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### ► **To cite this version:**

Estelle Crochelet, Nicolas Barrier, Marco Andrello, Francis Marsac, Aurélie Spadone, et al.. Connectivity between seamounts and coastal ecosystems in the Southwestern Indian Ocean. *Deep Sea Research Part II: Topical Studies in Oceanography*, 2020, 176, pp.104774. <10.1016/j.dsr2.2020.104774>. <hal-03410867>

**HAL Id: hal-03410867**

**<https://hal.umontpellier.fr/hal-03410867v1>**

Submitted on 16 Sep 2024

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## Connectivity between seamounts and coastal ecosystems in the Southwestern Indian Ocean

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### Abstract :

Understanding larval connectivity patterns is critical for marine spatial planning, particularly for designing marine protected areas and managing fisheries. Patterns of larval dispersal and connectivity can be inferred from numerical transport models at large spatial and temporal scales. We assess model-based connectivity patterns between seamounts of the Southwestern Indian Ocean (SWIO) and the coastal ecosystems of Mauritius, La Réunion, Madagascar, Mozambique and South Africa, with emphasis on three shallow seamounts (La Pérouse [LP], MAD-Ridge [MR] and Walters Shoal [WS]). Using drifter trajectory and a Lagrangian model of ichthyoplankton dispersal, we show that larvae can undertake very long dispersion, with larval distances increasing with pelagic larval duration (PLD). There are three groups of greater connectivity: the region between the eastern coast of Madagascar, Mauritius and La Réunion islands; the seamounts of the South West Indian Ridge; and the pair formed by WS and a nearby unnamed seamount. Connectivity between these three groups is evident only for the longest PLD examined (360 d). Connectivity from seamounts to coastal ecosystems is weak, with a maximum of 2% of larvae originating from seamounts reaching coastal ecosystems. Local retention at the three focal seamounts (LP, MR and WS) peaks at about 11% for the shortest PLD considered (15 d) at the most retentive seamount (WS) and decreases sharply with increasing PLD. Information on PLD and age of larvae collected at MR and LP are used to assess their putative origin. These larvae are likely self-recruits but it is also plausible that they immigrate from nearby coastal sites, i.e. the southern coast of Madagascar for MR and the islands of La Réunion and Mauritius for LP.

**Keywords :** Seamounts, connectivity, larval duration, larval drift, Lagrangian modelling, biophysical model, surface drifters, Southwestern Indian Ocean, Ichthyop.

## 51 **1. Introduction**

52 Marine resources are under threat from the combined effects of climate change, overfishing,  
53 pollution, diseases, tourism and coastal development (FAO, 2018). As marine ecosystems  
54 degrade, so do the well-being and livelihoods of populations that depend directly on the  
55 ecosystem goods and services they provide (Moberg and Folke, 1999). Managing marine  
56 resources effectively is therefore crucial, from both social and ecological perspectives.  
57 Connectivity is recognized as a key factor affecting marine populations dynamics, population  
58 persistence and stock sustainability (Hastings and Botsford, 2006), as well as the efficiency of  
59 management strategies in the face of global changes. It is defined as “the exchange of  
60 individuals among geographically separated subpopulations” (Cowen et al., 2007). Transport  
61 processes are believed to connect distant populations. Despite early genetic studies showing a  
62 fair degree of homogeneity between populations over large spatial scales (Doherty et al.,  
63 1995), accumulating recent evidence suggests that populations are not as open as initially  
64 thought. High levels of local retention and low levels of long-distance dispersal could be  
65 maintained by mesoscale and sub-mesoscale eddies capable of transporting larvae back to  
66 their location of origin despite long pelagic larval durations (Cowen et al., 2000; Warner and  
67 Cowen, 2002), thereby contributing to maintain endemic species around isolated islands  
68 (Boehlert et al., 1992).

69

70 The majority of marine organisms have a bipartite life history and experience pelagic larval  
71 stages before they settle and become sedentary (Leis, 1991). Larvae remain in the midwater  
72 layers for days to months while they acquire swimming and sensory capabilities that enable  
73 them to control part of their dispersal (Kingsford *et al.*, 2002; Leis, 2002). This pelagic stage  
74 facilitates the transport of individuals among spatially isolated populations. It has been  
75 suggested that the pelagic larval duration (PLD) is the most important factor determining the

76 level of larval dispersal and connectivity (Riginos and Victor, 2001; Selkoe and Toonen,  
77 2011; Luiz et al., 2013). Connectivity between distant populations may indeed be favoured by  
78 long PLD, whereas larval settlement close to the natal habitat can result from short PLD and  
79 entail increased population differentiation over short scales (Planes et al., 2001). However,  
80 larval dispersal is also mediated by both complex and dynamic oceanographic features and  
81 biological properties (Pineda et al., 2009).

82

83 The effective management of marine resources requires estimating the realized levels of  
84 connectivity between populations, but empirical estimates are scarce (Manel et al., 2019).  
85 Indeed, marine larvae are notoriously difficult to monitor, due to their small size and possibly  
86 long dispersal distances, up to hundreds of kilometers from their initial release site (Leis,  
87 1984; Victor, 1987). Patterns of larval dispersal and connectivity also vary between species.  
88 Various methods such as population genetics and phylogeography, microchemical  
89 fingerprinting, stable isotopes, otolith microchemistry, otolith shape analysis and biophysical  
90 dispersal models have been developed to assess patterns of larvae dispersal and population  
91 connectivity across the marine environment (Schultz and Cowen, 1994; Roberts, 1997;  
92 Cowen et al., 2000; Hellberg, 2007; Treml et al., 2008; Jones et al., 2009; Mora et al., 2012,  
93 Bryan-Brown et al., 2018).

94

95 The South West Indian Ocean (SWIO) has a high level of marine biodiversity, and marine  
96 species in the region are widely used as food resources and provide economic benefits to a  
97 rapidly growing human population. However, the SWIO is one of the less studied regions of  
98 the world (Obura, 2012; UNEP-Nairobi Convention and WIOMSA, 2015).

99

100 The SWIO has many seamounts. Seamount ecosystems are recognized as critical habitats for  
101 a wide array of species (Clark et al., 2012) and are subject to anthropogenic exploitation  
102 (Rowden et al., 2010). Despite an increased focus on these particular ecosystems, the natural  
103 processes involved to sustain biodiversity at seamounts remain largely unknown, in particular  
104 in the SWIO. Seamounts are generally geographically isolated structures, but currents can  
105 ensure connectivity between them and with adjacent ecosystems.

106

107 In this paper, we consider nine seamounts of the SWIO, ranging from latitudes 15°S to 45°S  
108 (Figure 1), which were the focus of previous oceanographic campaigns (Southern Indian  
109 Ocean Seamounts Project in 2009: Read and Pollard, 2017; Rogers et al., 2017; Pollard and  
110 Read, 2017). Five of them belong to the South West Indian Ridge (SWIR, 25–50°S), an area  
111 delineated by elevated rims reaching up to 2000 m below sea level, with several seamounts on  
112 its flanks rising to only a few hundred metres below the surface (Guinotte, 2011): Atlantis  
113 Bank, Sapmer Bank, Middle of What Seamount, Melville Bank and Coral Seamount. The  
114 SWIR is crossed by subtropical and Agulhas Return Current convergences (Figure 1). These  
115 strong hydrological discontinuities are almost impassable by small size organisms, both in the  
116 adult and larval stages. There is therefore no genetic connectivity between populations north  
117 and south of the subtropical convergence line (Rogers, 2012). We include three other  
118 seamounts located on the Madagascar Ridge: two unnamed pinnacles – hereafter called  
119 MAD-Ridge and Un-named seamount respectively) and Walters Shoal. The rugged  
120 topography and numerous shoals on this portion of the Madagascar Ridge interact with ocean  
121 currents (Roberts et al., 2020, this issue; Vianello et al., 2020, this issue). MAD-Ridge is a  
122 steep pinnacle (33 km north–south; 22 km east–west) located 240 km south of Madagascar  
123 and rises to 240 m below the surface. It is under the influence of a highly dynamic ocean  
124 circulation (the East Madagascar Current and its retroflexion, Figure 1; de Ruijter et al.,

125 2004) inducing strong mesoscale activity (Pollard and Read, 2017; Vianello et al., 2020, this  
126 issue). Indeed, it is frequently crossed by mesoscale eddies spinning off the South East  
127 Madagascar Current. These eddies may become trapped over the seamount and have an  
128 influence on the assemblages and diel vertical migrations patterns of micronekton  
129 communities (Annasawmy et al., 2020, this issue). Walters Shoal and Un-named seamount  
130 are very isolated features (>800 km south of Madagascar, 1300 km off the South African  
131 coastline) located at the southern end of the Madagascar Ridge. Both seamounts are classified  
132 as Benthic Protected Areas by the Southern Indian Ocean Fisheries Agreement (Shotton,  
133 2006; SIOFA, 2019). Walters Shoal is a large seamount rising to 18 m below the surface  
134 located 855 km south of Madagascar. Previous investigation showed a 400 km<sup>2</sup> caldera-like  
135 shape of the summit (RV Marion Dufresne cruises in 1973 and 1976, unpublished data). It has  
136 moderate mesoscale dynamics (Pollard and Read, 2017). The last seamount considered, La  
137 Pérouse, is located 160 km northwest of La Réunion Island. It is under the influence of the  
138 west-flowing South Equatorial Current (SEC, Figure 1) (Tomczak and Godfrey, 2003;  
139 Chapman et al., 2003) and has moderate mesoscale dynamics. As an old volcano, La Pérouse  
140 rises steeply to 55-60 m depth from the abyssal plain at 5000 m and is 10 km long (Marsac et  
141 al., 2020, this issue).

142

143 We also considered eight coastal sites, where knowledge on species and/or circulation were  
144 available, to assess exchanges with the seamounts: (i) two Mascarene archipelago sites, the  
145 west coast of Mauritius (Morne Brabant) and La Réunion (La Saline); (ii) four sites in  
146 Madagascar (Sainte-Marie and Mamanjary on the east coast, Fort-Dauphin in the south and  
147 Tulear in the southwest); and (iii) two sites on the African coast (Tofo in Mozambique and  
148 Saint Lucia in South Africa) (Figure 1). As these coastal sites are not fully representative of  
149 the respective coastlines, we also defined buffers around countries (Mauritius, La Réunion,

150 Madagascar, Mozambique and South Africa),  $1/3^\circ$  from shore, to highlight larval export from  
151 seamounts to surrounding countries.

