Artificial reefs geographical location matters more than its age and depth for sessile invertebrate colonization in the Gulf of Lion (NorthWestern Mediterranean Sea)

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ABSTRACT

Artificial reefs (ARs) have been used to support fishing activities. Sessile invertebrates are essential components of trophic networks within ARs, supporting fish productivity. However, colonization by sessile invertebrates is possible only after effective larval dispersal from source populations, usually in natural habitat. We tested the relevance of geographic location, duration of immersion and depth on ARs colonization processes in the Gulf of Lion. Five species sessile invertebrates species, with contrasting life history traits and regional distribution in the natural rocky habitat, were inventoried on ARs deployed during two immersion periods (1985 and 2000-2009) and at different depths. At the local level, neither depth nor immersion duration differentiated ARs assemblages. At the regional scale, colonization patterns differed between species, resulting in diverse assemblages.

This study highlights the primacy of geographical positioning over immersion duration and depth in ARs colonization, suggesting it should be accounted for in maritime spatial planning.

KEY WORDS: ARTIFICIAL REEF, BENTHIC INVERTEBRATES, DEPTH, IMMERSION DURATION, GEOGRAPHICAL LOCATION, LIFE TRAITS

INTRODUCTION

The decline of fish stocks and natural marine habitat degradation resulting from human exploitation have been documented worldwide for decades (Claudet and Fraschetti, 2010; Jackson, 2001; Pauly et al., 2002).

Artificial reefs (ARs) have been primarily implemented to reduce the pressure of fisheries in coastal areas, complementing other management tools such as marine protected areas or regulatory measures such as fishing licenses (Claudet and Pelletier, 2004; Seaman, 2007; Wilson, 2002). Moreover, ARs could provide economic benefits linked to recreational activities such as recreational fishing and scuba diving (Chen et al., 2013). Beneficial effects such as fish biomass and capture efficiency increase near ARs have been reported (reviewed by Bohnsack and Sutherland, 1985; Tessier et al., 2014). However, the quick colonization by fish and mobile invertebrates (Powers et al., 2003; Relini, 2002; Santos and Monteiro, 2007) led to a debate opposing attraction vs production regarding the effects of ARs on fishery (Grossman et al., 1997). The fish production argument is based on the hypotheses of a better protection against predators and an increase in available substrate area for larval establishment thanks to habitat complexification and an increase of available trophic resource (Bohnsack, 1989). In natural rocky habitats, benthic invertebrates play an essential role in fish trophic networks (Ardizzone et al., 1996; Martens et al., 2006), and ARs trophic network showed similarity with natural rocky habitat one, with dominance of filter-feeders using phytoplanktonic primary production and fish predation on crustacean colonizing the ARs (Cresson, 2013). Moreover, AR deployed in sandy areas are expected to enhance fish productivity given that epifauna secondary production per ARs unit surface has been estimated to be 30 times greater than that of natural sandy infauna (Steimle, 2002). However, those estimates were made shortly after immersion and do not prove the long-term fish production in ARs and supporting this argument would require extending, in the long-term, data on colonization by benthic invertebrates (Svane and Petersen, 2001). Indeed, the age since deployment has been described as a key factor to explain ARs coverage by benthic invertebrates (Svane and Petersen, 2001). The assemblages of benthic communities are expected to

53 change over time in a succession between pioneer and specialist species (Connell and Slatyer, 1977).
54 In contrast with pioneer species, specialist ones have slower colonization dynamics, because of their
55 lower fecundity (Fava et al., 2016). However, after colonization, specialists are expected to
56 outcompete pioneer species due to their more efficient use of environmental resources (Connell and
57 Slatyer, 1977). Among these, light availability is an essential factor shaping marine benthic
58 communities across the water depth gradient (Odum, 1971). Several studies have shown a decrease
59 in the density of benthic invertebrates with depth on ARs (Lewbel et al., 1986.; Moura et al., 2007;
60 Shinn and Wicklund, 1989; van der Stap et al., 2016) explained by the decrease in light intensity (Relini
61 et al., 1994). The structural complexity has also been put forward as important characteristics linked
62 to ARs efficiency in ecological restoration (Strain et al., 2018). Structural complexity increases available
63 surface for colonization and niches diversity with various shelter and light exposure conditions, the
64 latter being related to different benthic assemblage compositions (Glasby, 2000; T. M. Glasby, 1999)
65 and higher productivity (Vivier et al., 2021). The recent 3D printing techniques using concrete, allow
66 the design of ARs mimicking natural habitats (Ly et al., 2021). However, those studies concerned short-
67 term colonization (<3.5 years) (Wendt et al., 1989) hence based on pioneer species with high dispersal
68 capacities which colonization is likely mainly regulated by post-settlement processes such as
69 competition, predation and physical disturbance (Todd, 1998). In contrast to mobile species,
70 sessile benthic invertebrates can only colonize reefs after larval dispersal which is limited by
71 reproduction frequency (Thorson, 1950). Colonization implies thus an effective dispersal between
72 natural areas and ARs, which depends on source population spatial distribution, species fecundity,
73 dispersive larval traits and ocean circulation. Nevertheless, until now dispersal drivers have been
74 disregarded while colonization disparities among ARs may result from differences in both larval
75 connectivity (which in turn depends on fecundity, dispersal capacities and adult distribution in the
76 natural habitat) and post-recruitment processes.
77 The objective of the present study was to test the hypothesis that the geographical location of ARs
78 deployment with respect to the natural habitat can condition ARs colonization in the long term. To this

aim we investigated the effects of local (depth and immersion duration) and regional (geographic area) factors on the presence and abundance of five species of sessile invertebrates with different life history traits, endemic to the Gulf of Lion (GDL) (Northwestern Mediterranean Sea) and frequently found on natural hard substrates. Data were collected on ARs immersed for more than 10 years in the GDL and assemblage composition analysis at three nested spatial scales (~ 1kms; ~5kms; >30 kms) were combined.

MATERIALS AND METHODS

Study area and spatially stratified sampling design

The study area extended along 160 km of the GDL coastline (Figure 1). The GDL is a wide micro-tidal continental shelf dominated by soft-bottom habitat with few small rocky habitat patches of less than 20 km^2. The GDL is a homogeneous and isolated hydrodynamic unit (Rossi et al., 2014), delimited by the northern current (Millot, 1990).

