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## **Functional Connectivity improves the efficiency of the extension of a network of highly protected marine areas (Gulf of Lion, North Western Mediterranean sea)**

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1 **Functional Connectivity improves the efficiency of the extension of a**  
2 **network of highly protected marine areas (Gulf of Lion, North Western**  
3 **Mediterranean sea)**

4

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6

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10

11 **Abstract**

12

13 The creation of networks of interconnected highly protected marine areas is one way of  
14 increasing population resilience and halting the long-term loss of biodiversity in the oceans.

15 In this study, we evaluated the efficiency of systematic conservation planning (SCP) varying  
16 the adequacy resulting from connectivity- in the fragmented hard bottom habitat in the Gulf  
17 of Lion. Twelve sets of conservation plans- with objectives of conserving 10% and- 30% of  
18 the hard bottom habitat surface were established by crossing current pressures with three  
19 types of connectivity : (i) structural connectivity (ii) early summer and (iii) late summer  
20 connectivity arising from a one week larval dispersal, considering or disregarding existing  
21 highly protected areas. These connectivities are likely estimates of the functional  
22 connectivity of two umbrella species, the gorgonians *Eunicella singularis* and *Leptogorgia*  
23 *sarmentosa*. The efficiency of each conservation plan in protecting populations in the Gulf  
24 of Lion was then assessed against independent observations of the spatial distribution of the  
25 two species. When functional connectivity replaced structural connectivity, the spatial

26 distribution of highly protected areas was significantly modified targeting sites in the central  
27 Gulf of Lion, and the efficiency (ratio of proportion of individuals under protection to  
28 protection cost) increased by 300 % (20 %, respectively) in the objective of conserving 10%  
29 (respectively, 30%) of the hard bottom habitat surface. Moreover, SCP was more focussed  
30 when functional connectivity replaced structural connectivity. The present study suggests  
31 that using marine functional connectivity is all the more important that the conservation  
32 target is low.

33

34 **Keywords:** marine functional connectivity, spatial conservation planning, hard bottom  
35 habitat, Marxan Connect, gorgonian, NW Mediterranean Sea

36

### 37 **Impact statement**

38 First operational systematic conservation planning integrating functional connectivity due to  
39 larval dispersal in the NW Mediterranean sea

40

### 41 **Introduction**

42 The on-going collapse of marine biodiversity urges to revise the current marine protected  
43 areas (MPAs, Watson et al. 2009) system to ensure the long-term conservation of nature and  
44 the ecosystem services and cultural values associated with it (Halpern et al. 2012; 2019). At  
45 COP15, the Global Biodiversity Framework agreed that MPAs coverage should be  
46 drastically extended to reach at least 30% of the seas by 2030. In 2024, the coverage of  
47 designated MPAs at global scale is 8,4% of the ocean surface  
48 (<https://www.protectedplanet.net/en/thematic-areas/marine-protected-areas>, accessed Sept.  
49 11, 2024). However, protection levels can largely vary among MPAs (Grorud-Colvert et al.  
50 2021) and if focussing on fully or highly protected areas only, the figure drops to 2,9%

51 (<https://mpatlas.org/>, accessed Sept. 11, 2024). In addition, candidate areas should emerge  
52 from a selection process based on hierarchical scientifically sound criteria highlighting  
53 representativeness of the full range of biodiversity, adequacy meaning long-term persistence  
54 and efficiency (Wilson et al. 2009). Building connected networks is now put forward as a  
55 priority to reach adequacy (Goetze et al. 2021). Indeed, it is recognized that the exchange of  
56 individuals plays a fundamental role in improving conservation outcomes by promoting the  
57 resilience and adaptation potential of populations to global change (Carr et al. 2017).  
58 However, the integration of connectivity as an ecological criterion is still limited compared to  
59 other criteria such as the presence of heritage, endemic or protected species or habitats with  
60 high ecosystem values in decisions to create or manage marine protected areas (11% of  
61 MPAs, Balbar and Metaxas 2019). Furthermore, when included, population connectivity  
62 have been mainly estimated by the physical continuity of habitats fostering an ecological  
63 continuum or corridor (i.e. structural connectivity, Balbar et al. 2020). The adequacy of  
64 promoting corridors of habitat continuity to justify spatial conservation plans has been  
65 documented for terrestrial populations (McRae, 2006). However, given the dominance of  
66 pelagic displacement among marine species, habitat fragmentation is less of a barrier to  
67 population connectivity (Cheminée et al. 2014 ; Lett et al. 2020). Specifically, for sessile  
68 benthic invertebrates, population connectivity mainly happens thanks to larval dispersal  
69 through ecological routes drawn by marine currents structure in a fragmented habitat  
70 (Villamor et al. 2014; Padron et al. 2018; Schunter et al. 2019). However, the identification  
71 of species-specific ecological routes in the three-dimensional ocean is less obvious than  
72 structural connectivity and relies on various methods used separately or combined (marine  
73 functional connectivity, Sturrock et al. submitted). Those methods have shown that the  
74 probability of exchange between two areas of the same habitat that are geographically close  
75 may not be necessarily higher than between two areas that are further apart (Bandelj et al.

76 2020). Thus, the adequacy of structural connectivity, which is based on the geographical  
77 continuity of sites in order to limit habitat fragmentation to optimize exchanges, is  
78 questionable for the conservation of marine sessile invertebrates.

79 In this study we explored how efficiency of SCP varied with the adequacy of the connectivity  
80 criteria used. Representativeness of the SCP study was ensured by targeting a single and  
81 unique habitat of the Gulf of Lion (NW Mediterranean sea), the rocky and coralligenous  
82 habitat (hereinafter called hard bottom) which representativity for the Mediterranean  
83 biodiversity has been put forward to position existing highly protected areas. Gorgonian  
84 species such as *Eunicella singularis* (Esper, 1791) and *Leptogorgia sarmentosa* (Esper,  
85 1789) which are commonly found in the Gulf of Lion hard bottom habitat, are monitored in  
86 the marine protected areas management plans for being considered as umbrella species for  
87 the hard bottom habitat biodiversity (True, 1970 ; Hong, 1980). Twelve sets of conservation  
88 plans were built in the objective to protect 10% (respectively 30%) of the hard bottom habitat  
89 surface, varying the connectivity type among (i) structural connectivity, (ii) early summer  
90 (corresponding to *Eunicella singularis*) and (iii) late summer (corresponding to *Leptogorgia*  
91 *sarmentosa*) functional connectivity arising from larval dispersal, and considering or  
92 disregarding existing highly protected areas. The efficiency of each conservation plan to  
93 protect the two gorgonian species was ultimately evaluated independently based on  
94 observations of the spatial distribution of their abundance in hard bottom habitats.

95

## 96 **Material and methods**

### 97 **Study area**

98 The coastline of the Gulf of Lion stretches 350 km from Marseille to Cerbère. Along this  
99 coastline, the coastal benthic habitat is mainly made up of soft bottoms, with a few small  
100 patches of hard bottom habitat ranging in size from 0,5 to 34 km<sup>2</sup>, totalling a surface of 80

101 km<sup>2</sup>. The study area comprises a set of eight sites (Parc Marin de la Côte Bleue: PMCB,  
102 Aigues Mortes : AGM, Aresquiers: ARES, Agde: AGD, Valras: VLR, Leucate: LEU, Saint-  
103 cyprien: CST, Côte Vermeille: CVM; Figure S1). Four sites include a highly protected area  
104 (according to the classification of Horta e Costa et al. 2016: Fully protected) with different  
105 surface areas (PMCB: 289 ha, AGM: 100 ha; AGD: 310 ha, CVM: 69 ha; Figure S1),  
106 representing 5.45 % of the hard bottom habitat surface.

107

### 108 **MPA network design**

109 We used Marxan (V 4.0.6) and Marxan Connect (V 1.0.0) to design a network of  
110 conservation areas. These two software packages optimize a networked conservation area  
111 layout among a set of planning units (PU) according to conservation objectives and targets,  
112 minimizing layout costs and maximizing a type of connectivity. Both Marxan software  
113 programs require two types of information for each PU: data in relation to the conservation  
114 objective (species population density, species biomass, habitat area, etc.) and implementation  
115 cost data (action costs, indirect costs, opportunity costs).

116 Marxan maximizes structural connectivity defined as reduced landscape fragmentation and  
117 increased geographic continuity by compacting boundaries (Ball et al. 2009). Thus, structural  
118 connectivity favors large PU and common boundaries between PUs to form clusters and  
119 corridors linking these clusters across the seascape. This type of connectivity appears to be  
120 well suited to habitat-following species and, above all, reduces the cost of monitoring  
121 (Ardron et al. 2010). When the connectivity type is structural connectivity, boundary cost  
122 weighting is controlled by a multiplier called the "boundary length modifier" or BLM. The  
123 higher the BLM value, the greater the weight given to boundary cost and the more compact  
124 the conservation plan is. Reversely, the lower the BLM, the less costly the conservation plan  
125 is.

126

127 Marxan Connect replaces the structural connectivity criterion with functional connectivity,  
128 enabling sites that may be spatially distant but ecologically connected by a functional flux to  
129 be maintained (Daigle et al. 2020). Marxan Connect deals with functional connectivity in two  
130 ways. One way is to integrate functional connectivity (symmetrical or asymmetrical) through  
131 links between PUs (flow, migration, transfer probability) by creating high penalties in  
132 conservation plans that fail to protect a pair of highly connected PUs (Beger et al. 2010). The  
133 other way is to integrate functional connectivity in the form of a feature ranking PUs  
134 according to their influence in the connectivity network (e.g. degree of entry, intermediate  
135 centrality, local retention, Google pagerank, <https://marxanconnect.ca/>). In the present study,  
136 functional connectivity was implemented as spatial dependency with asymmetrical  
137 connectivity. Like the BLM, the connectivity strength modifier (CSM) adjusts the  
138 importance of connectivity in the conservation plan design by applying a penalty when  
139 connected PUs are not included (Beger et al. 2010).