152

153 The aim of this paper is to assess the degree of connectivity, deduced from hydrodynamic  
154 larvae dispersion, between the nine selected SWIO seamounts and nearby coastal ecosystems  
155 represented by the eight coastal sites and also nearby countries. Emphasis is placed on the  
156 three shallow seamounts which are the focus of the present Special Issue: La Pérouse (LP –  
157 doi:10.17600/16004500), MAD-Ridge (MR – doi:10.17600/16004900) and Walters Shoal  
158 (WS – doi:10.17600/17002700) (Roberts et al., 2020, this issue). In order to characterize  
159 connectivity patterns, we first used drifter trajectory data as evidence for possible  
160 hydrodynamic connectivity. Then, to gain a broader view of connectivity patterns, we used  
161 Ichthyop, a Lagrangian model (Lett et al., 2008) to simulate ichthyoplankton dispersal. This  
162 model was forced by near-surface ocean current estimates (OSCAR). A wide range of PLD  
163 values were considered to provide a synoptic view of seamount connectivity. Finally, we used  
164 information on PLD and the age of larvae collected at MR and LP by Harris et al. (2020, this  
165 issue) to assess their putative origin.

166

## 167 **2. Material and methods**

### 168 *2.1 SWIO marine species*

169 More than 800 fish species have been recorded on seamounts worldwide (Morato et al.,  
170 2004). Most are robust demersal fish species, with good swimming capabilities, high food  
171 consumption and energy expenditure. Some of them also exhibit great longevity (over 100  
172 years) with late maturation (50-60 years) and low fertility, making them extremely vulnerable  
173 to intensive fishing (Koslow et al., 2000).

174

175 Soviet and Ukrainian fisheries operating from 1969 to 1998 in the SWIO identified 81 fish  
176 families including four *Beryx* species (alfonsinos, including *Beryx splendens* and *B.*  
177 *decadactylus*) and orange roughy (*Hoplostethus atlanticus*) of high commercial value, pelagic  
178 pentacerotidae (*Pseudopentaceros wheeleri*, *P. richardsoni*), rockfish (*Sebastes* spp.,  
179 *Helicolenus* spp.), oreos (Oreosomatidae), cardinal fish (*Epigonus* spp.), grenadiers (including  
180 *Coryphaenoides rupestris*) and Patagonian toothfish (*Dissostichus eleginoides*) (Romanov,  
181 2003). These fish are specifically associated with seamounts, although they also live on the  
182 continental slopes and slopes of oceanic islands. Soviet and Ukrainian fisheries also  
183 inventoried a minimum of 13 threatened species of shark (Romanov, 2003) and benthic  
184 resources such as crustaceans (lobsters, crabs), molluscs, sponges, and cold-water corals. A  
185 new species of spiny lobster, *Palinurus barbarae* (Groeneveld et al., 2006), appears to be  
186 endemic to the Walters Shoal (WS), as well as the crab *Beuroisia duhameli* (Guinot and  
187 Richer de Forges, 1981) caught during the MD08 campaign of RV Marion-Dufresne in 1976.  
188 More recently, cruises to La Pérouse (LP), MAD-Ridge (MR) and the WS seamounts allowed  
189 identification of several micronekton species. Annasawmy et al. (2019) reported vertically  
190 migrating common open-water species of gelatinous crustaceans, squid and fish concentrated  
191 over the summit and flanks, and also an important community of seamount-  
192 associated/resident fish. Harris et al. (2020, this issue) also collected mesopelagic fish larvae  
193 during the current cruises, Myctophidae and Gonostomatidae being the most dominant  
194 families at all three seamounts.

195  
196 Despite these valuable recent data, biological data on marine species inhabiting SWIO  
197 seamounts are generally lacking, as underlined in several publications (Rogers, 2012; FFEM,  
198 2013; Rogers et al., 2017; Zucchi et al., 2018). In particular, there is only limited information  
199 available on their PLD for ichthyological species recorded during sea campaigns (e.g.

200 *Pseudopentaceros richardsoni*, *Hoplostethus atlanticus*, *Beryx splendens*), which have PLDs  
201 ranging from one to several months. Hence, *Beryx* spp. may have a PLD of around one year  
202 (Shotton, 2016). *Jasus* spp. (spiny lobsters) were recorded in seamount habitats in the  
203 southern hemisphere and are also known to have long PLDs. Hence, Booth (2006) reported  
204 PLDs between 8 and 12 months for *J. verreauxi*, and between 12 and 24 months for *J.*  
205 *edwardsii*. Harris et al. (2020, this issue) provided information on specimens collected at MR  
206 of the acanthurid *Naso* sp. having a PLD of 84 d, *Labrid* spp. with a PLD of 26–28 d, *Apogon*  
207 spp. with a PLD of 18–34 d and *Synodus* sp. with a PLD of 42 d (Stier et al., 2014). Thus, the  
208 different species inhabiting the SWIO seamounts cover a large range of PLD values.

209

## 210 2.2 Oceanographic drifter trajectories

211 As a first approach to assessing dispersal and connectivity in the SWIO, we downloaded 6-h  
212 interpolated trajectories of 1104 drogued oceanographic surface drifters located in the SWIO  
213 over the period 15/02/1979 to 30/06/2018 from the Global Drifter Program database  
214 (<https://data.nodc.noaa.gov/cgi-bin/iso?id=gov.noaa.nodc:AOML-GDP>, Lumpkin and  
215 Centurioni, 2019). From that dataset, we selected drifters that came close (<50 or 100 km) to  
216 one of the three focus seamounts (LP, MR and WS) and plotted their trajectories. We also  
217 searched for drifters that came close to two of the same seamounts, as an indication of  
218 possible hydrodynamic connectivity between seamounts.

219

## 220 2.3 Ichthyop larval dispersal model

221 To gain a broader perspective of dispersal and connectivity in the SWIO, we used the larval  
222 dispersal tool Ichthyop, a free Lagrangian tool designed to study the effects of physical and  
223 biological factors on ichthyoplankton dynamics (Lett et al., 2008). Ichthyop can integrate the  
224 most important processes involved in the early life stages of marine larvae: spawning,

225 transport, behaviour, growth, mortality and settlement. As we wished to obtain a synoptic  
226 view of connectivity patterns, rather than focus on a particular species, we used a large range  
227 of PLD values (15, 30, 45, 60, 90, 120, 180, 270 and 360 d) and assumed that all seamounts  
228 had habitats and populations capable of both producing and receiving larvae. This latter  
229 assumption is supported by the findings of Harris et al. (2020, this issue) who reported all  
230 developmental stages of oceanic and some neritic taxa from preflexion to postflexion at LP,  
231 MR and WS, an indication that the corresponding species spawn in the vicinity of these  
232 seamounts. We also assumed that larvae were transported passively depending only on  
233 horizontal surface currents. The term “larvae” used in the modelling part of this paper really  
234 stands for “virtual larvae” because there were no ground truth data to calibrate and validate  
235 the model. Particles were released every 5 d over 9 years, i.e. 10 000 particles at each of the  
236 considered release locations, a number that was shown to be large enough to provide precise  
237 estimates of connectivity values (Andrello et al., 2013). Release locations (Figure 1) were the  
238 nine SWIO seamounts and the eight coastal sites described in the introduction. Potential larval  
239 destination areas were the nine SWIO seamounts, the eight coastal sites and the shorelines of  
240 the five countries (Mauritius, La Réunion, Madagascar, Mozambique and South Africa;  
241 Figure 1). Simulations were performed with two sizes of buffer around locations used as  
242 release and destination areas,  $1/3$  of a degree and 1 degree.

243

244 As expected, the simulated values of connectivity were overall greater with a  $1^\circ$  buffer than  
245 with a  $1/3^\circ$  buffer, but as the connectivity patterns (i.e. sites that are more/less retentive,  
246 more/less connected, etc.) were similar, we only present the  $1/3^\circ$  case and refer the reader to  
247 Appendix Figure E for the  $1^\circ$  buffer results. The Ichthyop model was forced by current fields  
248 provided by the OSCAR product (see below) interpolated linearly at the location and time of

249 each larva, and their movement was solved using the Runge Kutta 4<sup>th</sup> order scheme, diffusion  
250 being added with a dissipation rate  $\varepsilon=1 \text{ E}^{-9} \text{ m}^2 \text{ s}^{-3}$  (following Peliz et al., 2007).

251

#### 252 *2.4 OSCAR current product*

253 OSCAR (Ocean Surface Current Analyses – Real Time) provides estimates of ocean near-  
254 surface currents by combining satellite-derived altimetry observations (sea-surface height; e.g.  
255 TOPEX/Poseidon), scatterometer data that estimate ocean wind vectors, and sea surface  
256 temperature sensors (e.g. AVHRR). OSCAR provides more precise ocean current estimates  
257 than those based exclusively on altimetry, particularly in the tropics, by combining  
258 geostrophic shear dynamics, Ekman and Stommel transport and a complementary term of  
259 surface buoyancy gradient (Bonjean and Lagerloef, 2002). Products are available worldwide  
260 at  $1/3^\circ$  horizontal resolution every 5 d and represent currents at a depth of  $\sim 15$  m. Here we  
261 used the currents data for the SWIO (latitude  $10\text{--}50^\circ\text{S}$ , longitude  $20\text{--}70^\circ\text{E}$ ) over the period  
262 2010–2018, downloaded from the NASA data center website ([ftp://podaac-](ftp://podaac-ftp.jpl.nasa.gov/allData/oscar/preview/L4/oscar_third_deg/)  
263 [ftp.jpl.nasa.gov/allData/oscar/preview/L4/oscar\\_third\\_deg/](ftp://podaac-ftp.jpl.nasa.gov/allData/oscar/preview/L4/oscar_third_deg/)). OSCAR products were validated  
264 for the northern part of the Indian Ocean by Sikhakolli et al. (2013).

265

#### 266 *2.5 Model outputs and post-processing*

267 We calculated connectivity matrices between seamounts, between seamounts and coastal  
268 ecosystems, and between coastal ecosystems and seamounts for all the considered PLD values  
269 averaged over all release dates. Connectivity can be interpreted as either the proportion of  
270 larvae exported to each seamount or coastal ecosystem (larval export, lines of the connectivity  
271 matrices), or the proportion of larvae coming from each seamount or coastal ecosystem (larval  
272 import, columns of the connectivity matrices). Local retention, i.e. the proportion of released  
273 larvae that stayed at their natal sites, is the diagonal of the connectivity matrices. We also

274 computed the dispersal distance as the “great-circle distance” between the initial and final  
275 positions of larvae, averaged for all larvae and release dates. We plotted maps of simulated  
276 larval density, the average number of all larvae per cell at a given time. The cell size was set  
277 as  $1/3^\circ$ , equivalent to the OSCAR resolution. Analyses were carried out using the software  
278 ArGIS 10.4.1 and Spyder (Python 2.7).

