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1 **High resolution modelling of ocean circulation can reveal retention spots important for**
2 **biodiversity conservation**

3

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13

14

15 **ABSTRACT:**

16 1. Larval transport by ocean circulation and its emerging property at the population level, i.e.
17 connectivity, have received increasing attention thanks to the Aichi target 11 of protecting 10% of
18 ocean surfaces. Furthermore, it is also important to investigate retention within a site as it
19 determines a population's self-persistence in an isolated marine protected area.

20

21 2. Mediterranean rocky substrates host a conspicuous and diverse biota, which explains that MPA
22 designation targetted the rocky habitat. Retention rates in the fragmented rocky habitat of the Gulf
23 of Lion were established at two spatial scales (10- and 1-km²) using dispersal simulations. To this
24 end we computed three dimensionnal flow simulations with high spatial resolution nearshore (80 m)
25 combined with a high density of release spots (every 100 m).

26

27 3. This study shows that among the six rocky 10-km² patches, marine protected areas (MPAs) were
28 designated in the four ones with highest average retention rates for Pelagic Larval Duration (PLD),
29 of up to 42 days. Furthermore, within each MPA, small zones where special protection measures are
30 applied correspond to 1-km² subpatches where highest local retention rates were found. Yet, the
31 2% most retentive subpatches of the rocky habitat do not exhibit retention rates large enough to
32 ensure the local persistence of most species.

33

34 Keywords: coastal, dispersal, Marine Protected Area

35

36

37 **Introduction**

38

39 Larval transport by ocean circulation and its emerging property at population levels, i.e.
40 connectivity, have gained increasing attention in the past 10 years as displayed by the ten-fold
41 increase in number of citations of papers referring to marine or ocean connectivity between 2005 and
42 2015 (Web of Science, June 1, 2017). This increase was in part, at least stimulated by Cowen,
43 Lwiza, Sponaugle, Paris, & Olson (2000), who questioned the broadly accepted paradigm of open
44 marine populations. Interestingly, the beginning of ocean connectivity studies traces back to a
45 pioneering study that linked connectivity to spatial planning of marine resources management
46 through MPA networks (Roberts, 1997). However, to date networks of MPAs are rarely found,
47 given that they require joint efforts of several players (local authorities, government, etc.) that are
48 more difficult to set and manage than single MPAs promoted by local communities (IUCN-WCPA,
49 2008). Within such a context, it is therefore crucial to test the efficacy of single MPAs based on
50 local retention values and in terms of ensuring species persistence through generations, in particular
51 if new protected areas are to be designated (Halpern & Warner, 2003; Guizien, Belharet, Marsaleix,
52 & Guarini, 2012).

53 Due to major advances in computing performances in the last decade, the use of ocean circulation
54 models in ecological studies has greatly increased, providing insight at both higher spatial
55 resolutions and broader scales compared with flow measurements. Several studies of regional
56 connectivity for coastal species have recently been carried out using high resolution configurations
57 of Regional Ocean Circulation Models (ROCMs) with horizontal resolutions of 1-2 km (e.g., Di
58 Franco et al., 2012: 2.2km; Nicolle, Dumas, Foveau, Foucher, & Thiébaud, 2013: 2km; Myksovoll,
59 Jung, Albrechtsen, & Sundby, 2014: 800m). Additionally, the efforts of climatologists to make high
60 resolution downscaled versions of Global Ocean Circulation Models (e.g. NEMO-MED12 and
61 NEMO-OPA 1/16: 6-8km) available to the scientific community has also facilitated their spread
62 among ecologists interested in large scale connectivity studies (Andrello et al., 2013; Rossi, Ser
63 Giacomi, Lopez Cristobal, & Hernandez-Garcia, 2014). Nevertheless, the terminology 'high
64 resolution' may have proved misleading in the field. 'High resolution' refers here to the level of
65 computing power effort devoted to the simulation – e.g., a large number of grid points to cover the
66 simulated area - and not the actual resolution of ocean flow spatial structures. A spatial resolution of
67 6-8 km is currently termed 'high' in simulations covering the Mediterranean basin while it would be
68 termed 'coarse' in coastal simulations. In fact, for any given level of computing effort, spatial
69 coverage and resolution are inversely related : if one is to increase the spatial coverage, resolution
70 would have to decrease in order to maintain the same computing effort (the reverse holds too).

71 Crucially, prior to performing any connectivity study using biophysical models, it is thus necessary
72 to compromise between resolving the spatial range of the flow relevant for populations connectivity
73 (spatial coverage) and that relevant for larval dispersal (spatial resolution).

74 With regard to empirical spatial coverage, although long range connections should not be totally
75 excluded, frequent and demographically efficient larval transfer was estimated over distances
76 ranging from 10 to 100 kms, due to the limitation imposed by larval survival (Cowen, Paris, &
77 Srinivasan, 2006) and large-scale ocean current shaping hydrodynamical provinces (Rossi, et al.,
78 2014). With regard to spatial resolution, larval dispersal simulations led to very different level of
79 retention in a bay in the south-west of the Gulf of Lion when either varying spatial resolution from
80 250 m to 100 m or the distance between spawning grounds and the coastline in flow simulations
81 (Guizien, Brochier, Duchêne, Koh, & Marsaleix, 2006). Along jagged coastlines, eddies developing
82 in the lee of capes may act as accumulative and retentive structures for particle dispersal (Denniss,
83 Middleton, & Manasseh, 1995; Graham & Largier, 1997; Roughan et al., 2005; Mace & Morgan,
84 2006).

85 In simulations it is thus of utmost importance to resolve in 3D these flow structures in order to
86 accurately compute larval dispersal around these geomorphological features (Doglioli, Griffa, &
87 Magaldi, 2004). Until recently, in 3D ROCMs resolving flow equations with finite-difference
88 numerical methods applied on cartesian grid computational limitations imposed a tradeoff between
89 spatial resolution and spatial coverage. Nesting multiple simulations of increasing resolution and
90 decreasing coverage was the only possibility to yield a resolution of 100 m, necessary to describe
91 nearshore eddies (Guizien et al., 2006). The introduction of bipolar curvilinear grids transformed
92 from Earth spherical coordinates in those ROCMs (Bentsen, Evensen, Drange, & Jenkins, 1999)
93 enables to yield wide spatial ranges with increased spatial resolution around specified poles.
94 Nevertheless, bipolar curvilinear grids, although allowing differential spatial resolution over the
95 simulation domain, do not reach the meshing flexibility of models resolving flow equations with
96 finite-element numerical method. However, up to date, those latter models have only been used in
97 2D depth-integrated version for regional ocean simulations (Lambrechts et al., 2008).

98 Besides, another important question for biophysical modellers of larval dispersal is the spatial
99 density of particles that have to be released to account for the spatial variability of hydrodynamics.
100 So far, particles or larvae have been released at coarse resolutions (Guizien et al., 2012: from 1/11
101 km^{-2} to 1/216 km^{-2} ; Di Franco et al., 2012: 1/3.25 km^{-2} ; Myksvoll et al., 2014: 1/16 km^{-2}). Di
102 Franco et al. (2012) reported that increasing the spatial density of particles did not show significant
103 difference in dispersal trajectories given the coarse resolution (2.2 km on the horizontal) of the
104 underlying flow simulations they used. However, a relationship between the spatial resolution of

105 flow simulations and the distance between release spots is to be expected, and to our knowledge its
106 influence on retention has yet to be explicitly assessed.

107

108 The aim of the present study is to investigate the local retention and potential connectivity within
109 the fragmented hard-bottom habitat of the Gulf of Lion (NW Mediterranean), which hosts a high
110 biodiversity (Laubier, 1966; True, 1970; Hong, 1980) and where marine protection measures have
111 been taken (MAPAMED, 2016). The originality of the study is to perform larval dispersal
112 simulations using ad hoc simulations of the ocean circulation over a 100,000 km² area, yielding a
113 spatial resolution of 80 m along its jagged coastline. To the best of our knowledge, these
114 simulations feature the highest spatial resolution ever used in 3D larval dispersal studies over such
115 large spatial coverage. This study tested the importance of resolving (1) small scale (hundreds of
116 metres) hydrodynamical structures, and (2) spawning timing (a few days) in larval dispersal when
117 studying retention rates. We argue that adapting the spatial and temporal resolution of ocean
118 circulation and the seeding spatial density in larval dispersal simulations to resolve flow transport at
119 kilometric scale provides reliable estimates of local retention and potential connectivity, with
120 important implications for guiding marine protection extension.

121

122 **Material and Methods**

123

124 *Area of study*

125

126 The Gulf of Lion is a wide, micro-tidal continental shelf in the North-western Mediterranean,
127 delineated by a steep shelf-break along which the Northern Current (NC, return branch of the
128 western Mediterranean basin cyclonic circulation) flows south-westward (Millot, 1990). The
129 infralittoral area (down to 40 m) consists mainly of soft bottoms delimited along the shore by a
130 smooth coastline, except at its two extreme tips (Côte Bleue to the east and Côte Vermeille-Cap de
131 Creus to the west, Fig. 1) where the coastline becomes jagged and rocky sea beds extend down to a
132 depth of 80 m (Aloisi, Got, & Monaco, 1973). Aside these two large hard-bottom areas, only a few
133 small areas of less than 20 km² are found, complementing the fragmented rocky shallow habitat
134 (Figure 1). Coralligenous assemblages on these rocky shallow substrates host a high biodiversity
135 (Laubier, 1966; True, 1970; Hong, 1980), including sponges, gorgonians, molluscs, bryozoans,
136 tunicates, crustaceans and fishes. Their vast biodiversity together with their proximity to the coast
137 makes this coralligenous habitat highly vulnerable to anthropogenic pressures such as recreational
138 and professional fisheries (Font & Lloret, 2014), scuba-diving (Sala, Garrabou, & Zabala, 1996),
139 and recreational boats' anchoring (Millazo, Chemello, Badalamenti, Camarda, & Riggio, 2002). In

140 order to protect these assemblages from anthropogenic pressure, four locally managed MPA have
141 been designated along the Gulf of Lion coastline (Aire Marine Protégée Agathoise, Parc Naturel
142 Marin du Golfe du Lion, Parc Marin de la Côte Bleue, and Réserve Naturelle Marine de Cerbère-
143 Banyuls (MAPAMED, 2016).

144 The coastal circulation in the Gulf of Lion is a wind-buoyancy driven circulation resulting from
145 meteorological forcings prevalence over tidal influence, with rare intrusions of the NC on the shelf
146 under specific wind and stratification conditions (Millot & Wald, 1981; Petrenko, 2003; Barrier,
147 Petrenko, & Ourmières, 2016). Two wind regimes can be distinguished in the Gulf of Lion: 1)
148 strong continental northerly (Mistral) and north-westerly (Tramontane) winds that blow
149 approximately 2/3 of time, for periods ranging from a few hours to a few days (Guénard, Dobrinski,
150 Caccia, Campistron, & Benech, 2005), and 2) easterly and south-easterly sea winds that blow less
151 frequently (1/3 of time) and with lower intensity (Fichaux, Poglio, & Ranchin, 2005). Despite the
152 fact that circulation patterns related to wind regimes in the Gulf can be identified (Estournel et al.,
153 2003), the erratic temporal variability in wind conditions translates into highly variable currents in
154 both space and time (Petrenko, Dufau, & Estournel, 2008), with localized up- and down-wellings
155 throughout the area (Millot, 1979; Millot & Wald, 1981; Hua & Thomasset, 1982; Johns,
156 Marsaleix, Estournel, & Véhil, 1992), and mesoscale eddies (Hu, Petrenko, Doglioli, & Dekeyser,
157 2011).