140 Both versions of Marxan use a simulated annealing algorithm that tests at each iteration a  
141 portfolio of PUs achieving the conservation objective, aiming to decrease the portfolio score  
142 after a finite number of iterations. This score is the sum of the cost of PUs related to  
143 pressures, the cost of connectivity and a penalty if the conservation objective is not reached.  
144 Thus, a reserve network with a more connected distribution will be favored (e.g. total edge  
145 length of selected PUs lowest for structural connectivity (Ball and Possingham 2000). The  
146 simulated annealing algorithm is repeated several times (number of runs) to obtain several  
147 optimal prospective conservation plans.

148

149 **Marxan implementation**

150 As PUs, we targeted plots of less than 1.5 km<sup>2</sup>, which is in the order of magnitude of the  
151 smallest surface area of current strong protection zones and a spatial scale consistent with the  
152 variability of local retention linked to marine currents in the Gulf of Lion (Figure S2, Briton  
153 et al. 2018). In total, the 8 sites were described by 138 PUs in natural habitat (with surface  
154 areas ranging from 0.01 to 1.4 km<sup>2</sup>).

155 Socio-economic data for calculating costs per PU were extracted from IMPACTS (Modeling  
156 coastal anthropogenic pressures and vulnerability thresholds; 20 x 20 m resolution);  
157 <https://medtrix.fr/>, Holon et al. 2015). We selected activities for which conservation could  
158 lead to a drop in income or conflicts of use. Four activities were selected: small boat mooring  
159 (<24 m) and large boat mooring (>24 m), artisanal fishing and beach tourism. The maximum  
160 value for each activity was extracted for each PU.

161 The mapping of anthropogenic impacts, obtained by interpolating pressure as a function of  
162 distance between proven pressure sites (100%) and habitat boundaries (0%), did not take into  
163 account existing activity regulation. Existing activity regulations could be taken into account  
164 by setting fishing and beach tourism pressures to zero in PUs located in highly protected  
165 areas ([www.medamp.org](http://www.medamp.org)). For PUs that overlap two types of zoning (protected and  
166 unprotected), the value of the pressures is proportional to the surface area of the type of  
167 zoning. The final cost for each PU was calculated by summing the pressure values of the  
168 activities. Two cost scenarios were considered for setting up conservation plans, one with  
169 existing highly protected areas and one without them, to test for the relevance of existing  
170 highly protected areas that were proposed long before pressures and connectivity assessments  
171 (Figure S2 A and B).

172

173 **Marxan Connect implementation: functional connectivity scenarios**



174 Functional connectivity by larval dispersal for *E. Singularis* and *L. Sarmentosa* is described  
175 as a probability of larval transfer from a source PU to a destination PU after a pelagic  
176 dispersal duration (PLD, Figure 1). Larval dispersal was simulated by a Lagrangian method  
177 integrating the transport by ocean currents of virtual particles of neutral buoyancy, according  
178 to measured larval traits of *E. Singularis* (Guizien et al. 2020). Currents were simulated on a  
179 curvilinear grid with high spatial resolution (from 80 m to 300 m near the coast) and  
180 temporal resolution (every 1h) in the Gulf of Lion during 3 consecutive summer periods  
181 (from June to October, in 2010-2011 and 2012, Briton et al. 2018). A virtual particle is  
182 released at 1 m above the seabed every hour and every 100 m in the PUs from June 1 to July  
183 10 for *E. singularis* (early summer) and from August 1 to September 10 for *L. sarmentosa*  
184 (late summer) in the three years (2010, 2011 and 2012). The probability of larval transfer  
185 from a source PU to a destination PU was computed as the median of the probability of larval  
186 transfer obtained after a one-week PLD for twelve (four per year) 10-day release periods per  
187 species. Larval transfer probability was calculated as the ratio of the number of particles that  
188 were released in a source PU and reached a destination PU to the total number of particles  
189 released in the source PU, multiplied by the ratio of surface areas of source PU to destination  
190 PU.

191 A PLD of one week was chosen because larvae of *E. singularis* settle massively after this  
192 duration (Zelli et al. 2020) and this larval dispersal duration best explained gene flow among  
193 natural populations of *E. singularis* living in the fragmented hard bottom habitat of the Gulf  
194 of Lion (Padron et al. 2018). For *L. sarmentosa*, the lack of knowledge of PLD leads us to  
195 hypothesize a one-week PLD (Rossi and Gili, 2009). Hence, differences in functional  
196 connectivity by larval dispersal between the two species only arises from the different release  
197 periods, with a greater number of PUs connected in late summer than in early summer  
198 (Figure 1).

## 200 **Configurations and simulations with Marxan**

201 The simulations were carried out considering two conservation targets of 10% and 30% of  
202 the hard bottom habitat (Tables 1 and S1). Extending the surface area of highly protected  
203 zones to 10% is the objective for 2030 of the French government  
204 (<https://biodiversite.gouv.fr/la-strategie-nationale-biodiversite-2030>). This objective  
205 reformulates the Aichi biodiversity target 11 of the Strategic plan for Biodiversity 2011-2020  
206 of the United Nation Convention on Biological Diversity. Extending the surface area of  
207 highly protected zones to 30% is the current objective of the United Nation Convention on  
208 Biological Diversity for 2030 and corresponds to a value generally applied in conservation  
209 planning studies (Schill et al. 2015; Chen et al. 2022), as according to the neutral theory of  
210 biodiversity distribution, which links the surface area of an area to the number of species  
211 present, 30% of a habitat would be sufficient to protect between 60 and 80% of species  
212 (Hubbell, 2001).

213 Twelve configurations were tested (Tables 1 and S1). In each configuration, the model  
214 sensitivity to the scaling factor (BLM or CSM) between cost and connectivity measure that  
215 adjusts the score's sensitivity to these two quantities was explored. The most compact  
216 solution was explored by setting BLM value equal to 1 and the least cost solution was  
217 explored by setting BLM value equal to 0. The optimal BLM of 0.004 in the structural  
218 connectivity configurations was calibrated using ©Qmarxan software (Figure S3). In the  
219 functional connectivity configurations, the sensitivity to the choice of the CSM was explored,  
220 varying its value from 3 (medium penalty), 10 (high penalty) to 100 (very high penalty) and  
221 finally set to 3, this value leading to a reasonable compromise between cost and connectivity  
222 (Stewart and Possingham, 2005).

223 In all configurations, the number of executions was set to 100 times with 10 million  
224 iterations (Figure S3), generating 100 conservation plans. The selection frequencies for each  
225 PU obtained from the 100 conservation plan were classified into 5 classes adapted to the  
226 conservation objective. For the conservation objective of 10%, the classes were : 10-20%  
227 (low), 20-40%, 40-60%, 60-80%, 80-100% (high). For the conservation objective of 30%,  
228 the classes were : 30-44% (low), 44-58%, 58-72%, 72-86%, 86-100% (high). Similarity  
229 between conservation plans in the different configurations and species was estimated by the  
230 Pearson coefficient between PU selection frequencies. Selection frequency maps were  
231 produced using GIS software (©QGIS).

232

### 233 **Conservation plans assessment**

234 The two species display different spatial distributions in the hard bottom habitat (Blouet et al.  
235 2024).The population density of both species was assessed in 2013 and in 2021 at 601  
236 georeferenced stations spaced by 100 m to 800 m, depending on the bathymetric gradient of  
237 each zone and covering the hard bottom habitat at all sites (Guizien et al. 2022;  
238 [https://cardobs.mnhn .fr/](https://cardobs.mnhn.fr/)). *E. singularis* is frequently observed and abundant throughout the  
239 hard bottom habitat of the Gulf of Lion (Figure S4 A). Conversely, *L. sarmentosa* is eight  
240 times less abundant than *E. singularis* in the hard bottom habitat (Figure S4 B). The  
241 abundance of each species in the PUs was calculated by multiplying the maximum  
242 population density measured during inventories by the effective surface area of substrate in  
243 each PU.

244 For each of the 100 conservation plans, the proportion of individuals of the known  
245 population of *L. sarmentosa* and *E. singularis* and the proportion of the total cost in the PUs  
246 selected in the plan was calculated. Conservation plan efficiency was defined as the ratio

247 between the proportion of individuals of the known population that are proposed to be put  
248 under protection and the proportion of the total cost.

249

## 250 **Results**

251 In both conservation objectives of 10 and 30 %, the conservation target in terms of surface  
252 area was almost always achieved, except in a few conservation plans, whatever the  
253 connectivity or cost scenarios considered. Nevertheless, the surface area of the hard bottom  
254 habitat selected, on average across the 100 conservation plans, was lower with structural  
255 connectivity (9 % and 28.4%, respectively when extending the current highly protected  
256 areas) than with functional connectivity (at least 9.5 % and 29.3 %, respectively, Table 1).  
257 More importantly, the average costs of the 100 conservation plans with structural  
258 connectivity always exceeded the ones with any of the functional connectivity by at least  
259 20 % (10 % target with existing highly protected areas and early summer functional  
260 connectivity) and up to 135 % (10 % target with existing highly protected areas and late  
261 summer functional connectivity, Table 1).

262 The spatial arrangement of conservation plans in both conservation objective of 10 % and  
263 30 % varied more with the type of connectivity (sharing less than 9% of the variance in PU  
264 selection frequencies, panels A versus B and panels C versus D in Fig. 2 and 3 respectively)  
265 than with accounting or not for the existing highly protected areas with structural  
266 connectivity (sharing more than 72 % of variance in PU selection frequency, panels A versus  
267 C in Fig. 2 and 3, respectively). This difference is even more marked in the 30% objective, in  
268 which conservation plans with functional connectivity consisted of a network of small highly  
269 protected areas distributed throughout the region (Fig. 3B and D).

270 In the conservation objective of 10 %, conservation plans with structural connectivity,  
271 targeted isolated PUs (having no boundary with other PUs) in PMCB, CST and CVM (Fig.

272 2A and C). None of these conservation plans reflected the least cost of large PUs located in  
273 AGD, ARES and AGM, that would have been prioritized with BLM=0 (Fig. S5A and C).  
274 Interestingly, conservation plans seeking for most compact solutions (BLM=1) excluded the  
275 isolated PUs selected with BLM=0.004, but were not selective with no difference in  
276 frequency selection among PUs (Fig. S5B and D). In contrast, conservation plans with  
277 functional connectivity which included PUs from the center of the Gulf of Lion (Fig. 2B),  
278 and mainly them if disregarding existing highly protected areas (Fig. 2D) as proposed in the  
279 most compact solutions, were more focussed. Noteworthy, with functional connectivity, PUs  
280 from CVM were not prioritized in conservation plans in the 10 % objective when  
281 disregarding existing highly protected areas. As expected, conservation plans tended to favor  
282 existing highly protected areas, when taking into account their reduced cost, resulting in little  
283 variability among conservation plans in the conservation objective of 10 %.

