

The spatial ecology of juvenile loggerhead turtles (*Caretta caretta*) in the Indian Ocean sheds light on the "lost years" mystery

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Abstract :

While our understanding of the early oceanic developmental stage of sea turtles has improved markedly over recent decades, the spatial context for this life history stage remains unknown for Indian Ocean loggerhead turtle populations. To address this gap in our knowledge, 18 juvenile loggerheads were satellite tracked from Reunion Island (21.2A degrees S, 55.3A degrees E) between 2007 and 2011. Nine turtles swam north toward Oman (20.5A degrees N, 58.8A degrees E), where one of the world's largest rookeries of loggerheads is located. Three individuals traveled south toward South Africa and Madagascar, countries that also host loggerhead nesting grounds. Fourteen of the transmitters relayed diving profiles. A dichotomy between diurnal and nocturnal diving behavior was observed with a larger number of shorter dives occurring during the day. Diving behavior also differed according to movement behavior as individuals spent more time in subsurface waters (between 10 and 20 m) during transit phases. The study provides an understanding of the oceanic movement behavior of juvenile loggerheads in the Indian Ocean that suggests the existence of an atypical trans-equatorial developmental cycle for the species at the ocean basin scale in the Indian Ocean. These results address a significant gap in the understanding of loggerhead oceanic movements and may help with the conservation of the species.

Introduction

Loggerhead sea turtles (*Caretta caretta*) have a global distribution throughout tropical and warm temperate waters, and the species is classified as endangered in the IUCN Red List (IUCN 2012). A striking feature of the life history of loggerheads is the large-scale, oceanic basin, development cycle. After entering the sea, hatchlings execute an intense, but brief, swimming phase known as the “swimming frenzy” (Wyneken and Salmon 1992). They then enter a neritic transitional phase lasting from a few days to a few months (Musick and Limburg 1997), after which they enter the oceanic zone. Juvenile and subadult loggerheads remain in the

44 open ocean for many years, a phase referred to as the juvenile oceanic stage (Bolten 2003),
45 during which their movements are driven essentially by the oceanic currents (Carr 1986).
46 This stage of the development cycle was first referred to as the “lost year” (Carr 1952; Carr
47 1986) and later as the “lost decade” (Musick and Limpus 1997) since it has long remained a
48 stage of which little was known due to the difficulty of following the movements of
49 hatchlings once they had departed the coastline. After this temporally variable oceanic stage
50 (Bolten 2003), loggerhead juveniles return to neritic habitats before reaching sexual maturity
51 (Bjorndal et al. 2000; Bolten 2003). It has been demonstrated, however, that some juveniles
52 can frequent the oceanic environment until sexual maturity (McClellan and Read 2007;
53 Mansfield et al. 2009; McClellan et al. 2010). Similarly, many adults also establish feeding
54 ranges far removed from coastal zones (Hawkes et al. 2006; Hughes 2012). It has been
55 suggested that these two strategies provide survival advantages. Whereas a neritic foraging
56 strategy might be more energetically favorable for turtle development, an oceanic foraging
57 strategy may reduce exposure to predation (Peckham et al. 2011).

58 In the North-Atlantic Ocean, the loggerhead development cycle is spread across the
59 entire basin (Bolten 2003), with turtles drifting from the western Atlantic nesting sites to the
60 islands of Azores, Madeira and Canary Islands (Putman et al. 2012; Scott et al. 2012).
61 Similarly, in the Pacific Ocean, genetic studies have demonstrated that the development cycle
62 occurs on an even greater scale, originating from breeding sites in Japan, Australia and New
63 Caledonia, and reaching as far as the coasts of Baja California in Mexico (Bowen et al. 1995;
64 Bowen and Karl 2007; Boyle et al. 2009).

65 Whilst genetic and oceanographic studies have provided a better understanding of
66 large scale movement patterns of the loggerhead juvenile stage in the Atlantic and Pacific
67 Oceans, information on their diving behavior remains scant. A diel diving behavior has been
68 exhibited by loggerheads during the open sea juvenile stage (Godley et al. 2003; Polovina et

69 al. 2004; Howell et al. 2010), with daytime dives being significantly shorter and more
70 numerous than nighttime dives. Recently, Howell et al. (2010) showed that, in the North
71 Pacific Ocean, oceanic juveniles spend 80% of the time, day and night, at very shallow (0-
72 5m) depths (90% in 0-15m). Moreover, this study revealed that the diving behavior was
73 variable across meso-scale oceanic features, with turtles making deeper and longer dives
74 when encountering more dynamic waters (Howell et al. 2010).

75 In the Indian Ocean, significant nesting sites for loggerheads are located at the edge of
76 the western part of the basin in the northern and the southern hemispheres and on the northern
77 coast of Western Australia (Baldwin et al. 2003; Halpin et al. 2009). Masirah Island (Sultanate
78 of Oman; 20.5°N, 58.8°E) in the North, is considered one of the world's largest nesting sites
79 (ca. 30,000 nesters per year ; Ross and Barwani 1995; Ross 1998; Rees et al. 2010). South
80 Africa (27.1°S, 32.8°E), Mozambique (26.3°S, 32.9°E) and Western Australia are also known
81 to host important nesting populations (ca. 500-1000 nesters per year ; Hughes 2010; Nel et al.
82 2013; Baldwin et al. 2003). In the south-western coast of Madagascar (23.8°S, 43.7°E),
83 nesting events have also been reported, but nesting activity in this area is poorly documented
84 and thought to be limited (Martel 2003; Rakotonirina 2011). Other minor nesting sites have
85 also been identified in Yemen and Sri Lanka (Halpin et al. 2009).

86 Whereas recent studies have focused on the spatial dynamics of adult loggerheads in
87 the western Indian Ocean (Oman: Rees et al. 2010; South Africa: Luschi et al. 2006), only one
88 study focused on the juvenile stages (*e.g.* Hughes 1973), which produced few data on oceanic
89 movements.

90 The main objective of our study was to document the foraging strategies of juveniles
91 by determining the environmental conditions with which they were associated from their
92 satellite-recorded large scale oceanic movements. Our study thus aimed to provide a better
93 understanding of these oceanic movements and the diving behavior of juvenile loggerheads,

94 so as to provide key information for the survival of this species, which is of major concern
95 both in the Indian Ocean (Petersen et al. 2009) and worldwide (Lewison et al. 2004).

96

97 **METHODS**

98

99 **Study area and sea turtle tracking**

100 Late juvenile loggerheads are captured as bycatch by long-lining fishing boats from Reunion
101 Island (21.15°S, 55.27°E). These vessels operate in French and Madagascar exclusive
102 economic zones (between 25°S and 16°S, and 49°E and 57°E; Online Resource 1 - Fig.1).

103 Following a collaboration protocol, fishermen declare to the official authorities
104 (CROSS Réunion) any accidental captures of loggerheads for which on-board hook extraction
105 is not possible. Individuals are then brought to 'Kélonia Sea Turtle Observatory and Care
106 Centre' (www.kelonia.org) where they receive veterinary surgery for hook extraction and are
107 placed in tanks at the care centre. General behavior and physiological parameters are regularly
108 monitored.

109 A set of criteria has to be fulfilled before deciding that the animal has recovered
110 sufficiently to be released: (1) the injuries have to be healed completely, (2) individuals must
111 be able to ingest prey efficiently and regain body mass, (3) active swimming behavior must be
112 resumed and (4) individuals must be free of anemia or infectious disease (confirmed through
113 blood analysis). Between 2007 and 2011, a total of 56 individuals were brought to the care
114 centre. Fourteen individuals (25%) died following the operation. To date, 27 (48%) have been
115 released, of which 18 were fitted with Argos Platform Terminal Transmitters (PTTs). The
116 mean ± SD curved carapace length of individuals released with a satellite tag was 67.7 ± 5.4
117 cm (n = 18).

118 We used four types of PTTs: A: TAM-4225, B: TAM-4325 and C: A-225 (Telonics, Inc.,
119 Mesa, Arizona), and D: SPOT-5 (Wildlife Computers, Inc., Bellevue, Washington). PTTs were
120 attached on the second vertebral carapace scute with epoxy resin (Power-Fast and Pure2k;
121 Powers Fasteners Inc., Wieringerwerf, Nederland). PTTs of types C and D were programmed
122 to transmit data continuously whereas PTTs of types A and B transmission followed a duty
123 cycle involving 24 hours "on" followed by 12 hours "off" to extend life expectancy. Turtles
124 were released approximately 3 km off the west coast of Reunion Island (21.15°S, 55.27°E)
125 after periods of captivity ranging from 28 to 876 days (mean ± SD : 277 ± 209 days; Table 1).

126

127 **Location and dive data acquisition**

128 The mean ± SD lifetime of PTTs was 158 ± 112 days (maximum 401 days, type A: 168 ± 53,
129 type B: 148 ± 21, type C: 40 ± 17, type D: 268 ± 162, see Table 1). Location data were filtered
130 in two successive stages: (1) *ad-hoc* heuristic pre-filtering and (2) state-space model (SSM)
131 filtering. Pre-filtering consisted in removing 0 and Z class locations (which, according to
132 CLS/Argos hierarchy, are of low precision), as well as on-ground locations (i.e. which
133 appeared more than 1m above sea level on Gebco Gridded Global Bathymetry Data (Arendt
134 et al. 2012; Mansfield et al. 2009) and locations involving a speed exceeding 15 km h⁻¹. SSM
135 filtering was run using the hierarchical correlated random walk model described in Breed et
136 al. (2009) under R and WinBUGS (5000 iterations, a burn-in of 3000, a thin of 5 and two
137 MCMC chains, as in Hoenner et al. (2012) who previously used this procedure on sea turtles
138 and demonstrated that location accuracy was improved significantly).