279

### 280 **3. Results**

281

#### 282 *3.1 Drifters*

283 We found 13, 11, and 14 drifters passing less than  $<50$  km from the LP, MR and WS  
284 seamounts, respectively, at some time in their travel in the SWIO (Figure 2). Most (11/13)  
285 drifters that came close to LP ended up to the south in the direction of the other seamounts  
286 (Figure 2a). One drifter (#45958) that came very close to LP ( $\sim 7$  km) was also close to MR  
287 ( $\sim 8$  km) 85 d later (the trajectory of that drifter is highlighted by a white background in  
288 Figure 2a). Drifters that travelled close to MR moved to the west or to the east and none  
289 travelled to LP or WS (Figure 2b). Most (10/14) drifters that came close to WS ended up to  
290 the west (Figure 2c), but along the way one drifter (#63941330) came close ( $\sim 43$  km) to MR  
291 after 75 d (the trajectory of that drifter is highlighted by a white background in Figure 2c).

292

293 We found 32, 23 and 21 drifters that travelled  $<100$  km from LP, MR and WS, respectively  
294 (Appendix Figure A). Among those, six drifters came close to LP and then MR (with 46–189  
295 d spent in between), two drifters travelled close to MR and then WS (29 and 70 d spent in  
296 between) and two drifters came close to WS and then MR (75 and 143 d spent in between).  
297 One of those drifters (#9108691) is of particular interest because it came close to first LP ( $\sim 51$   
298 km), then MR ( $\sim 71$  km) and finally WS ( $\sim 18$  km), and was the fastest drifter, travelling from

299 LP to MR in 46 d and from MR to WS in 29 d (the trajectory of that drifter is highlighted by a  
300 white background in Appendix Figure A).

301

### 302 *3.2 Mean dispersal distances*

303 In the simulations, as expected, the mean dispersal distances travelled by the virtual larvae  
304 leaving seamounts increased with PLD, ranging from 217 km for PLD = 15 d to 1366 km for  
305 PLD = 360 d, all seamounts averaged (Table 1). Larvae leaving Atlantis Bank had the shortest  
306 average dispersal distances (around 0.6 times less than the mean) except for PLD = 15, where  
307 the shortest distance was for larvae leaving WS (Table 1). Conversely, larvae from Coral  
308 Seamount had the highest mean dispersal distances for all PLD (1.5–2.15 times above the  
309 mean). For the three focal seamounts, larvae released from WS travelled the shortest average  
310 distances, whereas larvae leaving MR travelled farthest.

311

### 312 *3.3 Connectivity matrices between all sites*

313 Matrices presented in Figure 3 show the mean simulated larval connectivity obtained between  
314 all nine seamounts and eight coastal sites for three of the considered PLD values: 15, 120 and  
315 360 d (matrices for the six other PLD values are provided in Appendix Figure B). For a PLD  
316 of 15 d (Figure 3a), there were bilateral exchanges between Morne Brabant (Mauritius coastal  
317 site), La Saline (La Réunion coastal site) and LP, one of our three focal seamounts. For the  
318 other two seamounts, there was also bilateral exchange between WS and Un-named Seamount  
319 (which are close) and between MR and Fort Dauphin. The highest local retention values were  
320 for WS (11.1%), Atlantis Bank (7.5%) and LP (5.3%), in decreasing order. For a PLD of 120  
321 d (Figure 3b), there was bilateral connectivity between the five sites situated East of  
322 Madagascar (Maurice, La Réunion, LP, Mamanjary, Ile Ste Marie) and most of the seven sites  
323 located south of Madagascar and in the Mozambique Channel (WS, Un-named Seamount,

324 MR, Fort Dauphin, Tulear, Tofo, Saint Lucia). Finally, there was connectivity between most  
325 of the five seamounts situated on the SWIR (Atlantis Bank, Sapmer Bank, Middle of What  
326 Seamount, Melville Bank, Coral Seamount), attaining an elevated degree between Sapmer  
327 Bank, Middle of What seamount and Melville Bank. There was also bilateral exchange  
328 between WS and MR, LP and MR, and WS and LP. For a PLD of 360 d (Figure 3c), most  
329 sites were connected in both directions to some extent: the SWIR and South Madagascar  
330 seamounts group tended to join. WS, MR and LP were connected bilaterally to all seamounts  
331 and coastal sites, with the sole exception of LP which did not receive any larva from Saint  
332 Lucia. We assessed the temporal variability (seasonal and interannual combined) of simulated  
333 connectivity for the different PLD values (Appendix Figure C) and obtained little variability  
334 with coefficients of variation (CV) of 2.7 at most. The CV tended to decrease with PLD, and  
335 to have similar values for seamounts within the three different identified groups, i.e. east  
336 Madagascar, south Madagascar and Mozambique Channel, and SWIR, and also between two  
337 different groups (hence the “blocks” of similar colours in Appendix Figure Cc).

338

### 339 *3.4 Connectivity matrices between LP, MR and WS seamounts and coastal ecosystems*

340 Figure 4 represents exchanges from seamounts to coastal ecosystems (coastal buffers) for  
341 PLD values of 15, 120 and 360 d (matrices for the six other PLD values are in Appendix  
342 Figure D).

343 After 15 d of dispersal, connectivity ranged from 0 to 2.1%. Larvae released at LP reached the  
344 coastal ecosystems of Mauritius (0.007%), Madagascar (0.03%) and La Réunion (2.1%),  
345 whereas larvae from MR only reached Madagascar. After 120 d, larval connectivity values  
346 were divided by ~5, ranging between 0 and 0.42%. Larvae from LP reached all coastal  
347 ecosystems (Mauritius, La Réunion, Madagascar, Mozambique and South Africa). The two  
348 highest connectivity values were between LP and Madagascar (0.42%) and between LP and

349 La Réunion (0.21%). Larvae from MR also reached all coastal ecosystems, but with lower  
350 connectivity values. Larvae from WS reached all coastal ecosystems except Mauritius, with  
351 even lower connectivity values. After 360 d of dispersal, larval connectivity values were  
352 divided by ~10 relative to PLD = 120 d. All larvae leaving LP, MR and WS reached all  
353 coastal ecosystems. Overall, the lowest connectivity was from WS, except to Mozambique  
354 where it was the highest.

355

### 356 *3.5 Larval dispersal from LP, MR and WS*

357 The patterns of weak connectivity between seamounts and the coast described above result  
358 from a high degree of dispersal towards offshore locations, as shown by maps of larval  
359 density over the entire region. Figure 5 presents mean larval density maps for larvae released  
360 at LP, MR and WS seamounts after 15, 120 and 360 d of PLD (with the locations of the  
361 drifters of Figure 2 superimposed). Larvae released from LP remained concentrated at high  
362 density on the eastern side of Madagascar for a PLD of up to 120 d, and then tended to drift  
363 east. After 120 d, larvae released at MR split into two separate plumes, one directed east and  
364 the other west towards the South African coast. Larvae released at WS remained concentrated  
365 around that seamount for a longer time, eventually spreading east and west, similarly to larvae  
366 released at MR.

367

### 368 *3.6 Local retention and connectivity between LP, MR, and WS*

369 Local retention decreased with increasing PLD for all three seamounts, but at a faster rate for  
370 LP than for MR and WS (Figure 6). Conversely, connectivity between pairs of seamounts  
371 initially increased with increasing PLD values (Figure 7). Patterns of connectivity change  
372 with PLD and were similar for MR to WS, MR to LP, and WS to MR, first increasing  
373 strongly, then peaking around 120 d and eventually decreasing slightly for longer PLDs.

374 Connectivity between the most distant sites, WS and LP, was much weaker and continued to  
375 increase with PLD in the range of values tested. Connectivity from LP to MR was at an  
376 intermediate level and showed the least change with PLD.

377

### 378 *3.7 Larval import at LP, MR and WS*

379 The origin of larvae reaching LP, MR and WS is shown in Figure 8 after PLDs of 15, 120,  
380 and 360 d. At 15 d, larvae reaching WS, MR and LP were mostly self-recruits (95%, 95% and  
381 77%, respectively). For a PLD of 120 d, there was still a lot of self-recruitment at WS (42%)  
382 and MR (38%), but not at LP (15%), at which 57% of larvae came from Madagascar. At 360  
383 d, there was still 27% of self-recruitment on WS and no larvae coming from LP. The pattern  
384 was similar for MR, but with only 17% of self-recruitment. For LP, there was only 9% of self-  
385 recruitment, with the balance of larvae originating from MR (15%), WS (2%), Mauritius and  
386 La Réunion (20%), Madagascar (37%) and other seamounts (10%).

387

### 388 *3.8 Link with ichthyoplankton data*

389 It is difficult to interpret the above results in a biological sense because the larval durations of  
390 the species inhabiting the seamounts are poorly known. However, Harris et al. (2020, this  
391 issue) provide useful information on PLD and age for a set of larvae they collected at MR and  
392 LP. In particular, at MR, they collected larvae of four species with estimated PLDs close to 30  
393 d (*Labrid* and *Apogon* spp.), 45 d (*Synodus* sp.) and 90 d (the acanthurid *Naso* sp.). Assuming  
394 that these species reproduce at all the sites under consideration, dispersal patterns can be  
395 obtained for these PLD values (Figure 9) and also larval import and export for MR, where  
396 most larvae were collected (Figure 10). For a PLD of 30 d, virtual larvae arriving at MR  
397 originated from Fort Dauphin, MR and Un-named seamount (Figure 10). For a PLD of 45 d,

398 virtual larvae arriving at MR originated from Saint Lucia, Tofo, Fort Dauphin, MR, Un-  
399 named seamount and WS. For a PLD of 90 d, they originated from all 17 release sites.

400

401 Harris et al. (2020, this issue) also provide age estimates for some of the larvae they collected.

402 All larvae collected at MR were in the range 1.4-16.2 d, a range is largely consistent with the  
403 ages of virtual larvae transported from Fort Dauphin to MR in our simulations (Figure 11a).

404 Ages of virtual larvae transported from Mamanjary to MR (>10 d, Figure 11b) suggest that  
405 the oldest larvae collected, such as *Synodus* and *Trachinocephalus myops*, may also have been

406 transported from there. At LP, all larvae collected except one (a macrourid species) have  
407 estimated ages >5 d and may therefore have been transported from La Saline (Figure 11c),

408 whereas collected larvae >10 d (*Vinciguerria* spp.) may also have come from Morne Brabant  
409 (Figure 11d). Of course, all larvae collected could also have been self-recruits.

410

#### 411 **4. Discussion and perspectives**

412 The aim of this work was to assess the degree of connectivity between nine seamounts of the  
413 South West Indian Ocean (SWIO) and nearby coastal ecosystems, with emphasis on three  
414 shallow seamounts: La Pérouse (LP), MAD-Ridge (MR) and Walters Shoal (WS). The  
415 Lagrangian model of larval dispersal allowed us to explore a wide range of pelagic larval  
416 durations (PLDs) and revealed robust patterns of larval connectivity.