284 In the conservation objective of 30 %, conservation plans with structural connectivity could  
285 include PUs from all zones except AGM, with low selection frequency, except in CST and  
286 highly protected areas when their reduced cost was considered (Figure 3A and C). In  
287 contrast, conservation plans with functional connectivity targeted PUs from the center of the  
288 Gulf of Lion with high selection frequency (Figure 3B and D), and mainly them if  
289 disregarding existing highly protected areas (Figure 3D). Like in the conservation objective  
290 of 10 %, conservation plans included existing highly protected areas, when taking into  
291 account their reduced cost in the 30 % objective (Figure 3B). Noteworthy, conservation plans  
292 included existing highly protected areas from AGD, AGM and PMCB as well when their  
293 reduced cost was not taken into account when considering functional connectivity (Figure  
294 3D). In contrast, with functional connectivity, PUs from CVM were not prioritized in  
295 conservation plans in the 30 % objective when disregarding existing highly protected areas  
296 (Figure 3D).

297 Conservation plans obtained using early or late summer functional connectivity were very  
298 similar to each other, under the same conditions of costs and conservation objectives, sharing  
299 over 70% of the variance in PU selection frequencies (Fig. S6A versus Fig. 2B –  $R^2=0.82$  ;  
300 Fig. S6C versus Fig. 2D -  $R^2=0.73$ ; Fig. S6B versus Fig. 3B –  $R^2=0.89$  ; Fig. S6D versus Fig.  
301 3D –  $R^2=0.76$ ).

302 In terms of protection effect, there was a large variability in the proportion of the Gulf of  
303 Lion individuals concerned by conservation plans with 10% objective whatever the  
304 connectivity type, varying from 0 % to 24% for *E. singularis* and 0% to 32% for *L.*  
305 *sarmentosa* (Figure S7). When extending existing highly protected areas, a minimum of 5 %  
306 (2.5 %, respectively) of the Gulf of Lion individuals of *E. singularis* (*L. sarmentosa*,  
307 respectively) was included in conservation plans, while disregarding existing highly  
308 protected areas could lead to no protection at all, whatever the type of connectivity (Figure  
309 S7). In the 10 % conservation plans, the proportion of the Gulf of Lion individuals for *E.*  
310 *singularis* (*L. sarmentosa*, respectively) was at least 10.4 % (12.8%, respectively) with  
311 functional connectivity compared to 6.6 % (6.9%, respectively) with structural connectivity  
312 in half of plans (Fig. S7). When the conservation objective was raised to 30 %, protection  
313 effect increased whatever the connectivity type, but increased more with structural  
314 connectivity (at least 43.3 % for *E. singularis* and 73 % for *L. sarmentosa* in half of the  
315 plans) than with functional connectivity (36 % for *E. singularis* and 33% for *L. sarmentosa*,  
316 in half of the plans). It could reach up to 48 % of the *E. singularis* and 86 % of *L.*  
317 *sarmentosa* individuals of the Gulf of Lion in some 30 % conservation plans with structural  
318 connectivity while yielding a maximum of 45 % of *E. singularis* and 55 % for *L. sarmentosa*  
319 with late summer functional connectivity. However, some 30 % objective conservation plans  
320 could also protect less than 20 % of the *L. sarmentosa* Gulf of Lion individuals (Fig. S8).  
321 Finally, the most striking effect of considering functional connectivity (early or late summer)

322 compared to structural connectivity was to reduce the cost of the protection whatever the  
323 conservation objective by a factor 1.5 to 3, and even more when extending existing highly  
324 protected areas (Fig. S7 and S8).

325 Combining the reduced cost with effective protection of the two target species, the median of  
326 10 % conservation plans efficiency increased from 0.8 to 3 (4.5, respectively) for *E.*  
327 *singularis* and from 0.9 to 3.9 (6.3, respectively) for *L. sarmentosa* when replacing structural  
328 connectivity by early summer (late summer, respectively) functional connectivity (Fig. 4).  
329 However, the median 30 % conservation plan efficiency only increased from 1.9 with  
330 structural connectivity to 2.3 (2.4, respectively) with early summer (late summer,  
331 respectively) functional connectivity for *E. singularis* (Fig. 4A). For *L. sarmentosa*,  
332 structural connectivity led to more efficient conservation plans than functional connectivity  
333 in more than half of the conservation plans but could lead to totally inefficient plans as well  
334 (Fig. 4B).

335

## 336 **Discussion**

337 The value of population connectivity in improving population persistence and resilience has  
338 been widely demonstrated theoretically (Hanski, 1998; Hanski and Gaggiotti, 2004; Hastings  
339 and Harrison, 1994). Theoretically, metapopulation persistence requires the identification of  
340 closed exchange circuits known as persistence loops of stepping stones that can extend over  
341 more than a pair of populations (Hastings and Botsford, 2006). Spatially explicit  
342 metapopulation modeling in realistic seascapes showed that persistence is facilitated by  
343 connectivity through a complex network involving many populations (Moffitt et al. 2011;  
344 Guizien et al. 2014). Moreover, beyond lowering the persistence threshold, connectivity  
345 between MPAs also enables the recovery of impacted populations, as shown theoretically  
346 (Hanski and Gaggiotti, 2004 ; Guizien et al. 2014) and empirically (Cupido et al. 2009;

347 Padron et al. 2018; Giménez et al. 2020). Ignoring where populations will be impacted  
348 encourages to consider multiple connectivity routes between populations to promote species  
349 resilience. The present study confirms that systematic conservation planning (SCP) focused  
350 on conservation objectives while minimizing costs and conflicts with resource or space users  
351 were modified when functional connectivity estimated from larval dispersal modeling  
352 replaces structural connectivity within a fragmented natural habitat network. Furthermore,  
353 the efficiency of SCP incorporating functional connectivity was higher than those based on  
354 structural connectivity by reducing the cost for protecting the same proportion of individuals  
355 of two sessile species. The present study thus supports the old consensus that a network of  
356 small to medium-sized MPAs achieving persistence by mutualizing their offspring through  
357 exchange between MPAs, and thus limiting losses, is a more socially acceptable and  
358 profitable alternative than extending the size of an MPA to promote self-persistence by  
359 increasing the recovery of locally produced larvae returning to the MPA, especially for  
360 highly dispersive species (Gerber et al. 2003 ; Halpern and Warner, 2003).

361 Yet, and despite advances in tools for measuring connectivity, the adoption and  
362 transferability of population connectivity estimates, whatever the method used, to decision-  
363 makers remains limited (Beger et al. 2022). Including population connectivity into systematic  
364 conservation plans faces various challenges, of which some are specific to the marine  
365 environment (Virtanen et al. 2020). At sea, systematic conservation planning tools need to  
366 incorporate the diffuse directional population connectivity at distances larger than 1km,  
367 overpassing habitat physical fragmentation (Kinlan and Gaines 2003). This is the first study  
368 in a marine setting crossing real cost estimates with directed connectivity estimates using the  
369 recently developed systematic conservation planning tool, Marxan Connect (Daigle et al.  
370 2020). To our knowledge, the alternative decision-support tool for SCP, Zonation, has not  
371 been put into practice in similar conditions (Lethömaki and Moilanen 2013). In Marxan



372 Connect, transport can be incorporated directly as spatial dependencies (Beger et al. 2010 ;  
373 2015, Muenzel et al. 2022a) or after hierarchizing sites using graph-theoretic metrics  
374 characterizing node role in a network (Magris et al. 2018; White et al. 2014). The way to  
375 integrate functional connectivity due to larval dispersal is debatable. In the present study, we  
376 privileged the spatial dependence method, as a measure of functional connectivity,  
377 prioritizing pairs of habitat patches connected both ways, arguing this approach is a desirable  
378 prioritization approach for rebuilding and maintaining populations as it preserves functional  
379 loops across generations to ensure long term species persistence (Hastings and Botsford,  
380 2006). Indeed, metrics of node role in a network (such as centrality, strength, degree) are not  
381 correlated and taken separately are poor substitutes of causal influence in directed graphs  
382 (Dablander and Hinne 2019). As a consequence, they result in different node hierarchies in a  
383 network, leading to less focussed SCP combining different metrics, which renders decision-  
384 support tools of little relevancy. Magris et al. (2016) suggested combining three node metrics  
385 (local retention, outflux and betweenness centrality) which may increase focus by  
386 multiplying constraints. In any case, none of the two approaches, between node ranking and  
387 spatial dependencies fully integrates the long term persistence brought by functional  
388 connectivity over multiple generations in a metapopulation, as population demography is not  
389 accounted for (Moilanen 2011). Using spatially explicit metapopulation modeling to quantify  
390 the conservation plan efficiency in terms of proportion of the metapopulation size actually  
391 under protection would be totally relevant to compare methodologies to account for  
392 connectivity metrics into SCP tools, given a connectivity structure (Magris et al. 2018). Such  
393 a methodology should be particularly encouraged to explore the optimal trade-off between  
394 local retention and connectivity between separated patches to maintain the adaptation  
395 potential of populations while preserving population genetics diversity and avoid local  
396 extinction (Padron and Guizien, 2016). However, comparing the outputs of a SCP and a

397 metapopulation projection based on the same connectivity structure is a circular method to  
398 evaluate the reliability of the connectivity structure used. Indeed, connectivity structure can  
399 be incomplete or uncertain.

