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# Vulnerability of marine benthic metapopulations: implications of spatially structured connectivity for conservation practice in the Gulf of Lions (NW Mediterranean Sea)

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► **To cite this version:**

K. Guizien, M. Belharet, C. Moritz, J. M. Guarini. Vulnerability of marine benthic metapopulations: implications of spatially structured connectivity for conservation practice in the Gulf of Lions (NW Mediterranean Sea). *Diversity and Distributions*, 2014, 20 (12), pp.Pages 1392-1402. 10.1111/ddi.12254 . hal-01341743

**HAL Id: hal-01341743**

**<https://univ-perp.hal.science/hal-01341743v1>**

Submitted on 2 Dec 2022

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1                   **Vulnerability of marine benthic**  
2                   **metapopulations: implications of spatially**  
3                   **structured connectivity for conservation**  
4                   **practice**

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10 **RUNNING TITLE: Conservation and connectivity of marine benthic popula-**  
11 **tions**

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12 **ABSTRACT:**

13 Aim: Connectivity is currently considered to essential to enhance biodiversity conser-  
14 vation efforts and benefit adjacent areas. We evaluate the spatial structure of vulnerable  
15 marine benthic invertebrate populations based on connectivity to improve the placement  
16 of marine protected areas.

17 Location: Gulf of Lions, NW Mediterranean Sea.

18 Methods: We used a spatially explicit metapopulation model to explore how lar-  
19 val dispersal affects marine benthic invertebrate dynamics at local and regional scales.  
20 Minimum recruitment success (the proportion of larvae that settle in a site and survive  
21 between spawning and first reproduction, which is required to ensure species persistence)  
22 is proposed as a measure of vulnerability. Three contrasting simulations were constructed:  
23 closed versus connected populations, habitat loss versus recruitment failure disturbances,  
24 and varying patterns of oceanographic connectivity. The rescue factor (the ratio of mini-  
25 mum recruitment success in connected and closed populations) quantified the decrease in  
26 vulnerability due to oceanographic connectivity.

27 Results: In the Gulf of Lions, connectivity reduced population vulnerability by a rescue  
28 factor of 5.3. The minimum recruitment success for regional persistence decreased from  
29 3 % to 0.2 % when species' life expectancies increased from 2 to 50 years. Connectivity  
30 enabled the spread of individuals over the entire region, but there were higher densities  
31 in sink sites, where low retention rates do not allow for local persistence (western tip  
32 of the gulf). Source sites, defined as those sites bringing metapopulation resistance to  
33 recruitment failure and stresses from habitat loss, were located in the center of the gulf.

34 Main conclusions: Connectivity drives the spatial structure of regional adult distribu-

35 tions and population vulnerability in the absence of any other structuring factor. In the  
36 Gulf of Lions, marine protected areas are located in the western tip, where there are pop-  
37 ulation sink; however, if protection measures were taken in the central part, populations  
38 would benefit throughout the region via the rescue effect.

39 **Keywords :** larval dispersal, metapopulation, connectivity, numerical simulation,  
40 vulnerability, resistance, natural and anthropogenic stresses

## INTRODUCTION

41 Landscape connectivity is considered an essential factor for enhancing the resilience  
42 of biodiversity and ecosystem services in the face of climate change (Heller & Zavaleta,  
43 2009; Morecroft et al., 2012). The role of connectivity in biodiversity resilience (defined  
44 as the long-term persistence of a species) has been extensively examined theoretically in  
45 conservation biology and population ecology. Connectivity alters biodiversity in many  
46 ways, with both negative and positive outcomes. On the one hand, connectivity linked  
47 to anthropogenic actions (e.g. the opening of commercial routes, species introductions)  
48 has enabled the spread of alien species (Hulme, 2009; Katsanevakis et al., 2013), which  
49 has been identified as one of the major drivers of biodiversity loss (MEA, 2005). On  
50 the other hand, connectivity associated with propagule dispersal during reproduction  
51 has favored the wide geographical distribution of sessile species, which are dependent on  
52 the availability of suitable habitat downstream (Scheltema, 1986). Connectivity has also  
53 been recognized as a process that can reduce extinction threats due to invasive species  
54 by linking species refuges (Gilbert & Levine, 2013). Despite the adaptive disadvantage  
55 represented by dispersal to new sites, larval dispersal is also a way for sessile populations  
56 to recover following disturbances, such as extreme meteorological events or anthropogenic

57 stresses (Baker et al., 2008; Miller et al., 2009; Kendrick et al., 2012; Bernhardt & Leslie,  
58 2013).

59 Since the earliest metapopulation model of Levins (1969), a wealth of stochastic patch  
60 occupancy models have been used to address the fundamental question of the conse-  
61 quences of habitat fragmentation on the persistence of individual (Quinn and Hastings,  
62 1987; Hanski, 1989, 1994) and multiple species (Mouquet & Loreau, 2002). Increased satel-  
63 lite imaging capabilities have enabled the production of high-resolution maps of species'  
64 habitats in terrestrial environments, which have improved the spatially explicit modeling  
65 of species distribution (Schnell et al., 2013). Such an approach is limited in the marine  
66 environment, where habitat mapping is still incomplete. Conversely, dispersal is often  
67 described simplistically in terrestrial environments and is based solely on the distance  
68 between patches of a species' habitat (Roy et al., 2008; Dornier et al., 2011; Skelsey et al.,  
69 2013; Johansson et al., 2013). Yet in the case of propagule dispersal (pollen in the air,  
70 larvae in the ocean), transport mediated by an unsteady and non-uniform flow will often  
71 be asymmetrical (Aiken & Navarrete, 2011) and can cover long distances. In the ma-  
72 rine environment, larval transfer between sites has been calculated from larval dispersal  
73 simulations and summarized by oceanographic connectivity matrices (Melbourne-Thomas  
74 et al., 2011; Thomas et al., 2012; Jacobi et al., 2012; Morecroft et al., 2012; Moritz et  
75 al., 2013). Such connectivity matrices have been analyzed to elucidate population persis-  
76 tence using either graph theory methods (Tremblay et al., 2008) or eigenvalue decomposition  
77 (Hastings and Botsford, 2006). However, local demography may mitigate oceanographic  
78 connectivity (Moilanen, 2011); thus, assessing population persistence requires the integra-  
79 tion of oceanographic connectivity and local demography into models of metapopulation  
80 dynamics (Watson et al., 2012; Williams & Hastings, 2013). Of the local demographic pa-

81 rameters, recruitment success (the proportion of settling larvae that survive from spawning  
82 to the adult stage) ultimately drives the persistence of a population, although flow does  
83 bring larvae to a settling area. Persistence requires a 'minimum recruitment success' to  
84 compensate for the loss of adults in the population during the same period. The order of  
85 magnitude of recruitment success is virtually unknown for most species due to limitations  
86 in observing the supply of settled larvae (Grüss et al., 2012), and this parameter is the  
87 missing link between dispersal and local demography. Integrating demographic connec-  
88 tivity in spatially explicit metapopulation models is a challenge for the practical design  
89 of conservation strategies for the marine environment (Kaplan et al., 2009; Moffitt et al.,  
90 2011). It would be particularly interesting to identify sites, by considering the functional  
91 connections within self-persistent sites or between sites, where protection efforts aimed at  
92 minimizing adult loss would ensure persistence (Berumen et al., 2012; Olds et al., 2014).  
93 Furthermore, if persistence is achieved within the protected network, then dispersal export  
94 may further benefit populations in non-protected areas (Harrison et al., 2012).