417

##### 418 *4.1 Mean drift velocities and larval dispersal distance*

419 Larvae dispersed far from their site of origin, with travelled distances increasing with PLD.

420 Mean drift velocities, obtained by dividing the mean larval distances reported in Table 1 by  
421 PLD, reached values as high as 10 km d<sup>-1</sup> (about 0.1 m s<sup>-1</sup>). Such values are consistent with

422 current surface velocities found by Pollard and Read (2017) and Vianello et al. (2020, this

423 issue) during the MAD-Ridge cruise. They are also of the same order of magnitude as other  
424 estimates obtained by Lagrangian simulations in other regions. For example, median drift  
425 velocities were about  $4 \text{ km d}^{-1}$  in the Mediterranean Sea (Andrello et al., 2013). Other  
426 connectivity studies performed in the SWIO have highlighted long-distance colonization,  
427 possibly over several generations, between coral reefs (Crochelet et al., 2016), between South  
428 African ecosystems and La Réunion for vagrant dusky groupers (Reid et al., 2016), between  
429 Mauritius and La Réunion for honeycomb groupers (Crochelet et al., 2013), between the  
430 Mascarene archipelago and Madagascar for tropical eel (Pous et al., 2010) and Seychelles for  
431 Sargassum algae (Mattio et al., 2013), between the east African coast and Madagascar for  
432 mangrove propagules (Van der Stocken and Menemenlis, 2017) and for coral reef species  
433 (Gamoyo et al., 2019; Schleyer et al., 2019), and between ABNJ (Areas Beyond National  
434 Jurisdiction) and coastal zones (Popova et al., 2019, Maina et al., 2020). Our results focusing  
435 on seamounts show that currents around SWIO seamounts can be powerful means of larval  
436 dispersal over relatively long distances. The longest dispersal distances were obtained from  
437 the Coral Seamount, the southernmost seamount considered in this study, which is affected by  
438 the strong current velocities of the Agulhas Return Current.

439

#### 440 *4.2 Potential colonization of coastal sites by larvae originating from seamounts*

441 Connectivity from seamounts to coastal ecosystems was weak, with a maximum of 2.1%  
442 larvae originating from seamounts reaching coastal ecosystems. It is difficult to conclude  
443 whether such a low percentage of dispersal is good enough to influence the communities of  
444 the receiving sites, because the magnitude of immigration depends on survival during the  
445 pelagic phase and on local dynamics (Armsworth, 2002; Burgess et al., 2014). If a population  
446 is not self-sustaining as a consequence of high mortality or low fecundity rates, then  
447 immigration from other populations contributes to population persistence. Although some of

448 the seamounts mentioned herein are subject to fishing (with strong impacts on stocks of long-  
449 living species), coastal ecosystems are affected by greater anthropogenic pressure (e.g.  
450 fishing, dredging, pollution) and generally have smaller biomasses than isolated sites (Edgar  
451 et al., 2014; Cinner et al., 2016). Therefore, seamounts could be important sources of larvae  
452 for coastal sites, if connectivity is strong enough to transport sufficiently high numbers of  
453 larvae over long oceanic distances and the receiving habitat is appropriate. Owing to the lack  
454 of data on local population dynamics and abundance in both the seamounts of origin and the  
455 coastal sites of destination, however, this hypothesis cannot be tested here.

456

#### 457 *4.3 Local retention at seamounts and connectivity between seamounts*

458 Local retention (within a  $1/3^\circ$  buffer) at the three focal seamounts (LP, MR and WS) was also  
459 low, peaking at about 11.1% at the shortest PLD and decreasing sharply at longer PLDs.  
460 These values may be an underestimation of actual patterns of local retention, however,  
461 because of the relatively coarse spatial resolution of the ocean current product (OSCAR) and,  
462 perhaps more importantly, the assumption of passive larval dispersal, because active  
463 swimming and larval orientation mechanisms can increase local retention (Faillettaz et al.,  
464 2018). Even if retention probabilities seem low, though, they might be sufficiently high to  
465 replenish populations and ensure their persistence because of high fecundities of the fish  
466 species. For example, large female alfonsino (*Beryx splendens*) spawn a range of 0.8–2.4  
467 million eggs (Alekseeva, 1983). We also found that local retention was greater at WS than at  
468 MR (Figure 6), which is consistent with Vianello et al. (2020, this issue) showing that  
469 currents decrease from north to south along a transect going from MR to WS.

470

471 Maina et al. (2020) recently used a modelling approach similar to the one used here to assess  
472 connectivity between seamounts of the SWIO using a PLD of 30 d. Here, we used a range of

473 PLD values from 15 to 360 d and showed that connectivity patterns change dramatically with  
474 PLD. Here we obtained large differences in dispersal and connectivity patterns for PLD  
475 values of 30, 45 and 90 d, which correspond broadly to labrid and *Apogon* spp., *Synodus* sp.,  
476 and acanthurid *Naso* sp., respectively, collected by Harris et al. (2020, this issue) at MR  
477 (Figure 10). Therefore, differences in the putative origin of these collected larvae were  
478 significant (Figure 9), although a local (i.e. MR) origin was the most likely for all of them.  
479 For some species, the presence of larvae, juveniles and adults around the same seamount  
480 suggests that their populations are self-sustaining (Cherel et al., 2020, this issue). For neritic  
481 reef-associated species, it is also plausible that some of the larvae collected at MR originated  
482 from the south-east coast of Madagascar (Harris et al., 2020, this issue). Indeed, MR has a  
483 strong connection with the shelf waters through cross-shelf transport. This suggestion is  
484 supported by our age analysis of larvae, which shows that larvae arriving at MR may come  
485 from Fort Dauphin or Mamanjary (Figure 11). Similarly, it is also possible that larvae  
486 collected at LP come from the islands of La Réunion and Mauritius (Figure 11).

487  
488 Connectivity patterns between seamounts revealed three groups of greater connectivity: the  
489 region between the eastern coast of Madagascar, Mauritius and La Réunion islands; the  
490 seamounts of the SWIR; and the pair Walters Shoal – Un-named seamount. Connectivity  
491 between these three groups was only at long PLDs.

492  
493 With the exception of the two lowest connectivity values (between WS and LP), connectivity  
494 peaked at around 120 d PLD and remained stable or slightly decreased at longer PLDs (Figure  
495 7). However, that pattern does not consider the effects of larval mortality, which are likely to  
496 reduce connectivity proportionally to PLD.

497

498 We found little temporal variability in simulated connectivity patterns, which is consistent  
499 with Vianello et al. (2020, this issue) who reported no clear seasonality or interannual  
500 variability in currents along the Madagascar Ridge.

501

#### 502 *4.4 Complementarity of drifter data and Lagrangian simulations*

503 Drifter data were used as ground-truth information of hydrodynamic dispersal and  
504 connectivity, and they consolidated the results of Lagrangian modelling. Indeed, the  
505 trajectories followed by drifters passing close to each of the three focal seamounts were  
506 consistent with the general patterns followed by particles released there. In addition, we found  
507 drifters passing LP and then MR, passing WS and then MR, and passing LP and then MR and  
508 WS, which were also among the strongest connections found between seamounts in the  
509 Lagrangian model (Figure 7). Besides this, the range of time spent by drifters travelling from  
510 LP to MR (46–189 d) corresponded well with the PLD values for connectivity between these  
511 seamounts in the model. The range of time spent by drifters between the other seamounts (29–  
512 70 d from MR to WS, 75–143 d from WS to MR) were also consistent with the model results,  
513 although slightly slower. However, we found no drifter passing MR and then LP, although  
514 that is one of the strongest connections according to simulation results (Figure 7).

515

#### 516 *4.5 Limitations of the modelling approach*

517 Numerical transport models are increasingly being used to determine patterns of larval  
518 dispersal as well as connectivity between populations in the marine environment. Larval  
519 dispersal simulations are relatively simple and quick to implement in any study region.  
520 Indeed, data necessary for model input (coastline, release sites, etc.) are freely available  
521 online at high resolutions. Nevertheless, the work accomplished during this study could be  
522 improved by taking into account additional oceanographic and biological factors.

523

524 We used an ocean current product (OSCAR) that relies on remote-sensing data to force the  
525 Lagrangian larval dispersal model. OSCAR currents are available globally and over long  
526 periods of time. Despite their coarse spatial resolution ( $1/3^\circ$ ), OSCAR and other products  
527 providing near-surface ocean current estimates have been shown to allow the simulation of  
528 surface drifter trajectories with similar accuracies as outputs from oceanographic models of  
529 similar spatial resolution (Liu et al., 2014; Amemou et al., submitted).

530

531 However, OSCAR does not take into account the vertical stratification of currents in the water  
532 column, which may affect larval dispersal patterns. In this study, larvae were considered as  
533 passive particles drifting in the surface layer, because we had no knowledge of the larval  
534 biology of local species. However, the larvae of many species have good swimming ability  
535 (Fisher et al., 2005) and are capable of changing their behaviour (e.g. by changing their depth)  
536 in response to the environment (Leis and Carson-Ewart, 2002; Tolimieri et al., 2000). This  
537 affects how larvae are carried by currents (Irisson et al., 2010; Cherubin et al., 2011), because  
538 transport is usually faster close to the surface than in the deeper layers. Larvae might therefore  
539 rely on vertical migration to reduce their dispersal and promote local retention (Cowen, 2002).  
540 When such information is available, it is therefore important to consider larval behaviour and  
541 swimming capability during larval ontogeny (Leis, 2010), and physical data such as vertical  
542 stratification of currents.

543

544 Vianello et al. (2020, this issue) reported no clear seasonality or interannual variability in  
545 currents along the Madagascar Ridge. Nevertheless, Annasawmy et al. (2019) highlighted a  
546 strong seasonality in primary productivity at LP and MR, with maximum values reached in  
547 July, as a result of intense mixing caused by the austral winter trade winds, and minimum

548 values during the austral summer (December–March). Moreover, chlorophyll a (Chl-a)  
549 concentrations were twice as high at MR than at LP all year round. This seasonality and the  
550 differences between seamounts may have consequences on secondary productivity and thus  
551 on food availability, growth and survival for larvae. Harris et al. (2020, this issue) also  
552 showed that different environmental variables such as temperature, Mixed Layer Depth  
553 (MLD), Depth of Chlorophyll Maximum (DCM), zooplankton settled volume and integrated  
554 Chl-a, influence larval fish communities at LP, MR and WS. Therefore, environmental factors  
555 and their effect on biological processes such as larval growth and mortality are important  
556 factors to consider in future modelling studies.