158

159 *Three-dimensional coastal circulation and particle tracking simulations*

160

161 Three-dimensional currents were computed with the free-surface ocean model Symphonie (ver.
162 2015) for the extended summer period (May, 28 to November, 15) over three years (2010, 2011 and
163 2012). The Symphonie model solves hydrostatic primitive equations with a finite-difference method
164 on a C curvilinear grid under Boussinesq approximation and with an energy conserving numerical
165 scheme (Marsaleix et al., 2008). In the current configuration, turbulent closure scheme was set to
166 two-equation K- ϵ (Michaud et al., 2012). Horizontal meshing was a 680 by 710 curvilinear grid
167 with the same local resolution in orthogonal directions. The curvilinear grid was adapted to the
168 geomorphology of the Gulf of Lion thanks to a conformal mapping (i.e., a transformation that
169 preserves local angles) of the Earth spherical coordinates (Bentsen, Evensen, Drange, & Jenkins,
170 1999, details in legend of Figure 1). This bipolar grid allowed differential horizontal resolution
171 across the domain while conserving coordinates orthogonality, with high resolution over the
172 continental shelf in order to resolve small scale vortices and coarse resolution in the open sea in
173 order to ensure continuity when applying matching conditions with a large-scale oceanic model at
174 the open boundaries. Horizontal resolution ranged from 80 m along the Côte Vermeille-Cap de

175 Creus coastline to 400 m over the continental shelf break, to 2.7 km over the abyssal plain. The
176 bathymetry was smoothed prior vertical meshing in order to avoid large bottom steepnesses that
177 would create spurious vertical velocities due hydrostatic inconsistency (Beckmann & Haidvogel,
178 1993). Smoothing consisted in limiting relative water depth variation to 15 % between grid points
179 applying an iterative laplacian diffusion to the initial bathymetry. Generalized σ -coordinates were
180 used for vertical meshing, with 29 vertical levels regularly spaced for water depth lower than 100
181 m. For water depth larger than 100 m, the spacing between vertical levels became irregular, with a
182 value of about 3.5 m at the surface (the vertical resolution at 100 m water depth) and increasing
183 values towards the bottom, where spacing matched the spacing of regular σ -coordinates at that
184 water depth. Sea surface and open-sea boundary conditions were updated every 3 h from regional
185 downscaled climatic simulations (6-7 km horizontal resolution, NMFREE ; Hamon et al., 2016),
186 performed at the Mediterranean basin scale by coupling the atmospherical model ALADIN forced
187 by ERA-interim atmospherical reanalysis (12 km horizontal resolution, tri-hourly) with the
188 oceanical model NEMO-MED12 (6-7 km horizontal resolution). Open-boundary forcings included
189 measured discharge from the eight main rivers of the Gulf of Lion (Grand Rhône, Petit Rhône,
190 Hérault, Orb, Aude, Agly, Têt, Tech) and the Var river in the Ligurian sea. Hydrodynamical outputs
191 were stored at the computing grid resolution every hour for subsequent 'offline' simulations.
192 Neutrally buoyant particles were dispersed 'offline' using a pure Lagrangian approach, i.e.
193 integrating along individual tracks, the 3D velocity field linearly interpolated in space and time
194 between hourly discrete velocity outputs. In particular, no species-specific motility behaviour was
195 included and dispersal duration lasted up to 42 days so as to not restrict the study to a specific
196 species. The present study concerned larval dispersal of any species dwelling on rocky substrates
197 and reproducing in summer, the most frequent reproductive season (D. Cortese, Personal
198 communication). Release spots were spread evenly with a spatial density of 100/km² over the only
199 rocky habitat of the Gulf of Lion (1 release spot every 100m, Figure 1). Only those locations in
200 which flow velocity was computed according to land/sea mask were taken into account. In each
201 spot, one particle was released 1 m above the bed (benthic species) every hour from beginning of
202 June until the end of August, summing up to 16.2 million particles for each summer season.

203

204 *Upscaling particles dispersal into connectivity matrices*

205

206 Particle tracking simulations were post-processed to compute larval connectivity matrices,
207 integrating individual tracks at the population level. A larval connectivity matrix contains larval
208 transfer rates T_{ij} between release (rows) and destination (columns) patches. T_{ij} is the proportion of
209 the total number of particles released in a patch i per unit area of release during a given period of

210 release that reach the destination patch j per unit area of the destination after a dispersal duration
211 (the PLD). Connectivity matrices may thus vary according to : (1) the size and location of the
212 patches they connect, and (2) the duration and timing of the release period it summarizes. Building
213 connectivity matrices thus require choosing spatial and temporal scales of aggregation that are
214 ecologically relevant. Hence, as initial conditions, spatial and temporal scales of aggregation were
215 defined according to usual ecological drivers: environment fragmentation and seasonality. Larval
216 transfer rates were computed among habitat patches delineated by expected meso-scale
217 hydrodynamical structures and the rocky habitat fragmentation.

218 Six rocky habitat patches were identified in the Gulf of Lion (Figure 1, Table 1): Cap de Creus
219 (CC, 21km²), Côte Vermeille (CV, 4.2km²), Cap Leucate (CL, 6.5km²), Cap d'Agde (CA, 16.4km²),
220 Plateau des Aresquiers (PA, 16km²) and Côte Bleue (CB, 10.4km²). A larva was counted as
221 reaching a destination patch after the dispersal duration if its position was less than 100 m of at
222 least one of the release spots of this patch. Connectivity matrices were built for the entire summer
223 season in three consecutive years (2010, 2011 and 2012), and for PLD ranging from 3.5 to 42 days.
224 Local retention rates T_{ii} correspond to the diagonal of the connectivity matrix. The Relative Out-
225 strength RO of each release patch within the patch network was defined as the proportion of out-
226 strength (Bocaletti, Latora, & Moreno, 2010) of a patch that connects to any other patch except
227 itself:

$$228 \quad RO_i = \left(1 - \frac{T_{ii}}{\sum_{j=1}^6 T_{ij}} \right) * 100$$

229

230 *Sensitivity of retention rate to release spots spatial distribution*

231

232 Given the ecological importance of local retention for population persistence (Halpern & Warner,
233 2003), the sensitivity of retention rates estimated at the habitat patch scale to the spatial density of
234 release spots within the habitat patch was examined. Sensitivity analysis was performed for a 3-
235 week PLD. To do so, the spatial density of release spots was gradually reduced by varying the
236 distance distance (spatial resolution) from 100 m to 120 m, 200 m, 350 m, 500 m, 700 m, 1 km, 1.5
237 km, 2 km, 3 km and 5 km. For each spatial density (or spatial resolution) of release spots, many
238 subsets of the original set of release spots were generated (Table 1).

239 For a given density of release spots to be sufficient to describe the habitat patch retention, the
240 retention rate should not vary between the subsets of release spots. For each spatial resolution, the
241 frequency distribution of retention rate estimates across all subsets was computed. For each habitat
242 patch, convergence of local retention rates estimates was obtained when the frequency distribution

243 reaches a unimodal and narrow distribution. This is equivalent to the limit when the median value
244 Q_{50} for the next higher resolution remains unchanged compared to current resolution, (see
245 Supplementary Material 1 and Supplementary Figure 1). As a criteria for converging to an
246 unimodal distribution, a threshold of 20% of uncertainty was applied, defined as the relative
247 interquantile range $(Q_{90}-Q_{10})/Q_{50}$ with Q_{90} and Q_{10} being the 90% and 10% quantiles of the retention
248 rate distribution, respectively.

249 The sensitivity of the local retention rates to the density of release spots may reflect small-scale
250 hydrodynamical spatial structures of retention. Thus, contribution of each release spot to the
251 retention rate of the habitat patch it belongs to was calculated and used to define subpatches in
252 which retention rate was spatially homogeneous (see Supplementary Material 1). Finally, high
253 spatial resolution connectivity matrices were build using 115 subpatches ranging in area from 0.16
254 to 1.4 km² (0.66 km² on average, Supplementary Figure 5). The cumulative area distribution of
255 local retention rate, i.e. the proportion of the rocky surface area where local retention rate is lower
256 than a threshold value, was computed using these 115 subpatches, for PLD ranging from 3.5 to 42
257 days.

258

259

260 *Sensitivity of connectivity to release timing variability*

261

262 Whilst the summer reproductive season is from June to August, species display variations in their
263 spawning timing (e.g. among sponges: Mariani, Uris, & Turon, 2005; among gorgonians:
264 Santangelo, Carletti, Maggi, & Bramanti, 2003, Gori, Linares, Rossi, Coma, & Gili, 2007).
265 Furthermore, the coastal circulation in the Gulf of Lion is also driven by erratic wind regimes,
266 leading to high spatio-temporal variability of ocean currents (Millot, 1990; Petrenko, 2003). We
267 thus questioned if summer connectivity patterns for a week-long spawning event were pre-
268 dominantly driven by meteorological, seasonal or climatic (inter-annual) variability. To this end, 39
269 different connectivity matrices (13 per year in 3 years), each representing a non-overlapping week-
270 long release period were built spanning the entire summer reproductive season (starting and
271 finishing dates are given in Supplementary Table 1). The variability of larval transfer probabilities
272 at various temporal scales (within month hereinafter called $Var_{intra-month}$, within season hereinafter
273 called $Var_{intra-summer}$, and between years hereinafter called $Var_{inter-summer}$) was computed as defined in
274 see also Supplementary Material 2.

275

276 **Results**

277

279

280 The average summer particle flows among the six main rocky habitat patches of the Gulf of Lion
281 were less than a few percent, and heterogeneous, regardless of the duration of dispersal (Figure 2).

282 The average connectivity pattern revealed two types of habitats: « closed » ones with retention rate
283 larger than export rates (relative out-strength lower than 50 %), and « open » ones with export rates
284 larger than retention rate (relative out-strength larger than 50 %). After seven days of dispersal,
285 retention rate clearly dominated over export rate in Cap de Creus, Côte Vermeille, Cap d'Agde,
286 Plateau des Aresquiers and Côte Bleue with retention rate values of 3.39, 1.65, 1.40, 0.89 and
287 1.94%, respectively (Figure 2A), and relative out-strength values RO ranging from 0 to 34% (Table
288 1). Conversely, Cap Leucate exhibited a much lower retention rate value of 0.15 % and a high
289 relative out-strength value (RO = 74 %), transferring particles predominantly to Côte Vermeille
290 (0.22 % after 7 days of dispersal). The connectivity matrix for a 7-day Pelagic Larval Duration
291 (PLD) was fairly symmetrical. It displayed three clusters of rocky habitat patches formed by closest
292 neighbouring patches exchanging a proportion of particles comparable to the proportion that
293 remained in their release grounds (more than 0.2 %): one cluster included Cap de Creus, Côte
294 Vermeille and Cap Leucate, another cluster included Cap d'Agde and Plateau des Aresquiers, while
295 Côte Bleue was disconnected from these two former clusters (Figure 2A).

296 Increasing the PLD up to 21 days, retention rate values decreased in all habitat patches, yielding
297 1.43, 0.60, 0.05, 0.50, 0.08 and 0.74 % from west to east (Figure 2B and 3). However, only Plateau
298 des Aresquiers rocky habitat shifted from a closed to an open habitat patch, with relative out-
299 strength increase from 33% to 82% (Table 1). In Cap de Creus, Côte Vermeille, Cap d'Agde and
300 Côte Bleue, retention remained dominant over export for a 21-day PLD (Figure 2B). Nevertheless,
301 relative out-strength increased in eastern habitat patches thanks to an increase in long distance
302 connections within the Gulf of Lion while it decreased in the western habitat patches due to a
303 decrease of the transfer rate to closest neighbours and export out of the Gulf of Lion (Table 1). The
304 connectivity matrix became asymmetrical, with a dominant North-east to South-west particle flow
305 (higher transfer rates above the diagonal, Figure 2B) and the three clusters of preferentially
306 connected habitat patches for a 7-day PLD merged into a single cluster when PLD was set to 21
307 days. Yet, it is noteworthy that Côte Bleue received a very low proportion of particles from the
308 other habitat patches of the Gulf for a dispersal duration up to 42 days (data not shown, incoming
309 transfer rates ranged between 10^{-4} and 10^{-3} % for a 21-day PLD). In contrast, outgoing transfer rates
310 from Côte Bleue to all other habitat patches were one order of magnitude higher than incoming
311 transfer rates. For PLD lower than 14 days, Côte Bleue was only supplying the closest neighbouring
312 habitat patch, namely Plateau des Aresquiers. For dispersal duration larger than 14 days, this pattern

313 was reversed: the closer the habitat patch is to Côte Bleue, the fewer particles it received, with Côte
314 Bleue now mainly supplying the Cap Creus, the furthest from Côte Bleue (transfer rates from Côte
315 Bleue to Cap de Creus, Côte Vermeille, Cap Leucate, Agde and Plateau des Aresquiers respectively
316 being 0.026; 0.017; 0.017; 0.008; 0.004 % after 42 days of dispersal).

317 Retention rates (the diagonal of a connectivity matrix) decreased rapidly up to a 21-day PLD and
318 reached a stable value for longer dispersal duration in all habitat patches, except in Cap Leucate in
319 which retention rate was always small (Figure 3). The habitat patch ranking with regard to retention
320 rate was maintained for all dispersal durations, Cap Creus being the most retentive, followed by
321 Côte Vermeille, Côte Bleue, and Cap d'Agde, than Plateau des Aresquiers and last, Cap Leucate.
322 Yet, average retention rate values should be taken with caution as retention rates varied
323 significantly among the different release periods of three consecutive summers
324 (2010, 2010 and 2012) with standard deviation yielding 100% of the mean in all habitat patches
325 and for all dispersal durations.

326

327 *Meteorological variability during release period drives connectivity*

328

329 Seasonal variability (between different months of reproduction within a year, $\text{Var}_{\text{intra-summer}}$) and
330 climatic variability (between the same month of reproduction in different years, $\text{Var}_{\text{inter-summer}}$) had
331 the same order of magnitude, whatever the dispersal duration (Figure 4A). Their ratio for any of the
332 36 pairwise transfer probabilities among the six habitat patches ranged from 0.3 to 2.6, whatever the
333 dispersal duration. Neither seasonal nor climatic variability dominated for dispersal durations of up
334 to 21 days (median of the 36 values of the ratio between climatic and seasonal variability was close
335 to 1). When dispersal duration increased from 21 to 42 days, climatic variability started to exceed
336 seasonal variability (median of the 36 values of the ratio between climatic and seasonal variability
337 larger than 1). This was the case in 26 out of the 36 possible pairwise connections among the six
338 habitat patches for a dispersal duration of 35 days.

339 In contrast, meteorological variability (between release periods within each month of reproduction,
340 $\text{Var}_{\text{intra-month}}$) clearly outweighed seasonal variability in all pairwise connections among the six
341 habitat patches for dispersal durations of up to 21 days (Figure 4B), with an effect as large as 7.8
342 times larger than the seasonal variability. The dominance of meteorological variability over
343 seasonal variability was observed for all dispersal durations, although decreasing when dispersal
344 duration increased: the median of the 36 values of the ratio of meteorological to seasonal variability
345 varied from 3 to 4 for PLD lower than 21 days and dropped below 2 for PLD larger than 21 days.