Between 1985 and 2009, 763 ARs with different shapes or material and a total volume of 37 575 m^3 (Tessier et al., 2015) have been deployed along the GDL coastline over 66 km^2 of state concessions (Cepralmar, 2015) between 10 and 35 m depth (Figure 1, Blouet et al., 2021). The ARs deployed in GDL represent 40% of the total AR volume in France (Tessier et al., 2015).

Deployment was performed during three major time periods: 1985, 1992-1999 and 2004-2009, but for the present study we examined only the oldest (1985) and the youngest (after 2000) ones. For the analysis of data, we followed a stratified sampling design. To this aim, the GDL coastline was regularly divided into 6 geographical sectors separated by a distance ranging from 12 to 117 km, with a median value of 49 km (AGM, AGD, VLR, GRU, LEU, CST, Figure 1). Each sector included ARs deployed during either the first (1985, CST geographical sector), the last (2004-2009, AGM, VLR, GRU, LEU geographical sectors) or both periods of immersion (AGD). In each sector, two sites separated by a distance ranging from 2.1 to 11.7 km (median value of 7.5 km) were defined, except in AGD where 5 sites were defined.

105 In each site, three sampling units separated by a distance between 4m and 3.6 Km (median distance
106 of 251 m) were set out by pooling neighboring ARs reaching a minimum surface of 89 m^2 per sampling
107 unit and totalling a minimum developed surface of 306 m^2 per site. Such large continuous sampling
108 units in each site aimed at limiting the effect of recruitment spatial variability over distances from 100s
109 meters to kilometers arising from the non-uniformity of the flow of larvae (Daigle et al., 2014; Glasby,
110 2000; Simpson et al., 2017; Smale, 2012). Such a spatial scale is consistent with the spatial scale of flow
111 homogeneity obtained in simulations over GDL soft-bottom habitat (Briton et al., 2018). This inventory
112 methodology enabled us to test for the existence of structuring factors at the local and regional scale.
113 In the geographical sector GRU, in one of the two sites, only two sampling units could be defined given
114 the ARs shapes, yielding a total surface of 600 m^2 (Supplementary Material Table 1). Developed reef
115 surface was calculated on the basis of technical specifications data present in the state concession
116 documents taking into account only the colonizable surface (surfaces in contact with the sediment
117 were excluded).
118
119 **Colonization assessment**
120 Assessment of ARs colonization was carried out by autonomous scuba-diving in 2020 by counting the
121 number of individuals of the five target species in the 44 sampling units (Supplementary Material
122 Table1, totalling 80 ARs fully inventoried). Among the species listed in previous ARs inventories in the
123 GDL, we selected five species that were present in most inventories, easy to identify by scuba diving
124 and spanning different phyla with contrasting life-history traits (Créocean, 2003 & 2004; Table 1). We
125 selected two gorgonians *Eunicella singularis* (Esper, 1791) and *Leptogorgia sarmentosa* (Esper, 1789),
126 one bryozoan *Pentapora fascialis* (Pallas, 1766), one annelida *Sabella spallanzanii* (Gmelin, 1791) and
127 one ascidian *Halocynthia papillosa* (Linnaeus, 1797) (Figure 2). The five species have a similar wide
128 natural repartition area along European coasts ranging from 1m to 250m depth (Giangrande et al.,
129 2005; Gori et al., 2011; Ponti et al., 2019; Turon, 1990; Weinberg and Weinberg, 1979). In addition, *S.*

130 *spallanzanii* has been recorded along the coasts of Brazil, Australia and New Zealand where it is
131 classified as an invasive non-indigenous species (Currie et al., 2000).
132 The five species are present in the rocky habitat of the NW Mediterranean Sea (Laubier, 1966; True,
133 1970; Hong, 1980). However, in the GDL, where natural rocky habitat covers uneven surfaces within
134 the 6 geographical sectors (from 3,123 10^7 m^2 for the AGM sector to 5 10^5 m^2 for the LEU sector), the
135 five species display different spatial distributions (Dutrieux et al., 2005; Dalias et al., 2011; Padron et
136 al., 2018; S. Blouet personal observation). *E. singularis* is frequently observed and abundant
137 throughout the GDL (from the AGM sector to the CST sector), while *L. sarmentosa,* less abundant, is
138 present mainly in the center of the GDL (AGD, VLR, LEU, CST). *P. fascialis* is abundant in the west of the
139 GDL (AGD, LEU, CST, and south of CST). The distribution of *H. papillosa* is not well known, however the
140 species has been observed in all the rocky areas of the GDL. *S. spallanzanii* is present but rare in natural
141 rocky habitat. Nevertheless, *S. spallanzanii* is very abundant in lagoons, ports and marinas of the GDL
142 (S. Blouet personal observation) which have been indicated as preferred habitat of the species (Currie
143 et al., 2000).
144
145 The five species display different life-history traits. All five species reproduce once a year in different
146 seasons and with different strategies (Table 1).
147 *S. spallanzani* reproduces in January-February, when water temperature is the coldest. The species
148 displays multiple reproductive strategies: internal fertilization, with larvae brooded either inside or
149 outside the mineral tube secreted around the body, and external fertilization broadcast spawning
150 (Giangrande et al., 2000). In addition, asexual reproduction by fission has been reported (Read et al.,
151 2011). *S. spallanzani* releases lecithotrophic larvae with a planktonic larval duration (PLD) of about 4
152 weeks (Giangrande et al., 2000). It's life span can exceed 5 years, with sexual maturity after one year
153 (Giangrande and Petraroli 1994; Giangrande et al., 2000). Like most gorgonians, *E. singularis* releases
154 lecithotrophic larvae in early summer (June to August). Even though larval competency period can
155 reach up to 2 months (Guizien et al., 2020; Zelli et al., 2020), PLDs ranging from 7 to 14 days best