95 In this paper, we present the results of numerical simulations of the spatio-temporal  
96 dynamics of soft-bottom worm populations in the Gulf of Lions driven by oceanographic  
97 connectivity. The generic metapopulation model of Hastings and Botsford (2006), which  
98 incorporates spatially structured parameters for survival, fecundity and dispersal was  
99 modified to account for density-dependent recruitment (Roughgarden et al., 1985) and  
100 time-varying connectivity. A set of twenty different connectivity matrices were estimated  
101 from larval dispersal simulations and were randomly picked in the simulations of the  
102 metapopulation dynamics to reflect the inter-annual variability in dispersal that arises  
103 from the conjunction of environmental (currents) and biological (spawning timing) vari-  
104 ability (Guizien et al., 2012). 'Minimum recruitment success', which is required to ensure

105 populations persistence under each oceanographic connectivity scenario was used as a  
106 measure of population vulnerability. Simulations were designed to test three hypotheses:  
107 (1) Connectivity decreases population vulnerability at the regional scale, (2) population  
108 vulnerability to stresses is spatially structured by connectivity and (3) adult spatial dis-  
109 tribution allows for the identification of sink sites but not sites essential for regional  
110 persistence (source). The findings were also used to propose an extension of the current  
111 protection measures in the Gulf of Lions.

## METHODS

### 112 **The generic metapopulation model for benthic invertebrates**

113 The spatio-temporal dynamics of benthic invertebrate populations with a dispersive  
114 pelagic larval stage were simulated after modifying the generic metapopulation model of  
115 Hastings and Botsford (2006). The model describes explicitly, in discrete times and for a  
116 set of sites with different areas connected by larval transfer, the spatial density dynamics  
117 of only the sedentary adult stage (Fig.1). Density dynamics at a given site result from spa-  
118 tially structured local survivorship and reproductive success input potentially contributed  
119 by all the other sites in the system. The original model of Hastings and Botsford (2006)  
120 was modified to account for (1) recruitment limitation due to space availability at the  
121 destination site (computed as the proportion of free space based on the saturating density  
122 of adults  $N_{max} = 1/\alpha_A$ , where  $\alpha_A$  is the mean cross-sectional area of one adult), and (2)  
123 the variability in propagule transfer rate. The model in matricial form is as follows:

$$N(t + \Delta t) = \min(G(t)N(t), N_{max}) \quad (1)$$

124 with a time step of  $\Delta t$  and a transfer matrix  $G$  defined by:

$$G_{ji} = b_j C_{ji}(t) a_i + s_{jj} \delta_{ji} \quad (2)$$

125 where  $N(t)$  is a vector  $\in R^p$  containing the spatial density of adults at each site  
 126  $i \in [1, p]$  at time  $t$ ,  $a_i$  [larva per adult] is the propagule production rate in site  $i$ ,  $C_{ji}$   
 127 **[no units] is the propagule transfer rate from site  $i$  (column) to site  $j$  (row)**  
 128 multiplied by the ratio of the areas of origin  $A_i$  to settling  $A_j$  sites,  $b_j$  [adult per larva] is  
 129 the recruitment success in site  $j$ ,  $s_{jj}$  [no units] is the adult survivorship rate at settling site  
 130  $j$ ,  $\delta_{ij}$  is the Kronecker symbol (1 when  $i = j$ , 0 otherwise) and  $N_{max}$  is the site's carrying  
 131 capacity. The propagule production rate is equal to the number of larvae produced by  
 132 each adult female  $FS_R f$  where  $F$  is the fecundity rate,  $S_R$  is the sex ratio in the adult  
 133 population, and  $f$  is the probability of an egg being fertilized. The adult survivorship  
 134 rate can be related to species life expectancy  $L_E$  as  $s_{jj} = \exp(\ln(0.01) \Delta t / L_E)$ , where life  
 135 expectancy is the age at which 99% of the individuals of the same generation have died.

136 Propagule transfer rates are the elements of a square connectivity matrix  $C$  and are  
 137 defined as the proportion of larvae coming from an origin site (columns) and arriving at a  
 138 settlement site (rows), multiplied by the ratio of the areas of the origin to the settlement  
 139 sites.

140 Recruitment success is the proportion of larvae settling in one site that has survived  
 141 dispersal and will finally reach sexual maturity. This parameter, with values of between 0  
 142 and 1 and accounting for all mortality losses since egg release until the first reproduction  
 143 by the new recruits, is unknown for all species and is very difficult to measure. An  
 144 alternative approach is to seek a minimum value of this parameter that would avoid  
 145 either population (based only on local retention) or metapopulation (allowing for transfer



146 within the network of populations) extinction. The minimum recruitment success of  
147 a population corresponds to the recruitment success that yields a population growth  
148 rate equal to 1. Thus, the minimum recruitment success co-varies with the fecundity  
149 value; when the fecundity value is increased by a factor of 10, the minimum recruitment  
150 success is decreased by a factor of 10. Such a minimum recruitment success provides  
151 a measure of population vulnerability: the lower the minimum recruitment success, the  
152 lower the population vulnerability. The minimum recruitment success is independent  
153 of the saturating capacity choice because the site carrying capacity is not reached. The  
154 rescue factor was defined as the ratio between the recruitment success required to maintain  
155 individuals in any connected site in the region (regional persistence) and the minimum  
156 recruitment success required to maintain individuals in at least one isolated site in the  
157 region (local persistence). The rescue factor is, by definition, independent of species  
158 fecundity.

### 159 **Application to the Gulf of Lions soft-bottom polychaete populations**

160 The Gulf of Lions is a wide, micro-tidal continental shelf, dominated by soft-bottom  
161 habitat and it is delimited along the shore at its two extreme tips by rocky beds extending  
162 to a depth of 40 m (Aloisi et al., 1973). Polychaetes dominate the soft-bottom benthic  
163 communities of the gulf and their community composition is related to the grain size  
164 distribution and organic matter content, which is strongly related to water depth in this  
165 region except for some restricted areas at the river outlets (Labrune et al., 2007a). In  
166 the simulations, demographic parameters were assumed to be spatially uniform for the  
167 10-30 m depth range to more clearly reveal the effect of connectivity on spatial structure.  
168 Species were differentiated by their life expectancy (ranging from 2 to 50 years) and their

169 mean fecundity (averaged over the duration of their reproductive life). According to the  
170 review of demographic parameters of 200 polychaete species by McHugh & Fong (2002),  
171 no trade-off can be found between fecundity and life-expectancy, but fecundity is related  
172 to larval development mode. Fecundity values for polychaete species with dispersive larval  
173 stages range from  $10^3$  to  $10^6$  (McHugh & Fong, 2002). As fecundity can be related to food  
174 availability, fecundity in the oligotrophic Mediterranean sea is expected to be in the lower  
175 part of the range. Fecundity was thus varied between  $10^3$  and  $10^5$  eggs per female in the  
176 simulations, resulting in a propagule production rate of  $5 \cdot 10^1$  to  $5 \cdot 10^3$  larvae per female  
177 (using a sex ratio of 1 : 1 and a fertilization rate of 10%), independent of species life  
178 expectancy. As site saturating capacity is an upper limit introduced to avoid unrealistic  
179 population explosion when population growth rate is greater than 1 and is not expected to  
180 be reached at equilibria, this parameter, by definition, should be larger than the natural  
181 density. Furthermore, to avoid the introduction of an artificial trade-off between life  
182 expectancy and site saturating density, site saturating density was overestimated and set  
183 to  $25,000 \text{ ind m}^{-2}$ , which corresponds to a value larger than any density observed in the  
184 area (Labrune et al., 2007a). Given these demographic parameters, recruitment success  
185 was also considered to be spatially uniform and varied from  $10^{-6}$  to 1 (10 regular steps  
186 within each  $\log_{10}$ -interval) to detect the minimum value  $R$  at which either local or regional  
187 persistence was reached (see above).