400 Including connectivity into SCP requires examining all possible connections within a set of  
401 planning units (Marxan Connect, Daigle et al. 2020) or on a grid (Zonation, Moilanen et al.  
402 2005). Population connectivity spatial scales can span over various order of magnitude,  
403 depending on the species or the dispersing stage, ranging from a few kilometers for most  
404 adult fish movements (Harmelin-Vivien et al. 2008; Pérez-Ruzafa et al. 2008), to tens to  
405 hundreds of kilometers in the case of larval dispersal (D'Aloia et al. 2015; Jessopp &  
406 McAllen, 2007; Palumbi, 2004). However, spatial scales of connectivity larger than  
407 hundreds of kilometers may be difficult to match the spatial scales at which systematic  
408 conservation planning can be actually put into practice (Watson et al. 2009). Only few SCP  
409 studies used connectivity estimates derived from observations such as telemetry tracking data  
410 (Beger et al. 2015; Lea et al. 2016) and genetic metrics (Beger et al. 2014). To date, the  
411 connectivity input to SCP has been mainly estimated by direction and strength of transport  
412 among sites using larval dispersal modeling, because it can explore exhaustively potential  
413 connections (Álvarez-Romero et al. 2018; Beger et al. 2015; Beyer et al. 2018; Daigle et al.  
414 2020; Magris et al. 2018; Muenzel et al. 2022b). However, connectivity estimates established  
415 from larval dispersal modeling should be taken with caution as they may vary significantly  
416 with modeling parameters. In particular, despite larval dispersal modeling in theory enables  
417 spanning thousands of kms using global ocean models, these models should be avoided to  
418 establish connectivity metrics for coastal SCP due to the poor representation of ocean flow  
419 near the coast in such models and the sensitivity of connectivity to ocean flow representation  
420 (Putman and He, 2013 ; Sciascia et al. 2022). In the present study, the early summer  
421 functional connectivity structure used for SCP was estimated from larval dispersal modeling

422 after selecting the adequate pelagic dispersal duration to be used in simulations by  
423 confronting larval transport to gene flow between PMCB, ARES, AGD and CVM  
424 populations of *Eunicella singularis* (Padron et al. 2018). Partial cross-validation of  
425 connectivity estimates helped to fine tune the connectivity estimates and likely explain the  
426 higher focus of SCP outputs established with functional connectivity compared to the ones  
427 with structural connectivity. Among the four recommendations on incorporating  
428 connectivity for MPA design, Balbar and Metaxas (2019) advocated that it is essential to  
429 identify the role each MPA plays in supporting connectivity. MPAs containing source, self-  
430 reconstructing and core populations are considered essential to the network (Magris et al.  
431 2018). Practically, the present study prioritized sites located in the center of the Gulf of Lion  
432 previously identified for both local persistence (Guizien et al. 2012) and regional persistence  
433 of soft substrate species with PLDs ranging from 1 to 6 weeks (Guizien et al. 2014). Among  
434 the five current MPAs in the Gulf of Lion, the AGD highly protected area therefore plays a  
435 key role in the network for the conservation of both *E. singularis* and *L. sarmentosa*, and  
436 should be enlarged in its south-eastern part to optimize their conservation. Finally, the ARES  
437 site also appears to be a major candidate for the creation of a new marine protected area, with  
438 effect on the gorgonian dominant species of the region, *E. singularis*.

439 Ideally, conservation spatial planning requires the definition of a biodiversity conservation  
440 objective, thus, targeting multiple species. The neutral theory approach whereby 30% habitat  
441 surface area would contain 60-70% of the species number has been widely used as a criteria  
442 in conservation spatial planning (Zhao et al. 2020). However, the neutral theory does not  
443 inform about species population density in a particular habitat subpart. This could be  
444 dramatic if the number of representatives of a species is too small to prevent the collapse of  
445 genetic diversity and demography (Allee, 1931). For species which are not evenly  
446 distributed like the two gorgonian species of the present study, a broad habitat criteria could

447 include sites where the species for which the functional connectivity was estimated was  
448 absent (Guizien et al. 2022). Most recent spatial conservation planning studies based on  
449 larval dispersal patterns of one or more species exhibited the same methodological bias and  
450 targeted a broad habitat category as the conservation goal without considering the actual  
451 distribution of the targeted species (White et al. 2014; Schill et al. 2015; Magris et al. 2016;  
452 D'Aloia et al. 2017; Krueck et al. 2017; Muenzel et al. 2022A and b). This could be improved  
453 using ecological niche modeling methods to refine species specific habitat delineation based  
454 on environmental predictors, as a basis for conservation planning studies (Sillero et al. 2021 ;  
455 Blouet et al. 2024). The present study suggests that using functional connectivity is all the  
456 more important that the conservation target is low. While aiming to protect 10 % of the  
457 habitat, more than 10 % of the Gulf of Lion metapopulation was put under protection using  
458 functional connectivity while it reaches only 6.6 % of the metapopulation using structural  
459 connectivity. However, for common species such as *E. singularis* and *L. sarmentosa* in the  
460 hard bottom habitat of the Gulf of Lion (Blouet et al. 2024), when the conservation target  
461 was increased to 30%, the importance of using functional connectivity vanished. We thus  
462 conclude the less ambitious the target, the more informed the decision should be.

463

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474

#### 475 **Author contributions**

476 SB and KG designed the study and wrote the manuscript, SB performed the Marxan  
477 simulations and TT, SH and KG performed the biophysical simulations of larval dispersal  
478 and established the ecological connectivity matrices. All reviewed and approved the final  
479 version of the manuscript.

480

#### 481 **Disclosure of conflicts of interest**

482 The authors of this publication declare that they have no financial conflicts of interest with  
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484

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	TARGET 10%				TARGET 30%			
	WITH EXISTING HIGHLY PROTECTED AREAS		NO PRE-EXISTING HIGHLY PROTECTED AREAS		WITH EXISTING HIGHLY PROTECTED AREAS		NO PRE-EXISTING HIGHLY PROTECTED AREAS	
	Cost	Surface (%)	Cost	Surface (%)	Cost	Surface (%)	Cost	Surface (%)
Structural connectivity (BLM=0.004)	12.0	9.0	14.1	8.8	37.3	28.4	40.6	28.3
Functional connectivity of early summer (CSM=3)	9.7	10.3	9.8	9.7	25.2	29.6	31.0	29.5
Functional connectivity of late summer (CSM=3)	5.1	10.1	9.8	9.5	24.9	29.3	30.6	28.8

720

721 Table 1 : Costs and proportion of the hard bottom habitat surface (average for the 100  
722 conservation plans) in the three connectivity scenarios (structural connectivity, functional  
723 connectivity of early summer, functional connectivity of late summer) and with or without  
724 existing highly protected areas in the objective of fully protecting 10% or 30% of the hard  
725 bottom habitat surface.

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732 **List of Figures**

733

734 Figure 1: Median larval transport (probability of transfer) in the study area after a pelagic  
735 dispersal duration of 7 days for a release from June 1 to July 10 (early summer, *Eunicella*  
736 *singularis*, A) and from August 1 to September 10 (late summer, *Leptogorgia sarmentosa*, B)  
737 during the 3 summers (2010, 2011 and 2012) between each of the 138 hard bottom habitat  
738 planning units (black polygons). The blue lines correspond to southward larval transport. The  
739 red lines correspond to northward larval transport.

740

741 Figure 2: Selection frequency of planning units obtained with Marxan in the objective of  
742 fully protecting 10% of the hard bottom habitat surface in 4 configurations: considering  
743 existing highly protected areas (upper panels) and structural connectivity (A) or early  
744 summer functional connectivity as asymmetric spatial dependence (B) and disregarding  
745 existing highly protected areas (lower panels) and structural (C) or early summer functional  
746 connectivity as asymmetric spatial dependence (D). The five classes of selection frequencies  
747 obtained from the 100 runs used were: 10-20% (low), 20-40%, 40-60%, 60-80%, 80-100%  
748 (high).

749

750 Figure 3: Selection frequency of planning units obtained with Marxan in the objective of  
751 fully protecting 30% of the hard bottom habitat surface in 4 configurations: considering  
752 existing highly protected areas (upper panels) and structural connectivity (A, BLM=0.004) or  
753 early summer functional connectivity as asymmetric spatial dependence (B, CSM=3) and  
754 disregarding existing highly protected areas (lower panels) and structural (C, BLM=0.004) or  
755 early summer functional connectivity as asymmetric spatial dependence (D, CSM=3). The

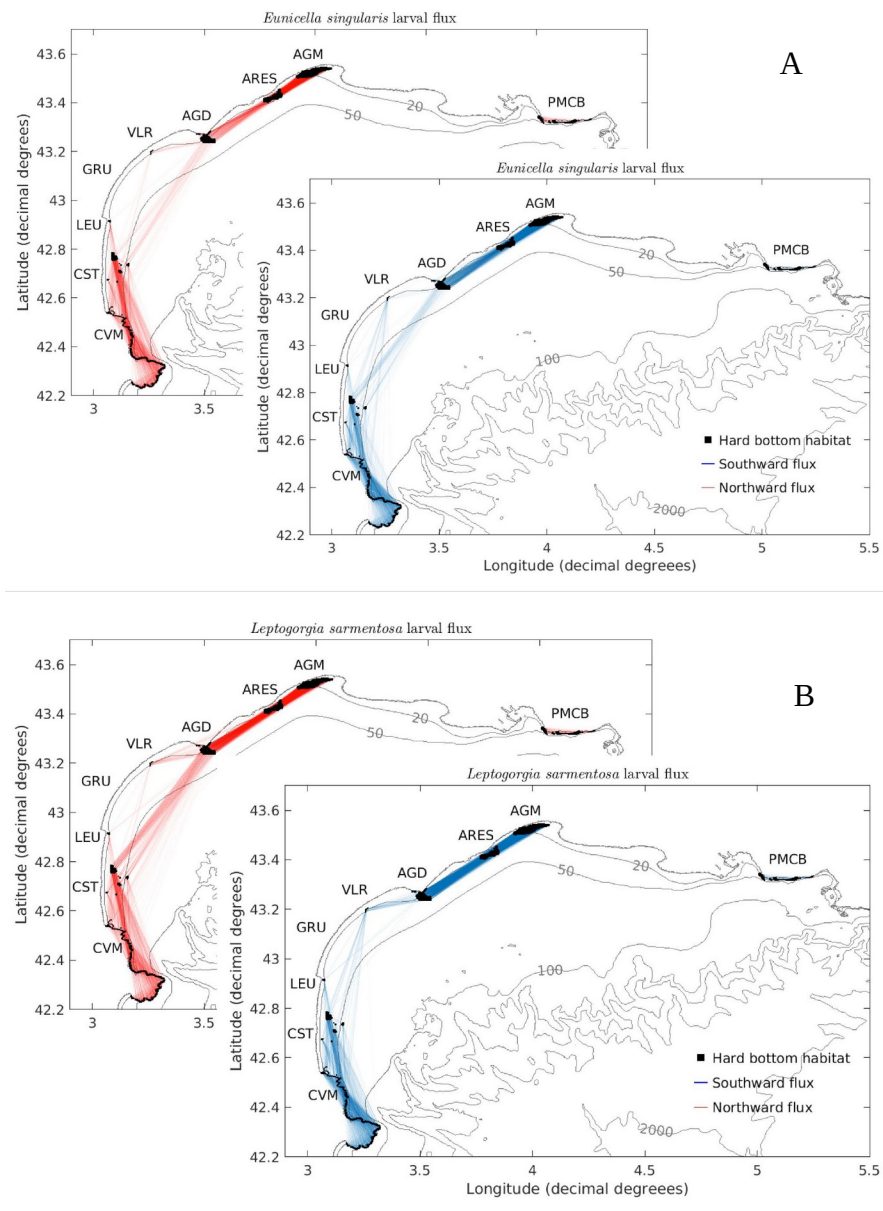


756 five classes of selection frequencies obtained from the 100 runs used were: 30-44% (low),  
757 44-58%, 58-72%, 72-86%, 86-100% (high).