156 explain gene flow among *E. singularis* natural populations dwelling in the fragmented rocky habitat of
157 the GDL (Padron et al. 2018). *E. singularis* life span can reach 25-30 years with sexual maturity before
158 6 years (Gori et al., 2007; Weinberg and Weinberg, 1979) (Weinberg and Weinberg 1979, Gori et al.
159 2007).
160 The other gorgonian, *L. sarmentosa* also releases lecithotrophic larvae but in the late summer
161 (September to October) and the PLD is unknown (Rossi and Gili 2009). *L. sarmentosa* life span can
162 reach 20 years with female sexual maturity within 2-3 years after settlement (Rossi and Gili 2009).
163 *H. papillosa* is a simultaneous hermaphrodite which releases larvae in late summer (September-
164 October; Becerro and Turon, 1992), presumably lecithotrophic. The PLD of *H. papillosa* larvae is
165 unknown but PLD shorter than 12 hours has been consistently reported for other solitary ascidian
166 species (Ayre et al., 1997). We did not find any data about the age at sexual maturity and the life span
167 of *H. papillosa*. However, the ascidians are considered as highly invasive, particularly because of their
168 rapid growth and early sexual maturity (Zhan et al., 2015), with some species such as C*iona*
169 *intestionalis* complex and *Ciona savigniy,* reaching sexual maturity at the age of 2 months (Zhan et al.,
170 2015) and continuous spawning (Carver et al. 2003).
171 *P. fascialis* displays both sexual and asexual reproduction. During sexual reproduction, most bryozoans
172 release lecithotrophic larvae which settle after a few minutes or a few hours, rarely beyond several
173 days (Keough, 1983). *P. fascialis* larval release has been inferred to happen in June based on
174 recruitment observations (Cocito et al., 1998a). Asexual reproduction happens by colony
175 fragmentation or budding extension (Cocito et al., 1998b). Individual life span is estimated to be about
176 10 years with early sexual maturity after 2 years (Cocito et al., 1998b).
177
178 **Statistical analysis**
179 We examined to which extent ARs colonization is affected by the location and timing of deployment.
180 To do so, we tested the effect of 4 factors (geographical sector being the regional factor, site being the
181 local factor, depth and age) on the presence/absence of the five species and on the dissimilarity

182 between their co-occurrence assemblages. In all analyses, site was a random factor, nested either in
183 year, age or the geographical sector factor. Due to AR deployment set up, the effect of factors age (2
184 levels, 1985, 2002-2009) and depth (2 levels, >20 m, <20 m depth) was tested within the AGD
185 geographical sector only. Factor age was tested in 3 sites at <20m and factor depth was tested in 4
186 sites deployed in 2009. To avoid any confounding effect due to age or depth, the regional factor vs
187 local factor were tested on the 5 geographical sectors where AR were deployed during the 2002-2009
188 immersion phase and at <20 m depth only (AGM, AGD, VLR, GRU, LEU: 5x2 levels). A Jaccard similarity
189 matrix was built on presence/absence data across all pairwise sampling units. Two multivariate
190 analyses were performed. Non-parametric multivariate analysis of variance with permutation was
191 applied to test for the effects of age, depth and geographical sector on species assemblages (NP-
192 manova: Anderson, 2001; Zar, 1999). Another multivariate analysis was performed to cluster most
193 similar species assemblages in the sector of AGD (SIMPROF : Clarke et al., 2008).
194 When significant differences between the five species co-occurrence assemblages were detected for
195 a factor, a non-parametric univariate analysis (ANOVA Kruskall-Wallis) was performed for each species
196 independently to detect the species driving the difference. Fisher post-hoc test was used to identify
197 the site where the difference arose. A same p-value of 0.05 was taken for detecting significant
198 differences. Analyses were performed with Matlab software using the Fathom package for multivariate
199 analyses (Jones, 2014) and the Matlab statistics toolbox for univariate analyses.
200
201 **RESULTS**
202 **Artificial reefs colonization by the five target species** at **regional scale**
203 Among the five target species, *S. spallanzanii* was the only one whose presence was recorded in all the
204 sampling units and geographical sectors (Figure 4). In only one out of 15 sites, it was the only species
205 detected. *H. papillosa* was detected in all geographic sectors but not in all the sampling units. *L.*
206 *sarmentosa* was detected in five of the six geographical sectors (not present in AGM) and *P. fascialis*
207 was detected in 3 of the 6 geographical sectors (CST, LEU and AGD). Finally, *E.singularis* was the least

208 frequently observed species, being detected in only three geographical sectors (AGM, AGD and LEU).
209 In all geographical sectors, at least three of the five target species were detected. Assemblages of two
210 species were found in only one site out of 15 (sector AGD), assemblages of three species were found
211 in 8 sites, assemblages of four species were found in 2 sites and assemblages of five species were found
212 in 3 sites.
213
214 **Age and depth effects on five target species at local scale**
215 Despite all five target species being detected on ARs in the AGD sector, assemblage composition
216 among sites differed (Figure 3). Clustering of sampling units within the 5 sites (A, B, C, D, E) in AGD
217 identified 2 clusters (SIMPROF: $P < 0.05$; Figure 4). The two sites (B and C) with same age (2009), depth
218 range (less than 20 m) and reef shape (pipe) were attributed to different clusters.
219 In fact, one cluster grouped ARs of different age at a same depth (1985 in site A and 2009 in site B)
220 while the other cluster grouped ARs of the same age but at different depths (less than 20 m in site C
221 and more than 20 m in sites D and E). In both clusters, different AR shapes were found (steel cage and
222 pipes in one cluster, pipes, Comin and Bonna in the other cluster, Figure 4). The geographic distance
223 between the two clusters (A-B) and (C-D-E) was 7.5 km and the median value of the intra-cluster
224 geographic distance was 3 km.
225 Multivariate analysis of variance confirmed that neither age (NP-MANOVA, $F=1.43$ $P<0.05$; Table 2)
226 nor depth (NP-MANOVA, $F=1.37$ $P<0.05$; Table 3) explained site differences in the five species
227 assemblages found on ARs in AGD ($P<0.05$; Tables 2 and 3). Differences among the five sites in AGD
228 were due to different ARs colonization by three species (Kruskall-wallis: *E. singularis*, *P. fascialis*, *H.*
229 *papillosa*: all $P<0.05$; Table 4). Site C differed from other sites by the presence of *E. singularis*, and sites
230 D and E differed from sites A and B due to the presence of *P. fascialis* and *H. papillosa* (Post-hoc tests).
231
232 **Geographical effect on five target species at local and regional scales**

