. During short trips, birds have to bring food frequently to

273   their chick so they feed in areas where preys are easily accessible, close to Europa Island.

274   They used preferentially attracting structures during daytime, probably because these

275   structures are conductive to the aggregation of preys. During long trips, birds avoid areas

276   near Europa Island probably because the foraging yield is less rich than that of more

277   distant waters, and/or because of strong interspecific competition near the island (10).

278   However, birds preferentially follow the LCSs in both cases.

279   In addition, seabirds follow LCSs not only for their foraging but also for their travelling

280   movements. The distributions of FSLEs during the outward and inbound journeys to the

281   colony indicate that they exhibit the same flying behaviour before and after their foraging

282   activity. Furthermore, the fact that the distribution of visited FSLEs is identical during day

283   and night indicate that they are able to use these LCSs to move during periods of

284   darkness. Frigatebirds move continuously during day and night at an average altitude of

285   200 m, and never completely stop moving when they forage, but they come to the sea

286   surface to eat only during day-time (10). If they used these structures only for food

287   availability, then the distribution of FSLEs for areas crossed by birds should be different

288   between day and night. This is not the case. This means that frigatebirds do not go to

289   FSLEs ridges only to forage but that they follow them most of the time as cues to

290   eventually find prey patches there.

291   It is relatively easy to understand why the attracting LCSs could be places for prey

292   accumulation, since horizontal flow will make passively advected organisms close to

293   these lines to approach them. More puzzling is to understand the role of the repelling

294   LCSs, which are also preferred locations for the frigatebirds. First we should mention that

295   at the vortex edges, lines of the attracting and the repelling types are very close and nearly

296   tangent. Thus, it may be the case that birds' positions located at repelling lines are

297   simultaneously located also on attracting ones: in SI we explain that a position is said to

298   be on a LCS if it is closer to it than 0.025 degrees. Thus, if the attracting and repelling

299   LCSs are close enough, the same bird position may be attributed to both structures. We

have checked that, among the 30.2% of bird positions which were found on repelling coherent structures, 53.7% of them were in fact visiting both structures, and thus the interpretation is that they are associated to vortex edges (or to other structures in which both types of lines are tangent). For the remaining fraction which does not seem to be associated to these edges, we believe that the three-dimensional dynamics of the flow close to these structures gives the clue for their association to birds' positions. Note that FSLE values have been calculated on the basis of the two-dimensional surface flow, and the FSLE methodology identifies these regions as places of filament and submesoscale structure formation by horizontal advection. But there is growing evidence (29,30) of strong links between submesoscale structures from different origins and vertical motions. Thus, in an indirect manner, the calculated LCSs may be indicating the places in the ocean where vertical upwelling and/or downwelling of nutrients and organisms could occur. This is obviously important for the birds, and may explain why they prefer to fly and to forage on top of them. The role of these LCSs on the biological activity is rather complex and may vary depending on the area and scale of study. For instance, (31) found an inverse relationship between mixing activity (high FSLEs) and phytoplankton stocks in very productive areas such as coastal eastern boundary upwelling.

The above arguments linking LCSs and vertical motion can be more easily justified for the attracting LCS case, because the vorticity involved in the interaction between vertical and horizontal motion will tend also to be aligned with these structures (30). But we note that in flows consisting on slowly moving eddies, we are close to the so-called integrable situation in which a large proportion of tangencies between attracting and repelling structures is expected (as indeed observed). As a consequence, it may happen that a bird starts a trip by following an attracting LCS, loses its surface signal, and finds itself on top of a repelling one simply by continuing its previous path in a more or less straight way.

325 We stress, however, that all explanations we give to the observed relationship between

326 LCSs and bird paths contain a number of hypothesis which need additional research.

327 Besides, one may ask how can frigatebirds "follow" the LCSs during day and

328 night. Several hypotheses can be put forward:

329 - First, because frigatebirds use atmospheric currents, especially to gain altitudes

330 by soaring, and then glide over long distances (32), we can suppose that the coupling

331 between the ocean and the atmosphere at meso and submesoscale generates atmospheric

332 currents followed by seabirds. Indeed some authors (33-36) underline the role of local

333 air–sea feedbacks arising from ocean mesoscale features. For example Chelton et al. (36)

334 showed that an ocean-atmosphere coupling is observed in the California Current System

335 during summer. They conclude that SST fronts generated by mesoscale activity (eddies

336 and upwelling) have a clear influence on the perturbation of summertime wind stress curl

337 and divergence. In the Mozambique Channel, mesoscale eddies and their interaction

338 would force the atmosphere and generate air-current favourable to Great Frigatebirds that

339 might take advantage of the wind to fly in spending the least possible energy.

340 - Second, we cannot exclude that birds may follow visual or, more likely,

341 olfactory cues. Foraging behaviour of seabirds is complex and results from a number of

342 behavioural parameters such as sight, smell (37, 38), memory effect (39) and

343 environmental parameters: chlorophyll concentration (10), or wind speed and direction.

344 Nevitt et al. (40) suggest that seabirds use olfaction to track high concentrations of odour

345 compounds such as dimethyl sulphide (DMS) and sight when they locate prey patches.