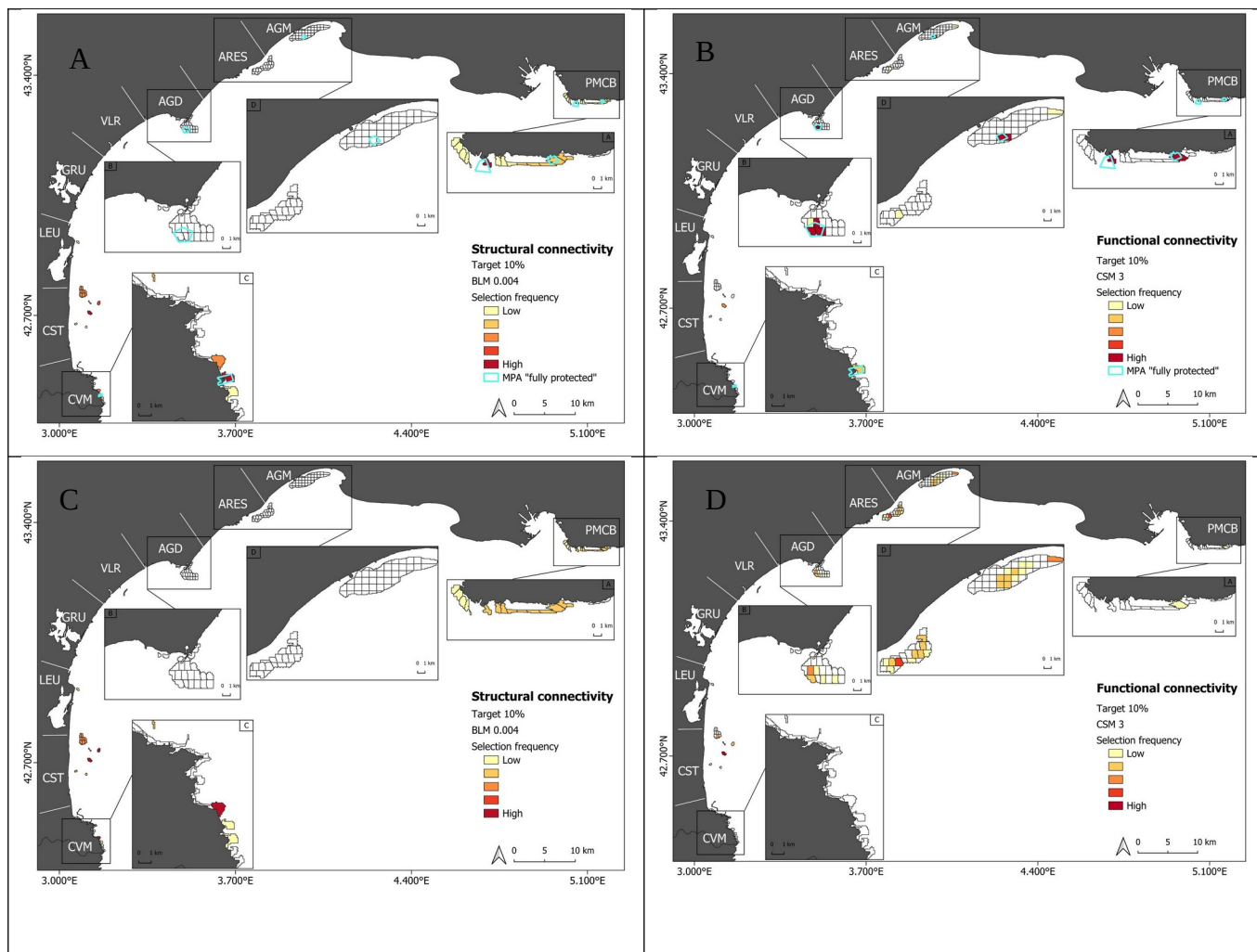
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759 Figure 4 : Boxplot of the efficiency of the 100 conservation plans in protecting *Eunicella*  
760 *singularis* (A) and *Leptogorgia sarmentosa* (B) for the targets of 10% and 30% protection of  
761 the hard bottom habitat in the different connectivity scenarios : structural (BLM=0.004),  
762 functional in the early summer (Es, CSM=3), functional in the late summer (Ls, CSM=3),  
763 extending the current highly protected. Cost of the conservation plans were calculated using  
764 the current cost with HPAs.

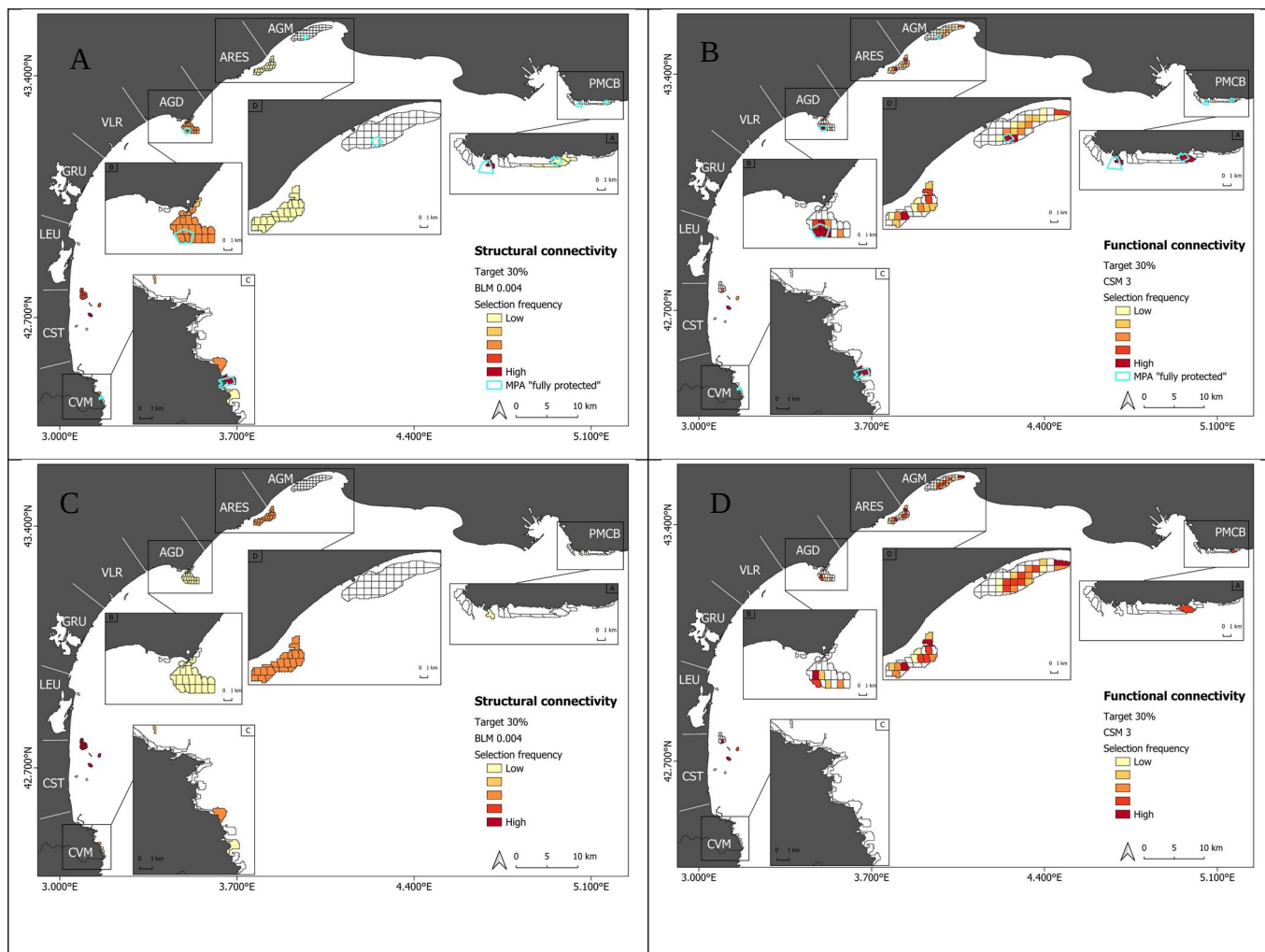
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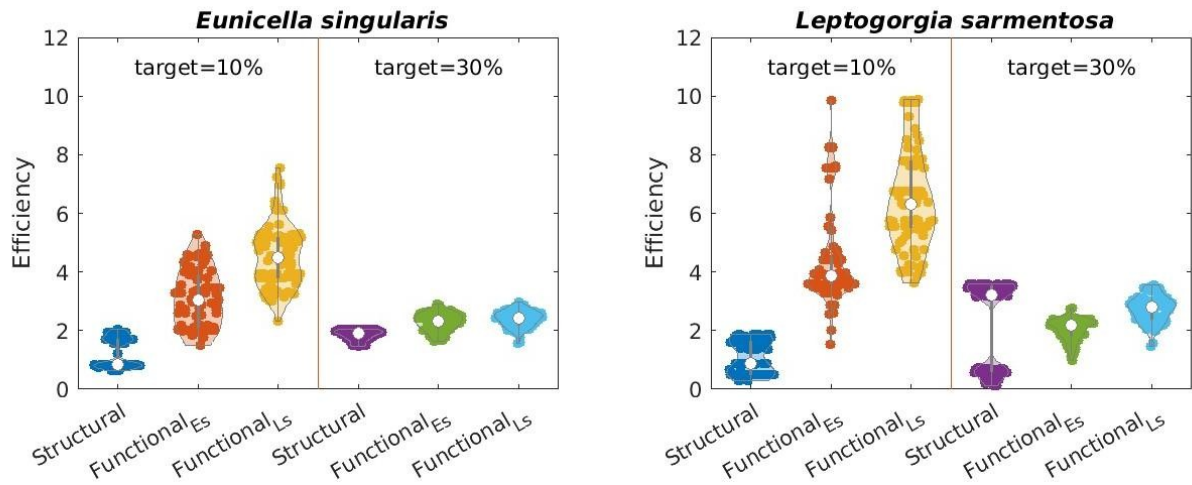
**Figure 1: Median larval transport (probability of transfer) in the study area after a pelagic dispersal duration of 7 days for a release from June 1 to July 10 (early summer, *Eunicella singularis*, A) and from August 1 to September 10 (late summer, *Leptogorgia sarmentosa*, B) during the 3 summers (2010, 2011 and 2012) between each of the 138 hard bottom habitat planning units (black polygons). The blue lines correspond to southward larval transport. The red lines correspond to northward larval transport.**