233 The five species co-occurrence assemblages on ARs deployed in the same period and at same depth
234 were significantly different at both regional and local scales (NP-MANOVA : geographical sector F=3.19
235 P<0.05; site (geographical sector) F=3.64 P<0.05; Table 5). These differences were due to different
236 colonization of ARs by three of the five species, *E. singularis*, *L. sarmentosa* and *P. fascialis*. For the
237 latter two species, regional differences (Kruskall-wallis: geographical sector P=0.0002) were more
238 significant than local differences (Kruskall-wallis: site P=0.001 for *L. sarmentosa* and P=0.003 for *P.*
239 *fascialis*; Table 6). Both species were not detected in the north of the GDL (AGM). In contrast, for *E.*
240 *singularis*, local differences (Kruskall-wallis: site P=0.01) were more significant than regional ones
241 (geographical sector P=0.036; Table 6), the species being detected in geographical sectors in the north,
242 center and south of GDL.
243
244 **DISCUSSION**
245 The study of effective integration of ARs into the rocky habitat network through their colonization by
246 species building up their natural biodiversity is essential to assess their ecosystem functions, prior and
247 after deployment. In the present study, we showed that ARs spread along the GDL coastline had been
248 colonized by five species found in the natural rocky habitat of the region, ten years after their
249 deployment. However, spatial colonization patterns differed among species, resulting in diverse
250 assemblages in different geographical sectors of the GDL. Locally, neither age, immersion depth or reef
251 shape significantly affected colonization patterns.
252 Colonization of ARs are expected to evolve toward a stable state comparable to that of the natural
253 environment, through the succession of opportunistic species (wide dispersal, high fertility, low
254 tolerance of reduced resource levels, short life-spans, minimal dietary specialisation) followed by
255 specialized species (limited dispersal, slow growth to a large size at maturity, delayed and limited
256 reproduction, optimization to reduced resources and long life-spans; (Platt and Connell, 2003; Faurie
257 et al., 2003). Monitoring of ARs short-term colonization (<3 years) have indeed shown a dominance of
258 pioneer species (hydroids, serpulids, barnacles and bivalves), most of them having life history traits

typical of opportunistic species (Fariñas-Franco et al., 2013; T. Glasby, 1999; Moura et al., 2007; Pamintuan and Ali, 1994; Ponti, 2015; Relini et al., 1994; Spagnolo et al., 2014; Toledo et al., 2020). Long-term studies confirmed successions in ARs colonization (Burt et al., 2011; Nicoletti et al., 2007; Perkol-Finkel and Benayahu, 2005; Whomersley and Picken, 2003), but none have described saturation (Svane and Petersen, 2001). In the Tyrrhenian Sea, Nicolleti et al., (2007) described colonization in 5 distinct phases: (i) A first recruitment by pioneer species (hydroids, serpulids, barnacles and bivalves) during the first months after immersion, followed by phases of (ii) cover dominance, (iii) regression and (iv) absence of *Mytilus galloprovincialis* for more than 10 years.The installation of diverse bio-builders bryozoans characteristic of the natural environment was recorded after 20 years only (v). Our study shows that bio-builder engineering species such as bryozoans (*P. fascialis*) and gorgonians (*E. singularis, L. sarmentosa*) colonized ARs as early as 10 years after their deployment, without significant difference between 10 years and 35 years old ARs. However, the presence of *S. spallanzanii* described as an opportunistic species (sexual precocity, various reproduction modes, rapid growth, short lived; Giangrande et al., 2000) on all ARs independently of their age of deployment suggests that ARs did not yet reach a stable state comparable to the natural environment. Thus, the presence of bio-builders is not a sufficient indicator of the ARs naturalization to the local biodiversity.

The GDL's ARs being located in the sandy coastal zone are likely regularly disturbed by sediment deposits due to river delivery or/and their resuspension by either trawling activities or the mechanical action of the swell (Dufois et al., 2014; Durrieu de Madron et al., 2005; Ulses et al., 2008). Testing the impact of swell and sediment deposit on ARs requires exploring the colonization of ARs along a gradient of depth and distance from the coast (van der Stap et al., 2016). However, current ARs deployment in the GDL ranged from 15 to 30 m depth and within 3 miles from the coast and did not allow testing for differential effect of sediment disturbances as swell impact occurs every year in this area (Guizien, 2009). Testing the impact of sediment disturbance on ARs colonization would require exploring reefs deployed deeper than 50 m, such as the anchorages of the floating wind farm that will be placed in the GDL in the next future (https://info-efgl.fr/le-projet/le-parc/#). Light is also expected

285 to be an important factor structuring benthic assemblages, along a depth gradient in natural and
286 artificial environments (T. Glasby, 1999a; T. M. Glasby, 1999b; Svane and Petersen, 2001) . Absence
287 of depth effect in the present study, although in the GDL light intensity strongly attenuates within the
288 upper 30 m of the water column (Durrieu de Madron et al., 2011) was potentially a bias due to the five
289 species selected in the present study whose distributions are not strongly structured by light intensity.
290 Another factor which has been shown to drive the intensity of ARs colonization is structural complexity
291 (see Bohnsack and Sutherland, 1985 for a review). Nevertheless, there is no consensus about the
292 relationship between complexity and subtidal benthic invertebrates abundance, due to potential bias
293 in controlling the surface and scale in ARs of different complexity (Rouse et al., 2019; Strain et al.,
294 2018). The similarity in the 5 species co-occurrence between different reef shapes at the same depth
295 found in the present study suggests structural complexity is less important than the geographical
296 location in AR colonization by benthic invertebrates.
297 Benthic invertebrate assemblages result from complex processes that operate at multiple spatial and
298 temporal scales (Smale, 2012). At the regional scale, larval availability can become a major factor
299 explaining colonization success. Change in the composition of assemblages during the early
300 colonization of artificial substrates by benthic invertebrates has been attributed to the availability and
301 abundance of larvae during the seasons rather than a sequence of distinct succession (Bramanti et al.,
302 2003; Turner and Todd, 1993). The larval behaviour (buoyancy and motility) and the characteristics of
303 the biological cycle of the species (spawning timing and PLD) can play a key role in determining the
304 dispersal distance (Todd, 1998), and consequently the possibility to reach habitat suitable for
305 settlement. Dispersion distance is generally correlated with PLD, thus, a species with a long PLD is
306 supposed to colonize habitats further away than species with a shorter PLD (Shanks, 2009). In this
307 study, the five species were chosen among different phyla known for their contrasting planktonic
308 durations, swimming abilities and larval dispersal periods, although these larval traits are only known
309 accurately for *E. singularis* (Guizien et al., 2020; Zelli et al., 2020). *P. fascialis* and *H. papillosa*, the two
310 species with short PLD (<24h and <48h, respectively) colonized ARs located close to the natural habitat