346 The use of models of odours transport suggests that olfaction plays a role in foraging

347 behaviour (40). Structures detected using FSLEs are dynamical and, as mentioned above

348 may induce vertical mixing favourable to phytoplankton enhancement (41, 42) and their

349 patchy distribution. The grazing of phytoplankton by zooplankton induces the production

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350   of DMS (43) which is very attractive for different species of seabirds (44). Even if there is

351   no study on the role of olfaction on Great Frigatebirds foraging behaviour, we can

352   hypothesize that they use olfaction to detect DMS and productive areas and find food

353   patches. The interaction between the ocean and the atmosphere at sub-mesoscale and

354   wind may allow the dispersion of the DMS or other odours and favour their detection by

355   seabirds that follow LCSs until they see a patch prey. These LCSs could be viewed as

356   moving habitat facilitating movement of seabirds. Indeed frigatebirds might use these

357   odourful corridors to move between food patches with efficacy.

358   Whatever is the cue used by frigatebirds to locate and follow these Lagrangian

359   coherent structures, our results provide the first evidence that a top predator tracks these

360   FSLE ridges to locate food patches. It allows us to better understand how top predators

361   search preys, and why they are able to concentrate precisely at LCSs. Since these

362   structures are mobile, a simple memory is not sufficient for a central place forager to

363   return to a productive prey area. Predators could thus take a general bearing where eddies

364   are likely to be found (e.g. to the northwest in the MC for a colony located in the central

365   MC) and then move until they cross a FSLE ridge, that they will follow until they

366   encounter a prey patch. Because they are unable to sit on the water, frigates are often in

367   association with sub-surface top predators to forage. We can suppose that if frigatebirds

368   track LCSs to locate preys, it is possible that they are associated to tuna schools around

369   foraging areas (10). Thus understanding the rationale behind their localization is crucial in

370   seabird's ecology but also in the detection of the presence of tuna schools. This kind of

371   multidisciplinary approach opens up interesting prospects in the management of

372   ecosystems and fisheries and can be useful in the ecosystemic approach to fisheries,

373   especially to better characterize temporary tuna habitats in the Mozambique Channel.

374   Future work is to identify the responsible mechanism by which an aerial predator may

375   spot and follow LCSs.

376

377   **MATERIAL AND METHODS**

378   In this part we provide a brief overview of the methodology; further details for each

379   section are explained in the Methods in *SI Text*.

380

381   **Great Frigatebirds**

382   Europa (22.3° S, 40.3° E) is one of the two colonies (with Aldabra) of Great

383   Frigatebirds in the West Indian Ocean. The island is located in the central part of the

384   Mozambique Channel. Great Frigatebirds have the ability to undertake long range

385   movements out of the breeding season (10) but they behave as central place foragers

386   when breeding. Their diet is composed essentially of flying-fish and Ommastrephid

387   squids (10), but Great Frigatebirds are also kleptoparasits meaning they can steal preys

388   from others. One of their particularities is that they cannot wet their feathers nor dive into

389   the water to feed. They forage mainly through association with tuna and dolphins schools,

390   which bring prey to the surface.

391   To track movements of frigatebirds, 8 birds were tracked with satellite transmitters and

392   altimeters between August 18 and September 30, 2003, resulting in 1864 Argos positions.

393   The mean time between each position is 0.07 days, with a minimum of 0.001 days and a

394   maximum of 1.1 days. All seabirds positions from a given week were collocated on the

395   time and space grid were the FSLEs were calculated (with 0.025° resolution).

396

397   **Lagrangian coherent structures by Finite Size Lyapunov Exponents**

398   *FSLE method*

399   Oceanic variability in surface velocities is not probably sensed directly by Great

400   Frigatebirds, but indirectly via transported substances. This calls for a Lagrangian

401   perspective of the problem. Thus, we quantify horizontal transport processes and

402   Lagrangian coherent structures by the Lagrangian technique of the Finite Size Lyapunov

403   Exponents (FSLE) (45), which is specially suited to study the stretching and contraction

404   properties of transport in geophysical data (20). Due to its Lagrangian character, FSLEs

405   describe submesoscale details which cannot be detected by other means, like the

406   inspection of the Sea Level Anomaly maps of the marine surface.

407   The calculation of the FSLE goes through computing the time, τ, at which two

408   tracer particles initially separated at a distance δ_0, reach a final separation distance δ_f,

409   following their trajectories in the marine surface velocity field. At position x and time t

410   the FSLE is given by:

$$\lambda\left(x,t,\delta_0,\delta_f\right) = \frac{1}{\tau}\log\left(\frac{\delta_f}{\delta_0}\right) . \quad (1)$$

412   We follow the trajectories for 200 days, so that if τ is larger than this, we define $\lambda = 0$. It is

413   clear that the FSLEs depend critically on the choice of two length scales: the initial

414   separation δ_0 and the final one, δ_f. δ_0 has to be close to the intergrid spacing among the

415   points x on which the FSLEs will be computed (20). In our case we calculate FSLE on all

416   the points of a latitude-longitude grid with a spacing of $\delta_0 = 1/40° = 0.025°$. On the other

417   hand, since we are interested in mesoscale structures, δ_f is chosen as $\delta_f = 1°$, i.e.,

418   separation of about 110 km. In this respect, the FSLE represents the inverse time scale for

419   mixing up fluid parcels between the grid and the characteristic scales of the Mozambique

420   Channel eddies. Maps of FSLE are calculated weekly. An alternative to FSLE are the

421   finite-time Lyapunov exponents (FTLE) (22, 46). At the scales and parameters we are

422 working no significant differences are expected for the locations of LCS by any of the two

423 methods.