188 The continuous sand facies bed spanning the 10 to 30 m isobaths along the gulf was  
189 discretized into thirty-two contiguous sites to describe the spatial distribution of the dif-  
190 ferent worm species living in this habitat (Fig. 2). Site boundaries were placed according  
191 to the natural coastline features forming bays or approximately every 20 km along the  
192 rectilinear shoreline, which yielded sites ranging in area from 6.2 to 121  $\text{km}^2$ . Connectivity

193 matrices, with local retention rates on the diagonal, and transfer rates between distant  
194 sites off of the diagonal, were quantified from Lagrangian larval dispersal simulations.  
195 Simulations of larval dispersal in the gulf used three-dimensional currents and turbulent  
196 kinetic energy computed at a resolution of 750 m  $\times$  750 m following interpolation be-  
197 tween the hourly outputs (Guizien et al., 2006). Spawning was simulated by releasing  
198 thirty neutrally buoyant larvae in the center of each of the 32 sites, on the 20 m isobath,  
199 every hour during the reproductive season. As temperate polychaetes reproduce in late  
200 winter-early spring in the NW Mediterranean Sea (Bhaud, 1972), a 100-day reproductive  
201 season (from January 5 at 0h until April 13 at 23h) was considered and divided into  
202 ten consecutive 10-day spawning events in 2004 and 2006 (see details in Guizien et al.,  
203 2012). In the absence of knowledge regarding sinking behavior that might differentiate  
204 species' dispersal capabilities (Guizien et al., 2006), connectivity was set as the same for  
205 all species in this study because most benthic invertebrates have a similar competency  
206 period of between 3 and 5 weeks (Mc Edward, 1995). Three connectivity matrices cor-  
207 responding to three different pelagic larval durations (3-, 4- and 5-week) were built for  
208 each spawning period, and the proportion of larvae coming from the center of any site  
209 and arriving in each of the thirty-two sites was multiplied by the ratio of the areas of  
210 origin to the destination sites. A composite connectivity matrix was then calculated as  
211 the weighted sum of the 3- (1/4), 4- (1/2) and 5- (1/4) week pelagic larval duration con-  
212 nectivity matrices. In total, twenty variant composite matrices were used to describe the  
213 interannual variability in connectivity arising from a conjunction between meteorological  
214 variability and the timing of spawning during a reproductive season, and this variability  
215 was assumed to affect all polychaete species. Then, the average and standard deviation of  
216 these twenty variant matrices were computed, and used as the average conditions matrix

217 in some of the simulations described in the next section.

## 218 **Simulation groups and statistical methods**

219 Three groups of spatio-temporal simulations over a duration of 50 life-expectancy cycles  
220 were carried out, starting with a low uniform spatial density of 0.4% of the site's carrying  
221 capacity. Asymptotic stable equilibrium was defined as the average of the population  
222 density between the 45 and 50 life-expectancy cycles. Connectivity was either set deter-  
223 ministically (the same matrix repeated every year) or stochastically (a random matrix  
224 picked up every year among the twenty variants). When connectivity was set stochasti-  
225 cally, ensembles of 500 simulations were performed for each set of the other parameters in  
226 order to evaluate the variability arising from the connectivity sequence. Redundant pat-  
227 terns among the ensemble of 500 stochastic simulations in the regional spatial distribution  
228 were sought by grouping spatial distributions that deviated by less than 20% (square root  
229 of the sum of normalized squared deviations in each site). **The spatial distribution  
230 of population density was described by the mean and standard deviation of  
231 the 500-simulation asymptotic stable equilibrium. The spatial distribution of  
232 relative density was described by the ratio between the population density in  
233 each site and the regional average of population density. The average regional  
234 coverage was defined as the ratio between the regional average of population  
235 density and the saturating capacity.**

236 Simulation settings are summarized in Table 1. Simulation groups 1 and 2 explored  
237 the effect of connectivity on population persistence and spatial distribution. Simulation  
238 group 3 explored the resistance of a short lived species to two types of scenarios (Fig.1B  
239 and C). By gradually increasing the number of unsuitable sites starting from each port,

240 group 3A aimed to quantify the resistance of the metapopulation to habitat loss around  
241 the four main ports: Port-Vendres, Port La Nouvelle, Sète and Marseille (Fig. 2). Group  
242 3B aimed to quantify the resistance of the **metapopulation** to different return periods of  
243 recruitment failure affecting either the Roussillon or the Languedoc Coasts. Recruitment  
244 failure is typically caused by extreme meteorological events (e.g. swell or heat waves,  
245 Durrieu de Madron et al., 2011) that affect populations over larger spatial scales than the  
246 scales affected by anthropogenic stresses.

## RESULTS

### 247 **Minimum recruitment success for local and regional persistence: the connec-** 248 **tivity effect (group 1)**

249 Connectivity matrices for the Gulf of Lions display a strong but highly variable spa-  
250 tial structure with variation coefficients for each connection spanning from 40 to 450 %  
251 (Fig. 3A and B). Amongst the twenty variants, three main connectivity structures could  
252 be identified and ranked according to drift direction: 65% with a dominant westward  
253 drift, 30% without dominant drift (diffusive connectivity) and 5 % with a dominant east-  
254 ward drift. On average, the local retention rates (matrix diagonal terms) were higher in  
255 the central gulf (ranging from 0.2 % to 1.41 %) than in the eastern and western tips (<  
256 0.05%). Sites located in the central gulf were also major larvae exporters, and can be split  
257 into two groups. Sites 10 to 13 predominantly exported individuals to the west, whereas  
258 sites 20 to 25 exported to both the east and the west (Fig. 3A). Larval transfer within  
259 and between the two groups of sites was also strong.

260 The spatial structure of local retention rates along the gulf coastline is depicted by  
261 the minimum recruitment successes required for the local persistence of species with life-

262 expectancies ranging from 2 to 50 years and a fecundity of  $10^4$  eggs per female (Fig. 4  
263 A). The minimum recruitment success would be multiplied by a factor of 10 for species  
264 with a fecundity of  $10^3$  eggs per female or divided by a factor of 10 for species with a  
265 fecundity of  $10^5$  eggs per female, but their relative values along the Gulf of Lions would  
266 be the same. In the nine sites along the western tip of the gulf (Roussillon coast, region  
267 of Port-Vendres) and also for three sites at its very eastern tip (region of Marseille), local  
268 retention rates were too small to achieve persistence for a species with a life expectancy of  
269 up to 10 years (up to 50-year life span in the five sites at the western tip). In contrast, the  
270 larger local retention rates in the central part of the gulf ensure the local persistence of  
271 the shortest-lived species (2-year) and of the longest-lived species (50-year) if recruitment  
272 success is larger than 70 % and 6 %, respectively. In fact, the recruitment success required  
273 for regional persistence without (in one isolated population with a maximum retention  
274 rate) and with connectivity decayed exponentially as species life expectancy increased, as  
275 it was divided by a factor of 2 between 2- and 7-year life expectancies (Fig. 4B).