**Figure 2: Selection frequency of planning units obtained with Marxan in the objective of fully protecting 10% of the hard bottom habitat surface in 4 configurations: considering existing highly protected areas (upper panels) and structural connectivity (A) or early summer functional connectivity as asymmetric spatial dependence (B) and disregarding existing highly protected areas (lower panels) and structural (C) or early summer functional connectivity as asymmetric spatial dependence (D). The five classes of selection frequencies obtained from the 100 runs used were: 10-20% (low), 20-40%, 40-60%, 60-80%, 80-100% (high).**



**Figure 3: Selection frequency of planning units obtained with Marxan in the objective of fully protecting 30% of the hard bottom habitat surface in 4 configurations: considering existing highly protected areas (upper panels) and structural connectivity (A, BLM=0.004) or early summer functional connectivity as asymmetric spatial dependence (B, CSM=3) and disregarding existing highly protected areas (lower panels) and structural (C, BLM=0.004) or early summer functional connectivity as asymmetric spatial dependence (D, CSM=3). The five classes of selection frequencies obtained from the 100 runs used were: 30-44% (low), 44-58%, 58-72%, 72-86%, 86-100% (high).**



**Figure 4 : Boxplot of the efficiency of the 100 conservation plans in protecting *Eunicella singularis* (A) and *Leptogorgia sarmentosa* (B) for the targets of 10% and 30% protection of the hard bottom habitat in the different connectivity scenarios : structural (BLM=0.004), functional in the early summer (Es, CSM=3), functional in the late summer (Ls, CSM=3), extending the current highly protected. Cost of the conservation plans were calculated using the current cost with HPAs.**

## Supplementary Material

### Functional Connectivity improves the efficiency of the extension of a network of highly protected marine areas (Gulf of Lion, North Western Mediterranean sea)

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1 CNRS-Sorbonne Université, Laboratoire d'Ecogéochimie des Environnements Benthiques, LECOB, Observatoire Océanologique de Banyuls Sur Mer, 66650 Banyuls sur Mer, France

2 Ville d'Agde, Aire marine protégée de la côte agathoise, 34300 Agde, France.

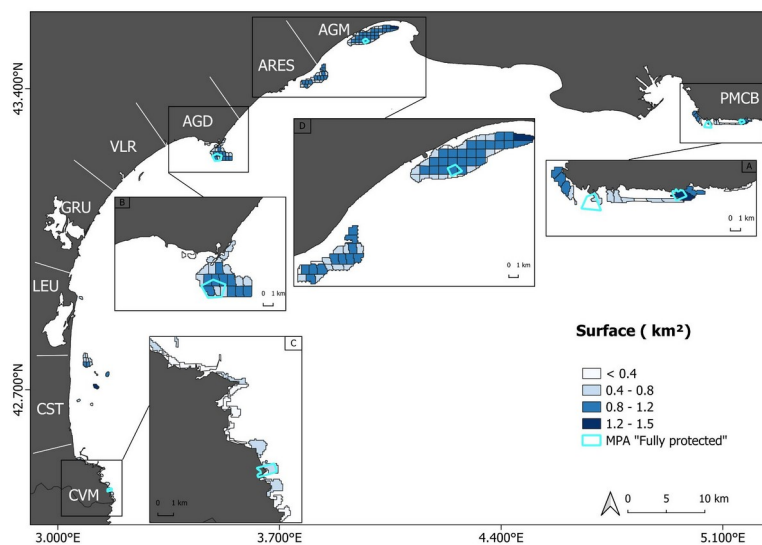
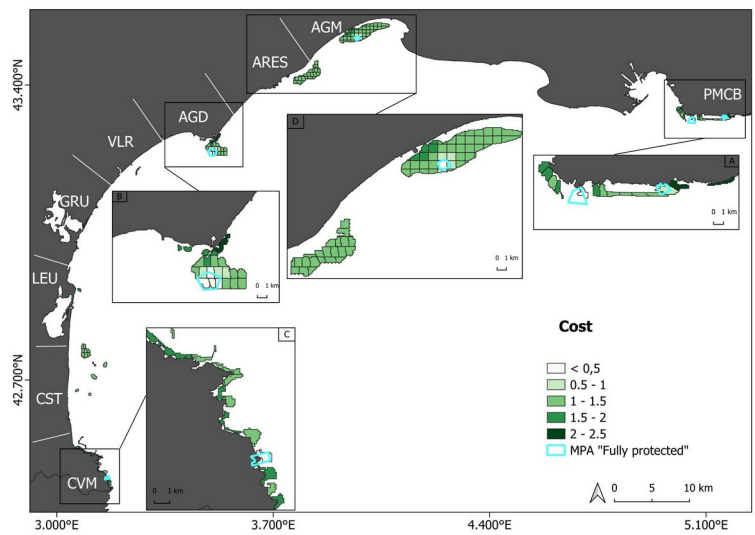
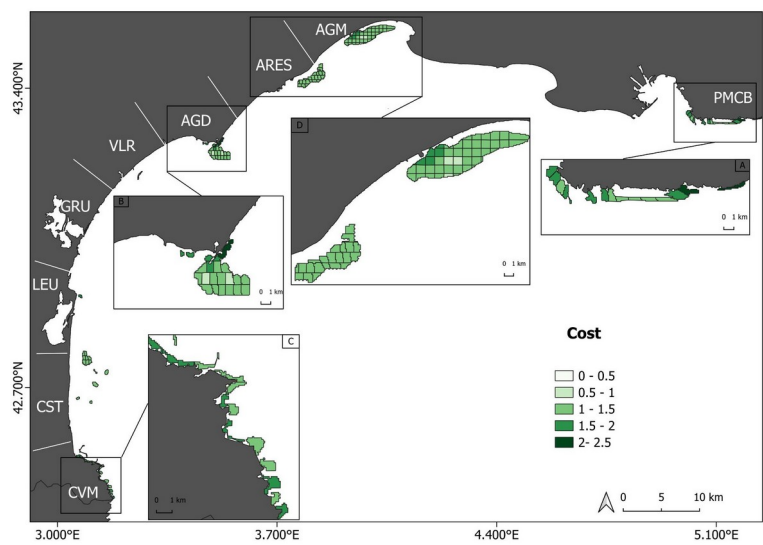


Figure S1: Surface areas of the 138 planning units used to describe the hard bottom habitat.



**Figure S2: Costs applied to the 138 planning units used to explore conservation plans in the configuration without pre-existing highly protected areas (A) and with existing highly protected areas (B).**

10% of Natural habitat 30% of Natural habitat	With existing highly protected areas	without existing highly protected areas
Structural continuity	BLM=0 <b>BLM=0.004</b> BLM=1	BLM=0 <b>BLM=0.004</b> BLM=1
Early summer functional connectivity	<b>CSM=3</b> CSM=10 CSM=100	<b>CSM=3</b> CSM=10 CSM=100
Late summer functional connectivity	<b>CSM=3</b> CSM=10 CSM=100	<b>CSM=3</b> CSM=10 CSM=100

Table S1: Summary of all simulations performed varying the conservation plan target (10 and 30% of the Natural Habitat), the type of connectivity (Structural, early summer functional, late summer functional), the cost with or without existing highly protected areas and the value of the Marxan parameter regulating the cost penalty if not taking into account connectivity.

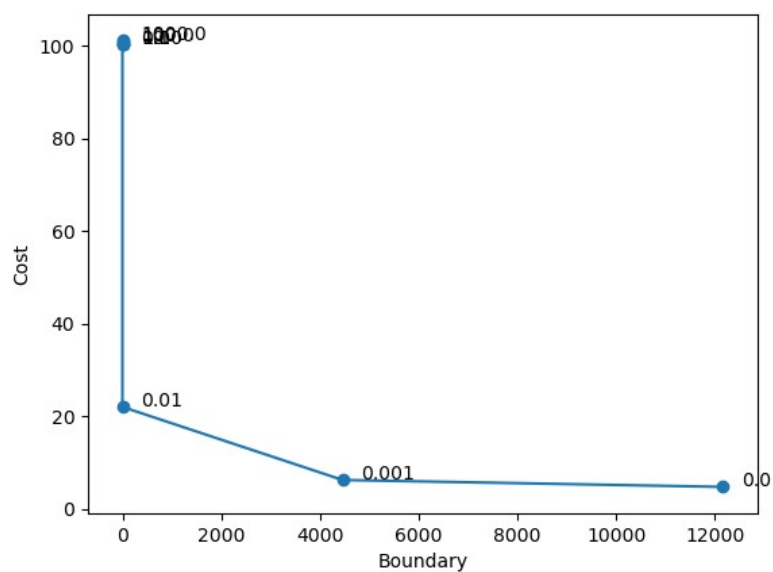




Figure S3 : Cost evolution with boundary length. The median point estimation is 0.004, which corresponds to a cost of 19.6 for a boundary length of 530 meters. Figure and values obtained with ©Qmarxan software.