424   The time integration of the particle trajectories can be performed in two different

425 ways: forward and backward in time. For the backward in time computation, maximum

426 values of FSLE organize in lines which are good approximations to the so called *unstable*

427 *manifolds of hyperbolic points*, which for our purposes are lines towards which

428 neighboring fluid trajectories, while escaping from hyperbolic points, approach at long

429 times (20, 23, 24). In consequence they are called attracting LCSs. FSLEs computed

430 integrating trajectories towards the future, i.e. forward-in-time, take large values on lines

431 (stable manifolds) from which neighbouring trajectories appear to be repelled (repelling

432 LCSs). These lines of maximum separation or convergence rates, or "ridges", delineate

433 fluid domains with quite distinct origin and characteristics. Such lines strongly modulate

434 the fluid motion since when reaching maximum values, and they act as transport barriers

435 for particle trajectories thus constituting a powerful tool for predicting fronts generated by

436 passive advection, eddy boundaries, material filaments, etc. In different sets of papers (20,

437 26, 27, 31, 42), it has been demonstrated the adequacy of the FSLE to characterize

438 horizontal mixing and transport structures in the marine surface, as well as its usefulness

439 when correlating with tracer fields like temperature or chlorophyll.

440

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451

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571   **Legend of figures**

23

572   Figure 1: Argos locations of Great Frigatebirds during long trips (black points) and short trips

573   (red points) in the Mozambique Channel, between August 18 and September 30, 2003. The green

574   point denotes Europa Island.

575

576   Figure 2: Overlays of seabirds' position on FSLE maps. Left panels (A and C): Backward

577   integration in time for FLSE computation (d^{-1}). Right panels (B and D): forward integration in

578   time (d^{-1}). A and B, week of September, 24, 2003. C and D, week of October, 6, 2003. Circles

579   represent seabirds trajectory and triangles foraging patches. Each color of points represents the

580   tag of a different bird (red, tag 8023; blue, tag 16255; green, tag 11377; magenta, tag 19827).

581

582   Figure 3: Histograms of relative frequency of FSLEs with percent of attracting (ALCSs) and

583   repelling LCSs (RLCSs). Positive values refer to $FSLE_f$ and negative to $FSLE_b$. A) areas crossed

584   by seabirds (long and short trips); B) in the whole MC and C) in the central part (16°S-24°S/30-

585   45°E)

586

587   Figure 4: Box plots of the distribution of FSLEs during short and long trips. The upper and lower

588   ends of the center box indicate the 75th and 25th percentiles of the data; the center of the box

589   indicates the median. Suspected outliers appear in a box plot as individual points + outside the

590   box. Dotted lines represent the threshold for detection of LCSs.

591

592   **Caption of table**

593   Table 1: Absolute frequency of seabirds' positions on LCSs and on no Lagrangian structures for

594   long and short trips per week and result of the G-test for Goodness of Fit. *Alpha 5%.*

595

week	All trips		Long trips		Short trips	
	LCSs: |FSLE|>0.1 day^{-1}	|FSLE|<0.1 day^{-1}	LCSs: |FSLE|>0.1 day^{-1}	|FSLE|<0.1 day^{-1}	LCSs: |FSLE|>0.1 day^{-1}	|FSLE|<0.1 day^{-1}
1	38	9	19	7	19	2
2	78	40	55	12	23	28
4	208	85	147	54	61	31
5	167	109	137	84	30	25
6	120	77	89	51	31	26
7	79	55	72	32	7	23
8	53	34	53	34	-	-
9	61	59	61	59	-	-
10	55	31	45	24	10	7
14	35	12	35	12	-	-
15	10	5	10	5	-	-
%	63.7	36.3	65.9	34.1	56.0	44.0
	G Test (Log-Likelihood ratio)		G Test (Log-Likelihood ratio)		G Test (Log-Likelihood ratio)	
N	1420		1097		323	
k	11		11		7	
df	10		10		6	
G	28.119		30.613		32.057	
p	0.00173		0.001		0.000	

One tailed tests. Ho: Seabird positions share equally LCSs (\|FSLE\|>0.1 day^{-1} and on no LCSs.