276 Connectivity decreased vulnerability independently of the species life expectancy (Fig. 4B).  
277 The rescue factor was independent of species life expectancy and varied from 1 to 6.6  
278 among the twenty connectivity matrix variants (3.8 on average). When a connectivity  
279 matrix was picked randomly every year from the twenty variants, the minimum recruit-  
280 ment success required for regional persistence was the same in the 500 simulations and  
281 was slightly higher or equal to the value when the averaged connectivity was repeated  
282 every year (data not shown). The rescue factor was 5.3 for the averaged connectivity and  
283 5.0 when the connectivity matrix was variable every year.

284 **Connectivity between distant sites (i.e. larval import) tended to decrease**  
285 **the sensitivity of the persistence thresholds to the variability of the hydrody-**

286 namics. The minimum recruitment success required for regional persistence  
287 was highly variable among the twenty different hydrodynamic periods when  
288 only local retention was included, which reflected the large variability in local  
289 retention rates (Fig. 4 B, without connectivity). In contrast, the minimum  
290 recruitment success required for regional persistence was less variable among  
291 the connectivity matrix variants when larval import from distant sites was  
292 included, with the exception of one matrix characterized by very low transfer  
293 rate values (Fig. 4 B, with connectivity).

#### 294 Connectivity and spatial distribution of population density at equilibrium 295 (groups 1 and 2)

296 The relationship between connectivity matrix structure and the spatial distribution of  
297 population density at equilibrium is illustrated in this section for a species with a 2-year  
298 lifespan but would be the same for any other life expectancy provided that recruitment  
299 success was set to the minimum value required to ensure regional persistence. When  
300 the same connectivity matrix was used every year and regional persistence was ensured,  
301 the spatial distribution of population density was significantly correlated with the spa-  
302 tial distribution of cumulated import rates in the settlement sites of the corresponding  
303 connectivity matrix (on average,  $R = 0.78$ ,  $p < 0.05$ ). When larval transfer drifted to  
304 the east, density was much lower in the western part of the gulf (Fig. 5 A). When larval  
305 transfer drifted to the west, individuals were mainly distributed in the western part of the  
306 gulf (Fig. 5B). As larval transfer rates were of the same order of magnitude regardless of  
307 the different connectivity structures, regional persistence was ensured by similar values  
308 of minimum recruitment success. Interestingly, in both cases, individuals were not only

309 present in the sites with the highest retention rates but also in sites where local retention  
310 was far too low to ensure local population persistence. When the averaged connectivity  
311 matrix was repeated every year in a simulation (deterministic case) with recruitment suc-  
312 cess set to its minimum value for regional persistence, density distribution was uneven in  
313 the gulf, which reflected the average spatial distribution of the cumulative import rates  
314 along the gulf ( $R = 0.94$ ,  $p < 0.05$ ). Individuals, although present everywhere, accumu-  
315 lated in the western half of the gulf with the highest densities in sites 13 to 17 and in sites  
316 1 and 2 at the very western tip (Fig. 5C).

317 When connectivity was variable each year (conserving the averaged connectivity dur-  
318 ing the 100-year simulation) and recruitment success was set to the minimum value for  
319 regional persistence, density spatial distribution displayed the same accumulation pat-  
320 tern as in the deterministic case, whereas the relative density disequilibrium between the  
321 eastern and western part of the gulf was smoothed (Fig. 5D). **It was not possible to**  
322 **identify a dominant pattern for the spatial distribution of population density,**  
323 **as the redundancy of the asymptotic equilibria density spatial distribution**  
324 **reached 4% at the maximum among the 500 simulations.** In fact, spatial distri-  
325 bution of population density displayed higher variability among the 500 simulations than  
326 among years in each simulation. This variability was also spatially structured, and was  
327 larger in the locations identified as the accumulation sites of the averaged connectivity  
328 matrix (Fig. 5D) as these locations also correspond to the areas of highest transfer rate  
329 variability (Fig. 3A and B). When recruitment success was increased, densities increased  
330 and their spatial distribution became more even (data not shown).

331 **Connectivity and resistance to habitats loss or periodic recruitment failure of**



332 **a 2-year lifespan species (groups 3A and 3B)**

333 The spatial structure of vulnerability to stresses affecting habitat availability or recruit-  
334 ment occurrence is described in this section only for a 2-year lifespan species, because the  
335 vulnerability of such short-lived species was already highest in the absence of any stress.  
336 Wherever habitat loss was occurring (western, central or eastern part of the Gulf of Lions),  
337 the average regional coverage decreased with habitat availability and reached metapopu-  
338 lation extinction before all of the suitable habitats were lost (Fig. 6A and B). However,  
339 resistance to habitat loss displayed a strong spatial structure. Applying a recruitment  
340 success value of 3% (which was the minimum value required for regional persistence in  
341 the absence of stress), resistance to habitat loss was much lower in Sète (central part of  
342 the Gulf of Lions, where extinction occurred as soon as 3 sites were lost) than in Marseille  
343 (western tip, where extinction occurred when 10 sites were lost) and Port La Nouvelle  
344 (central part, where extinction occurred when 12 sites were lost) or finally Port-Vendres  
345 (eastern tip, where extinction occurred when 16 sites were lost, Fig. 6A). Yet ultimately,  
346 the spatial structure of the resistance to habitat loss can be shaped by the recruitment  
347 success value (Fig. 6A and B). When recruitment success was doubled, resistance to habi-  
348 tat loss was increased globally but the spatial structure of vulnerability to habitat loss was  
349 modified. For example, Port La Nouvelle became as resistant as Port-Vendres (Fig. 6B).  
350 The spatial structure of vulnerability to habitat destruction was not sensitive to the his-  
351 tory of the connectivity sequence, as variability lead to less than a 5% standard deviation  
352 in species average regional coverage amongst the 500 simulations, irrespective of where  
353 habitat loss started.

354 When recruitment failure affected the western part of the Gulf of Lions (Roussillon  
355 coast), populations never went extinct and average regional coverage was insensitive to

356 recruitment failure frequency (Fig. 7A and B). In contrast, when recruitment failure  
357 affected the northern part of the Gulf of Lions (Languedoc coast), the species with a 2-year  
358 lifespan would go extinct with a recruitment failure return period greater than 4 years  
359 if recruitment success was the minimum required to ensure metapopulation persistence  
360 in the absence of stress (Fig. 7A). However, the metapopulation could resist recruitment  
361 failure of up to every other year (species life expectancy) when compensated by a higher  
362 recruitment success (Fig. 7B). In contrast to habitat loss, metapopulation resistance to  
363 recruitment failure was strongly dependent on the history of the connectivity sequence,  
364 when the northern part of the Gulf of Lions was impacted (the standard deviation in  
365 average regional coverage amongst the 500 simulations reaching approximately 50%).