139 PTTs of types A, B and C were equipped with depth sensors. Two kinds of parameters
140 were recorded: single dive parameters and integrated dive parameters. Single dive parameters
141 corresponded to last dive duration and maximum depth. Integrated parameters corresponded
142 to number of dives, average duration, maximum duration, maximum depth, underwater

143 percentage and time-at-depth histograms. They were computed over a given timeframe of
144 either 12 h (types A and B) or 24 h (type C). Details of measured parameters and sampling
145 frequency for each type of device are provided in Table 2.

146 Types A and B were programmed to tabulate integrated dive data into 12-h periods
147 06:00-18:00 and 18:00-06:00 GMT+4 (roughly corresponding to daytime and night periods in
148 the study area). The depth bins for the time-at-depth distributions were 10 m-width from
149 surface up to 60m, and 20 m-width from 60 m to 120m. Two additional bins were used for
150 deepest dives: 120-160-m and larger than 160 m. Type C was programmed to tabulate dive
151 data into 24-h periods with 20 m-width depth bins from the surface down to 180m.

152

153 **Oceanic environment**

154 The following environmental parameters were extracted along the filtered tracks using linear
155 temporal and bilinear spatial interpolation: (1) sea surface temperature (SST), (2) net primary
156 production (NPP), (3) sea surface currents and total kinetic energy per water mass unit (TKE).

157 (1) Satellite-derived SST data were taken from the Moderate Resolution Imaging
158 Spectroradiometer (MODIS), a major NASA EOS instrument aboard EOS-Aqua satellite
159 (<http://oceancolor.gsfc.nasa.gov>; Savtchenko et al. 2004). Datasets are available daily with a
160 spatial resolution of 4.63 km.

161 (2) Ocean NPP data were downloaded from Oregon State University
162 (<http://www.science.oregonstate.edu/ocean.productivity/>). NPP calculation is based on the
163 Vertically Generalized Production Model (Behrenfeld and Falkowski 1997). Datasets used for
164 NPP calculation include MODIS surface chlorophyll concentrations, sea surface temperature
165 and photosynthetically active radiation. Datasets are available at 8-days interval with a spatial
166 resolution of 9 km.

167 (3) The surface currents were extracted from the GEKCO database which provides a
168 satellite surface current product on daily basis at quarter degree resolution with a global
169 coverage from 82°N to 82°S (Sudre et al. 2013). These current estimates are the sum of
170 geostrophic current (resulting from the balance between the horizontal pressure gradient and
171 the Coriolis force) and Ekman transport (resulting from the balance between the frictional
172 stress due to the wind and the Coriolis force). These data were used both to compute motor
173 (water masses-related) movements from recorded (ground-related) tracks and TKE (TKE =
174 $1/2 s^2$ where s is the current speed; Howell et al. 2010).

175

176 **Movement behavior**

177 Turtles were divided into three groups based on latitude at last location: North (north of the
178 equator), South (south of 30°S) or Undetermined (all others), which were still in the vicinity
179 of the released site when their PTTs stopped transmitting. Horizontal movements (hereafter
180 simply refer to as movements) were classified as “oceanic transit” (OT), “coastal transit”
181 (CT), “oceanic residency” (OR), or “coastal residency” (CR). Transit and resident phases
182 were distinguished in terms of residence time (Barraquand and Benhamou 2008), which
183 corresponds to a well-behaved extension of the first passage time, leading to a less noisy time
184 series that therefore can be more easily segmented in different phases. Transit phases
185 correspond to movements characterized by lowest residence times, which were assumed to
186 occur in areas through which turtles were moving rapidly, whereas resident phases correspond
187 to movements characterized by highest residence times, which were assumed to occur in
188 concentrated-searching, food-rich areas. Because oceanic currents can have a major influence
189 on sea turtles movements, we first computed the current-corrected tracks, corresponding to
190 “motor” movements (*i.e.* performed with respect to water-masses) by subtracting the current
191 effects to the ground-related (*i.e.* Argos recorded) tracks (see Girard et al. (2006) for details).

192 Residence time was then computed, within a 200 km-radius circle, as the sum of the first
193 passage time within the circle and possibly of additional backward and forward time(s) spent
194 in the circle, with due care that the time(s) spent outside the circle before re-entry was not
195 larger than a given threshold. This was set at 10 days in the present study. The 200 km radius
196 was chosen because habitat selection of juvenile loggerheads is known to occur at a scale of
197 hundreds, rather than tens, of kilometres (Revelles et al. 2007). The limit of 10 days was set
198 up to avoid irrelevant movement portions (further or prior to location) being encompassed
199 within the residence time computation. The residence time series was segmented using the
200 Lavielle (2005) procedure, with a maximum number of 10 segments and a minimum of 20
201 locations in a segment. Segments were assigned to either transit or resident phases, based on
202 mean resident time over the segment, with higher residence times corresponding to the
203 resident period. The whole procedure was repeated with radii of 100 and 300 km, as well as
204 with an unlimited time allowed outside the circle before re-entry so as to check that our
205 results were not too sensitive to the choice of these parameters. No major differences were
206 observed in the identification of the resident and transit phases. These phases, when taking
207 place less than 100 km from any coastal area (continent or island) were considered coastal,
208 and beyond 100 km, oceanic.

209

210 **Diving behavior**

211 Based on distributions of dive depth and dive duration, we identified three categories of
212 dives: shallow and short dives (Dss: depth<30 m, duration<13 min), shallow and long dives
213 (Dsl: depth<30 m, duration >13 min) and deep and long dives (Ddl: depth>30 m, duration
214 >13 min). Cut-offs of 13 min and 30 m were chosen as limits between classes based on dive
215 depth and dive duration distributions (Fig. 1). When only dive duration was available (PTT
216 type C), dives were either assigned to long dives (Dl; duration >13 min) or to short and

217 shallow dives (Dss; duration < 13 min). The latter should have been considered simply as
218 short dives, but it appeared that dives with duration inferior to 13 min were rarely deeper than
219 30 m (0.27%, based on data from PTT types A and B). The dives that did not meet any of
220 these criteria (0.17%) were not assigned to any category.

221

222 **Computations and Statistical analyses**

223 All results are presented as median \pm IQR. For comparison of diving and environmental data,
224 we either used a Kruskal-Wallis test for multiple group comparison, a Wilcoxon signed-rank
225 test for paired comparison between two groups or a Mann-Whitney U test for unpaired
226 comparison between two groups. When possible, exact P-values were computed. Most
227 analyses were performed using R software (R Core Team, 2012). Current-correction and
228 residence time analyses were performed using Pascal programs developed by the authors.
229 Lavielle (2005) segmentation was performed using his Matlab script ([http://www.math.u-](http://www.math.u-psud.fr/~lavielle/programs/dcpc.zip)
230 [psud.fr/~lavielle/programs/dcpc.zip](http://www.math.u-psud.fr/~lavielle/programs/dcpc.zip)).

231

232 **RESULTS**

233

234 **Movement patterns**

235 The tracks of these 18 individuals are shown on Fig. 2. Nine turtles were assigned to the
236 northern group (N1-N9) and four to the southern group (S1-S4). Northern turtles reached the
237 latitude of Arabian Peninsula in the northern hemisphere while southern individuals traveled
238 beyond the latitude of South Africa. The remaining five either remained in the vicinity of the
239 release site (X2- X4) or their transmitter stop transmitting shortly after deployment (X1 and
240 X5; Table 1). There were no significant differences between the average sizes of individuals
241 per group (Kruskal-Wallis test, $H_2 = 4.12$, $P = 0.13$). The total distanced travelled was 2,932

242 km \pm 2,206 km (n = 18). The maximum straight distance travelled was 4,591 km (N5 reached
243 the coast of the Sultanate of Oman). Turtles from the northern and southern groups
244 respectively travelled $3,584 \pm 736$ km (22.1 ± 8.6 km/day, n = 9) and $2,386 \pm 857$ km ($10.6 \pm$
245 12.2 km/day, n = 4) away from the release point. The other turtles travelled 671 ± 505 km ($6.8 \pm$
246 26.7 km/day, n = 5). There were no significant differences between the groups in the
247 average daily straight-line distances travelled (Kruskal-Wallis test, $H_2 = 1.44$, $P = 0.49$).
248 Neither was there any significant relationship between the size of the animals and the average
249 daily straight-line distance travelled (Spearman rank correlation, $r_s = 0.04$, n = 18, $P = 0.97$).

250 The nine individuals of the northern group (N1-N9) displayed similar dispersal
251 patterns. Their mean traveling direction corresponded roughly to the direction of Masirah
252 Island (Oman) which hosts a major loggerhead rookery. N1-N5 traveled to the Omanese and
253 Yemeni coasts more than 3500 km away from the release point. N6-N9 headed to the south
254 coast of Somalia and followed the coast northwards. N9 remained in a narrow strip some 30
255 km long off the Somali coast for more than 3 months. The PTTs of N6-N8 stopped
256 transmitting while they were heading north.