557

#### 558 *4.6 Perspectives*

559 From the perspective of the conservation and management of ecosystems, in particular in  
560 areas beyond national jurisdiction (ABNJ) where most SWIO seamounts are located,  
561 improving the understanding and knowledge of larval dispersal is crucial. A new, legally  
562 binding instrument for the high seas has been discussed since 2006 under the United Nations  
563 Convention on the Law of the Sea for the conservation and sustainable use of marine  
564 resources beyond national jurisdiction. Larval dispersal will be a key point in designing  
565 regional networks of Marine Protected Areas (Andrello et al., 2017) to conserve biodiversity  
566 in the high seas efficiently. Studies using numerical models in combination with the data and  
567 knowledge gathered during at-sea expeditions could make a vital contribution to these efforts.  
568 Indeed, genetic data could be gathered for several species covering a range of PLD values in  
569 order to corroborate the connectivity patterns simulated here between seamounts. In addition,  
570 behavioural data such as larval and adult mobility, and demographic data including egg  
571 production and pre- and post-settlement mortality, should also be considered, because these

572 factors are as critical information as connectivity in determining the dynamics of populations,  
573 and therefore their persistence.

574

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575 Fig. 1. Main currents of the SWIO obtained from OSCAR current data averaged over the  
576 period 2010–2017, and the location of the nine studied seamounts, the eight coastal sites and  
577 surrounding countries (buffers).

578

579 Fig. 2. Trajectories of drifters passing less than 50 km from (a) La Pérouse, (b) MAD-Ridge  
580 and (c) Walters Shoal during their drift in the SWIO. Small white circles show the closest  
581 locations of drifters to seamounts used as the start of the represented trajectories, and small  
582 black circles are the final locations.

583

584 Fig. 3. Connectivity matrices between all seamounts and coastal sites for PLDs of (a) 15, (b)  
585 120 and (c) 360 d. The values represent the percentage of larvae released at each release site  
586 transported to each destination site at the given PLD. The cells in the diagonal of the matrices  
587 are values of local retention. White = no connectivity (0%). Note that the colour scale differs  
588 between panels.

589

590 Fig. 4. Connectivity matrices between seamounts and coastal ecosystems for PLDs of (a) 15,  
591 (b) 120 and (c) 360 d. The values represent the percentage of larvae released at each release  
592 site transported to each destination site at the given PLD. The cells in the diagonal of the  
593 matrices are values of local retention. White = no connectivity (0%). Note that the colour  
594 scale differs between panels.

595

596 Fig. 5. Maps of average density for virtual larvae released at La Pérouse (a, d, g), MAD-Ridge  
597 (b, e, h) and Walters Shoal (c, f, i) for PLDs of 15, 120 and 360 d. Pink dots are the locations

598 of the drifters shown in Figure 2 at the same time (i.e. 15, 120 and 360 d after they passed less  
599 than 50 km from the seamount).

600

601 Fig. 6. Local retention (%) at La Pérouse, MAD-Ridge and Walters Shoal for PLDs of 15, 30,  
602 45, 90, 120 180, 270 and 360 d.

603

604 Fig. 7. Connectivity (%) between La Pérouse, MAD-Ridge and Walters Shoal for PLDs of 15,  
605 30, 45, 90, 120, 180, 270 and 360 d.

606

607 Fig. 8. Origin of the larvae reaching La Pérouse, MAD-Ridge and Walters Shoal for PLDs of  
608 (a) 15, (b) 120 and (c) 360 d.

609

610 Fig. 9. Maps of average density for virtual larvae released at all seamounts and coastal sites  
611 for PLDs of (a) 30, (b) 45 and (c) 90 d. These PLD correspond broadly to labrid and *Apogon*  
612 *spp.*, *Synodus sp.*, and the acanthurid *Naso sp.*, respectively.

613

614 Fig. 10. Origin of larvae reaching MAD-Ridge (imports) for PLDs of (a) 30, (b) 45 and (c) 90  
615 d, and the destination of larvae leaving MAD-Ridge (exports) for PLDs of (d) 30, (e) 45 and  
616 (f) 90 d. These PLD correspond broadly to labrid and *Apogon spp.*, *Synodus sp.*, and  
617 acanthurid *Naso sp.*, respectively.

618

619 Fig. 11. Age distributions of virtual larvae arriving at MAD-Ridge from (a) Fort Dauphin and  
620 (b) Mamanjary, and arriving at La Pérouse from (c) La Saline and (d) Morne Brabant.

621

622 Table 1. Mean distances of larval dispersal (km) from each seamount for different Pelagic  
 623 Larval Durations (PLDs).

<b>FROM \ PLD</b>	<b>15</b>	<b>30</b>	<b>45</b>	<b>60</b>	<b>90</b>	<b>120</b>	<b>180</b>	<b>270</b>	<b>360</b>
<i>La Pérouse</i>	167	283	355	423	540	628	793	1031	1284
<i>MAD-Ridge</i>	337	460	575	665	804	901	1086	1368	1544
<i>Walters Shoal</i>	109	217	296	348	439	517	678	869	1014
<i>Atlantis Bank</i>	125	211	266	302	370	431	542	699	844
<i>Sapmer Bank</i>	164	236	292	356	443	530	674	854	1027
<i>Middle of What Seamount</i>	205	348	473	555	664	754	891	1061	1233
<i>Coral Seamount</i>	342	605	847	1070	1459	1718	2086	2393	2587
<i>Melville Bank</i>	311	551	719	830	979	1080	1256	1465	1638
<i>Un-named Seamount</i>	195	279	394	452	523	622	782	974	1122
<b>Mean</b>	<b>217</b>	<b>354</b>	<b>469</b>	<b>556</b>	<b>691</b>	<b>798</b>	<b>976</b>	<b>1190</b>	<b>1366</b>

624

625

626 Appendix Fig. A. Trajectories of drifters passing <100 km from (a) La Pérouse, (b) MAD-  
627 Ridge and (c) Walters Shoal during their drift in the SWIO. Small white circles show the  
628 closest locations of drifters to seamounts used as the start of the represented trajectories, and  
629 small black circles are the final locations.

630

631 Appendix Fig. B. Connectivity matrices between all seamounts and coastal sites for PLDs of  
632 (a) 30, (b) 45, (c) 60, (d) 90, (e) 180 and (f) 270 d. The values represent the percentage of  
633 larvae released at each release site transported to each destination site at the given PLD. The  
634 cells in the diagonal of the matrices are values of local retention. White = no connectivity  
635 (0%). Note that the colour scale differs between panels.

636

637 Appendix Fig. C. Variability (seasonal and interannual combined) of simulated connectivity  
638 for PLDs of (a) 15, (b) 120 and (c) 360 d. CV is the relative standard deviation (ratio of the  
639 standard deviation to the mean).

640

641 Appendix Fig. D. Connectivity matrices between seamounts and coastal ecosystems for PLDs  
642 of (a) 30, (b) 45, (c) 60, (d) 90, (e) 180 and (f) 270 d. The values represent the percentage of  
643 larvae released at each release site and transported to each destination site at the given PLD.  
644 The cells in the diagonal of the matrices are values of local retention. White = no connectivity  
645 (0%). Note that the colour scale differs between panels.

646

647 Appendix Fig. E. Connectivity matrices between all seamounts and coastal sites for all PLDs.  
648 The buffer used around all release and destination sites was  $1^\circ$  (instead of the  $1/3^\circ$  in Fig. 3  
649 and Appendix Fig. B). The values represent the percentage of larvae released at each release  
650 site transported to each destination site at the given PLD. The cells in the diagonal of the

651 matrices are values of local retention. White = no connectivity (0%). Note that the colour

652 scale differs between panels.

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997 10.2305/IUCN.CH.2018.14.en-fr  
998

Journal Pre-proof

999 **Formatting of funding sources**

1000 This work was partly carried out in the framework of the project P00917 entitled  
1001 "Conservation and sustainable exploitation of seamount and hydrothermal vent ecosystems of  
1002 the South West Indian Ocean in areas beyond national jurisdiction", funded by the French  
1003 Global Environment Facility (FFEM), and conducted from 2014 to 2018.

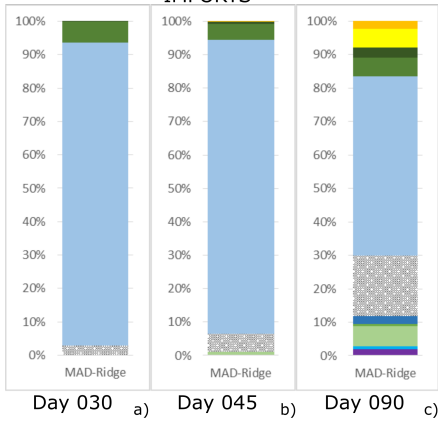
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Table 1. Mean distances of larval dispersal (km) from each seamount for different Pelagic Larval Durations (PLDs).

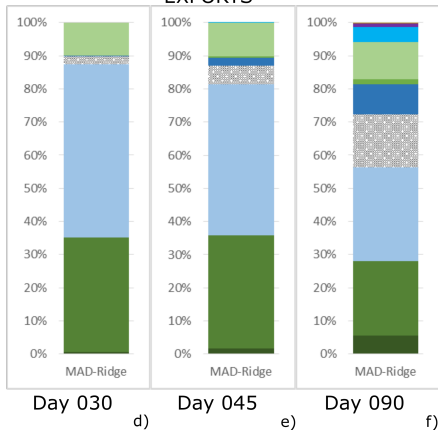
FROM \ PLD	15	30	45	60	90	120	180	270	360
<i>La Perouse</i>	167	283	355	423	540	628	793	1031	1284
<i>MAD-Ridge</i>	337	460	575	665	804	901	1086	1368	1544
<i>Walters Shoal</i>	109	217	296	348	439	517	678	869	1014
<i>Atlantis Bank</i>	125	211	266	302	370	431	542	699	844
<i>Sapmer Bank</i>	164	236	292	356	443	530	674	854	1027
<i>Middle of What Seamount</i>	205	348	473	555	664	754	891	1061	1233
<i>Coral Seamount</i>	342	605	847	1070	1459	1718	2086	2393	2587
<i>Melville Bank</i>	311	551	719	830	979	1080	1256	1465	1638
<i>Un-named Seamount</i>	195	279	394	452	523	622	782	974	1122
Mean	<b>217</b>	<b>354</b>	<b>469</b>	<b>556</b>	<b>691</b>	<b>798</b>	<b>976</b>	<b>1190</b>	<b>1366</b>