## DISCUSSION

366 The role of population connectivity in species persistence is currently emphasized  
367 in conservation biology and is translated into policy in the current Strategic Plan for  
368 Biodiversity 2011–2020 which formulated a conservation goal for the marine environment  
369 through 'ecologically representative and well connected systems of protected areas, and  
370 integrated into the wider seascapes' (<https://www.cbd.int/decision/cop/?id=12268>). At  
371 the same time, the openness of marine populations is being reconsidered using numerical  
372 simulations of larval dispersal that suggest that the scales of dispersal may not be as  
373 large as previously thought, with drastic reductions in realized long-distance connectivity  
374 due to larval mortality (Cowen et al., 2000). However, this concept does not imply that  
375 the closed-population hypothesis is valid (Cowen & Sponaugle, 2009). By subdividing  
376 the nearshore area of the Gulf of Lions into consecutive sites of tens of kilometers in  
377 width, we showed that local persistence would require different values of local recruitment  
378 success to compensate for different retention rates along an unfragmented uniform soft-

379 bottom habitat. This spatial structure was already identified in an earlier study concerned  
380 with the definition of self-persistent no-take reserves in this region (Guizien et al., 2012).  
381 The findings of the present study confirm the very low or non-existent potential for  
382 the conservation of soft-bottom species with a dispersive larval phase and a life span of  
383 up to 50 years in existing isolated marine protected areas located in the extreme tips  
384 of the Gulf of Lions (e.g. Parc Marin de la Côte Bleue, Réserve Naturelle Marine de  
385 Cerbère-Banyuls). These MPAs mainly target the conservation of hard-bottom species,  
386 which may experience higher retention rates in the boundary layer that develops around  
387 coralligenous three-dimensional structures (Moulin et al., 2007). Of greater concern is  
388 the location of the recently created Parc Naturel Marin du Golfe du Lion (PNM, Fig.2)  
389 which explicitly targets soft-bottom species as part of its sustainability goals for fisheries,  
390 while, according to our simulations, only including sink populations. The location of these  
391 sink populations is confirmed by the recurrent but transient extirpations of the 2-year life  
392 span serpulid *Ditrupa arietina* in Banyuls Bay followed by rapid recovery over the last 15  
393 years (Grémare et al., 1998; Medernarch et al., 2000; Labrune et al., 2007a, F. Charles,  
394 Pers. Comm.). Furthermore, the presence of many soft-bottom polychaete spawners in  
395 the western part of the Gulf of Lions (Labrune et al., 2007a), where local retention rates  
396 are too low to ensure species persistence as isolated populations, also indicate the existence  
397 of efficient larval transfer at the meso-scale. The rescue factor is proposed as a metric to  
398 rank the decrease in population vulnerability due to connectivity (regional persistence is  
399 not achieved by local persistence at any site, but implies a larval flux between sites) in  
400 different regions and for different species. In the Gulf of Lions, the rescue factor for species  
401 with a 4-week planktonic larval duration reached a value of 5.3 on average. Interestingly,  
402 this value was only 6% less when connectivity was variable among years, in contrast to

403 findings reported by Watson et al. (2012).

404 In the present study, scenarios of spatially structured disturbances based on existing  
405 meteorological and anthropogenic threats to a short-lived species were used to identify  
406 source sites that promote resistance to disturbances and thus are essential for regional  
407 persistence. As an example, *Ditrupa arietina*, which displays high densities in the absence  
408 of stress, is subject to local extirpations following successive recruitment failures due to  
409 mechanical disturbances and resuspension during swell events in Banyuls Bay (Charles  
410 et al., 2003; Labrune et al., 2007b). In the Gulf of Lions, swells impact different parts of  
411 the coast according to their origin: southerly swells impact the Languedoc coast whereas  
412 easterly swells impact the Roussillon coast (Fig. 2, Guizien, 2009). The recruitment failure  
413 scenario applied to *Ditrupa arietina* indicates that there is no risk of regional extirpation  
414 linked to the easterly swells impacting the Roussillon coast, which is consistent with the  
415 recolonization observed after two successive years of recruitment failure in Banyuls Bay  
416 (Roussillon coast). Another potential threat to species persistence in the Gulf of Lions is  
417 habitat loss due to boat traffic hazards spreading from ports (oil spill, invasive species).  
418 The present study identified source sites essential for metapopulation persistence around  
419 Sète. Our findings suggest that a re-evaluation of the boundaries of the Parc Naturel  
420 Marin should include the center of the Gulf of Lions and more generally account for  
421 connectivity when evaluating the ecological cost of habitat destruction.

422 This study showed that the few essential sites for regional persistence could not be  
423 depicted from the spatial distribution of population density along the gulf because, in the  
424 absence of disturbances, connectivity will enable individuals to spread to all importing  
425 sites. Consequently, traditional methods based on species inventories may fail to guide  
426 the design of protection measures to target source sites. Indeed, for a short-lived species,

427 connectivity patterns lead to a spatial distribution in the Gulf of Lions with a higher  
428 relative abundance in the western part than in the eastern part. Such disequilibrated  
429 spatial distribution is also present in long-lived species. These findings, which only account  
430 for the dispersal process in homogeneous habitat, are consistent with the community  
431 diversity throughout the muddy shelf sediment in the Gulf of Lions, which is separated  
432 into two clusters corresponding to the eastern and western parts of the gulf (Labruno et  
433 al., 2007a). These two clusters were originally differentiated by organic matter content,  
434 i.e., a habitat descriptor. In fact, the spatial distribution of organic matter in the gulf  
435 is likely to be driven by oceanographic dispersal as well. Such a result highlights the  
436 existence of co-variations among factors affecting the spatial distribution of individuals  
437 that may blur the assessment of connectivity using statistical inferences (Moritz et al.,  
438 2013).

439 In light of our findings, consideration should be given, when setting local protection  
440 measures to the oceanographic connectivity at the meso-scale (from tens to hundreds  
441 of kilometers) which drives regional distribution of population density and population  
442 vulnerability. In the Gulf of Lions, our results indicate that MPAs in the western tip are  
443 located in population sink for the soft-bottom species and establishing local protection  
444 measures in the central part of the gulf would benefit soft-bottom species over the entire  
445 region through the rescue effect. We highlight that metapopulation modeling integrating  
446 oceanographic connectivity, local demography and habitat mapping is a powerful tool  
447 that enables the inclusion of scenarios in the *a priori* design of conservation measures.

448 **Acknowledgments:** We thank METEO FRANCE for supplying atmospheric forcing  
449 data and the Banque Hydro for supplying the rivers discharge data for the hydrodynamical

450 simulations. We thank the national platform Sirocco and P. Marsaleix for their support  
451 in setting up the hydrodynamic simulations, L. Bramanti for fruitful discussion regard-  
452 ing demographic models, and J. Coston-Guarini and Wiley Editing Service for English  
453 language corrections.

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613 **Biosketch:** The research interests of the LECOB concern the ecogeochemistry, which  
614 is the integration of the interactions among the biotic and abiotic components of benthic  
615 ecosystems (<http://lecob.obs-banyuls.fr/>). K.G., J.M.G. and M.B. conceived the ideas;  
616 K.G. and M.B. performed the simulations; K.G. and M.B. analyzed the data; and K.G.  
617 and C.M. took the lead in writing the paper.