257 The four southern turtles (S1-S4) traveled more than 1500 km away from the release
258 point. S1-S3 travelled south-west whilst S4 first went southward and later eastwards in the
259 middle of the southern Indian Ocean. It was the only tracked individual that crossed the 70°E
260 meridian going eastward. All four turtles remained in the open ocean.

261 For the other turtles (X1-X5), last locations were within 1500 km from the release point.
262 X1 and X2 remained in the open ocean. They followed atypical westward pathways moving
263 toward Madagascar either straight (X1) or with loops (X2). X3 followed a northerly route and
264 remained in the vicinity of St-Brandon islands (670 km from Reunion Island) for more than 3
265 months. Similarly, X4 and X5 headed north but they remained in the oceanic zone. Their

266 movement patterns at the end of the transmission, around 1,100 km away from the release
267 site, were similar to the patterns displayed by the turtles of the northern group.

268

269 **Movement behavior types**

270 Behavioral modes – “oceanic transit” (OT), coastal transit (CT), oceanic residency (OR), or
271 coastal residency (CR) – along each current corrected track are shown in Online Resource 2.
272 Overall, turtles spent most of their time in transit, and more specifically in ocean transit (OT:
273 $51.5 \pm 36.6\%$, CT: $8.5 \pm 19.0\%$, OR: $1.8 \pm 35.0\%$, CR: $0.5 \pm 12.3\%$, n = 18). The PTTs of two
274 turtles, X1 and X2, stopped transmitting while they were considered in OT. X3 spent 100 days
275 in CR off St-Brandon islands and remained there until transmission was interrupted. Turtles of
276 the southern group (S1-S4) exhibited almost exclusively OT or OR. These individuals did not
277 travel along coastal areas except near the islands of Reunion and Mauritius shortly after
278 release. None of them exhibited coastal residency. S2 and S3 noticeably exhibited long OR
279 periods (113 days (72.7%) and 288 days (73.3%) respectively). Both turtles traveled along
280 large circles (150-300 km of radius) either clockwise or anti-clockwise. S4 exhibited a
281 slightly different movement behavior than other southern turtles as it spent most its time
282 (53.2%) in OT. Individuals of the northern group traveled longer distances either in the open
283 ocean or in the coastal areas of Somalia. N9 remained for 75 days in CR along a very narrow
284 area of the Somalian coast. Once reaching the Omani and Yemeni waters, N1, N2 and N5
285 alternated long OR with short CR phases. Other individuals did not reach latitudes north of
286 10°N during their tracking periods.

287

288 **Diving behavior**

289 A total of 23,362 dive durations (from 14 turtles) and 18,688 dives depths (from 10 turtles)
290 were recorded. The dive depth distributions show that $86.9 \pm 8.2\%$ (n = 10) of dives were

291 shallower than 30 m and that $98.5 \pm 1.2\%$ ($n = 10$) of dives were shallower than 100 m.
292 Another peak with larger dive frequencies appears around 55 m. Dive duration data
293 demonstrated that $57.1 \pm 12.9\%$ ($n = 14$) dives were shorter than 2 minutes and $88.9 \pm 6.6\%$
294 ($n = 14$) shorter than 30 minutes where a second peak appears in the number of dives.
295 Mean frequencies of dives assigned to each dive type Dss, Dsl, Ddl and Dl were respectively
296 $80.0 \pm 10.8\%$ ($n = 14$), $4.6 \pm 3.8\%$ ($n = 10$), $13.1 \pm 7.8\%$ ($n = 10$) and $9.9 \pm 15.8\%$ ($n = 4$; Fig.
297 1).

298 There was a clear daily dichotomy in turtles' diving behavior (Fig. 3 and Fig. 4), with
299 diurnal dives being significantly more numerous (Wilcoxon signed-rank test, $T = 55$, $P =$
300 0.002 , $n = 10$ Fig. 3a) and shorter (Wilcoxon signed-rank test, $T = 1$, $P = 0.002$, $n = 10$, Fig.
301 3e, Table 3) than nocturnal dives. In addition, maximum dive depth was also significantly
302 deeper at night (Wilcoxon signed-rank test, $T = 2$, $P = 0.006$, $n = 10$, Fig. 3c, Table 3). During
303 daytime, turtles spent significantly more time just below the surface ($53.5 \pm 19.1\%$ in 0-10 m,
304 $n = 10$, Table 3) than at night ($20.7 \pm 11.4\%$ in 0-10 m, $n = 10$, Table 3, Wilcoxon signed-rank
305 test, $T = 55$, $P = 0.002$). At night they spent half their time between 0-30 m ($51.4 \pm 22.2\%$ in
306 0-30 m, $n = 10$) with a relatively homogenous distribution in the water column (Online
307 Resource 1-Fig. 2). Time-at-depth for deepest layers (> 40 m) did not differ between day (4.3
308 $\pm 5.7\%$, $n = 10$, Table 3) and night ($5.2 \pm 5.7\%$, $n = 10$, Online Resource 1-Fig. 2, Table 3,
309 Wilcoxon signed-rank test, $T = 36$, $P = 0.43$). These differences in diving behavior were
310 confirmed by single dive parameters: short and shallow dives (Dss) were significantly more
311 frequent during day hours ($86.4 \pm 12.8\%$, $n = 14$, Table 3) than during night hours ($73.0 \pm$
312 8.9% , $n=14$, Table 3, Fig. 4, Wilcoxon signed-rank test, $T = 104$, $P < 0.001$).

313

314 **Relation between diving and movement behavior**

315 Time spent just below the surface (0-10 m) was not clearly related to movement phases (OR,
316 CR, CT, OT). A difference in the usage of the water column located between 10 m and 20 m
317 was observed, both during oceanic and coastal phases (Online Resource 1-Fig. 3). Turtles
318 spent more time in this layer while they were in resident phases ($24.9 \pm 2.5\%$, n = 6, Table 3)
319 than during transit periods ($8.8 \pm 6.4\%$, n = 6, Table 3, Mann-Whitney U test, U = 13, P =
320 0.036). The proportion of short and shallow dives (Dss) was slightly but not significantly
321 more important during transit phases ($85.5 \pm 9.5\%$, n = 14, Table 3) than during residency
322 phases ($74.5 \pm 5.4\%$, n = 7, Table 3, Mann-Whitney U test, U = 13, P = 0.055).

323 Slight differences were also observed in the usage of the deepest layers both during the
324 open ocean and coastal phases (Online Resource 1-Fig. 3). The maximum dive depth of
325 turtles during transit phases (121.2 ± 25.0 m, n = 9) was deeper than during resident phases
326 (100.0 ± 50.0 m, n = 9; Table 3, Mann-Whitney U test, U = 56, P = 0.039). Nevertheless, the
327 usage of the deepest layers (> 40 m) were not significantly different whether animals were
328 resident ($4.1 \pm 5.7\%$, n = 7, Table 3) or whether they were in transit ($6.5 \pm 5.1\%$, n = 14, Table
329 3, Mann-Whitney U test, U = 60, P = 0.44).

330

331 **Oceanic covariates**

332 The distributions of SST, NPP and TKE are illustrated in Fig. 5 and oceanic environment
333 values are summarized in Table 4 (An illustration of the oceanic covariates for each individual
334 track is provided in Online Resource 3). Most (95%) of the turtles locations were associated
335 with SSTs ranging from 17.12°C to 30.05°C . S4 experienced the coldest SST (11.5°C by
336 32.2°S) and N6 was exposed to the highest SST (31.9°C by 11.8°S). Turtles of the different
337 groups were exposed to various levels of SST (Kruskal-Wallis test, $H_2 = 9.30$, P = 0.009).
338 During residency phases (coastal and open ocean), individuals in the southern group were

339 exposed to colder SST ($19.4 \pm 0.72^\circ\text{C}$, $n = 3$) than individuals in the northern group ($27.7 \pm$
340 0.61°C , $n = 6$, Fig. 6a, Mann-Whitney U test, $U = 36$, $P = 0.028$). The other turtles were
341 exposed to high SST of the same order of magnitude as northern turtles ($27.8 \pm 0.03^\circ\text{C}$, $n = 2$,
342 Fig. 6a, Mann-Whitney U test, $U = 16$, $P = 0.44$).

343 NPP levels were extremely variable along tracks, with 95% of values ranging from
344 $125.0 \text{ mg C m}^{-2} \text{ day}^{-1}$ to $1141.6 \text{ mg C m}^{-2} \text{ day}^{-1}$. The highest levels of NPP were observed
345 along the coast of the Arabian Peninsula, with the highest level of NPP being recorded for N5
346 at $7801.1 \text{ mg C m}^{-2} \text{ day}^{-1}$ near the south-east coast of Oman. During residency phases,
347 individuals were exposed to varying levels of productivity, depending on their groups (Fig.
348 6a; Kruskal-Wallis test, $H_2 = 8.07$, $P = 0.017$). Individuals of the undetermined group ($231.1 \pm$
349 $51.7 \text{ mg C m}^{-2} \text{ day}^{-1}$, $n = 2$, for undetermined group) were exposed to significantly lower NPP
350 levels than individuals from the northern group ($424.7 \pm 345.3 \text{ mg C m}^{-2} \text{ day}^{-1}$, $n = 5$, Mann-
351 Whitney U test, $U = 5$, $P = 0.019$) or the southern group ($396.9 \pm 146.7 \text{ mg C m}^{-2} \text{ day}^{-1}$, $n = 3$,
352 Mann-Whitney U test, $U = 1$, $P = 0.016$).