IMPORTS

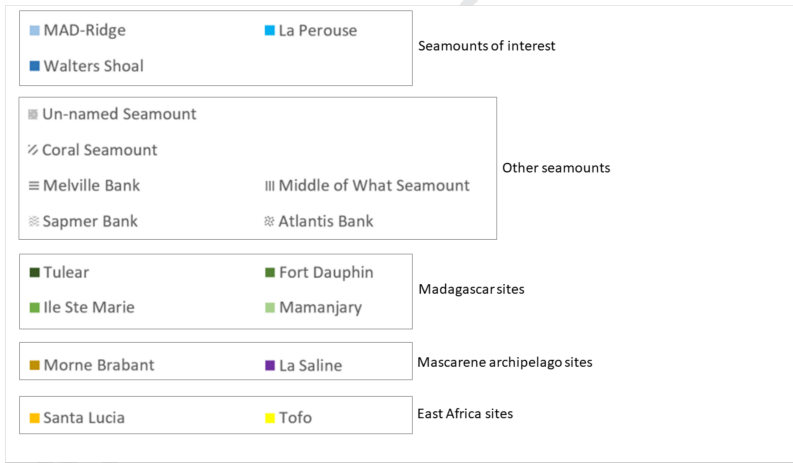


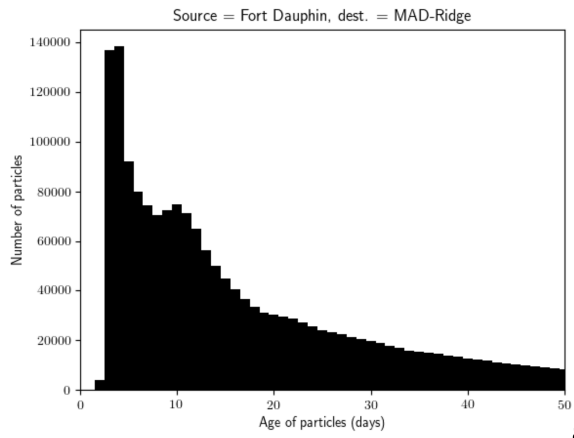
Day 030 a) Day 045 b) Day 090 c)

EXPORTS

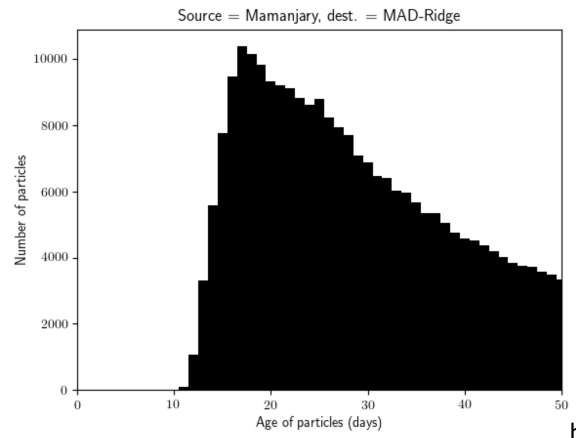


Day 030 d) Day 045 e) Day 090 f)

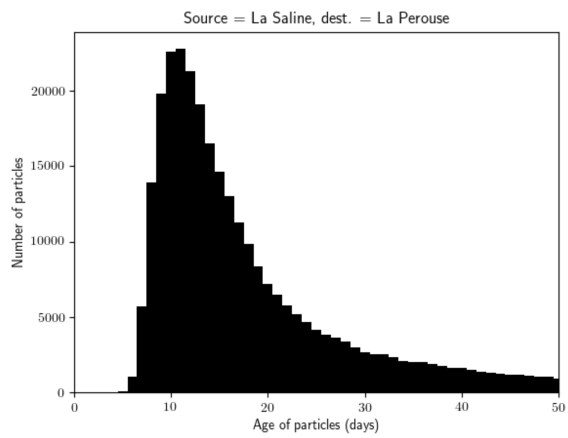




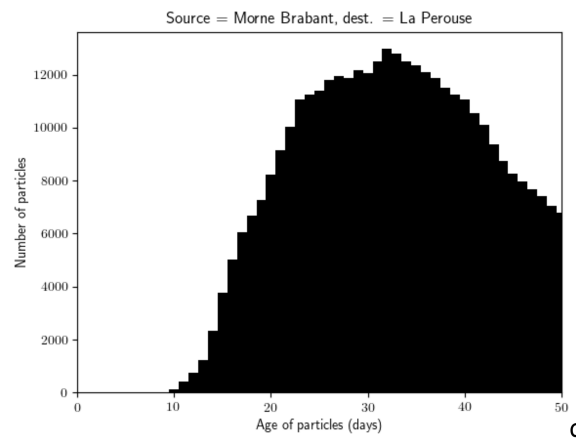
a)



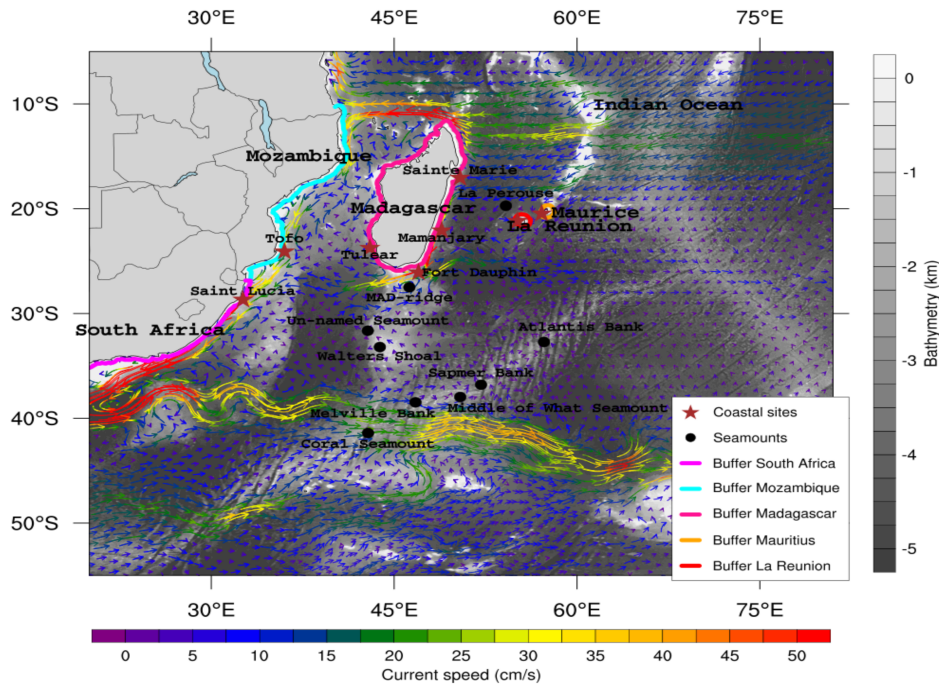
b)



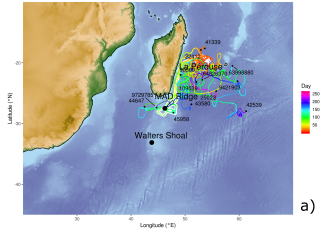
c)



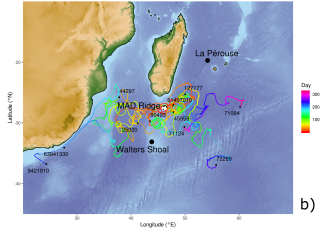
d)



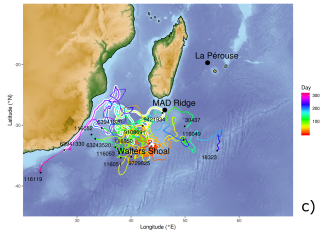
Name	Summit depth (meters)
Atlantis Bank	690
Sapmer Bank	261
Middle of What Seamount	876
Coral Seamount	175
Melville Bank	91
Un-named Seamount	1249
Walter's Shoal	18
La Pérouse	55
MAD-Ridge	240



a)

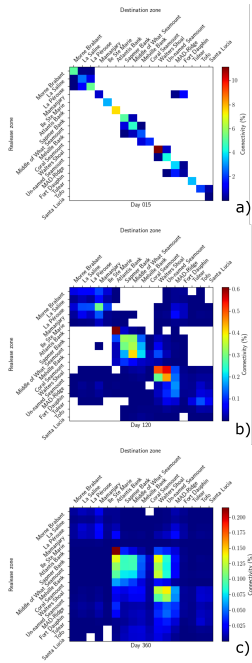


b)

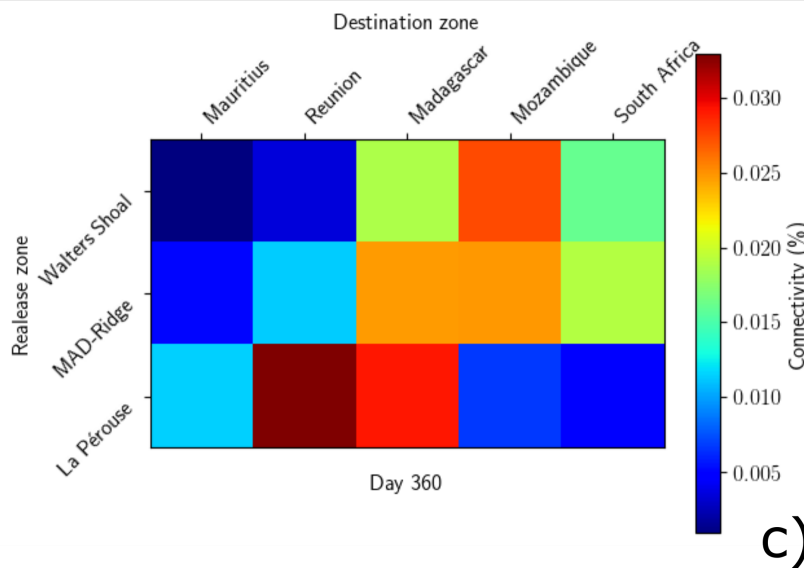
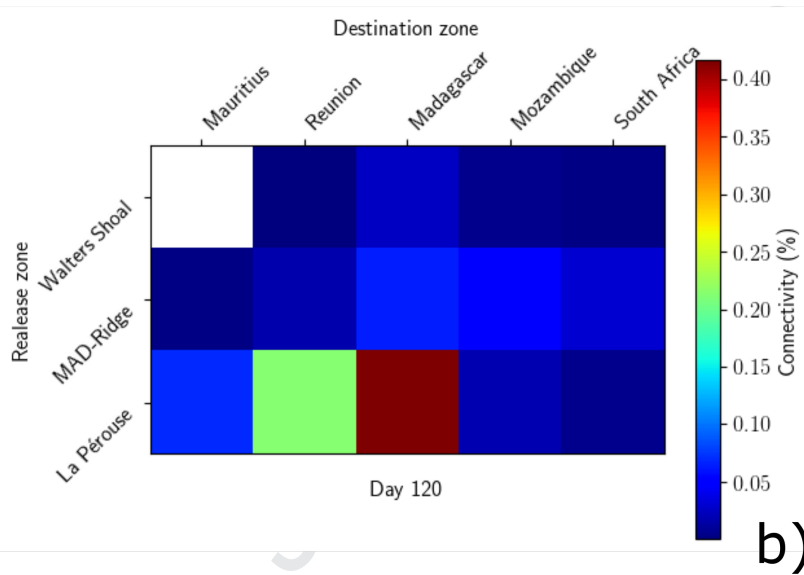
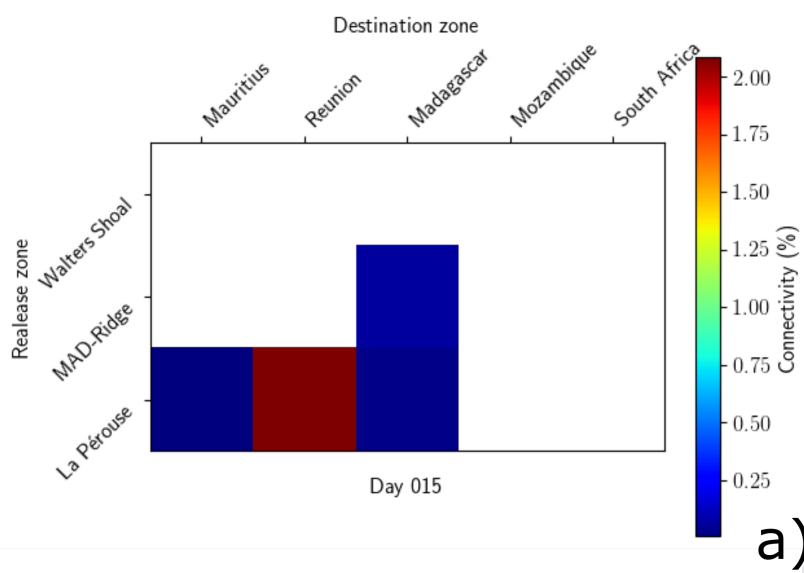