TABLE 1

Short trips
Long trips
Europa Island

FIGURE 1

A] ATTRACTING STRUCTURES

B] REPELLING STRUCTURES

C] ATTRACTING STRUCTURES

D] REPELLING STRUCTURES

Latitude degree

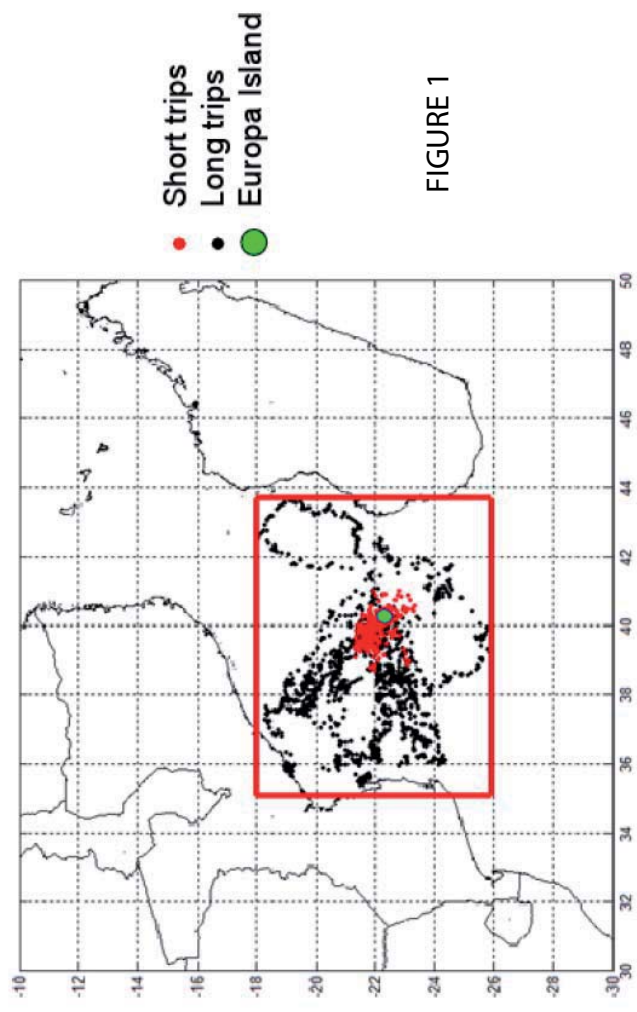Longitude degree

DAY⁻¹

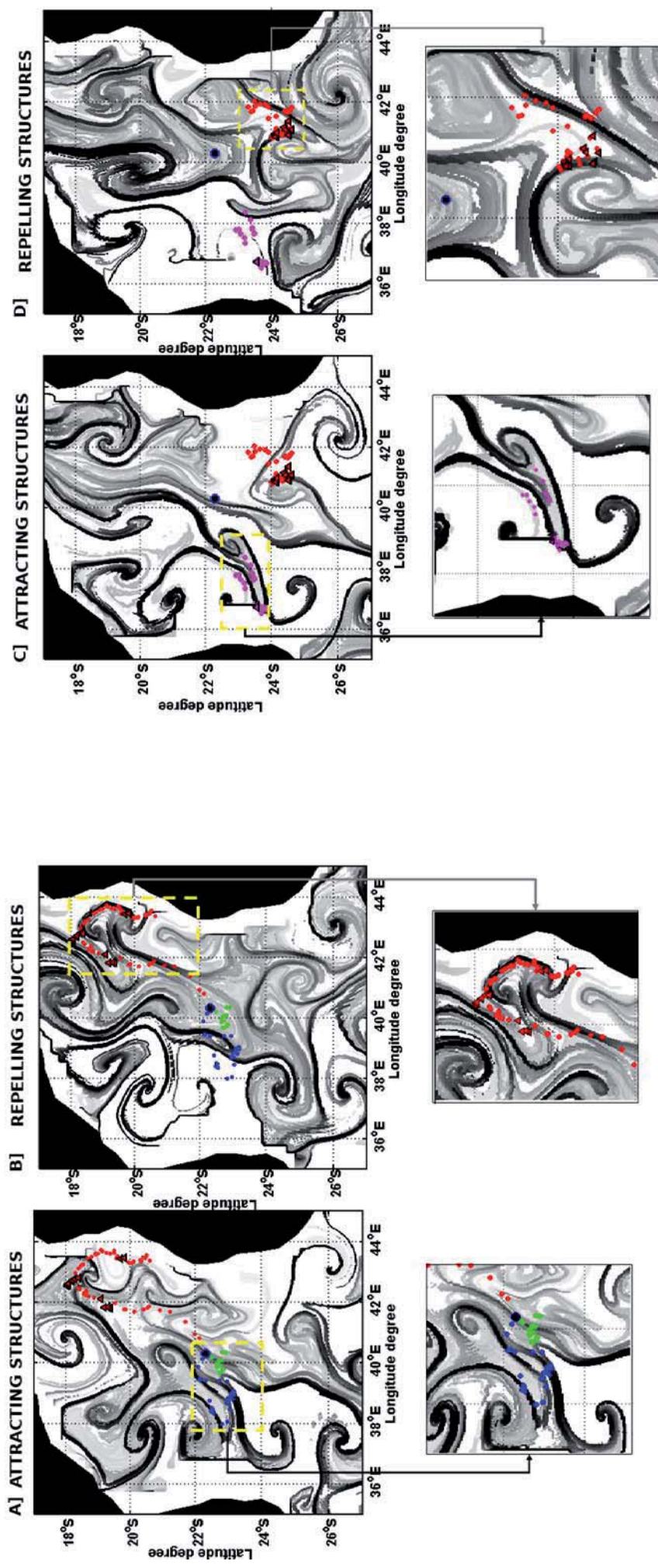0   0.05   0.1   0.15   0.2   0.25
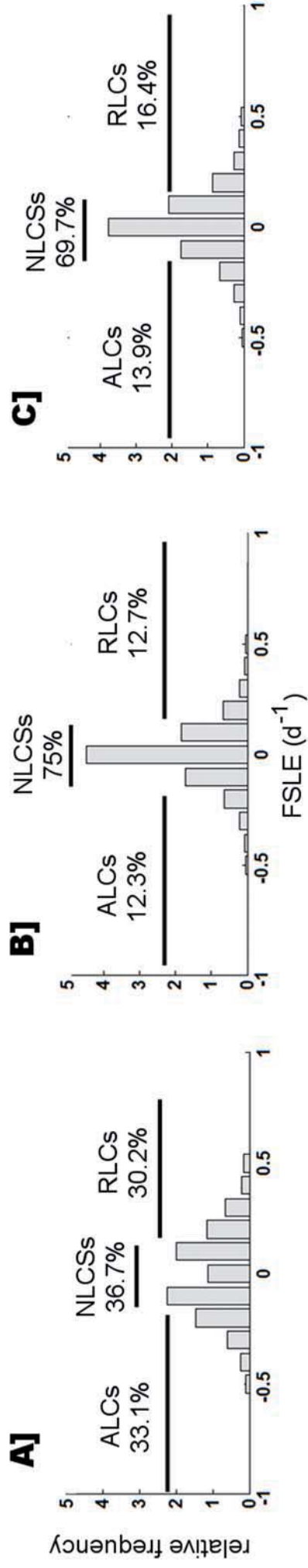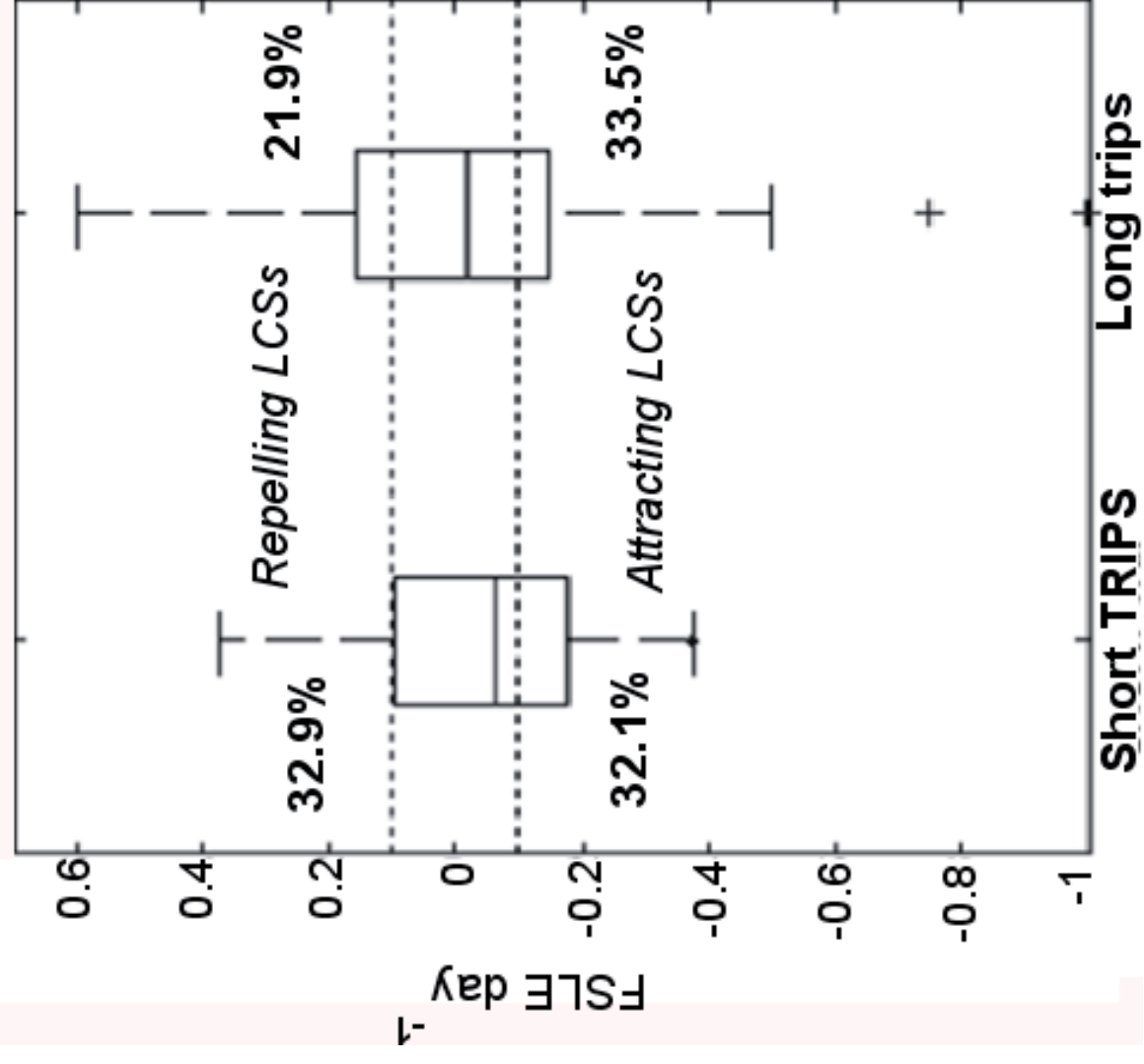
FIGURE 2