353 OR phases occurred most frequently, but not exclusively, either below 30°S or above
354 10°N . Several individuals then described circular movements (N1, N2, N5, N6, S2 and S3;
355 see respective figures in Online Resource 2). These OR phases were related to oceanic meso-
356 scale structures (Online Resource 1-Fig. 4), as supported by higher TKE values observed
357 along the tracks during OR phases ($505.5 \pm 451 \text{ cm}^2 \text{ s}^{-2}$, $n = 10$) in comparison with OT
358 phases ($449.0 \pm 202.5 \text{ cm}^2 \text{ s}^{-2}$, $n = 18$, Fig. 6b, Mann-Whitney U test, $U = 1$, $P = 0.61$). They
359 were also exposed to higher levels of NPP during OR phases ($405.2 \pm 300 \text{ mg C m}^{-2} \text{ day}^{-1}$, $n =$
360 10) than during OT phases ($262.0 \pm 80.6 \text{ mg C m}^{-2} \text{ day}^{-1}$, $n = 18$, Mann-Whitney U test, $U =$
361 39 , $P = 0.014$).

362

363 **DISCUSSION**

364 All living organisms have to move at some point of their life history either by passive or
365 active mechanisms (Holyoak et al. 2008). In a constantly changing and heterogeneous
366 environment, animals interact with the physical environment, the resources and the habitats
367 through their movement (Tilman and Kareiva 1997). Movement is therefore a key to the
368 ecological dynamics of numerous species (Kendall and Fox 1998; Nathan et al. 2008). Sea
369 turtles juvenile stage illustrates its importance. As our knowledge on juvenile loggerhead
370 spatial ecology improves, there is growing evidence that the spatial fate of individuals during
371 the early stages may have substantial effects on growth rates, life-stages duration and age at
372 sexual maturity (Bjorndal et al. 2013). The results of the satellite tracking of eighteen juvenile
373 loggerheads in the Indian Ocean provides new insight on the spatial ecology of the species in
374 the region, but also first evidence of trans-equatorial movements with high latitudinal range.

375

376 **Regional dispersal**

377 One half (50%) of the late juvenile loggerhead sea turtles tracked in this study went north
378 towards one of the world's largest rookeries for the species (Fig. 2). Another important
379 component (22%) went south-west towards smaller rookeries (Fig. 2). The average size of
380 first-time nesters is 84 cm in South Africa (Nel et al. 2013) and 91 cm in Oman (Ross and
381 Barwani 1995) whilst the size of sexual maturity for this species is usually considered to be
382 around 80 cm to 90 cm (Avens and Snover 2013). With an average curved carapace length of
383 68 cm, the individuals we tracked were likely to be close to sexual maturity, but not mature,
384 and therefore to be heading towards their natal site, as sea turtles tend to exhibit philopatry.
385 This suggests that late juvenile loggerheads frequenting the Reunion Island and East
386 Madagascar waters (location of capture, Online Resource 1-Fig. 1) may originate mainly from
387 northerly rookeries, and also, from southerly ones. This suggests a trans-equatorial

388 development cycle for the individuals originating from the northern rookeries. Population
389 genetics could be used to confirm this hypothesis as genetics have been used to characterize
390 the origin of individuals at large distance from their natal site (Monzon-Arguello et al. 2012;
391 Monzón-Argüello et al. 2010).

392 The distances travelled by the individuals were substantial as is generally the case for
393 juvenile sea turtles (Hays and Scott 2013). Nevertheless, while in the other oceans the
394 loggerhead development occurs typically over broad spatial scales (e.g. more than 10,000 km
395 in the Pacific Ocean; Bowen et al. 1995; Boyle et al. 2009), it is normally confined to a single
396 hemisphere (see exception in Bowen et al. 1995). The trans-equatorial development cycle in
397 the Indian Ocean appears therefore atypical.

398 The spatio-temporal pathways followed by juvenile loggerheads to reach the south-
399 west Indian Ocean are still to be determined. Ocean currents are known to play a crucial role
400 in the spatial fate of juveniles sea turtles (Musick and Limpus 1997). Noticeably, in both the
401 Atlantic and Pacific Oceans, large oceanic gyres are persistent and predominantly constrained
402 in a single hemisphere. In the Indian Ocean, the unique characteristics of the monsoon
403 phenomenon make hydrodynamics particularly complex: no annual, persistent, and ocean
404 scale gyre exists as cyclonic and anti-cyclonic complex gyres alternate during winter and
405 summer monsoon periods (Schott and McCreary 2001; Schott et al. 2009). The pathway
406 followed by hatchlings and early juvenile loggerheads from the Arabian Sea to the ocean
407 waters around Reunion and Madagascar is likely to be more complex than in the other oceans.

408 Following the general scheme of Indian Ocean circulation described in Schott et al.
409 (2009), we hypothesize that hatchlings from Oman may drift eastward with the South-
410 Equatorial Counter Current (SECC), possibly up to the eastern part of the Indian Ocean Basin.
411 They may then join the permanent South-Equatorial Current (SEC) and drift westward
412 towards the Mascarene archipelago. In the absence of strong supporting evidence, this

413 hypothesis should however be treated with caution. Furthermore, considering the seasonal
414 characteristics and the complexity of the oceanic circulation in the Indian Ocean, we can
415 surmise that more variability in the development cycle and hatching dispersal of loggerheads,
416 may exist in Indian Ocean hatchling dispersal than for loggerhead populations in other
417 oceans. Drift modeling should provide valuable information regarding these drift patterns as
418 they are now extensively used (Hays et al. 2010; Putman et al. 2012; Scott et al. 2012;
419 Shillinger et al. 2012; Gaspar et al. 2012).

420

421 **Space utilization**

422 In others oceans, various loggerhead foraging behaviors have been observed during the
423 development stages. Juveniles generally settle in neritic habitats but may occasionally remain,
424 or re-enter, the open ocean environment (McClellan and Read 2007; Mansfield et al. 2009;
425 McClellan et al. 2010). Both behaviors were observed in our study. Demographic implications
426 of this alternative foraging strategy are discussed in Peckham et al. (2011). For example,
427 while open ocean individuals may be exposed to slower growth rates due to lower prey
428 availability, this disadvantage may be negated through having a lower predation risk than a
429 purely coastal strategy.

430 It is noteworthy that three individuals remained in the vicinity of the coast of Yemen
431 and Oman and their movements were similar to the post-nesting movements of nesting adults
432 from Oman that forage in the same area (Rees et al. 2010). It is also worth noting that no
433 neritic settlement was observed in the southern group where all turtles remain in the open
434 ocean. In contrast, to the northern group, movements of late juveniles of the southern group
435 differed from the movements of adults nesting in South Africa that are known to forage in the
436 neritic zone along the coast of South Africa (even along the Atlantic side, Hughes 1974),
437 Mozambique (Luschi et al. 2006; Pereira, Pers. Com.), Tanzania (Luschi et al. 2006) or

438 Madagascar (Rakotonirina Berthin, IHSM, Pers. Com.). Nevertheless, circular movements
439 around the oceanic eddies of the Agulhas Rings have been observed in adult leatherback sea
440 turtles (Luschi et al. 2006; Doyle et al. 2008; Galli et al. 2012) demonstrating the interest of
441 the region for sea turtles during the oceanic phases.

442 Individual turtles did not generally spend much time around the island where they were
443 captured and tended to leave the area shortly after release. The region must be regarded as
444 transit zone or a migratory corridor for late juveniles heading towards more productive areas
445 in the South or in the North and simply passing through Reunion Island waters where they are
446 accidentally captured. More data are required to confirm this hypothesis.

447

448 **Diving behavior**

449 The diurnal vs. nocturnal dichotomy in diving behavior, with more dives occurring during the
450 day and longer dives at night, has already been observed (Renaud and Carpenter 1994;
451 Houghton et al. 2002; Godley et al. 2003; Howell et al. 2010). Howell et al. (2010) also found
452 that late juvenile loggerheads spend more time in the 0-15 m depth layer during the night than
453 during the day and that they make more dives deeper than 15 m during the day. With slightly
454 different bins (0-10m), we made similar observations. The dichotomy observed in the diving
455 behavior may result from nocturnal resting dives and diurnal subsurface active dives (Godley
456 et al. 2003).