where they are present (< 4.8 km and <10 km, respectively). The coastal circulation of the GDL allows such dispersal distance over periods of a few days (Guizien et al., 2012). *S. spallanzanii*, which has a PLD of 3 weeks, colonized all the inventoried ARs, in line with a dispersal distance of 40 km after 3 weeks (Guizien et al., 2012). In contrast, *E. singularis* did not colonize all ARs within geographical sectors of 30 km width where the species is present in the natural habitat, although a 2-week PLD was expected to enable such dispersal (Padron et al., 2018). The other gorgonian species, *L. sarmentosa* colonized more ARs located within distances of less than 30 km from its natural habitat than *E. singularis* while the PLD of the two species are presumably the same. This suggests that other factors influence the colonization failure of *E. singularis*.

Reproductive traits are another key to the success in colonising new settings (Stearns, 2000). In this regard, *E. singularis* colonization potential could be limited by its low fecundity (~25-40 larvae.cm^{-1} of colony branch, Ribes et al., 2007; Theodor, 1967) compared to that of *L. sarmentosa* (~75 larvae.cm^{-1} of colony branch, (Rossi et al., 2011; Rossi and Gili, 2009). The wide colonization of ARs by *S. spallanzanii* is in line with its reproductive traits typical of opportunistic species (early sexual maturity, high fecundity with more than 50 000 eggs per female, Currie et al., 2000, a fertilization close to 100%, Giangrande et al., 2000). Since arriving in the Pacific Ocean, *S. spallanzanii* has been declared one of the ten priority pest species in the marine environment by the Australian authorities and classified as an invasive species (Hayes et al., 2005). Similarly to *S. spallanzanii*, *H. papillosa* colonized nearly all ARs located within its 10-km dispersal distance from the natural habitat. Within the ascidian class, a wide disparity in species fecundity has been reported (Pandian, 2018). This suggests *H. papillosa* reproductive traits would be close to those of invasive ascidians (Zhan et al., 2015).

Ultimately, understanding ARs colonization requires a precise mapping of source populations in the natural environment. To this respect, the abundance of *S. spallanzan*i on ARs is surprising, as the species is not abundant in the natural rocky habitat of the GDL. For this species, other sources of larval supply than natural settings should be considered, such as the numerous ports and marinas along the coast of the GDL, as *S. spallanzanii* is very tolerant to environmental conditions (Currie et al., 2000). In

this case of intense colonization by an endemic benthic invertebrate species, ARs apparently extended its metapopulation, acting as stepping stones for further larval dispersal beyond its natural current colonization limits (Bishop et al., 2017; Wang et al., 2020). In the GDL, the 14 500 m^3 of ARs deployed 30 years ago are now decommissioned and the relevance of their removal is currently debated. Connectivity between natural populations has been shown to support species resilience after disturbances in fragmented habitat, and could be extended to ARs (Fahrig, 2003). However, ARs may also facilitate the spread of non-indigenous species introduced with maritime traffic in ports (Glasby et al., 2007). The present study advocates accounting for the geographical arrangement in planning ARs deployment to enhance fish productivity while avoiding the spread of invasive species.

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Authors contributions

SB and KG conceived the study, SB carried out sampling and statistical analysis. All contributed to manuscript writing.

LITERATURE CITED

Anderson, M., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x

Ardizzone, G.D., Belluscio, A., Gravina, M.F., Somaschini, A., 1996. Colonization and Disappearance of Mytilus galloprovincialis Lam. on an Artificial Habitat in the Mediterranean Sea. Estuarine, Coastal and Shelf Science 43, 665–676. https://doi.org/10.1006/ecss.1996.0095

Ayre, D.J., Davis, A.R., Billingham, M., Llorens, T., Styan, C., 1997. Genetic evidence for contrasting patterns of dispersal in solitary and colonial ascidians. Marine Biology 130, 51–61. https://doi.org/10.1007/s002270050224

Becerro, M.A., Turon, X., 1992. Reproductive Cycles of the Ascidians Microcosmus sabatieri and Halocynthia papillosa in the Northwestern Mediterranean. Marine Ecology 13, 363–373. https://doi.org/10.1111/j.1439-0485.1992.tb00360.x

Bishop, M.J., Mayer-Pinto, M., Airoldi, L., Firth, L.B., Morris, R.L., Loke, L.H.L., Hawkins, S.J., Naylor, L.A., Coleman, R.A., Chee, S.Y., Dafforn, K.A., 2017. Effects of ocean sprawl on ecological connectivity: impacts and solutions. Journal of Experimental Marine Biology and Ecology 492, 7–30. https://doi.org/10.1016/j.jembe.2017.01.021

Blouet, S., Quittet, L., Agin, G., Thorin, S., Dalias, N., Marobin, D., Lenfant, P., Guizien, K., 2021. Database of the location and typology of artificial reefs in the Gulf of Lion (NW Mediterranean Sea). https://doi.org/10.17882/81407

Bohnsack, J.A., 1989. Are High Densities of Fishes at Artificial Reefs the Result of Habitat Limitation or Behavioral Preference? Bulletin of marine science 44, 15.

Bohnsack, J.A., Sutherland, D.L., 1985. Artificial reef research. A review with recommendations for future priorities. Bulletin of marine science 37, 30.