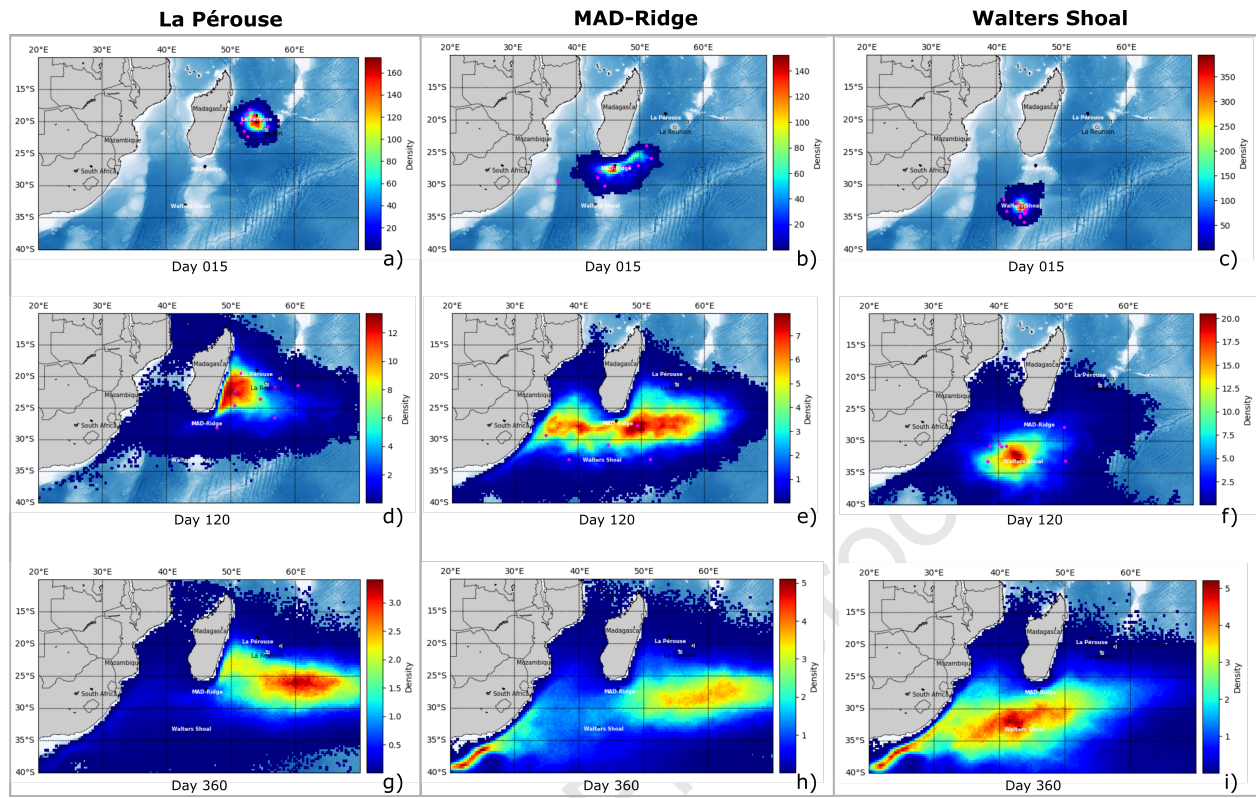
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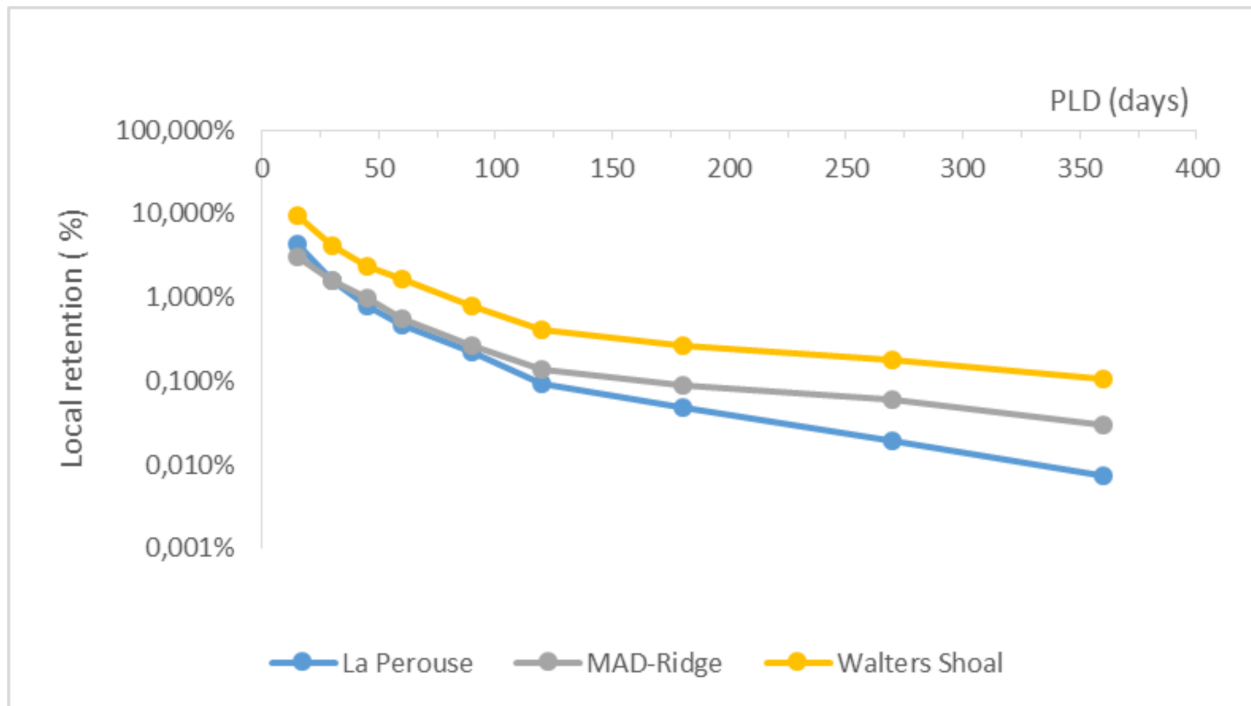
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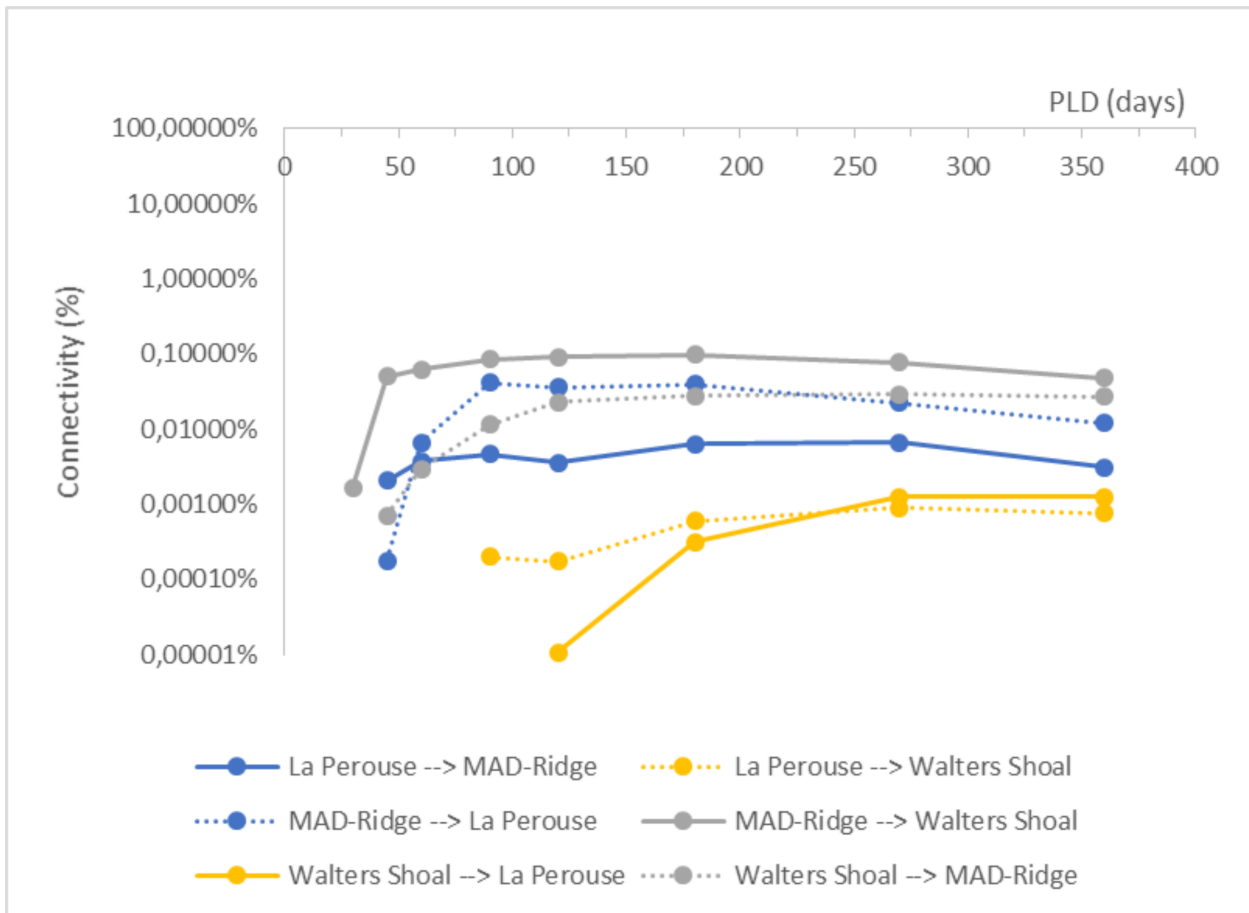