457 During residency phases, turtles made more use of the 10-20 m layer than during transit
458 periods, but made less use of the deeper layers (>40 m). This was observed for both coastal
459 and open ocean phases. For coastal phases, this may be explained by the shallower waters
460 allowing turtles to reach ocean bottom. During open ocean phases, prey availability at
461 shallower depth may occur under specific conditions, and could explain the observed behavior
462 of loggerheads. The association of oceanic residency phases with oceanic frontal zones, as

463 commonly observed in a variety of taxonomic groups such as birds and large pelagic fishes
464 (Fonteneau et al. (2008); Tew Kai et al. (2009); Tew Kai and Marsac (2010); Online Resource
465 1-Fig. 4) supports this hypothesis but needs to be investigated more deeply in the future.
466 Observations of occasional, and exceptionally deep dive events (>80 m) occurring mostly
467 during transit phases, are difficult to interpret. Individuals may be inspecting the water
468 column looking for prey as it has been suggested for the leatherback sea turtle (Houghton et
469 al. 2008). They may also attempt to reduce silhouetting against the surface and exposure to
470 predators, or eventually to reach the sea bottom to check for the proximity of seamounts or
471 coastal areas as these two behaviors have been suggested for green turtles (Hays et al. 2001;
472 Rice and Balazs 2008).

473

474 **Oceanic environment**

475 Environmental conditions for northern and southern groups were drastically different.
476 According to world Ocean partitioning of Longhurst (1998), the Indian Ocean consists mainly
477 of two large biogeochemical provinces: the Indian Monsoon Gyre Province (MONS) in the
478 north and the Indian South Subtropical Gyre Province (ISSG) in the south. MONS is bordered
479 by the Northwest Arabian Sea Upwelling Longhurst province (ARAB). This province,
480 included in the Arabian Large Marine Ecosystem, is considered a highly productive
481 ecosystem (Heileman et al. 2009) with intense large scale seasonal coastal upwelling and a
482 productive phytoplankton bloom system (Lévy et al. 2007). The southern region also exhibits
483 extensive coastal upwelling leading to the productive Agulhas Current large marine ecosystem
484 (Heileman et al. 2009). In addition, interactions, between meso-scale structures that take place
485 in the Mozambique Channel, generate strong frontal mixing zones favorable to the production
486 and aggregation of organic matter (Tew Kai and Marsac 2009). As a consequence, individuals

487 of the northern and southern groups frequented more productive waters than the individuals
488 that remained close to the release site.

489 There was a major difference in the sea surface temperature to which turtles were
490 exposed, with clearly higher temperatures for the northern group (27.6°C) than the southern
491 group (20.4°C; Fig. 6). Nevertheless turtles from the southern group remained in relatively
492 warm waters for loggerhead sea turtles. For example, in the Pacific Ocean, loggerheads
493 frequent waters with temperatures between 14.5°C and 20°C (Kobayashi et al. 2008), and
494 Coles et al. (2000) have suggested a lower thermal boundary of 13.3°C.. Such environmental
495 difference should potentially lead to contrasted life histories. For example, growth rates have
496 been shown to be strongly decreasing with lower sea surface temperatures and may therefore
497 lead to lower growth rates for the turtles exploiting the southern habitats (Hughes 1974).

498

499 **Conservation implications**

500 Pelagic longlines, through incidental bycatch, has a high impact on loggerhead populations.
501 (Lewison et al. 2004; Peckham et al. 2007). In the Western Indian Ocean, longline bycatch
502 was identified as one of the possible reason explaining the slow recovery of the South African
503 population (Petersen et al. 2009). The loggerheads tracked in this study were caught
504 accidentally by the small French longline fishing fleet operating around Reunion Island and
505 the East-Madagascar EEZs (Evano and Bourjea 2012). The number of individuals
506 accidentally caught by this fishery is assumed to be low (Miossec and Bourjea 2003). The fact
507 that most of the longline gears are set deeper than 40 m around Reunion Island, could explain
508 the relatively low incidence of turtle bycatch occurring within the area

509 Considering the large size of loggerhead populations in the northern Indian Ocean from
510 which a majority of individuals seems to originate, any negative impact of the Reunion Island
511 longline fleet is likely to be moderate. Encouraging collaboration between fishermen and the

512 local sea turtle care centre (Ciccione and Bourjea 2010) should contribute to a reduction of
513 this impact. Existing mitigation measures, such as the use of adapted circle hooks (Read
514 2007), the reduction of gear soak time, the avoidance of hotspots and the setting of gear below
515 turtle-abundant depths (Polovina et al. 2003; Gilman et al. 2006; Howell et al. 2010), are also
516 to be encouraged locally.

517

518 **Summary**

519 In the present study, the first evidence of ocean scale trans-equatorial movements was
520 demonstrated for juvenile loggerhead turtles. This has value for conservation, as threats are
521 identified and protection measures can be developed. It was also shown that southern and
522 northern open ocean juvenile loggerhead turtles target waters with high levels of productivity,
523 although the southern group was exposed to lower sea temperatures. The consequent
524 influence on growth rates and on survival rates might have high impact on population
525 dynamics, viability and recovery. While this is a modest advance in the knowledge of juvenile
526 loggerhead movement ecology, major questions remain. The routes followed by these
527 individuals from their original rookeries to Reunion island waters are yet to be determined
528 and whether the trans-equatorial development cycle suggested by the results for the northern
529 rookeries is prevalent or if it's only an artifact of the small number of loggerhead turtles
530 tracked, remains to be confirmed. Regional genetic and stable isotopes studies, as well as drift
531 simulations could help to answer key issues regarding the survival of loggerhead turtles from
532 hatchling to adult.

533

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775 **FIGURES**

776 **Fig. 1** Dive depth vs. dive duration for pooled single dives of 10 late
777 juvenile loggerhead sea turtles. Density plot clearly outline 2 modes
778 (dark grey) defined here as Dss and Ddl, respectively representing
779 short and shallow (<30m, <800sec) and long and deep (>=30m,
780 >=800sec) dives. Another number of dives, yet less numerous, was
781 identified and defined as Dsl dives, long and shallow (<30m,
782 >=800sec). Only dives superior to 30 sec and 2 m were considered
783 for the purpose of this analysis.

784 **Fig. 2** Satellite tracks of 18 late juvenile loggerhead individuals released
785 after accidental captured by long-line fishing boats in the vicinity of
786 Reunion Island. Individuals were classified in three groups: North
787 (red), and South (Blue).

788 **Fig. 3** Pooled distributions of integrated parameters of late juvenile
789 loggerhead sea turtles over 24h, 12h daytime and 12h night time: (a)
790 Number of dives (n = 14), (b) underwater percentage (n = 14), (c)
791 maximum dive depth (n = 10), (d) maximum dive duration (n = 14), (e)
792 mean dive duration (n = 14). Diurnal dives are more numerous and
793 shorter than nocturnal dives. Maximum dive depth is also
794 significantly deeper at night.

795 **Fig. 4 Percentage of Dss, Dsl and Ddl dives of 10 late juvenile loggerhead**
796 **sea turtles according to day hour (GMT+4). Dss are subsurface and**
797 **short dives (< 30 m, < 800 s), Dsl are shallow and long dives (<30 m,**
798 **>= 800 s) and Ddl are deep and long dives (>= 30 m, > 800 s). Short**
799 **and shallow dives are more frequent at day time while longer dives**
800 **are more frequent during night time.**

801 **Fig. 5 Distributions of environmental variables along the 18 turtle's**
802 **tracks: (a) Sea Surface Temperature (°C), (b) net primary production**
803 **(mgC m⁻² day⁻¹), (c) total kinetic energy (cm² s⁻²). Coldest SST**
804 **appears at the most southern locations. NPP levels are higher at**
805 **more extreme latitudinal locations in the South and in the North and**
806 **are lower in the equatorial locations. TKE values are more**
807 **homogeneously dispersed.**

808 **Fig. 6 (a) Comparison of Net Primary Production (NPP) and Sea Surface**
809 **Temperature (SST) between late juvenile loggerhead individuals**
810 **from the northern group (n = 11) and individuals from the southern**
811 **group (n = 4). NPP reaches higher levels for turtle of the northern**
812 **and southern group. Individual from the southern group are**
813 **exposed to lower SSTs. (b) Comparison of NPP and Total Kinetic**
814 **Energy (TKE) during oceanic transit phases (OT) and oceanic**
815 **resident phases (OR). NPP levels are higher during resident phases.**
816 **Higher TKE levels also occur during resident phases.**

817 **TABLES**

818 **Table 1 Demographic (CCL, body mass), distribution and migration**
 819 **parameters for 18 late juveniles loggerhead sea turtles satellite-**
 820 **tagged after accidental capture from long-liners from Reunion**
 821 **Island, Indian Ocean (Online Resource 1-Fig. 1). Spatial group,**
 822 **distance from released point and bearing from released point are**
 823 **evaluated from last tracking location. Mean travel speed is**
 824 **calculated using tracks interpolated with 3 locations per day.**

Turtle ID	Captivity period (days)	CCL (cm)	Mass (kg)	Tag model	Release date	Tracking period (days)	Distance from released point (km)	Bearing from released point (°)	Mean travel speed (km.day ⁻¹)
N1	171	69	44.7	A	19-Oct-10	244	4521	4	48
N2	51	64	29.6	A	12-Nov-10	182	3949	6	42
N3	199	66	40.3	B	23-Dec-10	134	3620	8	42
N4	215	54	29.3	B	28-Mar-11	126	3584	9	38
N5	338	61	26.5	D	15-Sep-11	219	4591	9	37
N6	238	73	50.2	A	23-Dec-10	101	2748	332	51
N7	876	72	54.4	A	23-Dec-10	144	3115	349	37
N8	143	69	36.4	B	29-Mar-11	141	3213	352	48
N9	44	61	28.5	D	16-Aug-11	260	3417	351	30
S1	470	64	33.4	C	14-Oct-09	48	1873	216	49
S2	212	68	44.0	B	23-Dec-10	157	2037	213	35
S3	141	71	50.0	D	16-Nov-11	394	2732	221	45
S4	332	65	32.4	D	11-Nov-11	401	3221	121	24
X1	453	77	58.7	C	4-Mar-09	20	602	292	46
X2	28	67	37.2	C	11-Dec-09	59	348	249	31
X3	293	71	37.7	B	23-Dec-10	180	671	43	20
X4	224	71	54.2	A	17-Sep-10	171	1157	331	29
X5	557	73	55.0	C	08-Oct-08	33	1107	357	41