Bramanti, L., Magagnini, G., Santangelo, G., 2003. Settlement and recruitment: The first stages in the life cycle of two epibenthic suspension feeders (*Corallium rubrum* and *Anomia ephippium)*. Italian Journal of Zoology 70, 175–178. https://doi.org/10.1080/11250000309356512

Briton, F., Cortese, D., Duhaut, T., Guizien, K., 2018. High-resolution modelling of ocean circulation can reveal retention spots important for biodiversity conservation. Aquatic Conserv: Mar Freshw Ecosyst 28, 882–893. https://doi.org/10.1002/aqc.2901

Burt, J., Bartholomew, A., Sale, P.F., 2011. Benthic development on large-scale engineered reefs: A comparison of communities among breakwaters of different age and natural reefs. Ecological Engineering 37, 191–198. https://doi.org/10.1016/j.ecoleng.2010.09.004

Carver, CE., Chisholm, A., Mallet, AL., 2003. Strategies to mitigate the impact of Ciona intestinalis (L.) biofouling on shellfish production. J Shellfish Res 22:621–631

Cépralmar, Région Languedoc-Roussillon., 2015. Guide pratique d'aide à l'élaboration, l'exploitation et la gestion des récifs artificiels en Languedoc-Roussillon : 236 pages.

Chen, J.-L., Chuang, C.-T., Jan, R.-Q., Liu, L.-C., Jan, M.-S., 2013. Recreational Benefits of Ecosystem Services on and around Artificial Reefs: A Case Study in Penghu, Taiwan. Ocean & Coastal Management 85, 58–64. https://doi.org/10.1016/j.ocecoaman.2013.09.005

Clarke, K.R., Somerfield, P.J., Gorley, R.N., 2008. Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. Journal of Experimental Marine Biology and Ecology 366, 56–69. https://doi.org/10.1016/j.jembe.2008.07.009

Claudet, J., Fraschetti, S., 2010. Human-driven impacts on marine habitats: A regional meta-analysis in the Mediterranean Sea. Biological Conservation 143, 2195–2206. https://doi.org/10.1016/j.biocon.2010.06.004

Claudet, J., Pelletier, D., 2004. Marine protected areas and artificial reefs: A review of the interactions between management and scientific studies. Aquat. Living Resour. 17, 129–138. https://doi.org/10.1051/alr:2004017

Cocito, Silvia, Ferdeghini, F., Sgorbini, S., 1998a. Pentapora fascialis (Pallas) [Cheilostomata: Ascophora] colonization of one sublittoral rocky site after sea-storm in the northwestern Mediterranean, in: Baden, S., Phil, L., Rosenberg, R., Strömberg, J.-O., Svane, I., Tiselius, P. (Eds.), Recruitment, Colonization and Physical-Chemical Forcing in Marine Biological Systems. Springer Netherlands, Dordrecht, pp. 59–66. https://doi.org/10.1007/978-94-017-2864-5_5

Cocito, S., Sgorbini, S., Bianchi, C.N., 1998b. Aspects of the biology of the bryozoan Pentapora fascialis in the northwestern Mediterranean. Marine Biology 131, 73–82. https://doi.org/10.1007/s002270050298

Connell, J.H., Slatyer, R.O., 1977. Mechanisms of Succession in Natural Communities and Their Role in Community Stability and Organization. The American Naturalist 111, 1119–1144. https://doi.org/10.1086/283241

CREOCEAN., 2003. Impact des récifs artificiels sur le milieu marin et la pêche professionnelle dans le golfe d'Aigues- Mortes, CREOCEAN, France, 53 pp.

CREOCEAN., 2004. Suivi scientifique des récifs artificiels immergés au large de Gruissan—Rapport Annuel 2003— Peuplements benthiques, CREOCEAN, France, 32 pp.

Currie, D.R., McArthur, M.A., Cohen, B.F., 2000. Reproduction and distribution of the invasive European fanworm Sabella spallanzanii (Polychaeta: Sabellidae) in Port Phillip Bay, Victoria, Australia. Marine Biology 136, 645–656. https://doi.org/10.1007/s002270050724

Daigle, R.M., Metaxas, A., deYoung, B., 2014. Fine-Scale Distribution and Spatial Variability of Benthic Invertebrate Larvae in an Open Coastal Embayment in Nova Scotia, Canada. PLOS ONE 9, e106178. https://doi.org/10.1371/journal.pone.0106178

Dalias, N., Astruch, P., Foulquié, M., Rouanet, E., 2012. Suivi à long terme de l'impact potentiel de la plongée sous-marine sur les peuplements d'invertébrés benthiques au sein de la Réserve Naturelle Marine de Cerbère-Banyuls (2007 - 2011) – Rapport final. Contrat Conseil Général des Pyrénées Orientales & SEANEO - GIS Posidonie. SEANEO - GIS Posidonie publ. Fr. : 136 P

Dufois, F., Verney, R., Le Hir, P., Dumas, F., Charmasson, S., 2014. Impact of winter storms on sediment erosion in the Rhone River prodelta and fate of sediment in the Gulf of Lions (North Western Mediterranean Sea). Continental Shelf Research 72, 57–72. https://doi.org/10.1016/j.csr.2013.11.004

Durrieu de Madron, X., Ferré, B., Le Corre, G., Grenz, C., Conan, P., Pujo-Pay, M., Buscail, R., Bodiot, O., 2005. Trawling-induced resuspension and dispersal of muddy sediments and dissolved elements in the Gulf of Lion (NW Mediterranean). Continental Shelf Research 25, 2387–2409. https://doi.org/10.1016/j.csr.2005.08.002