346

347 *Coastline indentation drives retention rates patchiness down to 1km² scale*

348

349 Retention rate estimates varied according to the density of release spot, but did so differently
350 according to habitat patches. While retention rate estimates did not vary much with release spot
351 distance in the Plateau des Aresquiers and Cap Leucate, uncertainty on retention rate estimates
352 notably decreased

353 when distance between release spots decreased below 1 km in Cap de Creus, Cap d'Agde, Côte
354 Bleue and Côte Vermeille, with a faster reduction of uncertainty in Cap de Creus than in the three
355 other habitat patches (Figure 5B). The distance between release spots required to reach a precision
356 of 20 % in retention rate estimates among different release spot subsets (relative interquartile range
357 less than 20%) was 700 m in Plateau des Aresquiers, 350 m in Cap Leucate and 200 m in Cap de
358 Creus, while it was 100 m in Cap d'Agde and Côte Bleue. In Côte Vermeille, with a distance of 100
359 m between release spots, the precision of 20 % around the median could not be obtained and the
360 deviation between the 10 % and 90 % quantiles was 35%.

361

362 Stabilization of the median retention rate values was reached for a distance between release spots of
363 250 m in all habitat patches except in Côte Vermeille (deviation by less than 5% between median
364 retention rate values for release spot spatial resolution of 100 m and 250 m, Figure 5A). In Côte
365 Vermeille, median retention rate still exhibited 25% deviation between the 120 m and the 100 m
366 release spots spatial resolution. However, such a deviation was four times lower than the variability
367 among retention rate values at different release periods (Figure 3).

368 The large uncertainty on retention rate estimates when distance between release spot was larger
369 than 1km in Cap Creus, Côte Vermeille, Cap d'Agde and Côte Bleue (Figure 5A) indicated that
370 retention rates could vary greatly over a 1 km distance within these habitat patches (Supplementary
371 Figures 2, 3 and 4 and Figure 6). Retention rates computed within 115 subpatches of about 1 km²
372 (defined in Supplementary Figure 5) showed highly retentive subpatches in Cap Creus, Côte
373 Vermeille, Cap d'Agde and Côte Bleue with retention rates greater than 2% for a 21-day PLD.
374 Crucially, those subpatches correspond to locations where special marine protection is implemented
375 (Figure 6). The highest local retention rate was found in one subpatch of Cap de Creus, ranging
376 from 5% for a 7-day PLD to 3.5% for a 42-day PLD. Altogether, in the Gulf of Lion, local retention
377 rate was higher than 5% in only 6.8% of the rocky surface area for PLD of 3.5 days (data not
378 shown), and equal or lower to 5% everywhere in the rocky habitat for PLD equal or larger to 7 days
379 (Figure 7). For a PLD of 7 days, local retention rates was less than 2 % over 90 % of the rocky
380 surface area and less than 4 % over 98 % of the rocky surface area (Figure 7). For PLD larger than 7
381 days, local retention rates was less than 1.5 % over 90 % of the rocky surface area and less than
382 2.5 % over 98 % of the rocky surface area .

383

384 Average connectivity matrices at high spatial resolution (that is, among the 115 subpatches, Figure
385 8) further indicated that highly retentive subpatches (displayed by vertical stripes in Figure 8C and
386 D) corresponded as well to sink areas that received particles from neighbouring or distant
387 subpatches (displayed by vertical stripes in Figure 8A and B). Conversely, source subpatches
388 displayed by horizontal stripes could be both retentive
389 and non-retentive. It is worth noting that regardless of the PLD, transfers within subpatches
390 of the southern part of Cap de Creus were high and bidirectional. On the other hand, the direction
391 of transfer to distant habitat patches varied with the PLD. For a 7-day PLD, the southern part of Cap
392 de Creus spread a higher proportion of particles to the Côte Vermeille than it received from it. For a
393 21-day PLD, it received particles from up to Cap d'Adge but spread only to Cap Leucate.

394

395 **Discussion**

396

397 The present study shows the strong spatial heterogeneity in local retention rates estimated at a scale
398 of 1 km² around a jagged coastline. The results reported here highlight the inadequacy of low
399 resolution flow simulations produced with global ocean climatic models for tackling the question of
400 retention in coastal MPAs (Andrello et al., 2013). Criticisms as to the realism of the *in silico*
401 approach of larval dispersal has mainly focused on the assumptions restricting larvae to neutrally-
402 buoyant particles, disregarding their motility behaviour (Cowen et al., 2006), ontogenic
403 development (Guizien et al., 2006) or mortality (Cowen et al., 2000). Furthermore, incorporating
404 this information is still currently limited by gaps in biological knowledge. Notwithstanding the
405 importance of such biological aspects in altering dispersal patterns, the choice of spatial and
406 temporal resolutions of ocean flow simulations in larval transport studies should be questioned
407 (Putman & He, 2013). For instance, spatial resolution as low as tens of metres were used to depict
408 flow variability in reef mosaic or complex costalines (Andutta, Kingsford, & Wolanski, 2012;
409 Herbert et al., 2012). Yielding such spatial resolution in flow simulations covering an area of
410 hundred of square kilometers representative for populations connectivity was only achievable in 2D
411 finite-element models. Yet, coastal flows influenced by wind forcing are not accurately resolved
412 with 2D models, and 3D models able to resolve Ekman layers should be used (Petrenko et al.,
413 2008).

414

415 Until recently, 3D models based on a finite-difference numerical scheme were limited by their
416 regular orthogonal meshing and required successive nested meshes to improve spatial resolution
417 (Blayo & Debreu, 1999). However, nested meshes can complicate particle tracking when they

418 disperse outside the smallest nested domain and return to it thanks to meso-scale eddies (Guizien et
419 al., 2006). In the present study, such retention processes were observed in rocky patches located a
420 few kilometers offshore (Cap Leucate and Plateau des Aresquiers) and resulted in evenly distributed
421 retention rates. The latter *a posteriori* justifies the coarse 750 m horizontal resolution used in
422 Guizien et al. (2012) to study soft-bottom species dispersal. Conversely, on other rocky patches
423 retained particles did not leave the habitat during their entire dispersal, regardless of the PLD used.
424 In those patches, retention resulted from either simulated weak flow velocities due to important
425 bottom friction in shallow areas in Cap d'Agde or from simulated retention structures with spatial
426 scales less than 200m in the lee of capes or in bays along the steep bathymetry of Côte Bleue, Côte
427 Vermeille and Cap de Creus.

428
429 Such small scale structures could not be simulated in a previous study using the same model but
430 with a 750 m horizontal resolution. Very low retention rates were reported in large soft-bottom
431 areas (11 to 216 km²), spanning water depths of 10 to 30 m, at three of the four rocky habitat
432 patches investigated (Guizien et al., 2012). Increasing horizontal resolution by a factor of about 10
433 in the same numerical model enabled simulation of small scale hydrodynamical structures
434 important for retention in rocky habitat patches adjacent to jagged coastlines and nearby soft
435 bottoms. Hence, incorporating curvilinear meshing into 3D finite-difference models such as the one
436 used in the present study opens the way for improved horizontal resolution in 3D ocean flow
437 simulations used for larval dispersal studies. This is of particular interest where the geomorphology
438 imposes high horizontal resolutions, in order to avoid computationally costly nesting procedures.

439
440 Nonetheless, one has to keep in mind that the true resolution of flow structures in ocean models
441 may be different from the theoretical grid resolution. Numerical schemes used to discretize
442 primitive equations constrain the effective resolution of flow dissipation and may alter flow
443 representation in simulations (Soufflet et al., 2016). However, in the absence of ground truth
444 validation versus flow measurements, larval dispersal simulation reliability is difficult to estimate.
445 For instance, high retention rates in isolated locations very close to the coast are most likely
446 artifacts: in the absence of a hydrodynamic calculation point between a release spot and the coast,
447 the logarithmic decay of flow velocity in the coastal boundary layer will be linearly interpolated and
448 the flow underestimated. Conversely, can several release spots spaced a 100 m from each other
449 (more than grid resolution) along the Côte Vermeille consistently depicting high retention rate be
450 considered as a reliable indicator of the existence of actual retention ? Strikingly, the four rocky
451 habitat patches with highest average retention for PLD up to 42 days, namely Cap de Creus, Côte
452 Vermeille, Cap d'Agde and Côte Bleue correspond to areas designated for marine protection in the

453 Gulf of Lion. Furthermore, areas with highest average local retention at the 1-km² scale in Cap
454 d'Agde and Côte Bleue, and partially in Côte Vermeille, correspond to areas where special marine
455 protection have been implemented. Given that the present study quantified for the first time the
456 retention in those places, this criterion was not used in their designation. Until now, MPA
457 designation has been largely based on the biotic richness of areas. Persistence of high biomass and
458 biodiversity in some locations indicates that in those locations, many species reached local
459 equilibrium, that is, colonization compensated local extinction. For species with a dispersive larval
460 stage which can potentially form metapopulations (Levins, 1969), colonization can result from
461 either local retention or import from distant populations. Both local retention rates as well as import
462 rates were higher in the small subpatches where marine protection had been designated based on
463 biotic richness. These finding validate the present simulations.

464

465 Designating areas with high local retention for marine protection is essential for at least two
466 reasons. On the one hand, such areas are highly vulnerable to contaminations. In a context of
467 limited dispersal, low dilution of organic or inorganic effluent is likely to lead to local
468 eutrophication and/or anoxia (Xu et al., 2010). On the other hand, such areas are the ones where
469 self-persistence of isolated populations can be expected. Hence, we advocate using biophysical
470 models with adequate spatial resolution to identify areas with high local retention to help guide
471 future marine spatial planning. Meanwhile, verifying that highly retentive areas effectively ensure
472 population self-persistence requires comparison of retention rates with the threshold defined by
473 species life-history traits. Neglecting losses during recruitment (taking a recruitment success equal
474 to 1, Hastings & Botsford, 2006), local retention rates should be ranging from 5.9 to 14.4% to
475 ensure population self-persistence for species with 3-yr life expectancy, a fecundity of 10⁴ eggs per
476 adult and a PLD ranging from 1 to 4 weeks (Guizien et al., 2012). Hence, self-persistence of species
477 with such life-history traits would not be achieved in any subpatch of the rocky habitat of the Gulf
478 of Lion. However, for a PLD ranging from 5 to 6 weeks and a fecundity of 10⁵ eggs per adult,
479 population self-persistence would be yielded in about 2% of the rocky surface area, although still
480 ignoring losses during recruitment. Indeed, increasing the coverage of no-take zones in the
481 Mediterranean Sea from the current value of 0.04% to 2% by 2020, targeting key functional areas is
482 the objective set up during the 2016 MEDPAN Forum (Tangier declaration,
483 http://www.medmpaforum.org/sites/default/files/tangier_declaration.pdf). Meanwhile, keeping in
484 mind that recruitment success is by definition less than 1, this means that even if marine protection
485 designation was directed towards those most retentive areas, self-persistence may not be achievable
486 for species whose life-history traits impose much higher local retention rates than the flow allows.
487 In such cases, populations persistence at a regional scale would rely on connectivity among distant

488 subpatches forming persistence loops over multiple generation (Hastings & Botsford, 2006).
489 Indeed, achieving species conservation objectives in the fragmented rocky habitat of the Gulf of
490 Lion relies on the identification of networks of connected subpatches. Indeed, protecting source
491 populations providing larvae to unprotected populations (identified by horizontal stripes in
492 connectivity matrices), may prove completely unefficient if those source populations do not
493 maintain themselves through receiving sufficient larvae. Yet, protecting sink populations receiving
494 larvae from unprotected populations is even more cynical. In addition to being unefficient because
495 depending on the wealth of unprotected supplying populations, it may give a false impression of
496 protection efficiency as sink populations have a higher resistance to local perturbations. Designating
497 efficient MPAs requires to go beyond the easy identification of source and sink populations from
498 connectivity patterns, by investigating the populations network functioning within a region. To this
499 aim, the present study provides ready-to-use connectivity matrices among 1-km² rocky subpatches
500 to analyze the persistence of rocky populations in the Gulf of Lion through metapopulation
501 modeling, accounting for demographical processes (Moilanen, 2011) . Such an approach will enable
502 to evidence the minimal set of populations necessary to achieve conservation objectives and test
503 future maritime spatial planning scenarios including MPA extension (Guizien, Belharet, Guarini, &
504 Moritz, 2014 ; Padron & Guizien, 2016).