## 619 List of Tables

620	1	<i>Settings for the three simulation groups. Connectivity was set either de-</i>	
621		<i>terministically using the same matrix every year (either one of the twenty</i>	
622		<i>variants or the averaged value <math>D</math>) or stochastically picking a different ma-</i>	
623		<i>trix among the twenty variants every year with a uniform probability in</i>	
624		<i>order to conserve the averaged connectivity during the simulation (<math>S</math>). . . .</i>	33

625

## 626 List of Figures

627	1	<i>(A) Schematic diagram for a spatially explicit model of a metapopulation,</i>	
628		<i>where gray intensity indicates adult abundance per unit area in each popu-</i>	
629		<i>lation and solid arrows indicate larval fluxes in the absence of disturbance.</i>	
630		<i>(B) Habitat loss disturbance: adult abundance in dashed sites is set to zero.</i>	
631		<i>(C) Recruitment failure disturbance: dashed arrows indicate useless larval</i>	
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633	2	<i>Gulf of Lions (NW Mediterranean Sea) bathymetric map with depth con-</i>	
634		<i>tours displayed in gray lines (depth contours are 20, 50, 100, 500 m and</i>	
635		<i>spacing is 500 m below 500 m deep). The nearshore sandy habitat (depth</i>	
636		<i>between 10 and 30 m) was meshed into 32 sites from the center of which</i>	
637		<i>(indicated by circles and numbered from west to east) larvae were released</i>	
638		<i>for dispersal simulations. Hollow circles indicate the release points off the</i>	
639		<i>Roussillon coast and filled circles indicate the release points off the Langue-</i>	
640		<i>doc coast used in the simulations, group 3B. Solid boxes show the extension</i>	
641		<i>of the two nested computational domains (1500 m and 750 m resolution</i>	
642		<i>grids) and the thick-lined box displays the extent of the Parc Naturel Marin</i>	
643		<i>du Golfe du Lion (PNM). The two stars indicate the location of the two</i>	
644		<i>other marine protected areas (Parc Marin de la Côte Bleue in the West</i>	
645		<i>and Réserve Naturelle Marine de Cerbère-Banyuls in the East). The four</i>	
646		<i>trade ports of the Gulf of Lions for the simulations group 3A are indicated</i>	
647		<i>by a filled square and a letter. From east to west, M stands for Marseille,</i>	
648		<i>S for Sète, PLN for Port La Nouvelle and PV for Port-Vendres. Banyuls</i>	
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651		<i>computed for twenty 10-day spawning periods and a 4-week pelagic larval</i>	
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653	4	<p><i>Simulation group 1: (A) Minimum recruitment success required to ensure local persistence considering only average local retention rates (without connectivity). The black line displays the location where recruitment success for local persistence was at a minimum along the Gulf of Lions, and this section is plotted in B. (B) Minimum recruitment success required to ensure regional persistence (persistence in at least one site of the region) with and without connectivity for each of the twenty connectivity variants. . . . .</i></p>	36
660	5	<p><i>Spatial distribution of the relative population density (ratio between the site population density and the regional average of population densities) of a 2-year lifespan species computed between 91 and 100 years and repeating the same connectivity matrix every year (simulations group 1): (A) for a connectivity matrix displaying a westward drift, (B) for a connectivity matrix displaying an eastward drift, (C) for the average connectivity matrix, and (D) for an ensemble of 500 simulations in which connectivity was picked every year with uniform probability amongst the 20 connectivity variants (simulation group 2). Black circles display the standard deviation of the 500 simulations replicated when connectivity was stochastic. R is the minimum recruitment success value to ensure species persistence in each connectivity case. . . . .</i></p>	37



- 672 6 *Average regional coverage of a 2-year lifespan species between 91 and 100*  
673 *years for the ensemble of 500 simulations of group 3A. Connectivity was*  
674 *picked every year with uniform probability amongst the 20 connectivity vari-*  
675 *ants and the number of habitat sites destroyed was increased from 1 to 32.*  
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680 *nectivity was picked every year with uniform probability amongst the 20*  
681 *connectivity variants and the return frequency of recruitment failure in the*  
682 *northern (Languedoc) and western (Roussillon) part of the Gulf of Lions*  
683 *varied from every ten years to every year. Recruitment success  $R$  was set*  
684 *to (A) 3%, and (B) 6%. The shaded area is delimited by the 5% and 95%*  
685 *quantiles of the average regional coverage between 91 and 100 years. . . . 38*

	Group 1	Group 2	Group 3	
			A	B
Connectivity	D	S	S	S
Fecundity	$10^3-10^5$	$10^3-10^5$	$10^4$	$10^4$
Life expectancy	2-50 years	2-50 years	2 years	2 years
Disturbance	NO	NO	habitat loss	recruitment failure
Number of simulations per life expectancy	21	500	500	500

Table 1: *Settings for the three simulation groups. Connectivity was set either deterministically using the same matrix every year (either one of the twenty variants or the averaged value D) or stochastically picking a different matrix among the twenty variants every year with a uniform probability in order to conserve the averaged connectivity during the simulation (S).*

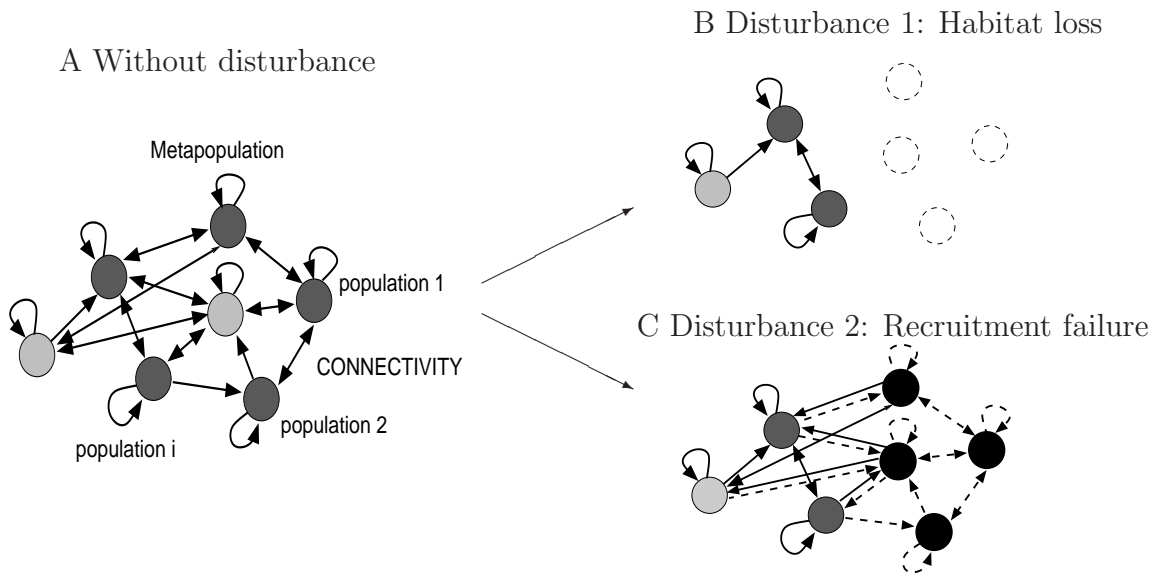


Fig. 1: (A) Schematic diagram for a spatially explicit model of a metapopulation, where gray intensity indicates adult abundance per unit area in each population and solid arrows indicate larval fluxes in the absence of disturbance. (B) Habitat loss disturbance: adult abundance in dashed sites is set to zero. (C) Recruitment failure disturbance: dashed arrows indicate useless larval transfers due to recruitment failure in sites displayed in black.