FIGURE 3

FIGURE 4

1 **Supporting Information**

2

3 **SI Figure legend**

4 **Figure S1**

5 Figure S1: Box plots of the distribution of FSLEs during flying and foraging part of short and

6 long trips. The upper and lower ends of the center box indicate the 75th and 25th percentiles

7 of the data; the center of the box indicates the median. Suspected outliers appear in a box plot

8 as individual points + outside the box. Dotted lines represent the threshold for detection of

9 LCSs.

10

11 **Figure S2**

12 Figure S2: Box plots of the distribution of FSLEs. The upper and lower ends of the center

13 box indicate the 75th and 25th percentiles of the data; the center of the box indicates the

14 median. Suspected outliers appear in a box plot as individual points + outside the box. A)

15 Outward and return part of short trips. B) Day and night short trips, C) outward and return

16 part of long trips, D) day and night long trips. Dotted lines represent the threshold for

17 detection of LCSs.

18

19 **Figure S3**

20 Figure S3: Comparison between the zonal and meridional components (cm/s) of the velocity

21 field used in our study with those of Lagrangian buoy data in the same oceanographic region

22 (Mozambique Channel). EGM currents are the sum of surface geostrophic anomalies (G), a

23 climatological mean (M) and the surface Ekman velocity field (E). N is the number of data

24 used for the comparison and the square of the correlation coefficient, r^2. In blue: all data

25 points from Lagrangian drifters for our area of interest; in red: all points from Lagrangian

26 drifters for our area of interest when |Udrifter -Uegm| < 30cm/s and |Vdrifter - Vegm| < 30

27 cm/s.

28

29 **SI Table legend**

30 **Table S1**

31 Table S1: Number of birds' positions at week t which are on the LCS of later weeks (t+i,

32 i=1,3,5). The G-test statistics show a decreasing association between birds and LCSs as time

33 lag between them increases.

34

35 **Table S2**

36 Table S2: Result of G-test statistics. Comparison between frequency of birds' positions on

37 repelling or attracting LCS during flying and foraging and short and long trips; Alpha 5%.

38

39 **Table S3**

40 Table S3: Result of G-test statistics. Comparison between frequency of birds' positions on

41 repelling or attracting LCS during outward and return part/day and night during short and

42 long trips. Alpha 5%.

43
44
45 **SI text**
46
47 *Methods*
48
49
50 **Great Frigatebirds**

51   Seabirds' positions were interpolated to the same resolution of FSLEs. Because of

52   Argos positioning errors and inherent errors in interpolating satellite data on a much

53   finer grid, we say that a bird position is on a LCS if it is within a radius of 0.025° from

54   a point where |FSLE|>0.1 d^{-1}. Following Weimerskirch et al. (1), trips were separated

55	in two categories, long and short ones. Typically Great Frigatebirds were doing long
56	trips, mainly during incubation (58.5% of birds), when birds forage long distances
57	from the colony, and shorter trips, mainly when they rear chicks (64.1%) and have to
58	bring food regularly to the nest. A threshold at 617 km was used to distinguish both
59	types of trips. 17 long trips and 33 short trips are separated and visualized on Figure 1.
60	Short trips are located around the breeding colony in Europa Island and positions of
61	long trips are mostly located in the western central part of the channel between 18°S
62	and 26°S, except for 2 trips. Foraging patches were defined as the areas where flight
63	speed between at least 3 successive Argos locations is lower than 10 km h^{-1} (2).
64	Therefore, only pairs of locations at sea separated by more than 30 min were used to
65	limit erroneous estimates of speed because of the relative inaccuracy of the locations
66	(1).

Surface currents data

The weekly global ¼° resolution product of surface currents developed by Sudre and Morrow (3) has been used over the time period January 1st, 2001 to December 31st, 2006. The surface currents are calculated from a combination of wind-driven Ekman currents, at 15 m depth, derived from Quikscat wind estimates, and geostrophic currents computed from time variable Sea Surface Heights. These SSH were calculated from mapped altimetric sea level anomalies combined with a mean dynamic topography from Rio et al (4). The weekly velocity data, which are then interpolated linearly to obtain a daily resolution with a 0.025° intergrid spacing, depend on the quality of their sources as the SSH fields and the scatterometer precision. However, they were validated with different types of *in situ* data such as

80   Lagrangian drifting buoys, ADCP and current meter mooring data. In the

81   Mozambique Channel (10°-30°S, 30°-50°E), zonal and meridional components of the

82   velocity field show an average correlation with for e.g. Lagrangian buoy data between

83   0.71 and 0.76 (see Figure 3 SI).

84   When calculating the FSLEs from velocity data with a resolution of ¼ degree and

85   interpolating down to 1/40° we are assuming that the small scale details of the velocity

86   field are not important for the dispersion dynamics. This situation is called non-local

87   dynamics (5) since it implies that the small scale transport is driven by the large

88   scales. The assumption is correct for flows with an energy spectrum steepest than k^{-3}

89   which corresponds to 2D turbulence. Although there is some uncertainty in energy

90   spectra for the marine surface, the calculations of Stammer (6) show that there is a

91   decay of the energy spectra, at mid-latitudes, close to k^{-3}. Thus we might expect a

92   weak sensitivity of FSLE computations of the surface ocean to the spatial resolution of

93   the velocity field.