505

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507

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519

520 **LITERATURE CITED**

521

522 Aloisi, J.C, Got, H., & Monaco, A. 1973. Carte géologique du précontinent languedocien au
523 1/250000ième. Netherlands : Enschede : International Institute for Aerial survey and Earth sciences.
524 (ITC), Netherlands.
525

526 Andrello, M., Mouillot, D., Beuvier, J., Albouy, C., Thuillier, W., & Manel, S. 2013. Low
527 Connectivity between Mediterranean Marine Protected Areas: A Biophysical Modeling Approach
528 for the Dusky Grouper. *Plos One*, 8(7), e68564.
529

530 Andutta, F.P., Kingsford M.J., & Wolanski, E. 2012. 'Sticky water' enables the retention of larvae
531 in a reef mosaic. *Estuarine, Coastal and Shelf Science*, 101, 54-63
532

533 Barrier, N., Petrenko, A., & Ourmières, Y. 2016. Strong intrusions of the Northern Mediterranean
534 Current on the eastern Gulf of Lion: insights from in-situ observations and high resolution
535 numerical modelling. *Ocean Dynamics*, 66, 313-327 , doi: 10.1007/s10236-016-0921-7
536

537 Beckmann, A., & Haidvogel, D.B. 1993. Numerical simulation of flow around a tall isolated
538 seamount. Part I : Problem formulation and model accuracy. *Journal Physical Oceanography*, 23,
539 1736-1752.
540

541 Bentsen, M., Evensen, G., Drange, H., & Jenkins, A.D. 1999 Coordinate transformation on a sphere
542 using conformal mapping. *Monthly Weather Review*, 127(12), 2733-2740, doi:10.1175/1520-
543 0493(1999)127.
544

545 Blayo, E., & Debreu, L. 1999: Adaptative mesh refinement for finite-difference ocean models: first
546 experiments. *Journal Physical Oceanography*, 29, 1239-1250.
547

548 Bocaletti, S., Latora, V., & Moreno, Y. 2010 Handbook on Biological networks. World Scientific
549 Lecture Notes in Complex Systems - vol. 10. World Scientific Publishing.
550

551 Cowen, R. K., Lwiza, K.M.M., Sponaugle, S., Paris, C.B., & Olson, D.B. 2000. Connectivity of
552 marine populations: Open or closed? *Science*, 287(5454), 857-859
553

554 Cowen, R.K., Paris, C.B., & Srinivasan, A. 2006. Scaling of connectivity in marine populations.
555 *Science*, 311 (5760), 522-527.
556

557 Denniss, T., Middleton, J.H., & Manasseh, R. 1995. Recirculation in the lee of complicated
558 headlands: A case study of Bass Point. *Journal Geophysical Research*, 100 (C8), 16,087-16,101
559

560 Di Franco, A., Coppini, G., Pujolar, J.M., De Leo, G.A., Gatto, M., Lyubartsev, V., al. ..., Guidetti,
561 P. (2012) Assessing Dispersal Patterns of Fish Propagules from an Effective Mediterranean Marine
562 Protected Area. *PLoS ONE*, 7(12), e52108. doi:10.1371/journal.pone.0052108
563

564 Doglioli, A.M., Griffa, A., & Magaldi, M.G. 2004. Numerical study of a coastal current on a steep
565 slope in presence of a cape: The case of the Promontorio di Portofino. *Journal Geophysical*
566 *Research*, 109, C12033, doi:10.1029/2004JC002422
567

568 Estournel, C., Durrieu de Madron, X., Marsaleix, P., Auclair, F., Julliand, C., & Vehil, R. 2003.
569 Observation and modelisation of the winter coastal oceanic circulation in the Gulf of Lion under
570 wind conditions influenced by the continental orography (FETCH experiment). *Journal*
571 *Geophysical Research*, 108(C3), doi:10.1029/2001JC000825
572

573 Fichaux, N., Poglio, T., & Ranchin, T. 2005. Mapping offshore wind resources: synergetic potential
574 of SAR and scatterometer data. *IEEE Journal Ocean Engineering*, 30(3), 516-525
575

576 Font, T., & Lloret, J. 2014. Biological and Ecological Impacts Derived from Recreational Fishing in
577 Mediterranean Coastal Areas. *Reviews in Fisheries Science & Aquaculture*, 22(1), 73-85.
578

579 Graham, W.M., & Largier, J.L. 1997 Upwelling shadows as nearshore retention sites: the example
580 of northern Monterey Bay. *Continental Shelf Research*, 17 (5), 509-532
581

582 Gori, A., Linares, C., Rossi, S., Coma, R., & Gili, J.M. 2007. Spatial variability in reproductive
583 cycle of the gorgonians *Paramuricea clavata* and *Eunicella singularis* (Anthozoa, Octocorallia) in
584 the Western Mediterranean Sea. *Marine Biology*, 151, 1571-1584
585

586 Guénard, V., Dobrinski, P., Caccia, J.L., Campistron, B., & Benech, B. 2005. An observational
587 study of the mesoscale Mistral dynamics. *Boundary Layer Meteorology*, 115, 263-288
588

589 Guizien, K., Brochier, T., Duchêne, J.C., Koh, B.S., & Marsaleix, P. 2006. Dispersal of *Owenia*
590 *fusiformis* larvae by wind-driven currents: turbulence, swimming behaviour and mortality in a
591 three-dimensional stochastic model. *Marine Ecology Progress Series*, 311, 47-66

592

593 Guizien, K., Belharet, M., Marsaleix, P., & Guarini, J.M. 2012. Using larval dispersal simulations
594 for marine protected area design: Application to the Gulf of Lions (northwest Mediterranean).
595 *Limnology Oceanography*, 57(4), 1099-1112 doi:10.4319/lo.2012.57.4.1099

596

597 Guizien, K., Belharet, M., Guarini, J.M., & Moritz, C. 2014. Marine benthic metapopulations
598 vulnerability: implications of spatially structured connectivity for conservation practice. *Diversity
599 and Distributions*, 20, 1392-1402 doi:10.1111/ddi.12254

600

601 Halpern, B.S., & Warner, R.R. 2003. Matching marine reserve design to reserve objectives
602 *Proceedings Royal Society London B*, 270,1871-1878, doi 10.1098/rspb.2003.2405

603

604 Hamon, M., Beuvier, J., Somot, S., Lellouche, J.-M., Greiner, E., Jord, G., Drevillon,..., Drillet, Y.
605 2016. Design and validation of MEDRYS, a Mediterranean Sea reanalysis over 1992-2013. *Ocean
606 Science*, 12, 577-599, doi:10.5194/os-12-577-2016

607

608 Hastings, A., & Botsford, L.W. (2006) Persistence of spatial populations depends on returning
609 home. *Proceedings of National Academy of Science of USA*,103(15), 6067-6072.

610

611 Herbert, R.J.H., Willis, J., Jones, E., Ross, K., Hübner, R., Humphreys, J., A..., Baugh, J. 2012.
612 Invasion in tidal zones on complex coastlines: modelling larvae of the non-native Manila clam,
613 *Rudipates philippinarum*, in the UK. *Journal Biogeography*, 39, 585-599

614

615 Hong, J.S. 1980. Etude faunistique dun fond de concrétionnement de type coralligène soumis un
616 gradient de pollution en Méditerranée nord-occidentale (Golfe de Fos). Thèse de Doctorat.
617 Université d'Aix Marseille II.

618

619 Hu, Z. Y., Petrenko, A. A., Doglioli, A. M., & Dekeyser, I. 2011. Numerical study of eddy
620 generation in the western part of the Gulf of Lion, *Journal Geophysical Research*, 116, C12030,
621 doi:10.1029/2011JC007074.

622

623 Hua, B.L., & Thomasset, F. 1983. A numerical study of the effects of coastline geometry on wind-
624 induced upwellings in the Gulf of Lions. *Journal Physical Oceanography*, 13, 678-694.

625

626 IUCN World Commission on Protected Areas (IUCN-WCPA) 2008. Establishing Marine Protected
627 Area Networks Making It Happen. Washington, D.C.: IUCN-WCPA, National Oceanic and
628 Atmospheric Administration and The Nature Conservancy. 118 p.
629

630 Johns, B., Marsaleix, P., Estournel, C., & Véhil, R., 1992. On the wind-driven coastal upwelling in
631 the Gulf of Lions. *Journal Marine System*, 3, 309-320
632

633 Lambrechts, J., Harnet, E., Deleersnijder, E., Bernard, P.E., Legat, V., Remacle, J.F., Wolanski, E.,
634 2008. A multi-scale model of the hydrodynamics of the whole Great Barrier Reef. *Estuarine,*
635 *Coastal and Shelf Science*, 79, 143-151.
636

637 Laubier, L. 1966. Le coralligène des Albères: monographie biocénotique. *Annales de l'Institut*
638 *Océanographique de Monaco*, 43, 139-166
639

640 Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for
641 biological control. *Bulletin of the Entomology Society of America*, 71, 237-240
642

643 Mace, A.J., & Morgan, S.G. 2006. Larval accumulation in the lee of a small headland: implications
644 for the design of marine reserves. *Marine Ecology Progress Series*, 318, 19-29.
645

646 MAPAMED. 2016. Base de données des sites d'intérêt pour la conservation de l'environnement
647 marin en Méditerranée. MedPAN, PNUE/PAM/CAR-ASP.
648

649 Mariani, S., Uris, M. J., & Turon, X. 2005. The dynamics of sponge larvae assemblages from north-
650 western Mediterranean nearshore bottoms. *Journal Plankton Research*, 27(3), 249-262.
651

652 Marsaleix, P., Auclair, F., Floor, J.W., Herrmann, M.J., Estournel, C., Pairaud, I., & Ulses, C. 2008.
653 Energy conservation issues in sigma-coordinate free-surface ocean models. *Ocean Modelling*, 20,
654 61-89. <http://dx.doi.org/10.1016/j.ocemod.2007.07.005>.
655

656 Michaud H., Marsaleix, P., Leredde, Y., Estournel, C., Bourrin, F., Lyard, F., Mayet, C., &
657 Arduin, F., 2012. Three-dimensional modelling of wave-induced current from the surf zone to the
658 inner shelf. *Ocean Science*, 8, 657-681, doi:10.5194/os-8-657-2012.
659

660 Millazo, M., Chemello, R., Badalamenti, F., Camarda, R., Riggio, S. 2002. The impact of human
661 recreational activities in Marine Protected Areas: what lessons should be learnt in the
662 Mediterranean sea ? *Marine Ecology*, 23(1), 280-290.

663

664 Millot, C. 1979. Wind induced upwellings in the Gulf of Lions. *Oceanologica Acta*, 2(3), 261-274.

665

666 Millot, C., & Wald, L. Upwelling in the Gulf of Lions. F.A. Richards. Coastal Upwelling, 1981,
667 United States. American Geophysical Union, 1, pp.160-166, 1981, Coastal and Estuarine Science
668 Series.

669

670 Millot, C. 1990. The Gulf of Lion's hydrodynamics. *Continental Shelf Research*, 10(9-11), 885-
671 894.

672

673 Moilanen, A. (2011) On the limitations of graph-theoretic connectivity in spatial ecology and
674 conservation. *Journal Applied Ecology*, 48, 1543-1547.

675

676 Myksovoll, M. S., Jung, K-M., Albretsen, J., & Sundby, S. 2014. Modelling dispersal of eggs and
677 quantifying connectivity among Norwegian coastal cod subpopulations. *ICES Journal of Marine
678 Science*, 71, 957-969.

679

680 Nicolle, A., Dumas, F., Foveau, A., Foucher, E., & Thiébaud, E. 2013. Modelling larval dispersal of
681 the king scallop (*Pecten maximus*) in the English Channel: examples from the bay of Saint-Brieuc
682 and the bay of Seine. *Ocean Dynamics*, 63, 661-678 DOI 10.1007/s10236-013-0617-1.

683

684 Padron, M., & Guizien, K. 2016. Modelling the effect of demographic traits and connectivity on the
685 genetic structuration of marine metapopulations of sedentary benthic invertebrates. *ICES Journal of
686 Marine Science*, 73(7), 1935-1945. doi: 10.1093/icesjms/fsv158.

687

688 Petrenko, A.A. 2003. Variability of circulation features in the Gulf of Lion NW Mediterranean Sea.
689 Importance of inertial currents. *Oceanologica Acta*, 26, 323-338.

690

691 Petrenko, A.A., Dufau, C., & Estournel, C. 2008. Barotropic eastward currents in the western Gulf
692 of Lion, north-western Mediterranean Sea, during stratified conditions. *Journal of Marine Systems*,
693 74, 406-428, doi:10.1016/j.jmarsys.2008.03.004.