825 **Table 2 Depth parameters recorded by transmitter models A-C. Model D**

826 **(5 tags) was not equipped with depth sensors.**

Recorded parameter	Model A and B	Model C
# of tags deployed	10	4
Dive duration (s)	Single dive	Single dive
Dive depth (m)	Single dive	-
Dive counter	12h	24h
Average dive duration (m)	12 h	24h
Maximum dive duration (m)	12 h	24h
Maximum dive depth (m)	12 h	-
Underwater percentage	12 h	24h
Time-at-depth histograms	12 h	24h
Dive qualification period	5s	30s

827

828 **Table 3 Distribution of diving parameters (median ± IQR (n)) for 14 late juvenile loggerheads over the all tracking**
 829 **period (overall), depending on day time (Day and Night) and depending on behavioural modes (OT, OT, CT and**
 830 **CR). (CR: Coastal Residency, CT: Coastal Transit, OR: Oceanic Residency and OT: Oceanic Transit, Dss: Short**
 831 **and shallow dives, Ddl: Deep and long dives, Dsl: Deep and shallow dives)**

	Overall	Day	Night	OT	OR	CT	CR
a. Dive summary							
Number of dives (24h)	300.3 ± 117.3 (14)	356.3 ± 81.3 (10)	215.1 ± 100.4 (10)	326.4 ± 128.5 (14)	268 ± 184.7 (7)	405.5 ± 175.4 (13)	268.5 ± 38 (4)
Under water ratio (%)	90.8 ± 4.6 (14)	92.5 ± 2.8 (10)	92.3 ± 3.2 (10)	91.6 ± 4.5 (14)	80.7 ± 15.3 (7)	88.7 ± 6 (13)	91.5 ± 10.4 (4)
Maximum depth (m)	114.7 ± 18.6 (10)	88.6 ± 27.8 (10)	139.1 ± 40.9 (10)	126.7 ± 17.5 (10)	118.9 ± 35.6 (6)	109.3 ± 22.6 (9)	78.1 ± 32.5 (4)
Maximum duration (min)	66.9 ± 27.2 (14)	68.7 ± 31.5 (10)	72.6 ± 27.1 (10)	65 ± 28.1 (14)	80.5 ± 47.7 (7)	57.7 ± 18.6 (13)	56 ± 29.1 (4)
Mean duration (min)	8.5 ± 4.9 (14)	6 ± 3.8 (10)	10.7 ± 6 (10)	7.9 ± 4 (14)	6.3 ± 12 (7)	5.7 ± 2.7 (13)	6.3 ± 7 (4)
b. Dive type							
Dss ratio (%)	75.9 ± 17.6 (10)	86.4 ± 12.8 (14)	73 ± 8.9 (14)	82.8 ± 12.1 (14)	72.1 ± 19 (7)	86.6 ± 8.4 (14)	76.4 ± 4.9 (4)
Ddl/(Ddl + Dsl)(%)	75.9 ± 17.6 (10)	64.6 ± 47.2 (10)	85.2 ± 28.2 (10)	86.6 ± 19.1 (10)	95.6 ± 33.5 (5)	79.3 ± 28.2 (10)	65.5 ± 15.2 (4)
c. Time-at-depth							
1-10m (%)	39.7 ± 11.2 (10)	53.5 ± 19.1 (10)	20.7 ± 11.4 (10)	37.6 ± 11.7 (10)	42.3 ± 13.8 (6)	43.2 ± 8.1 (9)	30.1 ± 6 (4)
11-20m (%)	15.4 ± 11.7 (10)	6.2 ± 8.3 (10)	21.8 ± 14.3 (10)	8.9 ± 8.6 (10)	8.8 ± 15.1 (6)	5.5 ± 3.1 (9)	25.8 ± 13.1 (4)
21-30m (%)	13.6 ± 6 (10)	8.2 ± 5.9 (10)	19.3 ± 9 (10)	15.1 ± 6.9 (10)	8.6 ± 9 (6)	8.8 ± 8.8 (9)	11.9 ± 4.4 (4)
31-40m (%)	7.8 ± 3.9 (10)	5.2 ± 2.1 (10)	10.7 ± 7 (10)	9.3 ± 4.9 (10)	5.7 ± 3.6 (6)	8.1 ± 2.7 (9)	7.6 ± 3.8 (4)
40m+ (%)	6.5 ± 6.2 (14)	4.3 ± 5.7 (10)	5.2 ± 5.7 (10)	6.4 ± 5.8 (14)	4.1 ± 5.4 (7)	6.5 ± 6 (13)	4.6 ± 5.5 (4)

832 **Table 4 Distribution of oceanic parameters (median \pm IQR (n) for the**
 833 **three spatial groups: North, South and Undetermined; and for the 4**
 834 **behavioral modes: Coastal Residency (CR), Coastal Transit (CT),**
 835 **Oceanic Residency (OR) and Oceanic Transit (OT).**

Group / Mode	SST ($^{\circ}$ C)	NPP ($\text{mgC m}^{-2} \text{day}^{-1}$)	TKE ($\text{m}^2 \text{s}^{-2}$)
North	27.61 ± 1.27 (9)	296.07 ± 98.76 (9)	459.95 ± 177.17 (9)
South	21.65 ± 1.03 (4)	365.61 ± 62.9 (4)	433.7 ± 301.22 (4)
Undetermined	27.25 ± 1.44 (5)	204.67 ± 53.57 (5)	410.97 ± 126.07 (5)
OT	27.05 ± 2.39 (18)	261.92 ± 80.62 (18)	448.98 ± 202.46 (18)
OR	27.45 ± 5.96 (10)	405.18 ± 299.99 (10)	505.46 ± 451.61 (10)
CT	27.16 ± 1.64 (18)	208.11 ± 58.8 (18)	294.64 ± 288.41 (18)
CR	27.75 ± 0.45 (6)	427.23 ± 602.34 (5)	233.02 ± 244.11 (6)

836

837 **ONLINE RESOURCE**

838 **Online Resource 1**

839 **OR1. Fig. 1** Capture positions of loggerhead sea turtles by long-liners fisheries from Reunion Island
840 between 2007 and 2011 ($n = 46$). Black symbol show capture positions for individuals released with
841 a satellite tag.

842 **OR1. Fig. 2** Time at depth histograms (Day (D) vs. Night (n)) of 10 late juvenile loggerhead sea
843 turtles. The subsurface layer (<10m) is the most frequented during the day while turtles make more
844 usage of layers between 11 and 40m.

845 **OR1. Fig.3** Time at depth histograms according to behavioral mode of 10 late juvenile loggerhead
846 sea turtles (OT: Oceanic Transit; OR: Oceanic Residency; CT: Coastal Transit; CR: Coastal
847 Residency). Turtles exhibit similar usage of the subsurface layer (<10 m) for all behavioral modes.
848 They made more usage of the 11-20 m layer during resident phases (OR and CR) but more usage of
849 the deepest layer (>40 m) during the transit phases (OT and CT).

850 **OR1. Fig. 4** Examples of tracks associated with oceanic eddies in the northern hemisphere for N5 (a)
851 and in the southern hemisphere for S2 (c) and S3 (c and d). (c) and (d) during an oceanic and resident
852 phase lasting 288 days, S3 clearly associated repeatedly with eddies in the Agulhas retroflection
853 region at large of the South African coast. This constitutes the most striking example of association
854 with eddies observed in the Western Indian Ocean.

855

856 **Online Resource 2**

857 Representation of individual's track and behavioral mode, time-at-depth distribution, and dive depth
858 distribution according to behavioral mode.