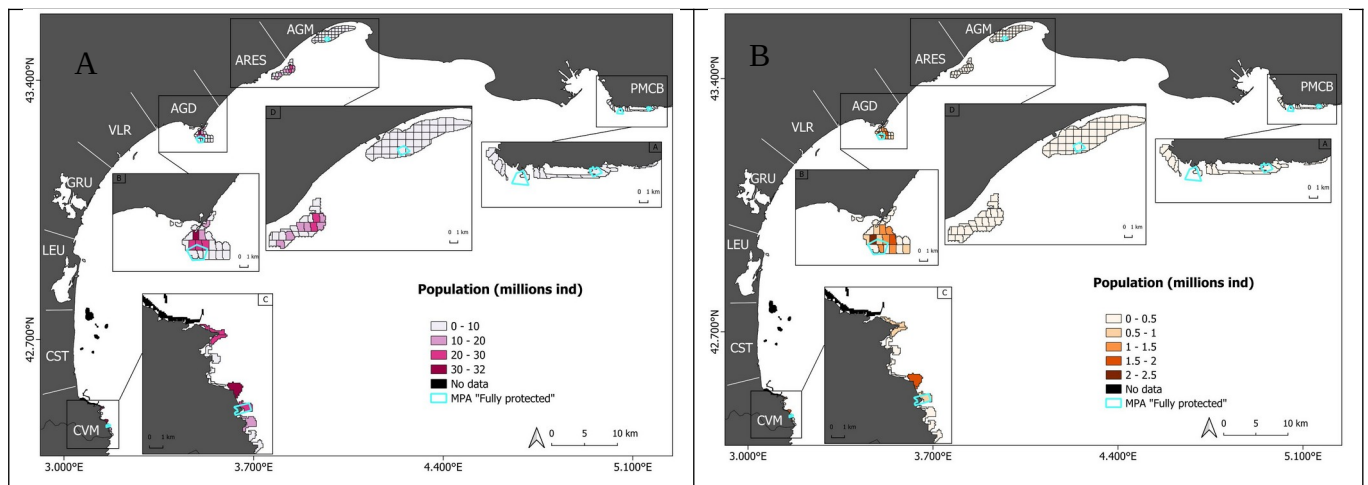


Figure S4 : Mapping of maximum population densities per planning units for (A) *Eunicella singularis* and (B) *Leptogorgia sarmentosa*

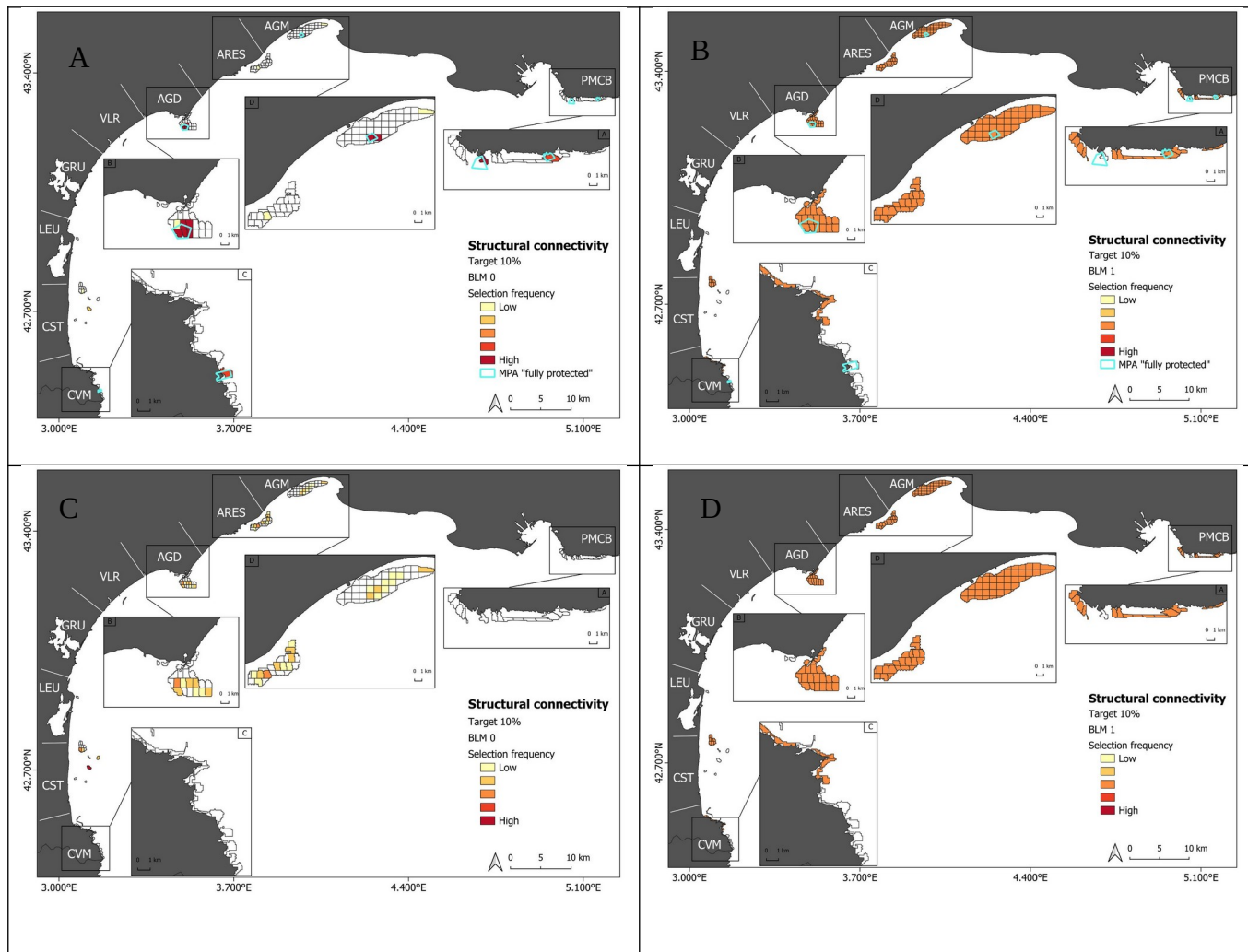
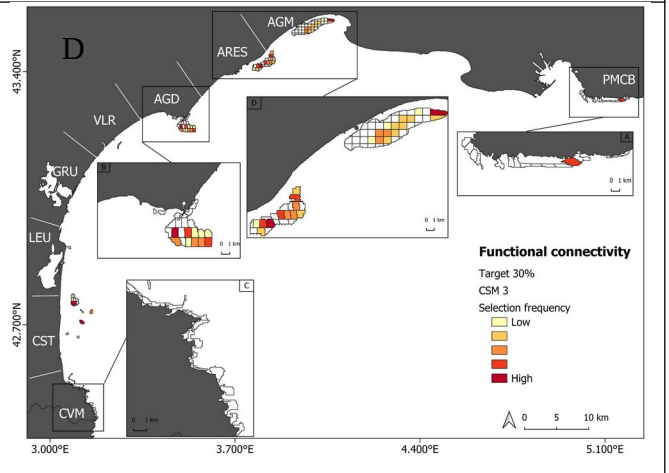
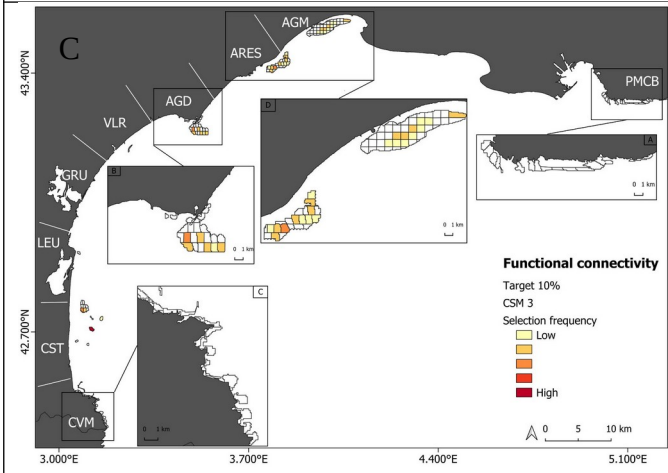
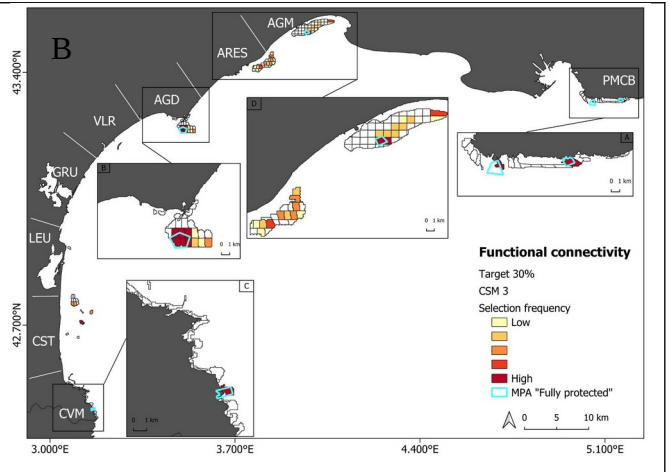
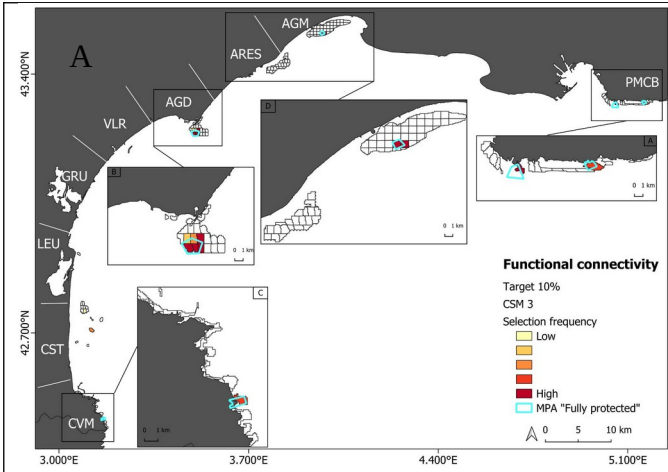
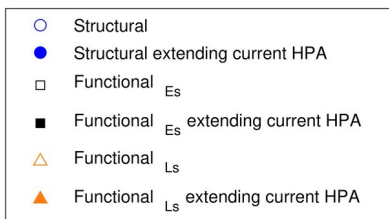
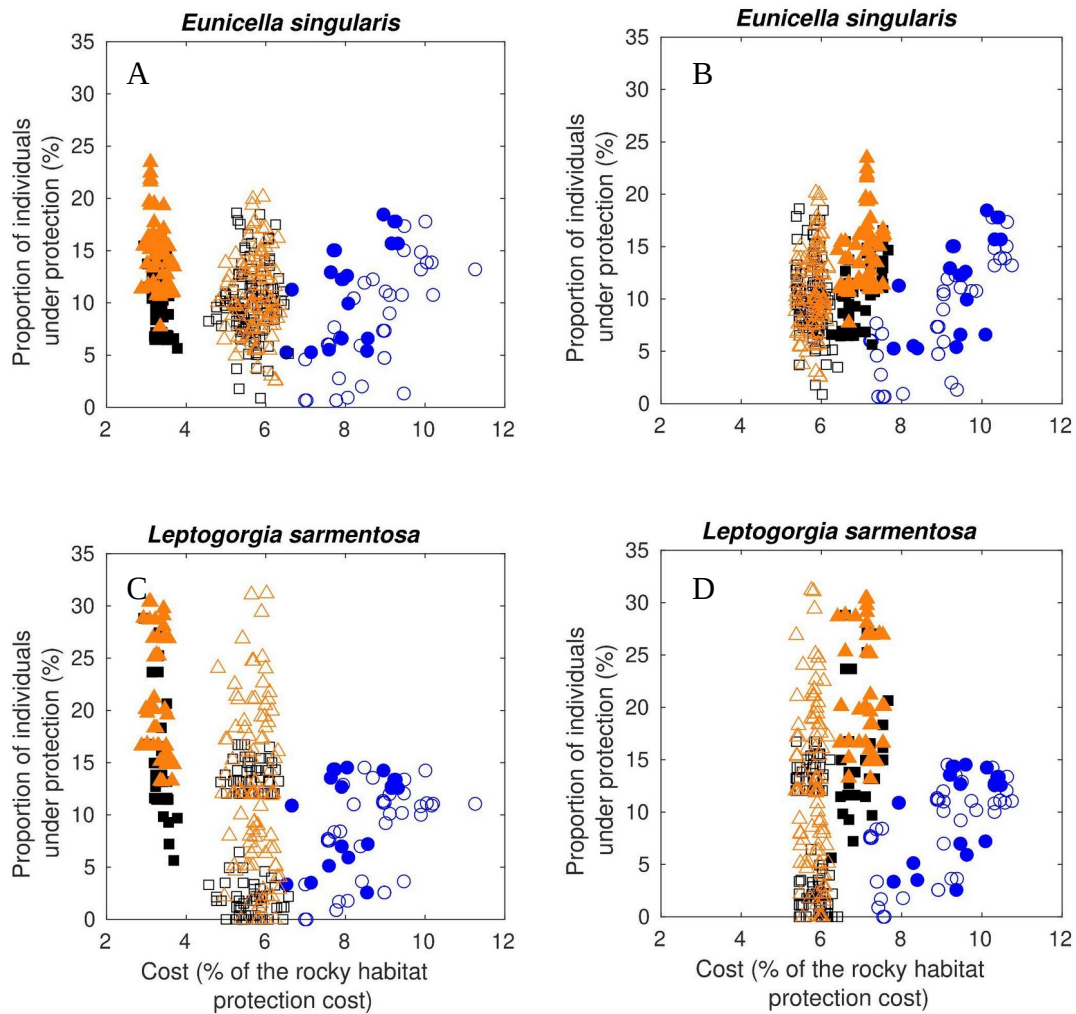