694

695 Putman, N.F., & He, R. 2013. Tracking the long-distance dispersal of marine organ- sensitivity to
696 ocean model resolution. *Journal Royal Society Interface*, 10, 20120979,
697 <http://dx.doi.org/10.1098/rsif.2012.0979>.
698

699 Roberts, C. M. 1997. Connectivity and management of Caribbean coral reefs. *Science*, New Series,
700 278 (5342), 1454-1457.
701

702 Rossi, V., Ser Giacomi, E., Lopez Cristobal, A.A., & Hernandez-Garcia, E. 2014. Hydrodynamic
703 provinces and oceanic connectivity from a transport network help designing marine reserves.
704 *Geophysical Research Letter*, 9(41), 2883-2891.
705

706 Roughan, M., Mace, A. J., Largier, J. L., Morgan S. G. , Fisher, J. L., & Carter, M. L. 2005.
707 Subsurface recirculation and larval retention in the lee of a small headland: A variation on the
708 upwelling shadow theme. *Journal Geophysical Research*, 110, C10027,
709 doi:10.1029/2005JC002898.
710

711 Sala, E., Garrabou, J., & Zabala, M. 1996. Effects of diver frequentation on Mediterranean
712 sublittoral populations of the bryozoan *Pentapora fascialis*. *Marine Biology*, 126, 451-459.
713

714 Santangelo, G., Carletti, E., Maggi, E., & Bramanti, L. 2003. Reproduction and population sexual
715 structure of the overexploited Mediterranean red coral *Corallium rubrum*. *Marine Ecology Progress*
716 *Series*, 248, 99-108.
717

718 Soufflet, Y., Marchesiello, P., Lemarié, F., Jouanno, J., Capet, X., Debreu, L., & Benshila, R. 2016.
719 On effective resolution in ocean models. *Ocean Modelling*, 98, 36-50.
720

721 True, M. A. 1970. Etude quantitative de quatre peuplement sciaphiles sur substrat rocheux dans la
722 région marseillaise. *Bulletin Institut Oceanographique Monaco*, 69(1401), 1-48.
723

724 Xu, J., Yin, K., Liu, H., Lee, J. H. W., Anderson, D. M., Ho, A. Y. T., & Harrison, P. 2010. A
725 comparison of eutrophication impacts in two harbours in Hong Kong with different hydrodynamics.
726 *Journal of Marine System*, 83 (3-4),276-286.
727
728
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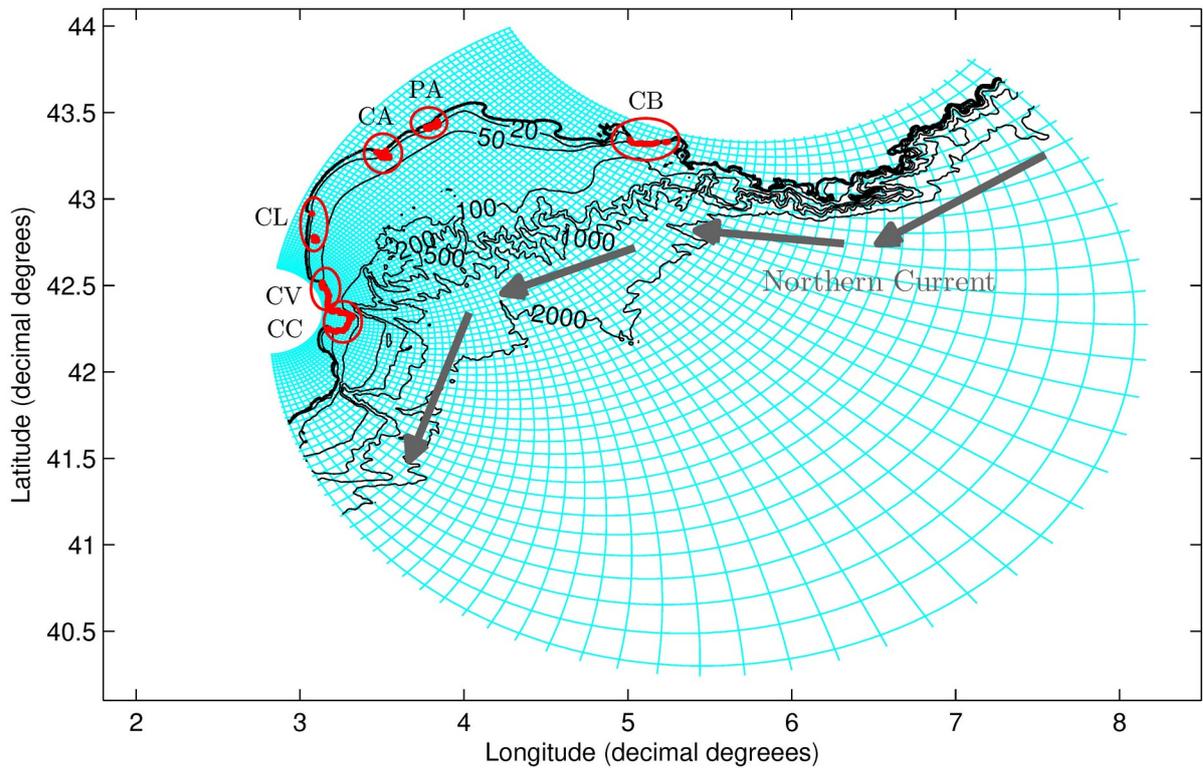
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753 Figure 1 : Spatial extent of the simulated domain with the dipolar grid (680 × 710; 1 blue line every
 754 10 cells) and the 20 m, 50 m, 100 m, 200 m, 500 m, 1000 m and 2000 m bathymetric contours.
 755 Parameters for the projection were: North pole (44.2° N ; 5.3° E) at indices (170; 710); South pole
 756 (42.37° N; 2.82° E); reference latitude for Mercator projection was 52° N. The 6 rocky habitats
 757 (CC= Cap de Creus, CV= Côte Vermeille, CL= Cap Leucate, CA= Cap d’Agde, PA= Plateau des
 758 Aresquiers, CB= Côte Bleue) are indicated in red and the coastline is depicted by a bold line.

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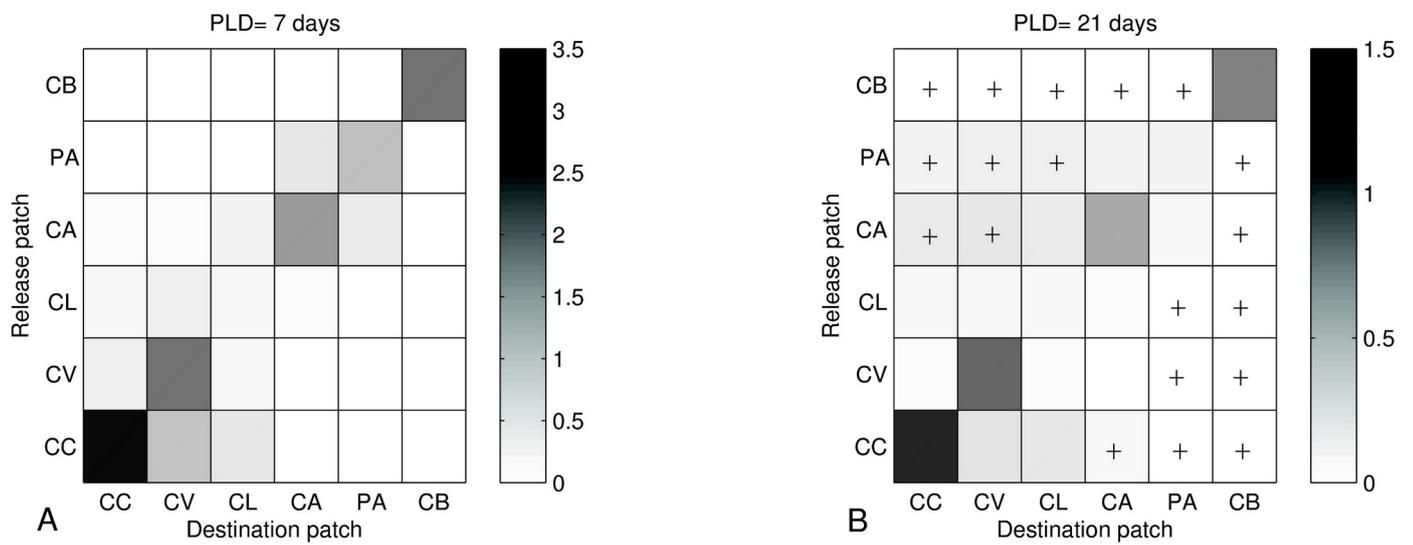
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Figure 2 : Connectivity matrices containing mean transfer rates (in %) computed for the summer seasons of 2010, 2011 and 2012 between the 6 main rocky habitat patches of the Gulf of Lion (CC= Cap de Creus, CV= Côte Vermeille, CL= Cap Leucate, CA= Cap d'Agde, PA= Plateau des Aresquiers, CB= Côte Bleue) (A) for a 7-day PLD and (B) for a 21-day PLD. Symbol (+) display those transfer rates that increased in the 21-day PLD compared to the 7-day PLD.

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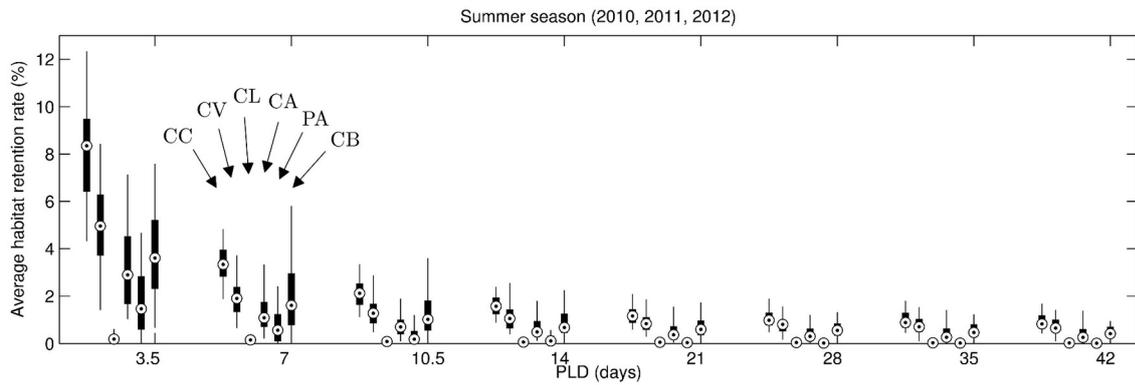


Figure 3 : Boxplots of the mean retention rate in the six main rocky habitat patches (CC= Cap de Creus, CV= Côte Vermeille, CL= Cap Leucate, CA= Cap d'Agde, PA= Plateau des Aresquiers, CB= Côte Bleue) computed for the thirteen 1-week release periods in 3 consecutive years (2010, 2011 and 2012) and for dispersal duration ranging from 3.5 days to 42 days.

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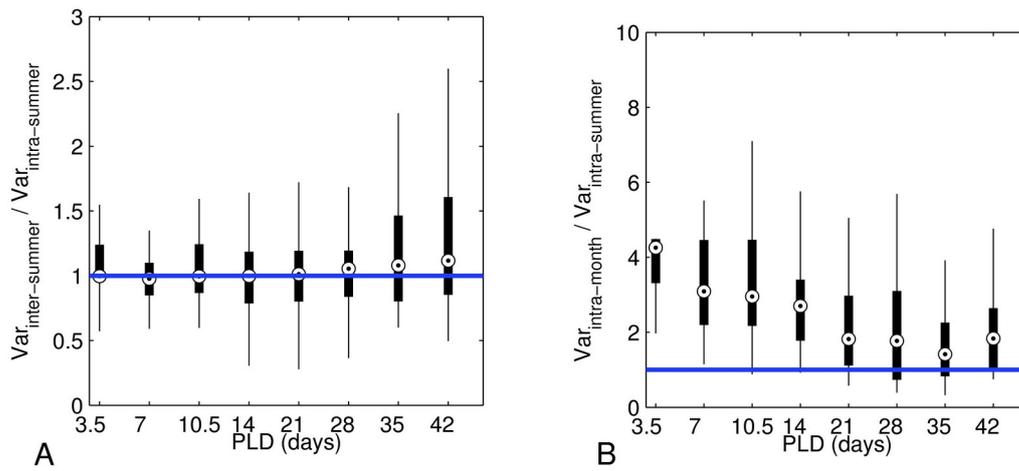
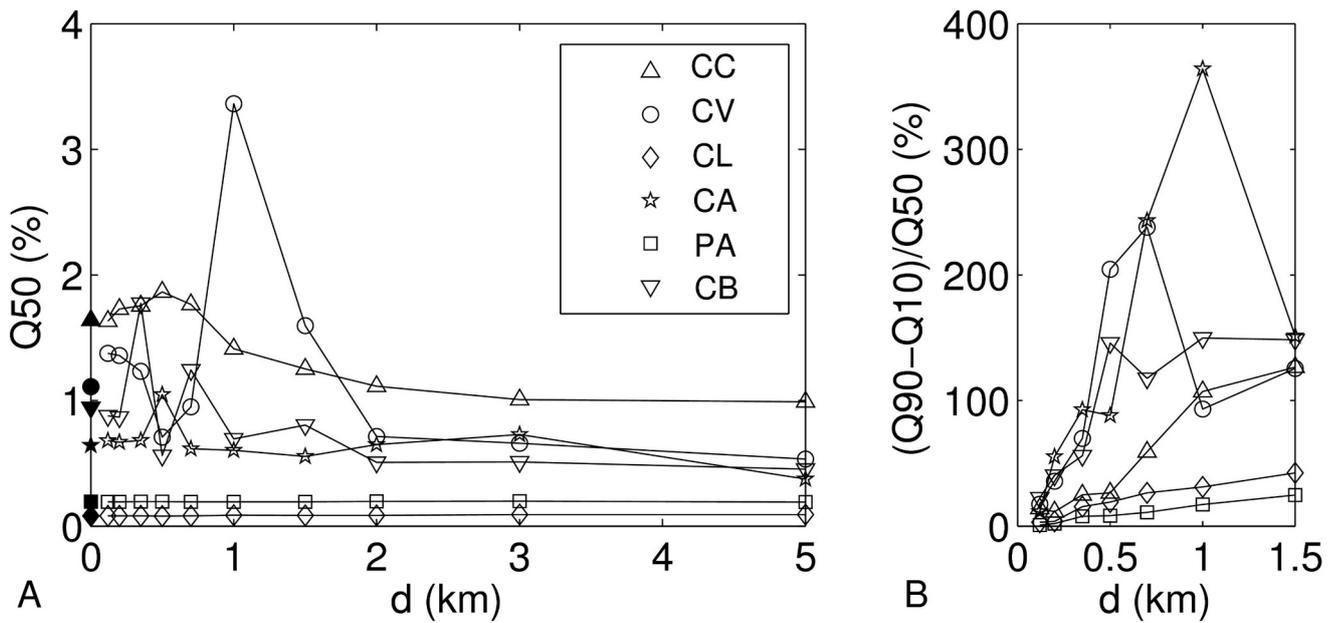


Figure 4 : Boxplot of (A) $\text{Var}_{\text{inter-summer}} / \text{Var}_{\text{intra-summer}}$ ratio and (B) $\text{Var}_{\text{intra-month}} / \text{Var}_{\text{intra-summer}}$ ratio of any element in the connectivity matrices computed for the thirteen 1-week release periods in 3 consecutive years (2010, 2011 and 2012) and for PLD ranging from 3.5 days to 42 days.