859 **Online Resource 3**

860 Animations representing the distributions of oceanic environmental variables along track.

Fig. 1

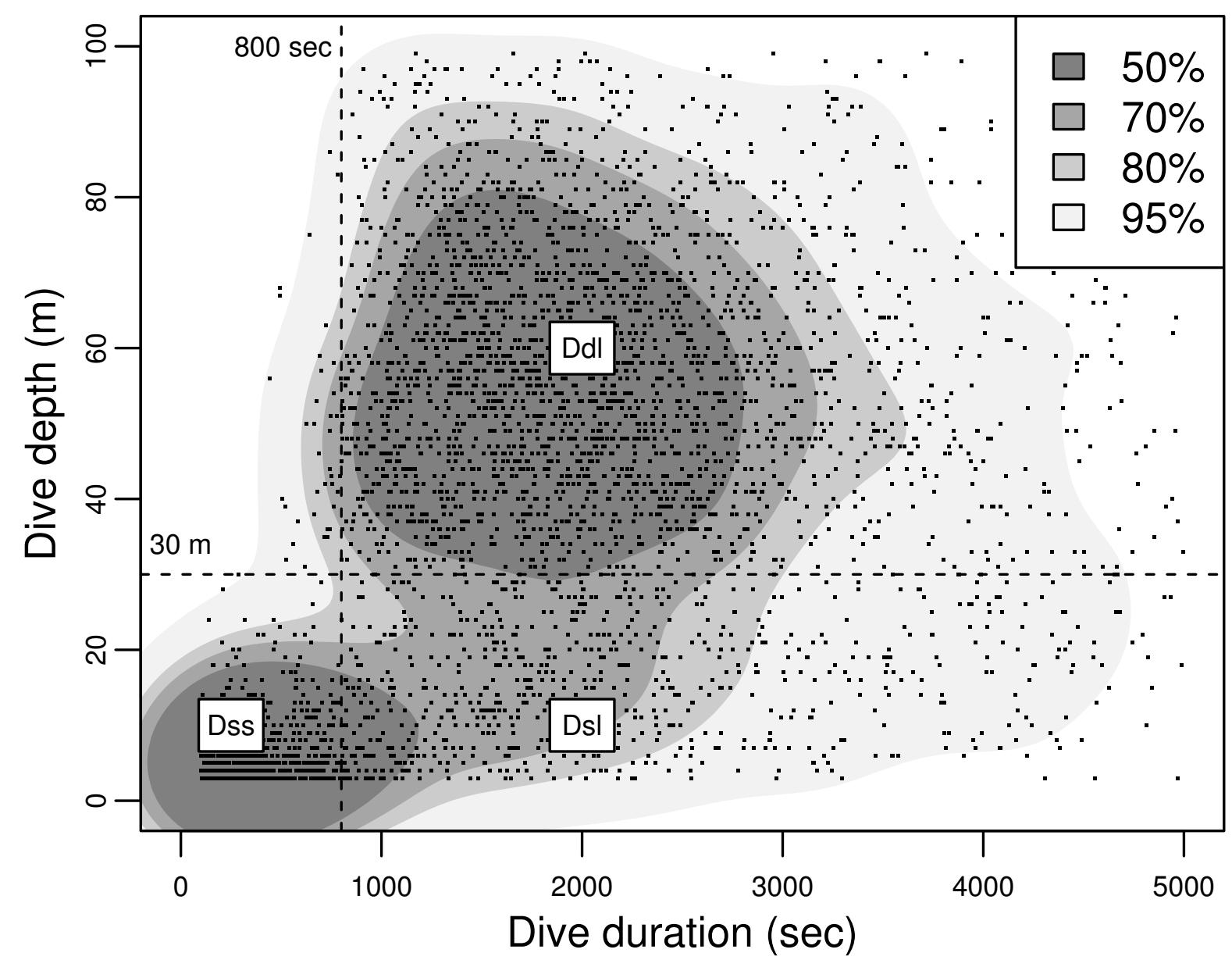
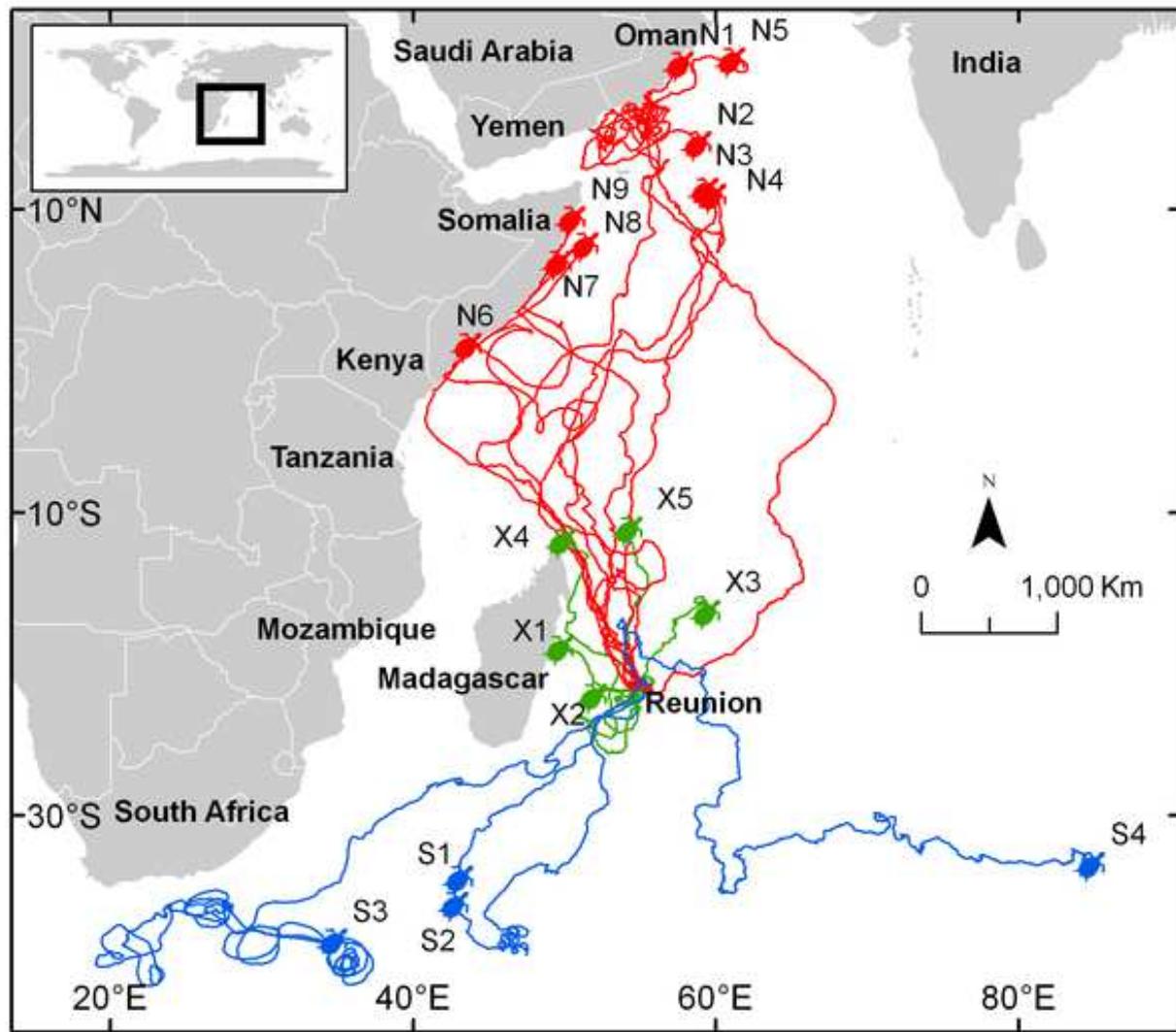