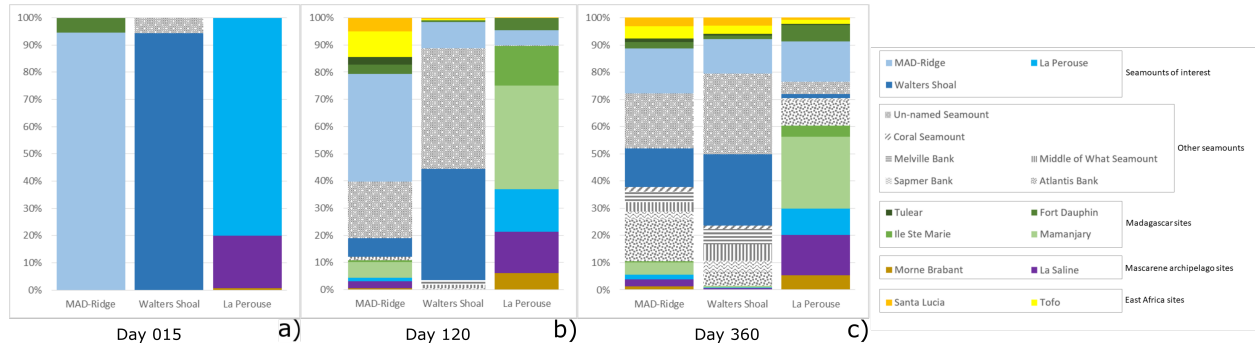
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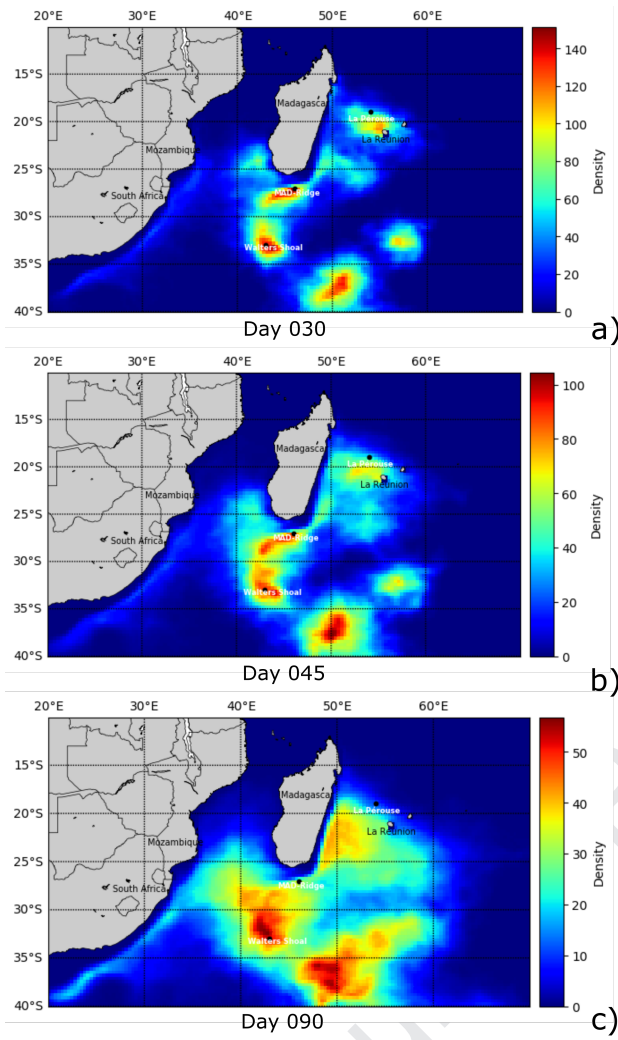


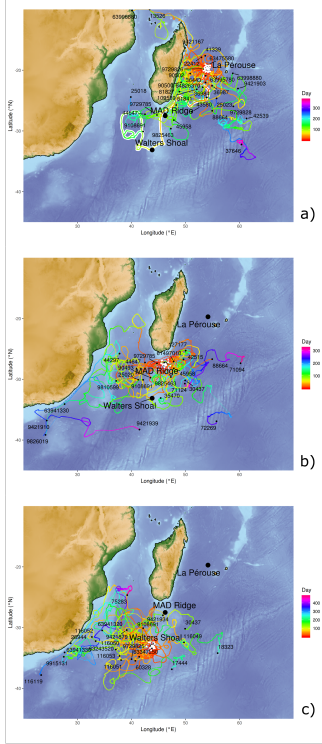




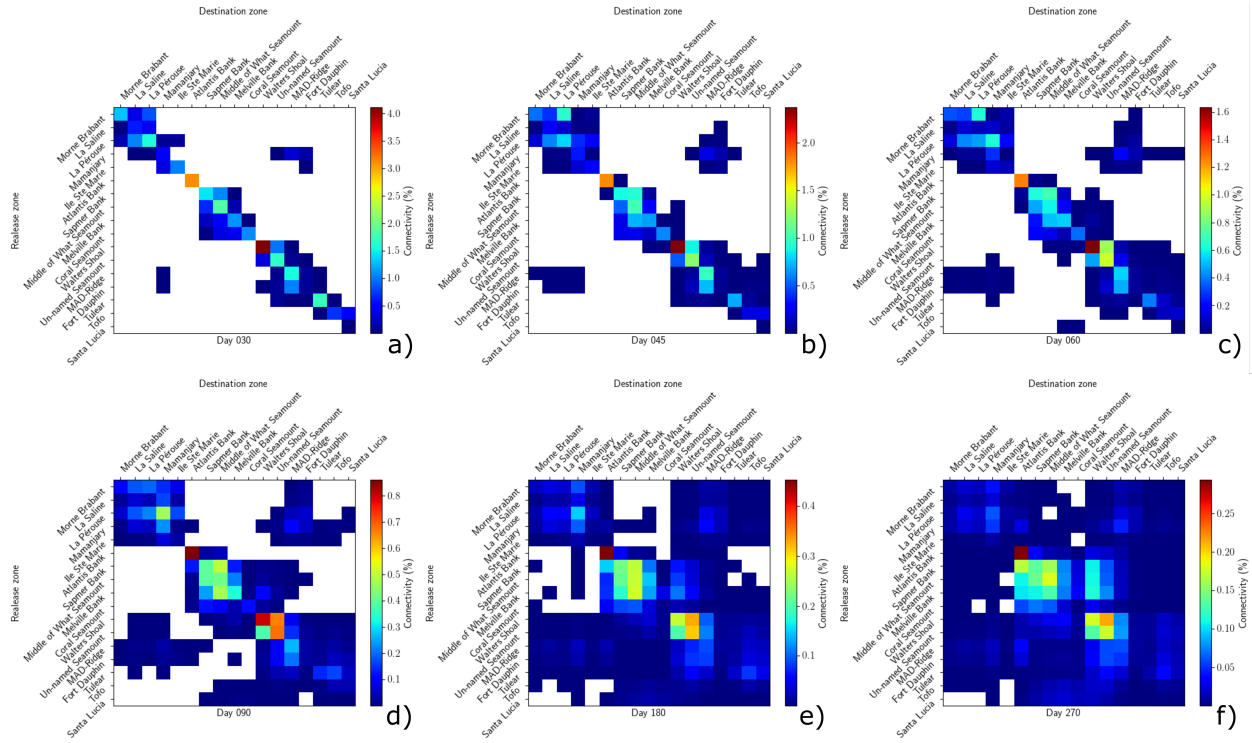


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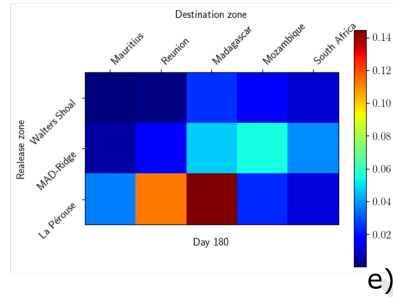
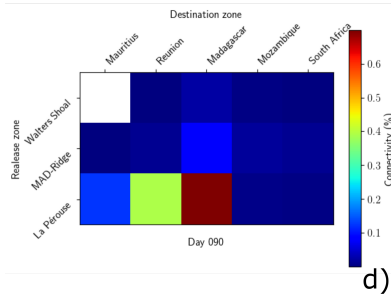
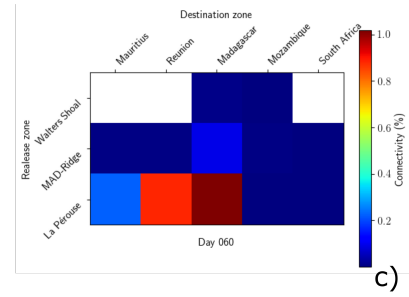
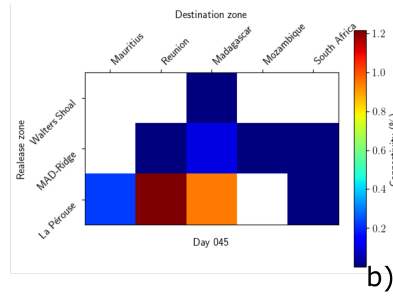
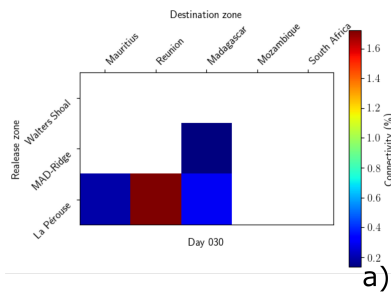




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**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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