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Figure 5 : (A) Median Q_{50} retention rate at habitat patch scale versus minimal distance between release spots d for each habitat and a 21-day PLD (open symbols, CC= Cap de Creus, CV= Côte Vermeille, CL= Cap Leucate, CA= Cap d'Agde, PA= Plateau des Aresquiers, CB= Côte Bleue). Filled symbols indicates the retention rate when all release spots are considered. (B) Difference $Q_{90} - Q_{10}$ as percentage of the median Q_{50} for each distance d .

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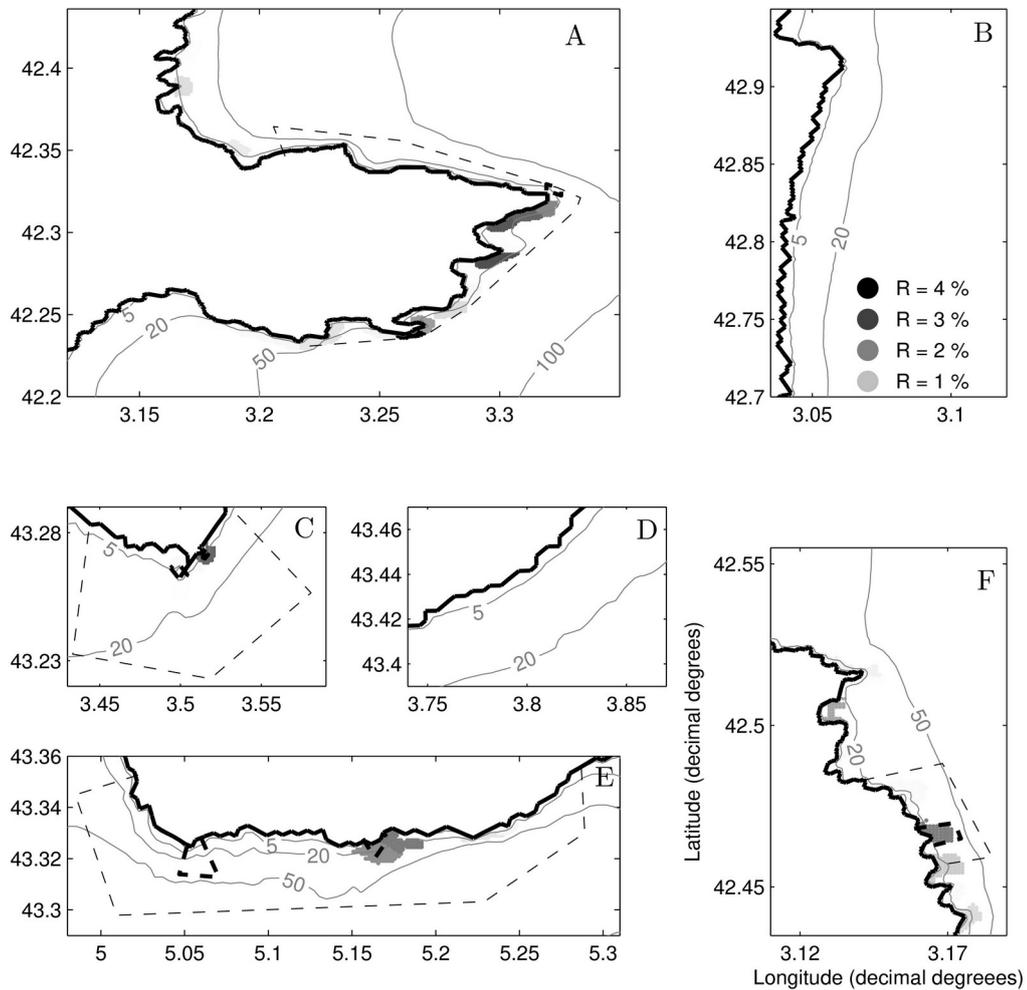


Figure 6 : Each panel is a close up of one of the six main rocky habitat patch showing the average retention rate over three years (2010, 2011 and 2012) in each of the 115 subpatches for a 21-day PLD (bold dots). A displays Cap de Creus, B displays Cap Leucate, C displays Cap d'Agde, D displays Plateau des Aresquiers, E displays Côte Bleue and F displays Côte Vermeille. Bathymetric contours are displayed in gray and labeled in meters, and coastline is displayed by the black thick line. Thin dashed line delimitates the areas designated for marine protection. Thick dashed line delimitates the areas where special protection is implemented.

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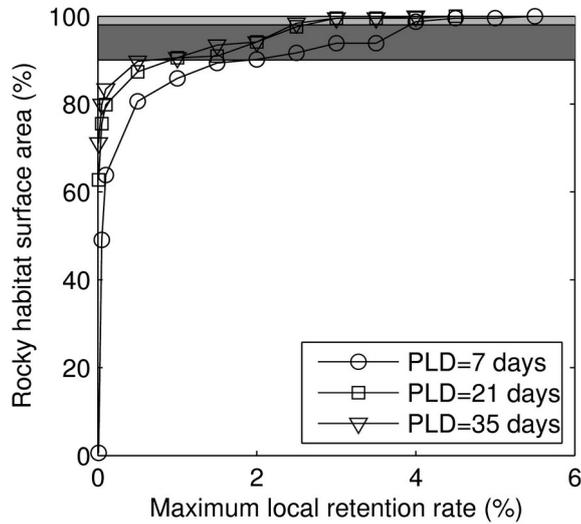
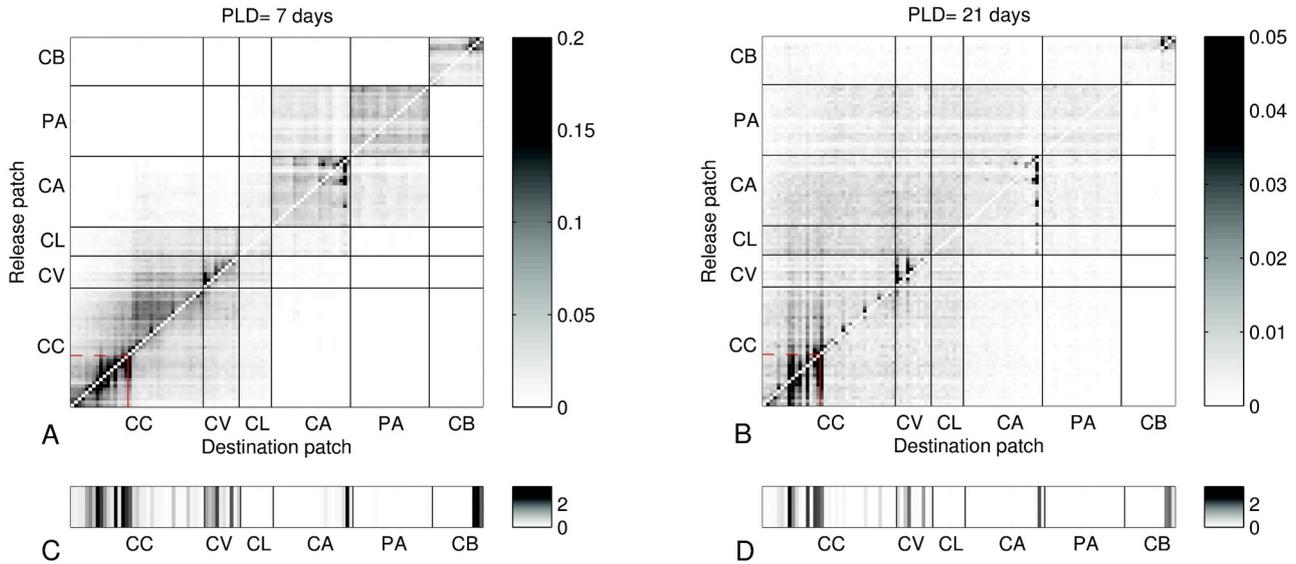


Figure 7 : Cumulative area distribution of local retention rate in the rocky habitat of the Gulf of Lion for a PLD of 1 week (circle), 3 weeks (square), and 5 weeks (triangle). Shaded dark grey area displays the maximum local retention values if the 10% MPA coverage extent targetted by the 10th United Nations Conference of the Parties for 2020 concerned the most retentive subpatches in the Gulf of Lion. Shaded light grey area displays the maximum local retention values if the 2% no-take zones coverage extent targetted by the MEDPAN Forum for 2020 concerned the most retentive subpatches in the Gulf of Lion.

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Figure 8 : Average connectivity matrices between 115 subpatches of 1-km² for summer 2010, 2011 and 2012 for a 7-day PLD (A and C) and for a 21-day PLD (B and D). To give more visibility to transfer rates between subpatches, (A) and (B) displays transfer rates between subpatches only (outside diagonal), and (C) and (D) displays the local retention in each subpatch (values on the diagonal). Horizontal and vertical lines delimitate the six main rocky habitat patches (CC= Cap de Creus, CV= Côte Vermeille, CL= Cap Leucate, CA= Cap d'Agde, PA= Plateau des Aresquiers, CB= Côte Bleue) used to establish low-resolution connectivity matrices. The southern part of the Cap de Creus is delineated with red dashed lines. Transfer rates are in %.

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969 **List of Tables**

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	Cap de Creus	Côte Vermeille	Cap Leucate	Cap d'Agde	Plateau des Aresquiers	Côte Bleue
Number of release spots	2085	421	654	1638	1595	1041
$d=120\text{m}$	1026 (175)	215 (57)	322 (29)	794 (449)	777 (83)	516 (36)
$d=200\text{m}$	524 (869)	115 (193)	162 (369)	394 (1107)	402 (869)	266 (471)
$d=350\text{m}$	189 (1591)	48 (295)	51 (585)	121 (1546)	119 (1505)	93 (832)
$d=500\text{m}$	102 (1818)	31 (358)	28 (551)	68 (1426)	67 (1245)	55 (817)
$d=700\text{m}$	64 (1897)	21 (340)	16 (571)	36 (1593)	35 (1434)	33 (860)
$d=1\text{km}$	42 (1891)	12 (320)	9 (570)	20 (1467)	18 (1457)	20 (882)
$d=1.5\text{km}$	27 (1892)	8 (326)	5 (494)	10 (1443)	10 (1509)	13 (822)
$d=2\text{km}$	20 (1947)	5 (323)	4 (583)	7 (1602)	6 (1456)	10 (841)
$d=3\text{km}$	13 (1877)	4 (314)	2 (583)	4 (1518)	3 (1333)	6 (859)
$d=5\text{km}$	7 (1920)	2 (305)	2 (653)	2 (1509)	2 (1220)	4 (819)
$RO_{7\text{days}}(\%)$	22	34	74	31	32	0
$RO_{21\text{days}}(\%)$	18	25	76	48	82	7

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974 Table 1 : First line indicates the original number of release spots regularly distributed over a 100 m
975 by 100 m grid for each habitat. Following lines provide the mean number of release spots per
976 subset, and between parenthesis the number of different subsets that were found for each minimum
977 distance d . Last two lines gives the relative out-strength values calculated for a 1 week and a 3 week
978 dispersal duration for each habitat.

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Supplementary Material 1 to High resolution modelling of ocean circulation can reveal retention spots important for biodiversity conservation: Sensitivity of retention rate to release spots spatial distribution