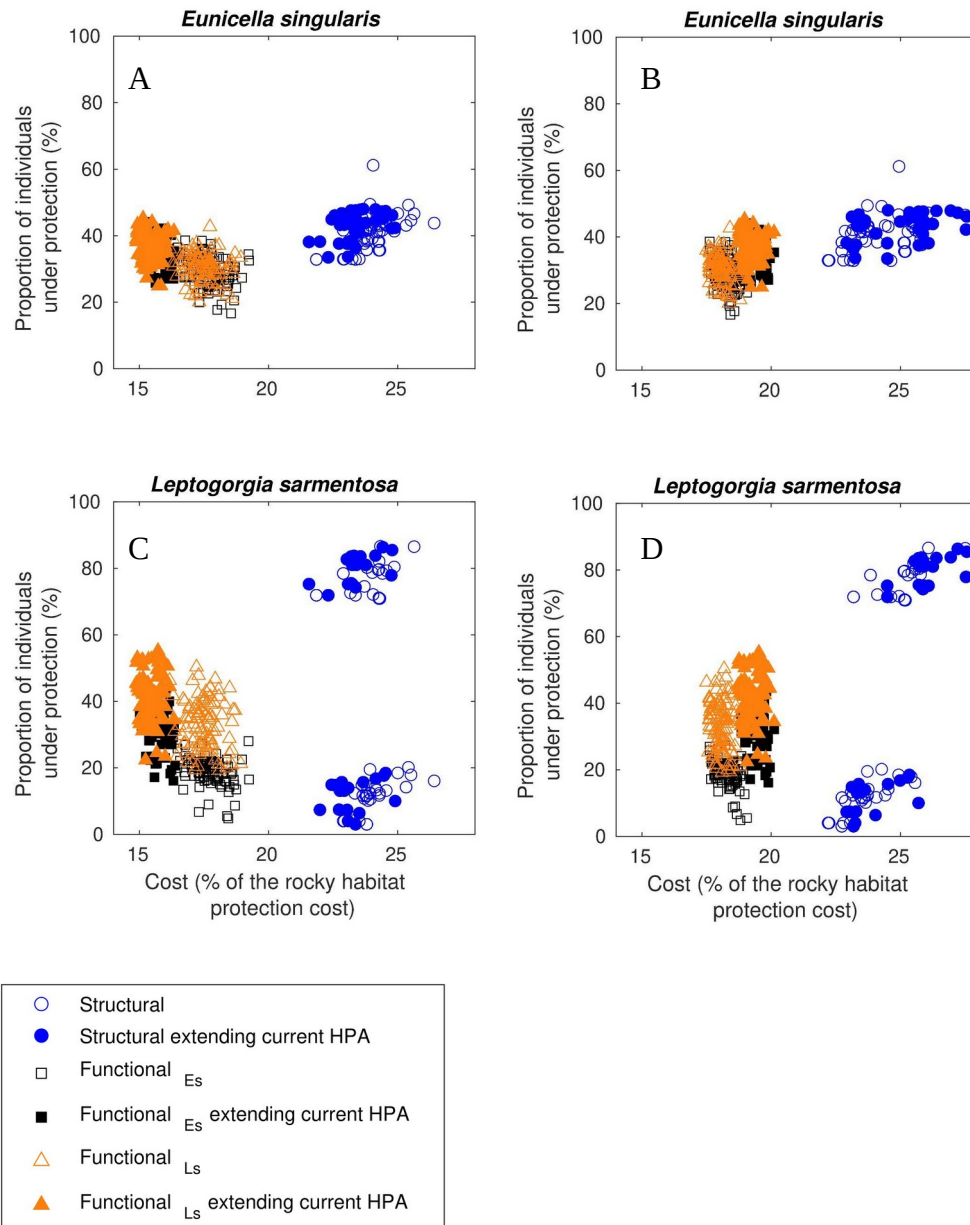
Figure S5: Sensitivity of selection frequency of planning units across the 100 conservation schemes in the objective of fully protecting 10% of the hard bottom habitat surface to the structural continuity scaling factor with current full protection areas (A: BLM=0 ; B: BLM=1). Same but without considering current full protection areas (C: BLM=0 ; D: BLM=1). The five classes of selection frequencies obtained from the 100 runs used were: 10-20% (low), 20-40%, 40-60%, 60-80%, 80-100% (high).



**Figure S6: Selection frequency of planning units obtained with Marxan in the objective of fully protecting 10% (left panels) and 30% (right panels) of the hard bottom habitat surface considering pre-existing full protection areas (upper panels) and disregarding existing full protection areas (lower panels) using late summer functional connectivity as asymmetric spatial dependence (CSM=3). Note that the five classes of selection frequencies obtained from the 100 runs differed with the protection objective. The five classes were: 10-20% (low), 20-40%, 40-60%, 60-80%, 80-100% (high) in the 10% objective and 30-44% (low), 44-58%, 58-72%, 72-86% and 86-100% in the 30% objective.**



**Figure S7 : Relationship between the proportion of individuals of *Eunicella singularis* (A, B) and *Leptogorgia sarmentosa* (C, D) under protection and the cost of the 100 conservation plans for a target of 10% protection of the hard bottom habitat in the different connectivity scenarios : structural, functional in the early summer (Es), functional in the late summer (Ls), extending or not the current highly protected. Cost of the conservation plans were calculated using the current cost with HPAs and the cost if no HPAs have been implemented in the region.**



**Figure S8 : Relationship between the proportion of individuals of *Eunicella singularis* (A, B) and *Leptogorgia sarmentosa* (C, D) under protection and the cost of the 100 conservation plans for a target of 30% protection of the hard bottom habitat in the different connectivity scenarios : structural, functional in the early summer (Es), functional in the late summer (Ls), extending or not the current highly protected. Cost of the conservation plans were calculated using the current cost with HPAs and the cost if no HPAs have been implemented in the region.**