Durrieu de Madron, X., Guieu, C., Sempéré, R., Conan, P., Cossa, D., D'Ortenzio, F., Estournel, C., Gazeau, F., Rabouille, C., Stemmann, L., Bonnet, S., Diaz, F., Koubbi, P., Radakovitch, O., Babin, M., Baklouti, M., Bancon-Montigny, C., Belviso, S., Bensoussan, N., Bonsang, B., Bouloubassi, I., Brunet, C., Cadiou, J.-F., Carlotti, F., Chami, M., Charmasson, S., Charrière, B., Dachs, J., Doxaran, D., Dutay, J.-C., Elbaz-Poulichet, F., Eléaume, M., Eyrolles, F., Fernandez, C., Fowler, S., Francour, P., Gaertner, J.C., Galzin, R., Gasparini, S., Ghiglione, J.-F., Gonzalez, J.-L., Goyet, C., Guidi, L., Guizien, K., Heimbürger, L.-E., Jacquet, S.H.M., Jeffrey, W.H., Joux, F., Le Hir, P., Leblanc, K., Lefèvre, D., Lejeusne, C., Lemé, R., Loÿe-Pilot, M.-D., Mallet, M., Méjanelle, L., Mélin, F., Mellon, C., Mérigot, B., Merle, P.-L., Migon, C., Miller, W.L., Mortier, L., Mostajir, B., Mousseau, L., Moutin, T., Para, J., Pérez, T., Petrenko, A., Poggiale, J.-C., Prieur, L., Pujo-Pay, M., Pulido-Villena, Raimbault, P., Rees, A.P., Ridame, C., Rontani, J.-F., Ruiz Pino, D., Sicre, M.A., Taillandier, V., Tamburini, C., Tanaka, T., Taupier-Letage, I., Tedetti, M., Testor, P., Thébault, H., Thouvenin, B., Touratier, F., Tronczynski, J., Ulses, C., Van Wambeke, F., Vantrepotte, V., Vaz, S., Verney, R., 2011. Marine ecosystems' responses to climatic and anthropogenic forcings in the Mediterranean. Progress in Oceanography 91, 97–166. https://doi.org/10.1016/j.pocean.2011.02.003

Dutrieux, E., Thorin, S., Jouvenel, J.-Y., 2005. 100 belles plongées en Languedoc-Roussillon, Edition GAP, 336 p.

Fahrig, L., 2003. Effects of Habitat Fragmentation on Biodiversity. Annu. Rev. Ecol. Evol. Syst. 34, 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fariñas-Franco, J.M., Allcock, L., Smyth, D., Roberts, D., 2013. Community convergence and recruitment of keystone species as performance indicators of artificial reefs. Journal of Sea Research 78, 59–74. https://doi.org/10.1016/j.seares.2012.10.008

Fava, F., Ponti, M., Abbiati, M., 2016. Role of Recruitment Processes in Structuring Coralligenous Benthic Assemblages in the Northern Adriatic Continental Shelf. PLOS ONE 11, e0163494. https://doi.org/10.1371/journal.pone.0163494

Giangrande, A., Petraroli, A., 1994. Observations on reproduction and growth of Sabella spallanzanii (Polychaeta, Sabellidae) in the Mediterranean Sea. In: Dauvin JC, Laubier L, Reish DJ (eds) Actes de la 4éme Conférence Internationale des Polychetes. Mus Hist nat Paris 162: 51±56

Giangrande, A., Cavallo, A., Licciano, M., Mola, E., Pierri, C., Trianni, L., 2005. Utilization of the filter feeder polychaete Sabella. Aquacult Int 13, 129–136. https://doi.org/10.1007/s10499-004-9025-3

Giangrande, A., Licciano, M., Pagliara, P., Gambi, M.C., 2000. Gametogenesis and larval development in Sabella spallanzanii (Polychaeta: Sabellidae) from the Mediterranean Sea. Marine Biology 136, 847–861. https://doi.org/10.1007/s002279900251

Glasby, T.M., 1999a. Interactive effects of shading and proximity to the seafloor on the development of subtidal epibiotic assemblages. Mar. Ecol. Prog. Ser. 190, 113–124. https://doi.org/10.3354/meps190113

Glasby, T.M., 1999b. Effects of shading on subtidal epibiotic assemblages. Journal of Experimental Marine Biology and Ecology 234, 275–290. https://doi.org/10.1016/S0022-0981(98)00156-7

Glasby, T.M., Connell, S., Holloway, M., Hewitt, C., 2007. Nonindigenous biota on artificial structures: Could habitat creation facilitate biological invasions? Marine Biology 151, 887–895. https://doi.org/10.1007/s00227-006-0552-5

Glasby, T.M., 2000. Surface composition and orientation interact to affect subtidal epibiota. Journal of Experimental Marine Biology and Ecology 248, 177–190. https://doi.org/10.1016/S0022-0981(00)00169-6

Gori, A., Linares, C., Rossi, S., Coma, R., Gili, J.-M., 2007. Spatial variability in reproductive cycle of the gorgonians Paramuricea clavata and Eunicella singularis (Anthozoa, Octocorallia) in the Western Mediterranean Sea. Mar Biol 151, 1571–1584. https://doi.org/10.1007/s00227-006-0595-7

Gori, A., Rossi, S., Berganzo, E., Pretus, J.L., Dale, M.R.T., Gili, J.-M., 2011. Spatial distribution patterns of the gorgonians Eunicella singularis, Paramuricea clavata, and Leptogorgia sarmentosa (Cape of Creus, Northwestern Mediterranean Sea). Mar Biol 158, 143–158. https://doi.org/10.1007/s00227-010-1548-8

Grossman, G.D., Jones, G.P., Seaman, W.J., 1997. Do Artificial Reefs Increase Regional Fish Production? A Review of Existing Data 22, 7.

Guizien, K., 2009. Spatial variability of wave conditions in the Gulf of Lions (NW Mediterranean Sea). Vie Milieu 11.

Guizien, K., Belharet, M., Marsaleix, P., Guarini, J.M., 2012. Using larval dispersal simulations for marine protected area design: Application to the Gulf of Lions (northwest Mediterranean). Limnology and Oceanography 57, 1099–1112. https://doi.org/10.4319/lo.2012.57.4.1099

Guizien, K., Viladrich, N., Martínez-Quintana, Á., Bramanti, L., 2020. Survive or swim: different relationships between migration potential and larval size in three sympatric Mediterranean octocorals. Scientific Reports 10, 18096. https://doi.org/10.1038/s41598-020-75099-1

Hayes, K.R., Australia, Department of the Environment and Heritage, CSIRO (Australia), Division of Marine Research, 2005. National priority pests. Part II, Part II,. Australian Government Dept. of the Environment and Heritage, Parkes A.C.T.

Hong, J.S., 1980. Étude faunistique d'un fond de concrétionnement de type coralligène soumis à un gradient de pollution en Méditerranée nord-occidentale (Golfe de Fos). Thèse de Doctorat. Université d'Aix -Marseille II. 134 pp.