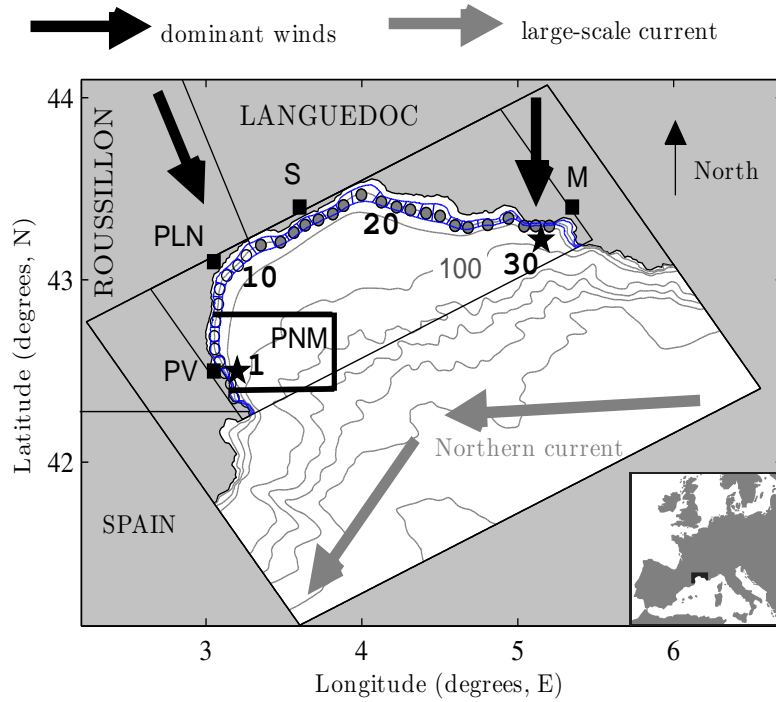


Fig. 2: Gulf of Lions (NW Mediterranean Sea) bathymetric map with depth contours displayed in gray lines (depth contours are 20, 50, 100, 500 m and spacing is 500 m below 500 m deep). The nearshore sandy habitat (depth between 10 and 30 m) was meshed into 32 sites from the center of which (indicated by circles and numbered from west to east) larvae were released for dispersal simulations. Hollow circles indicate the release points off the Roussillon coast and filled circles indicate the release points off the Languedoc coast used in the simulations, group 3B. Solid boxes show the extension of the two nested computational domains (1500 m and 750 m resolution grids) and the thick-lined box displays the extent of the Parc Naturel Marin du Golfe du Lion (PNM). The two stars indicate the location of the two other marine protected areas (Parc Marin de la Côte Bleue in the West and Réserve Naturelle Marine de Cerbère-Banyuls in the East). The four trade ports of the Gulf of Lions for the simulations group 3A are indicated by a filled square and a letter. From east to west, M stands for Marseille, S for Sète, PLN for Port La Nouvelle and PV for Port-Vendres. Banyuls Bay (not depicted) is located 10 km south of Port-Vendres.

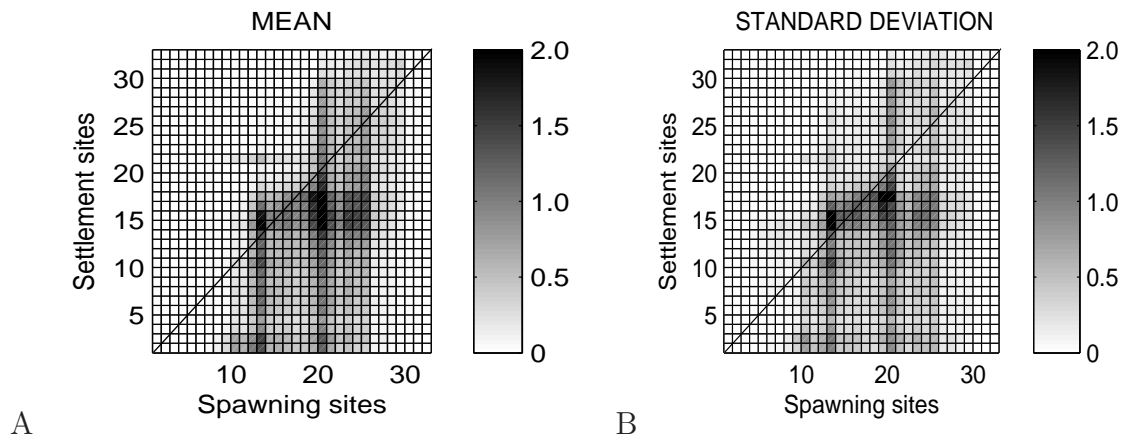


Fig. 3: (A) Mean and (B) standard deviation of the twenty connectivity matrices computed for twenty 10-day spawning periods and a 4-week pelagic larval duration.

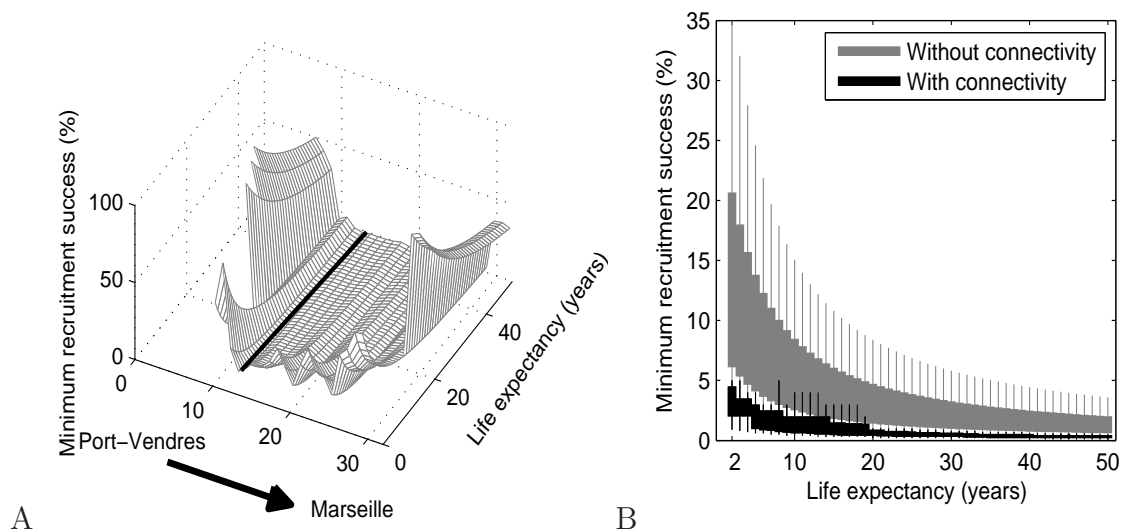


Fig. 4: Simulation group 1: (A) Minimum recruitment success required to ensure local persistence considering only average local retention rates (without connectivity). The black line displays the location where recruitment success for local persistence was at a minimum along the Gulf of Lions, and this section is plotted in B. (B) Minimum recruitment success required to ensure regional persistence (persistence in at least one site of the region) with and without connectivity for each of the twenty connectivity variants.