94

95   **Computation and analysis areas**

96   The full geographical area of the Mozambique Channel is used to make our

97   numerical computations of FSLEs. We then defined our analysis areas large enough to

98   cover the maximum extension of birds' trajectories and made the approximation to the

99   closest proper rectangle fitting the best. Note that the computation areas are larger than

100   the analysis ones, considering the fact that particles may leave the area before reaching

101   the fixed prescribed final distance δ_f.

102

103   **Statistical test Table S1:**

To compare the number of birds' positions at week t (from 1 to 10) which are on LCS at that given week, with the number of these birds' positions which fall on the LCS of different weeks t+i (i=1,2,…,9) we performed G-tests which quantify their independence. To do so, we consider all the seabirds' positions for a given week *t*. Then we compute the FSLE at week t, and identify which of the birds' positions correspond to LCS. Maintaining the original frigate positions at t, we compute the values of FSLEs for the whole time series of Lyapunov maps from t'=t to t'=t+i (i=1,2,…,9), identifying again which of the bird's positions are on LCSs. G-test were performed on these distributions of number of coincidences of LCSs at all times with the locations of birds at the given time t. Results are displayed on Table S1 for i=1,3,5 and show a decreasing association between birds and LCSs as time lag i between them increases.

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173 Table1

Positions at week t	on LCSs of week t	on LCSs of week t+1	on LCSs of week t+3	on LCSs of week t+5
WEEK1	19	14	9	21
WEEK2	55	49	34	56
WEEK4	146	106	106	99
WEEK5	137	114	112	118
WEEK6	89	69	89	81
WEEK7	72	67	81	71
WEEK8	53	50	41	28
WEEK9	61	59	48	66
WEEK10	45	28	46	48
Gtest		*0.81*	*0.19*	*0.12*

174
175
176 Table2

		Flying	Foraging
Long trips	Repelling LCS FSLE>0.1 day^{-1}	318	50
	Attracting LCS FSLE<-0.1 day^{-1}	333	37
G-test	*N* *G* *p*	*738* *2.29* *0.13021*	
Short trips	Repelling LCS FSLE>0.1 day^{-1}	76	9
	Attracting LCS FSLE<-0.1 day^{-1}	112	10
G-test	*N* *G* *p*	*207* *0.34* *0.55993*	

Two tailed tests. Ho: seabirds share out equally on repelling and attracting structures when they fly or forage

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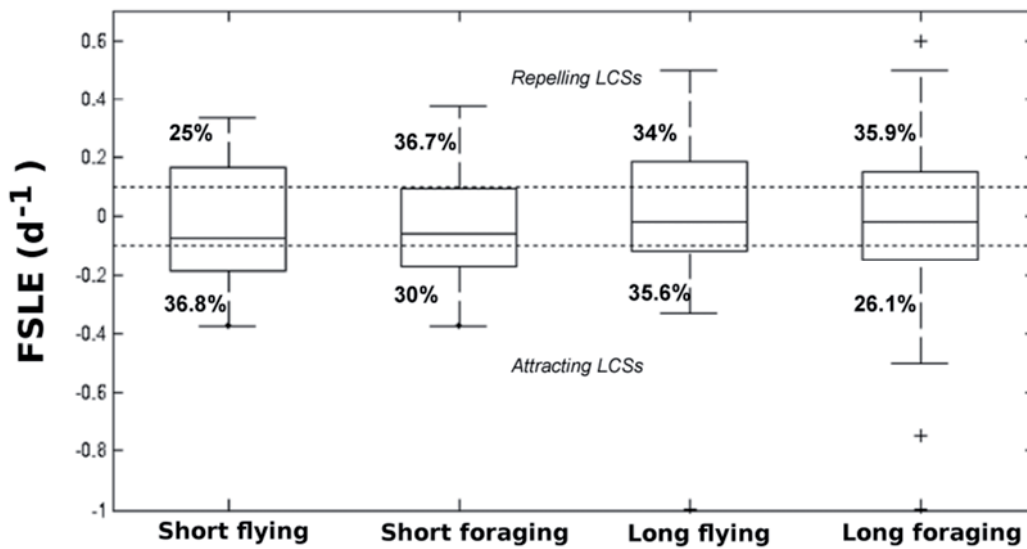185
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194   Table3
195

		OUTWARD	RETURN	DAY	NIGHT
Long trips	Repelling LCS FSLE>0.1 day^{-1}	196	156	188	162
	Attracting LCS FSLE<-0.1 day^{-1}	186	165	164	181
	N	703		695	
	G	0.513		2.655	
	p	0.47395		0.10325	
short trips	Repelling LCS FSLE>0.1 day^{-1}	33	29	27	33
	Attracting LCS FSLE<-0.1 day^{-1}	53	37	65	38
	N	152		163	
	G	0.474		5.003	
	p	0.49		**0.0253**	