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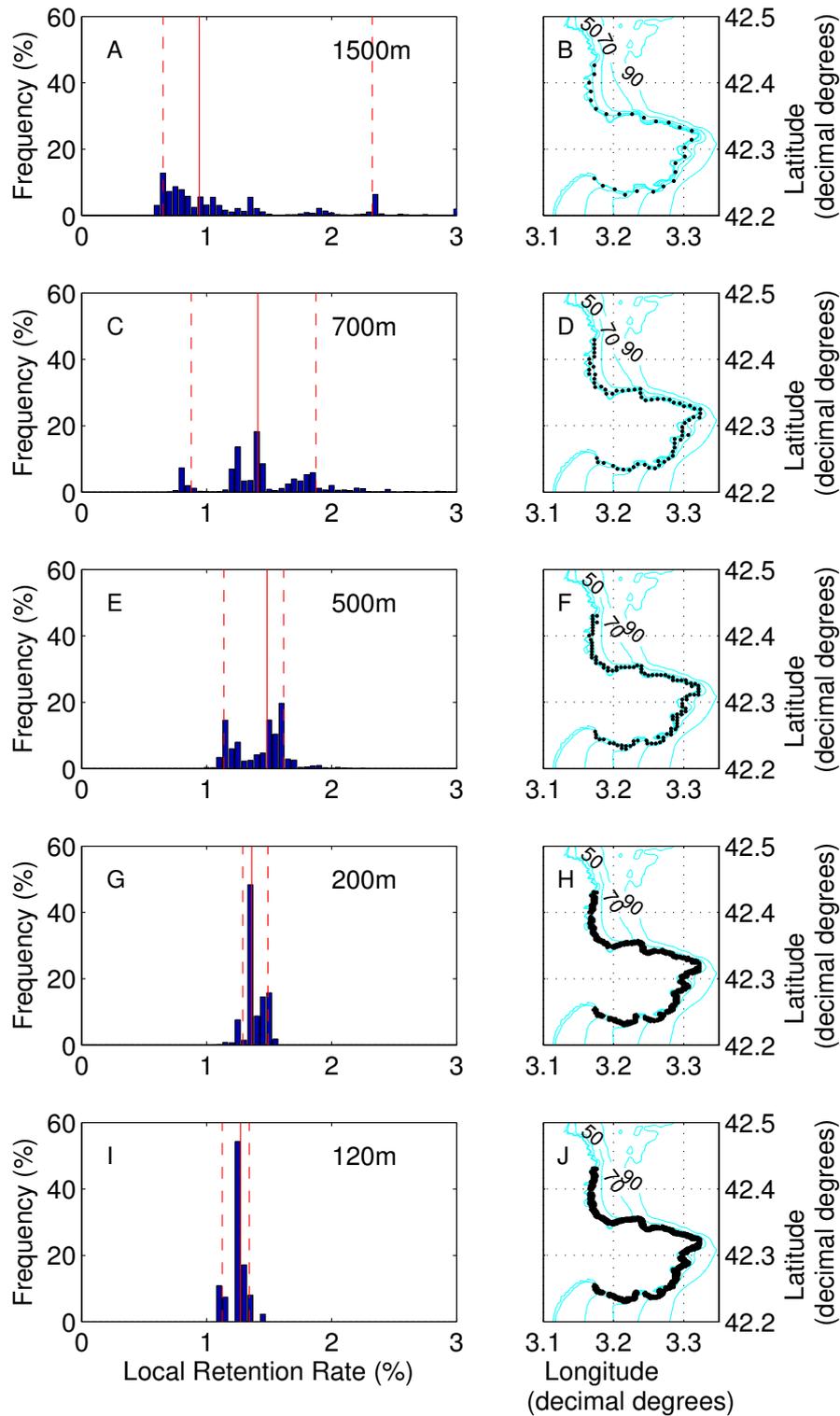
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Thanks to the high resolution of flow simulations (less than 300 m in each habitat patch), the sensitivity of habitat patch retention rate estimates to the spatial density of release spots (hereafter indicated by release spot distance) could be reliably assessed. The robustness of habitat patch retention rate estimates was determined by two criteria: the reduction of the uncertainty defined as the relative interquantile range $(Q_{90} - Q_{10})/Q_{50}$ and the stabilization of the median value Q_{50} of retention rate frequency distribution. As an example, in the Cap de Creus habitat patch, with low density of release spot ($d=1500\text{m}$, $d=700\text{m}$, Fig.1B and D), local retention rates are quite evenly distributed across a wide range of values, and the mode does not appear (Fig.1A and C): the median retention rate is not representative and increased from 1.85% for $d=1500\text{m}$ to 2.47% for $d=700\text{m}$. For a minimum distance of 500m between release spots (Fig.1F, H and J), the mode emerges, and the quantiles Q_{10} and Q_{90} get closer to the median (Fig.1E, G and I). Both stabilization of the median value Q_{50} and reduction of the relative interquantile range $(Q_{90} - Q_{10})/Q_{50}$ (herein called uncertainty) when release spot distance decreases define the convergence toward a stable unimodal

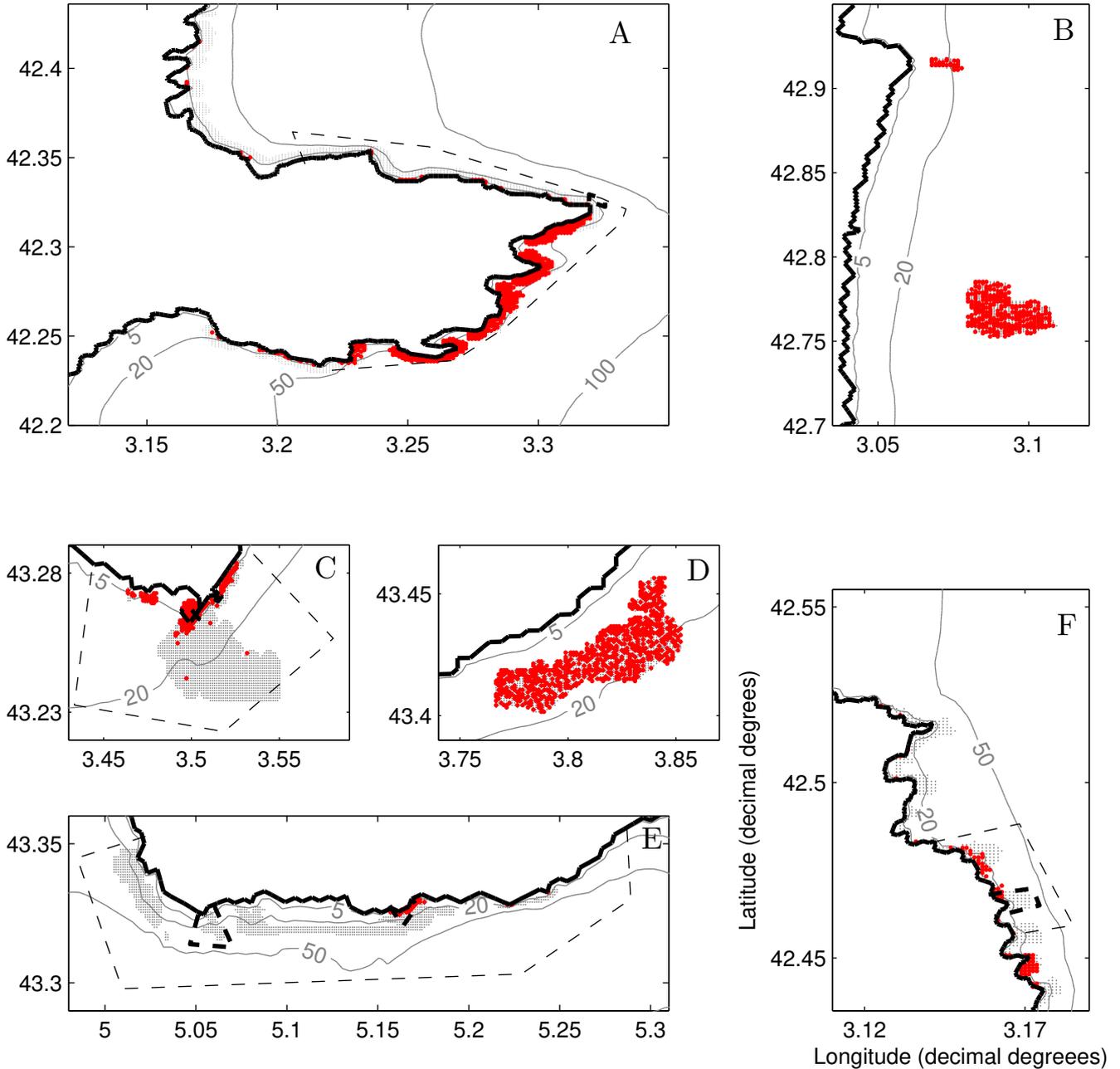
distribution. Convergence is reached when uncertainty becomes lower than 20% and the retention rate of the habitat is estimated by the median value of the converged distribution (Fig.1G).

The contribution of each release spot to the retention rate of the habitat patch it belongs to was calculated as the proportion of particles released in that spot during a release event that came back into its original habitat patch after a certain PLD. The history of the particle contributing to the local retention was investigated as well. Indeed, local retention can result from two different processes. Either the particles remained in the patch where they were released, kept by local hydrodynamics structures, or they are swept away from their release patch and find their way back through meso-scale recirculation structures. To arbitrate between the two possibilities, for each release spot the proportion of particles released there that contributed to the local retention staying in the patch during the whole dispersal period was also calculated.

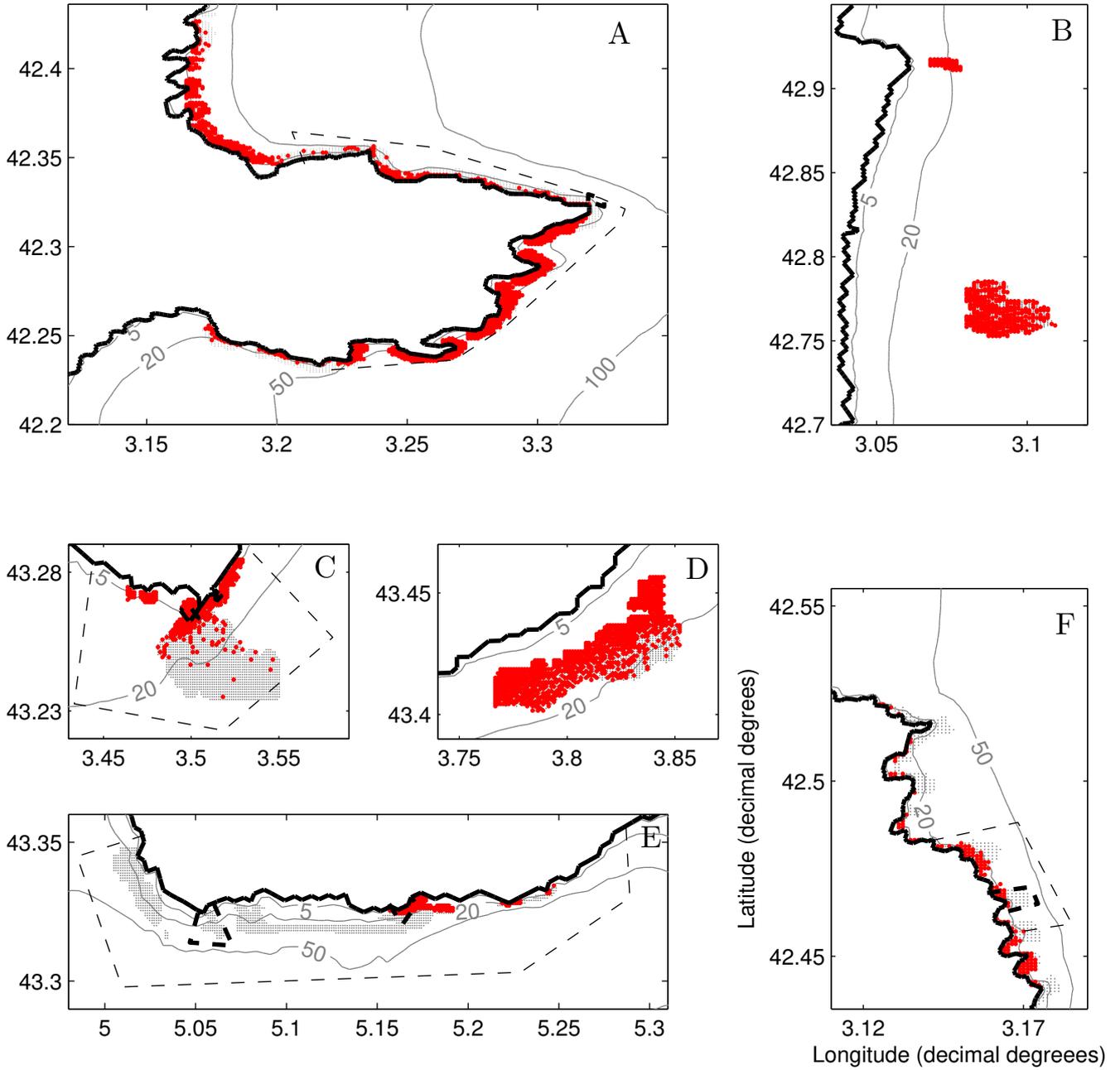
As an example, Supplementary Figure 2 displays the spatial distribution of the release spots having the highest retention rates in the habitat and cumulating 75% of the habitat patch retention rate for a 21-day PLD. These release spots were evenly distributed and represented 41% and 51% of the release spots in Plateau des Aresquiers and Cap Leucate, respectively. In Cap de Creus, 75% of the habitat patch retention rate is accounted for by 31% of the release spots which were regularly distributed along the southern half of the habitat. In contrast, 75% of the habitat patch retention rate was accounted for by only 17% of the release spots in Côte Vermeille, 16% in Cap d'Agde, and 3% in Côte Bleue. The latter were sometimes isolated but more often accumulated in subpatches of ten or more release spots. In Côte Vermeille, those spots were located around bays and capes. In Côte Bleue, there were a few retention pools close to the shore but in steep bathymetry in its eastern part. In Agde, they were concentrated near the coast at depths less than 5m. The most retentive release spots did not vary for PLDs larger than 21 days in Cap de Creus, Côte Vermeille, Cap d'Agde and Côte Bleue (Supplementary Figures 3 and 4) indicating that particles released in those most retentive spots did not leave the habitat patch during their dispersal period. In contrast, in Cap Leucate and Plateau des Aresquiers, no particles remained in their original habitat patch during their whole dispersal period (data not shown), and the ones contributing to habitat patch retention depended only on recirculation structures to return to their original habitat. This analysis guided the definition of 115 subpatches ranging in area from 0.16 to 1.4 km² (0.66 km² on average), in which retention rate was spatially homogeneous (Supplementary Figures 5).