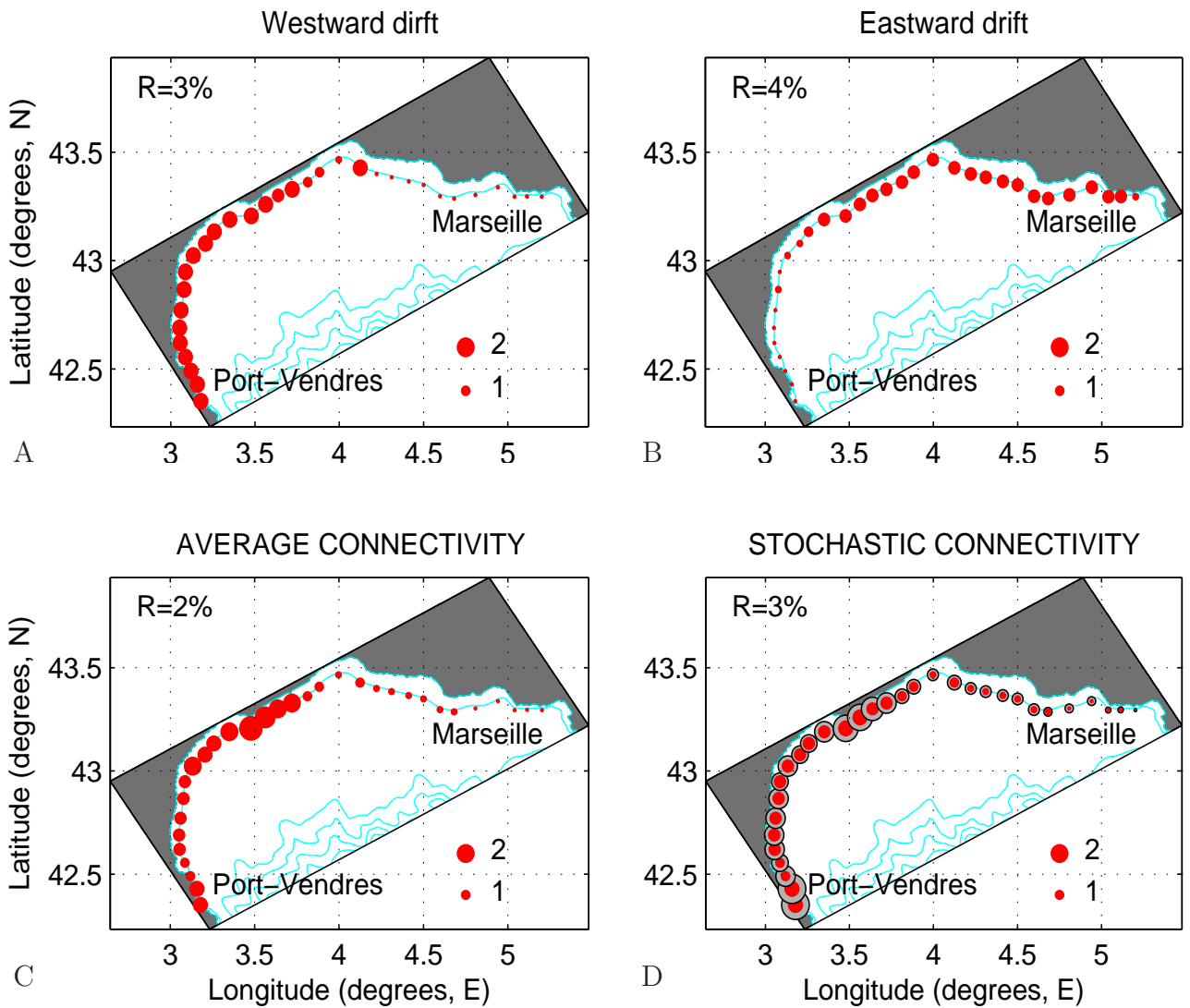


Fig. 5: Spatial distribution of the relative population density (ratio between the site population density and the regional average of population densities) of a 2-year lifespan species computed between 91 and 100 years and repeating the same connectivity matrix every year (simulations group 1): (A) for a connectivity matrix displaying a westward drift, (B) for a connectivity matrix displaying an eastward drift, (C) for the average connectivity matrix, and (D) for an ensemble of 500 simulations in which connectivity was picked every year with uniform probability amongst the 20 connectivity variants (simulation group 2). Black circles display the standard deviation of the 500 simulations replicated when connectivity was stochastic.  $R$  is the minimum recruitment success value to ensure species persistence in each connectivity case.

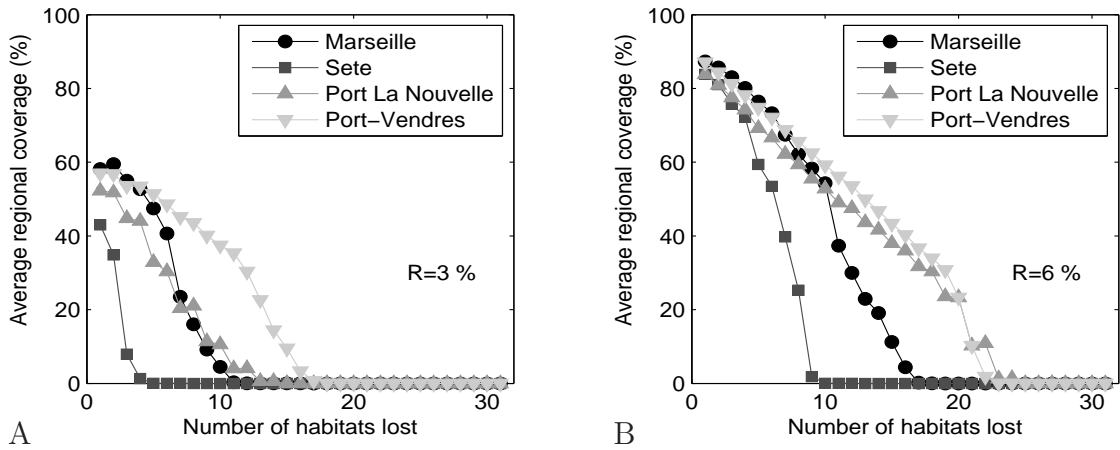


Fig. 6: Average regional coverage of a 2-year lifespan species between 91 and 100 years for the ensemble of 500 simulations of group 3A. Connectivity was picked every year with uniform probability amongst the 20 connectivity variants and the number of habitat sites destroyed was increased from 1 to 32. Recruitment success  $R$  was set to (A) 3% and (B) 6%. The errorbars displaying variability among the 500 simulations are smaller than the symbols.

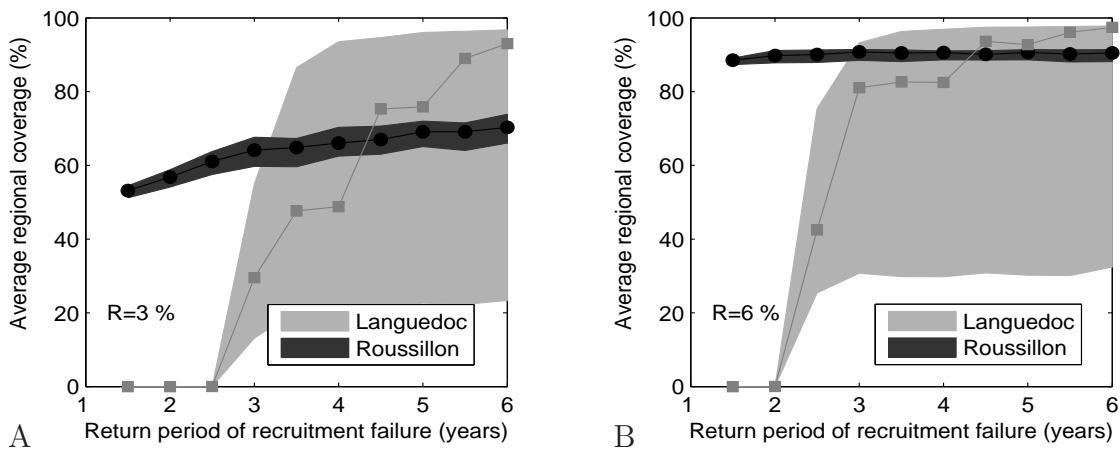


Fig. 7: Median of the average regional coverage of a 2-year lifespan species between 91 and 100 years for the ensemble of 500 simulations of group 3B. Connectivity was picked every year with uniform probability amongst the 20 connectivity variants and the return frequency of recruitment failure in the northern (Languedoc) and western (Roussillon) part of the Gulf of Lions varied from every ten years to every year. Recruitment success  $R$  was set to (A) 3%, and (B) 6%. The shaded area is delimited by the 5% and 95% quantiles of the average regional coverage between 91 and 100 years.