Ho:seabirds share out equally on repelling and attracting structures during day and night and seabirds share out equally on repelling and attracting structures during outward and return flights
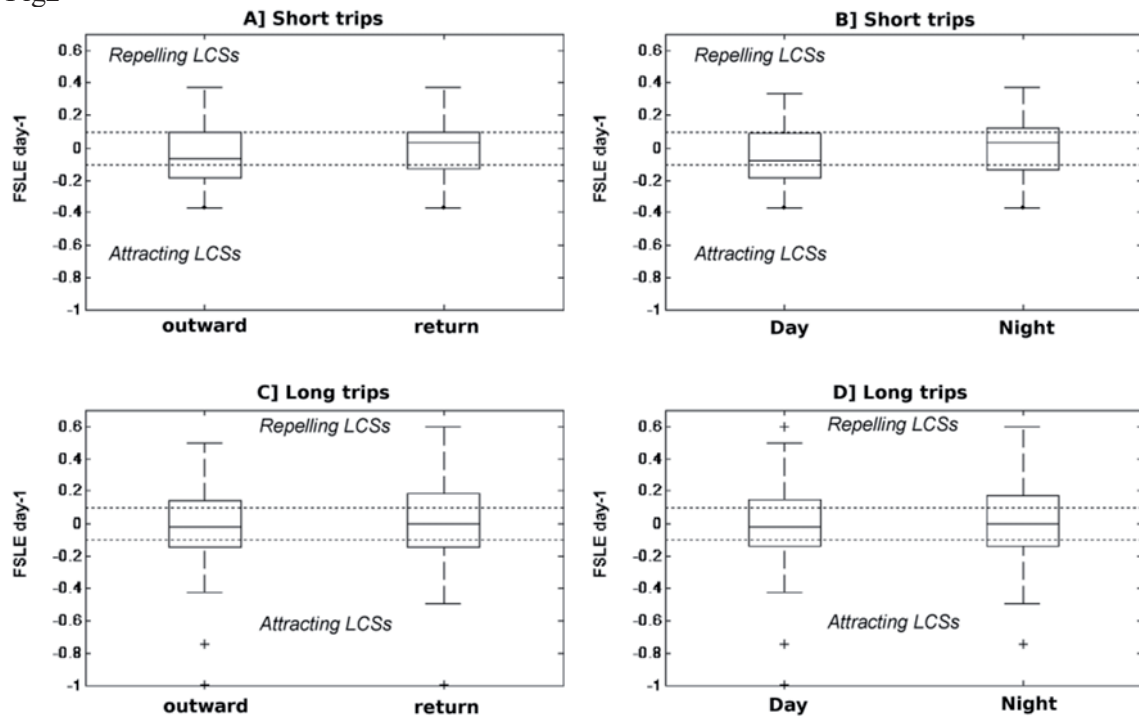
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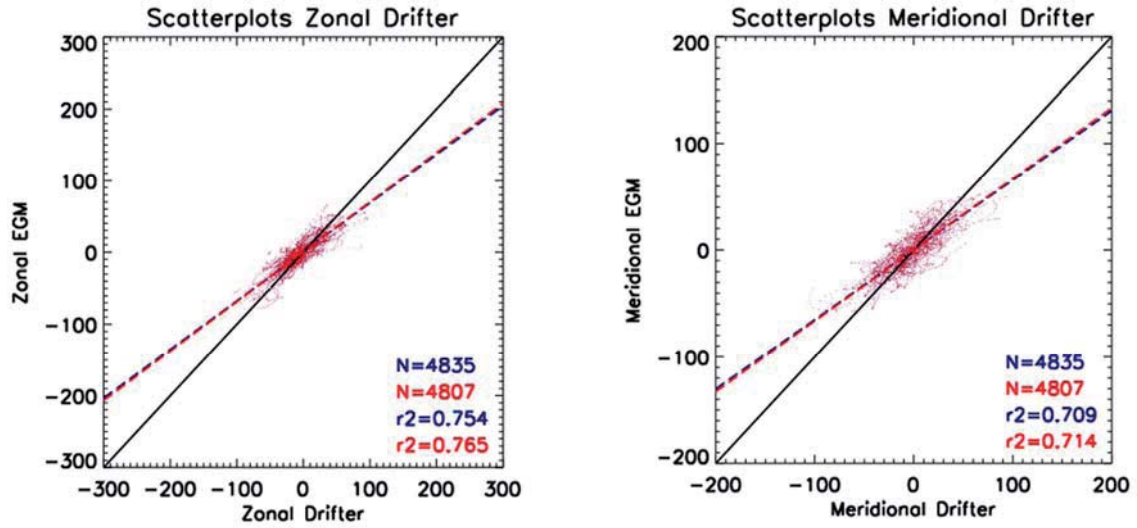200   Fig1

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209   Fig2

A] Short trips — FSLE day-1, Repelling LCSs / Attracting LCSs, outward / return

B] Short trips — FSLE day-1, Repelling LCSs / Attracting LCSs, Day / Night

C] Long trips — FSLE day-1, Repelling LCSs / Attracting LCSs, outward / return

D] Long trips — FSLE day-1, Repelling LCSs / Attracting LCSs, Day / Night

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212   Fig3

Scatterplots Zonal Drifter — Zonal EGM vs Zonal Drifter
N=4835
N=4807
r2=0.754
r2=0.765

Scatterplots Meridional Drifter — Meridional EGM vs Meridional Drifter
N=4835
N=4807
r2=0.709
r2=0.714

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