Fig. 2

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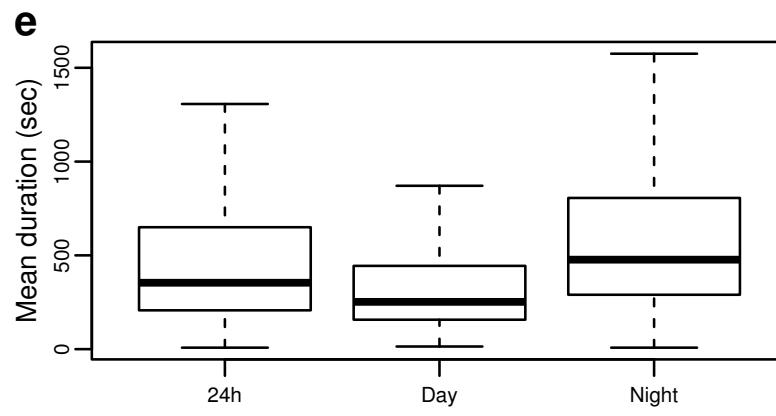
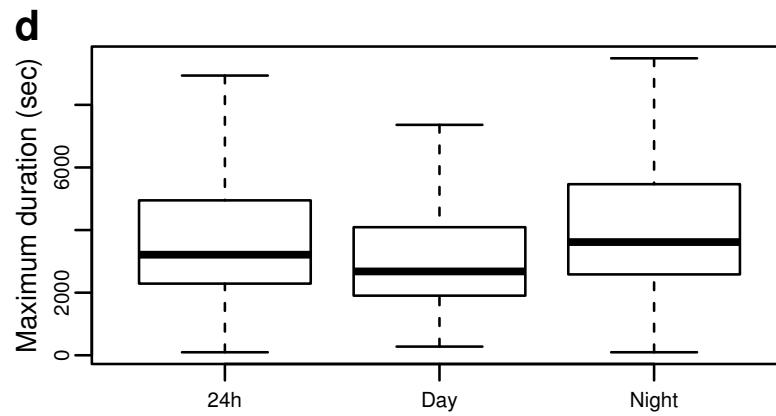
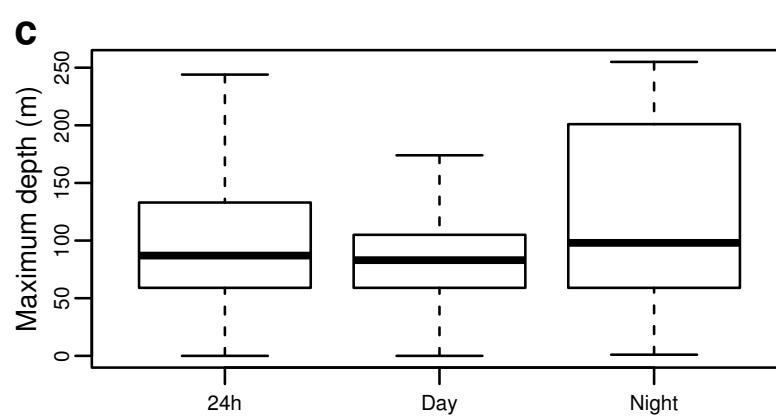
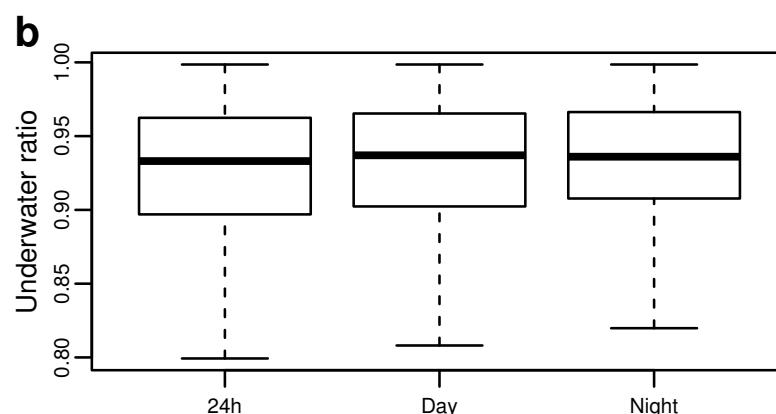
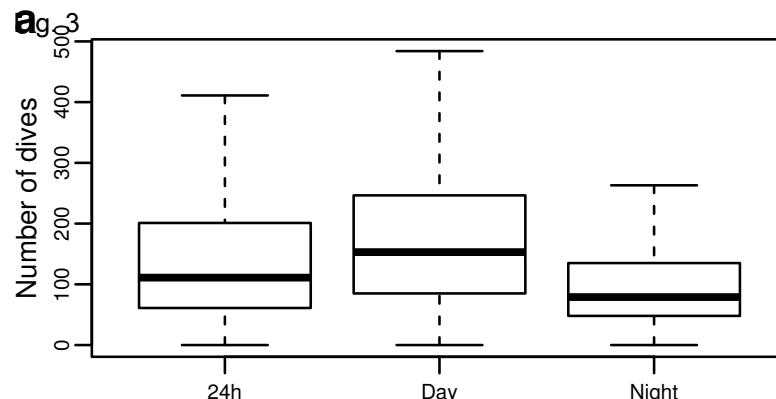


Fig. 4

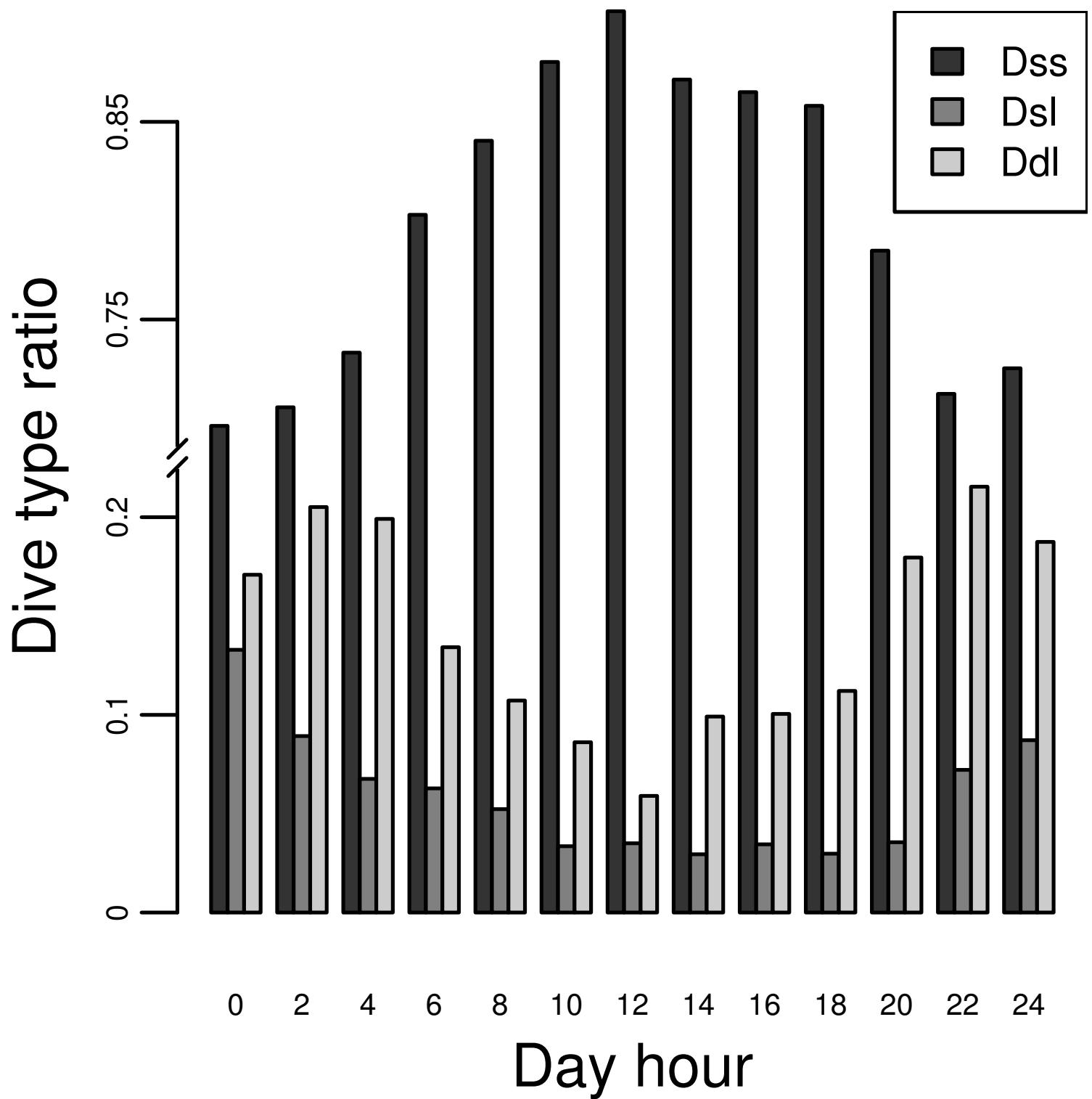


Fig. 5

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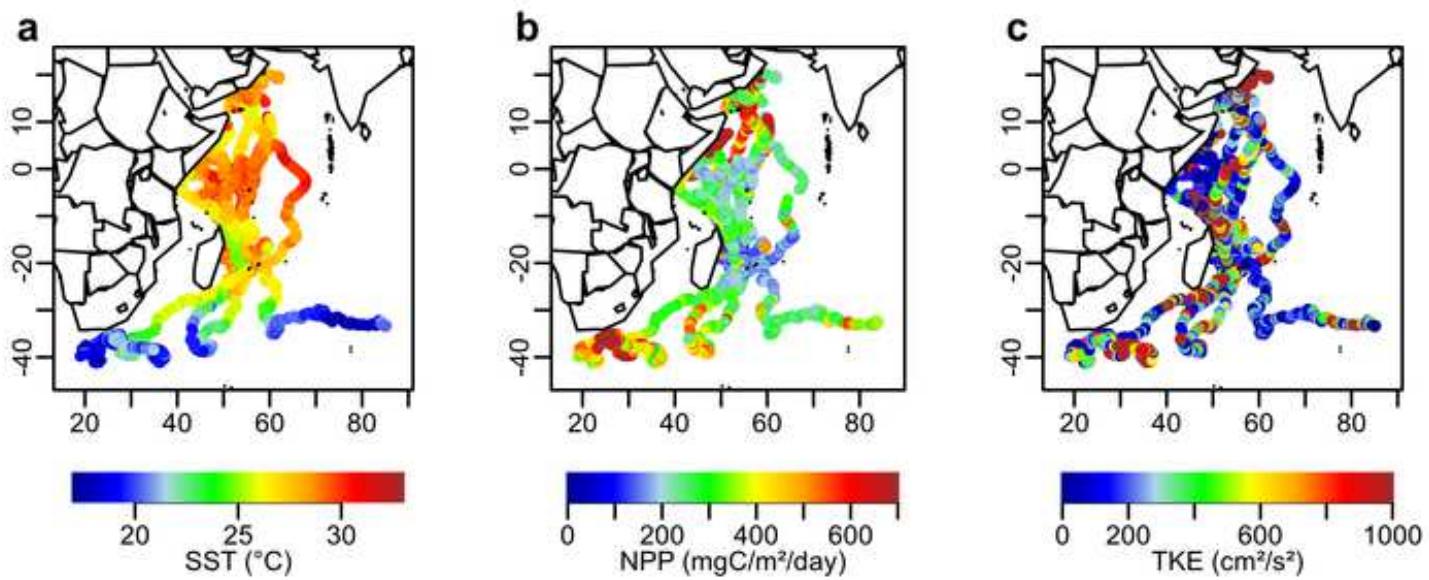


Fig. 6