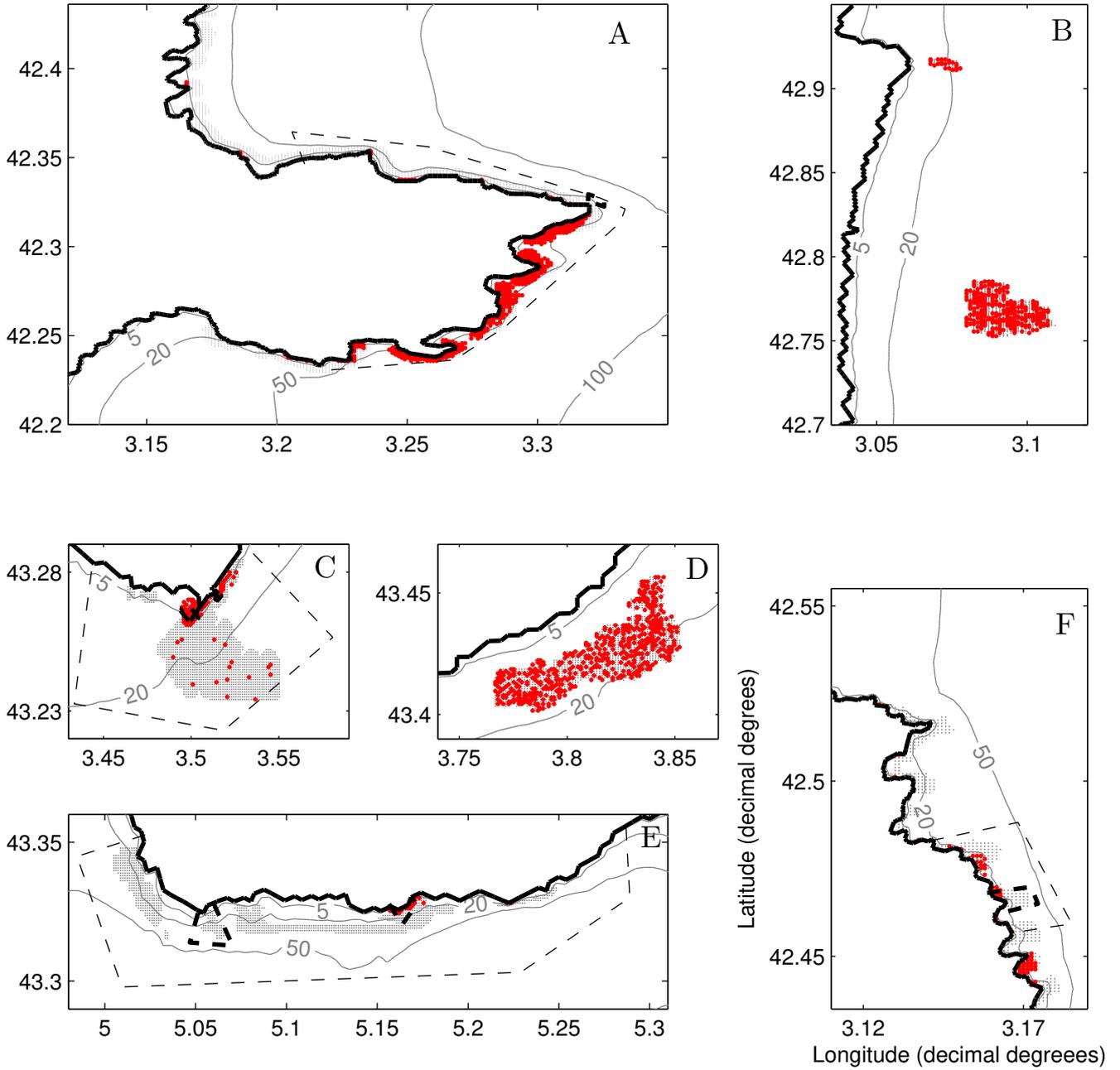
Supplementary Figure 1: Frequency distributions of local retention rates at Cap de Creus for increasing density of release sites (A: $d=1.5\text{km}$; C: $d=700\text{m}$; E: $d=500\text{m}$; G: $d=200\text{m}$; I: $d=120\text{m}$, where d is the distance between release sites). For each release spatial density, the number of samples is equal to the number of subsets that could be made from the original distribution at 100m resolution as indicated in Table 1. The solid line represents the median value Q_{50} , and the dashed lines the quantiles Q_{10} and Q_{90} . A sample of a release sites subset for each release spatial density is mapped on the right panels (B: $d=1.5\text{km}$; D: $d=700\text{m}$; F: $d=500\text{m}$; H: $d=200\text{m}$; J: $d=120\text{m}$).



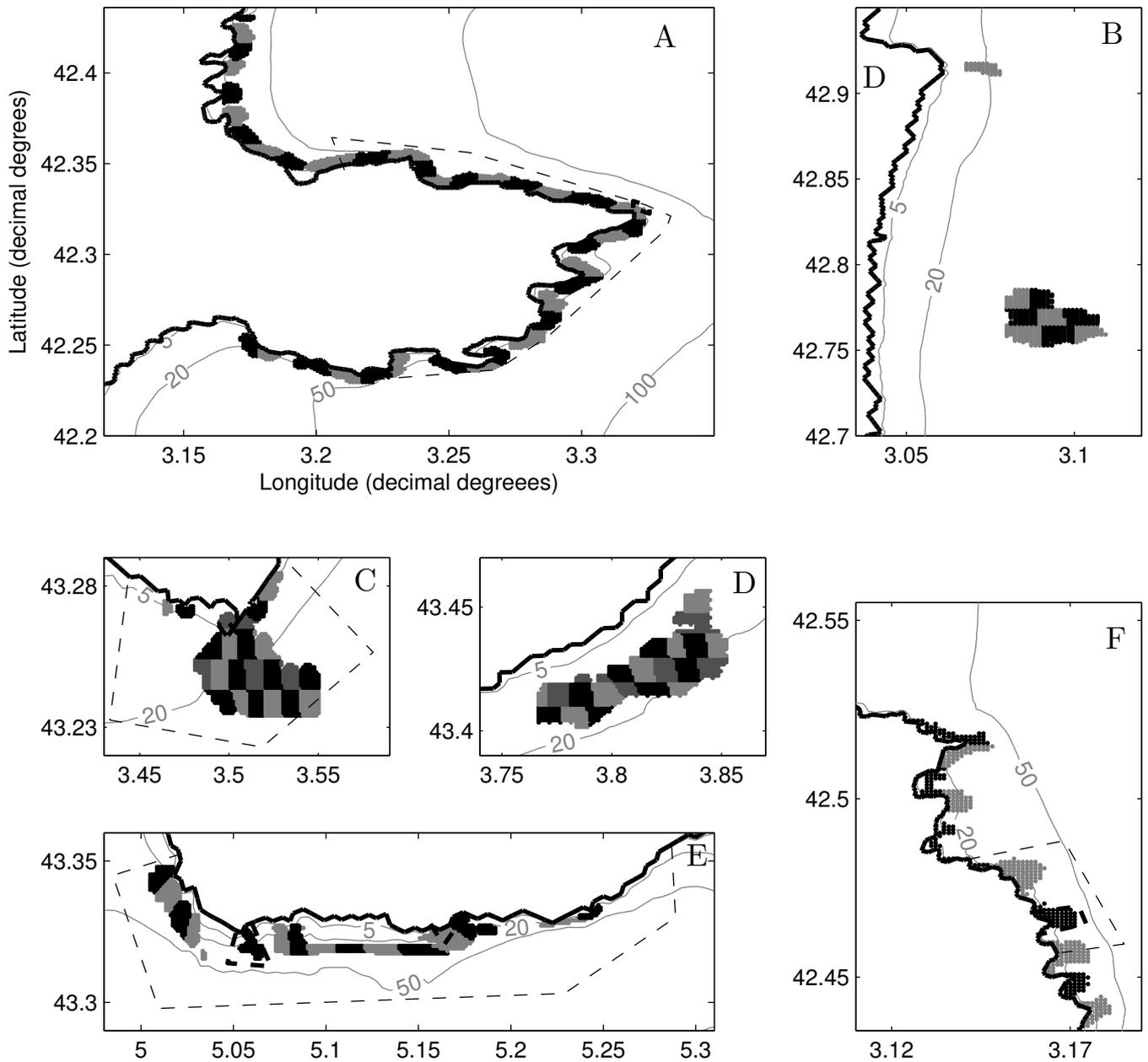
Supplementary Figure 2: Each panel is a close up of one of the six main rocky habitat patch showing the distribution of release spots spaced by a 100 m (small grey dots) and the most retentive release spots accounting for 75% of the average habitat retention rate over the summer of 2010, 2011 and 2012 for a 21-day PLD (bold red dots). A displays Cap de Creus, B displays Cap Leucate, C displays Cap d'Agde, D displays Plateau des Aresquiers, E displays Côte Bleue and F displays Côte Vermeille. Bathymetric contours are displayed in gray and labeled in meters, and coastline is displayed by the black thick line. Thin dashed line delimitates the areas designated for marine protection. Thick dashed line delimitates the areas where special protection is implemented.



Supplementary Figure 3: Same as Figure 2 but for a 7-day PLD.



Supplementary Figure 4: Same as Figure 2 but for a 35-day PLD.



Supplementary Figure 5: Each panel is a close up of one of the six main rocky habitat patch showing the distribution of 115 subpatches of about 1-km² grouping release spots spaced by a 100 m. The subpatches are individuated by different gray intensity. Bathymetric contours are displayed in gray and labeled in meters, and coastline is displayed by the black thick line. Thin dashed line delimitates the areas designated for marine protection. Thick dashed line delimitates the areas where special protection is implemented.

Supplementary Material 2 to High resolution modelling of ocean circulation can reveal retention spots important for biodiversity conservation: Sensitivity of connectivity to release timing variability

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The 39 non-overlapping week-long release periods (13 per year in 3 years) defined in Supplementary Table 1 were used to calculate connectivity matrices for different week-long release periods. The meteorological, seasonal and climatic (inter-annual) variability was quantified by intra-month $\text{Var}_{intra-month}$, intra-summer $\text{Var}_{intra-summer}$ and inter-summer $\text{Var}_{inter-summer}$ variabilities, respectively, and defined as follows:

Meteorological variability on any transfer rate T (an element of the connectivity matrix) was quantified by the intra-month (i.e between release periods within each month of reproduction) variability of the transfer rate defined as:

$$\text{Var}_{intra-month} = \frac{\sum_{y=1}^{N_{year}} \sum_{m=1}^{N_{month}} \left(\frac{\sum_{p=1}^{N_{period}} (T_{m,p}^y - \overline{T_m^y})^2}{N_{period}} \right)}{N_{year} N_{month}} \quad (1)$$

with the average transfer rate of month m in year y defined as:

$$\overline{T}_m^y = \frac{\sum_{p=1}^{N_{period}} T_{m,p}^y}{N_{period}} \quad (2)$$

Seasonality on any transfer rate T (any element of the connectivity matrix) was quantified by the intra-summer (i.e between different months of reproduction within a same year) variability of the transfer rate defined as:

$$\text{Var}_{intra-summer} = \frac{\sum_{y=1}^{N_{year}} \left(\frac{\sum_{m=1}^{N_{month}} (\overline{T}_m^y - \overline{T}^y)^2}{N_{month}} \right)}{N_{year}} \quad (3)$$

with the average connectivity matrix of year y defined as:

$$\overline{T}^y = \frac{\sum_{m=1}^{N_{month}} \overline{T}_m^y}{N_{month}} \quad (4)$$

Climatic variability on any transfer rate T (any element of the connectivity matrix) was quantified by the inter-summer (i.e between the same month of reproduction in different years) variability of the transfer rate defined as:

$$\text{Var}_{inter-summer} = \frac{\sum_{m=1}^{N_{month}} \left(\frac{\sum_{y=1}^{N_{year}} (\overline{T}_m^y - \overline{T}_m)^2}{N_{year}} \right)}{N_{month}} \quad (5)$$

with the average connectivity matrix of month m defined as:

$$\overline{T}_m = \frac{\sum_{y=1}^{N_{year}} \overline{T}_m^y}{N_{year}} \quad (6)$$

with $N_{year} = 3$ the number of years (2010, 2011, 2012), $N_{month} = 3$ the number of reproductive months (June, July, August), $N_{period} = 4$ the number of one-week long release periods per month. Thus, only the week-long release periods 1 to 12 (Table 1) were taken into account in the calculation of meteorological, seasonal and inter-annual variability, in order to maintain a same number of periods per month.

	2010	2011	2012	Assigned reproductive month
Period 1	June, 6 to June, 12	June, 5 to June, 11	June, 3 to June, 9	June
Period 2	June, 13 to June, 19	June, 12 to June, 18	June, 10 to June, 16	June
Period 3	June, 20 to June, 26	June, 19 to June, 25	June, 17 to June, 23	June
Period 4	June, 27 to July, 3	June, 26 to July, 2	June, 24 to June, 30	June
Period 5	July, 4 to July, 10	July, 3 to July, 9	July, 1 to July, 7	July
Period 6	July, 11 to July, 17	July, 10 to July, 16	July, 8 to July, 14	July
Period 7	July, 18 to July, 24	July, 17 to July, 23	July, 15 to July, 21	July
Period 8	July, 25 to July, 31	July, 24 to July, 30	July, 22 to July, 28	July
Period 9	August, 1 to August, 7	July, 31 to August, 6	July, 29 to August, 4	August
Period 10	August, 8 to August, 14	August, 7 to August, 13	August, 5 to August, 11	August
Period 11	August, 15 to August, 21	August, 14 to August, 20	August, 12 to August, 18	August
Period 12	August, 22 to August, 28	August, 21 to August, 27	August, 19 to August, 25	August
Period 13	August, 29 to September, 4	August, 28 to September, 3	August, 26 to September, 1	none

Supplementary Table 1: Starting and finishing date of the thirteen week-long release periods in the three consecutive years 2010, 2011 and 2012. Last column indicates the reproductive month to which each period was assigned for testing the intra-summer variability.