Jackson, J.B.C., 2001. Historical Overfishing and the Recent Collapse of Coastal Ecosystems. Science 293, 629–637. https://doi.org/10.1126/science.1059199

Jones, D. L., 2014. The Fathom Toolbox for Matlab: multivariate ecological and oceanographic data analysis. College of Marine Science, University of South Florida, St. Petersburg, Florida, USA. Available from: http://www.marine.usf.edu/user/djones/

Keough, M.J., 1983. Patterns of recruitment of sessile invertebrates in two subtidal habitats. Journal of Experimental Marine Biology and Ecology 66, 213–245. https://doi.org/10.1016/0022-0981(83)90162-4

Laubier, L., 1966. Le coralligène des Albères. Monographie biocénotique. Ann. Inst. Océanogr. : 137-316.

Lewbel, G.S., Howard, R.L., Gallaway, B.J., n.d. Zonation of Dominant Fouling Organisms on Northern Gulf of Mexico Petroleum Platforms 26.

Ly, O., Yoris-Nobile, A.I., Sebaibi, N., Blanco-Fernandez, E., Boutouil, M., Castro-Fresno, D., Hall, A.E., Herbert, R.J.H., Deboucha, W., Reis, B., Franco, J.N., Teresa Borges, M., Sousa-Pinto, I., van der Linden, P., Stafford, R., 2021. Optimisation of 3D printed concrete for artificial reefs: Biofouling and mechanical analysis. Construction and Building Materials 272, 121649. https://doi.org/10.1016/j.conbuildmat.2020.121649

Martens, K., Queiroga, H., Cunha, M.R., Cunha, A., Moreira, M.H., Quintino, V., Rodrigues, A.M., Seroôdio, J., Warwick, R.M. (Eds.), 2006. Marine Biodiversity: Patterns and Processes, Assessment, Threats, Management and Conservation. Springer Netherlands, Dordrecht. https://doi.org/10.1007/1-4020-4697-9

Millot, C., 1990. The Gulf of Lions' hydrodynamics. Continental Shelf Research 10, 885–894. https://doi.org/10.1016/0278-4343(90)90065-T

Moura, A., Boaventura, D., Cúrdia, J., Carvalho, S., da Fonseca, L.C., Leitão, F.M., Santos, M.N., Monteiro, C.C., 2007. Effect of depth and reef structure on early macrobenthic communities of the Algarve artificial reefs (southern Portugal). Hydrobiologia 580, 173–180. https://doi.org/10.1007/s10750-006-0455-y

Nicoletti, L., Marzialetti, S., Paganelli, D., Ardizzone, G.D., 2007. Long-term changes in a benthic assemblage associated with artificial reefs, in: Relini, G., Ryland, J. (Eds.), Biodiversity in Enclosed Seas and Artificial Marine Habitats, Developments in Hydrobiology. Springer Netherlands, Dordrecht, pp. 233–240. https://doi.org/10.1007/978-1-4020-6156-1_20

Odum, E.P., n.d. An understanding of ecological succession provides a basis for resolving man's conflict with nature. 164, 9.

Padron, M., Costantini, F., Baksay, S., Bramanti, L., Guizien, K., 2018. Passive larval transport explains recent gene flow in a Mediterranean gorgonian. Coral Reefs 37. https://doi.org/10.1007/s00338-018-1674-1

Pamintuan, I.S., Ali, P.M., n.d. Early Successional Patterns of Invertebrates in Artificial Reefs Established at Clear and Silty Areas in Bolinao, Pangasinan, Northern Philippines 11.

Pandian, T.J., 2018. Reproduction and Development in Echinodermata and Prochordata. CRC Press, Boca Raton. https://doi.org/10.1201/9780815364733

Pauly, D., Christensen, V., Guénette, S., Pitcher, T.J., Sumaila, U.R., Walters, C.J., Watson, R., Zeller, D., 2002. Towards sustainability in world fisheries. Nature 418, 689–695. https://doi.org/10.1038/nature01017

Perkol-Finkel, S., Benayahu, Y., 2005. Recruitment of benthic organisms onto a planned artificial reef: shifts in community structure one decade post-deployment. Marine Environmental Research 59, 79–99. https://doi.org/10.1016/j.marenvres.2004.03.122

Platt, W.J., Connell, J.H., 2003. Natural Disturbances and Directional Replacement of Species. Ecological Monographs 73, 507–522. https://doi.org/10.1890/01-0552

Ponti, M., 2015. Benthic assemblages on artificial reefs in the northwestern Adriatic Sea: Does structure type and age matter? Marine Environmental Research 10.

Ponti, M., Turicchia, E., Costantini, F., Gori, A., Bramanti, L., Di Camillo, C., Linares, C., Rossi, S., Abbiati, M., Garrabou, J., Cerrano, C., 2019. Mediterranean gorgonian forests: Distribution patterns and ecological roles.

Powers, S., Grabowski, J., Peterson, C., Lindberg, W., 2003. Estimating enhancement of fish production by offshore artificial reefs: uncertainty exhibited by divergent scenarios. Mar. Ecol. Prog. Ser. 264, 265–277. https://doi.org/10.3354/meps264265

Read, G., Inglis, G., Stratford, P., Ahyong, S., 2011. Arrival of the alien fanworm Sabella spallanzanii (Gmelin, 1791) (Polychaeta: Sabellidae) in two New Zealand harbours. AI 6, 273–279. https://doi.org/10.3391/ai.2011.6.3.04

Relini, G., 2002. Trophic relationships between fishes and an artificial reef. ICES Journal of Marine Science 59, S36–S42. https://doi.org/10.1006/jmsc.2002.1212

Relini, G., Zamboni, N., Tixi, F., Torchia, G., n.d. Patterns of Sessile Macrobenthos Community Development on an Artificial Reef in the Gulf of Genoa (Northwestern Mediterranean) 27.

Ribes, M., Coma, R., Rossi, S., Micheli, M., 2007. Cycle of gonadal development in Eunicella singularis (Cnidaria: Octocorallia): trends in sexual reproduction in gorgonians: Gametogenic cycle in a temperate gorgonian. Invertebrate Biology 126, 307–317. https://doi.org/10.1111/j.1744-7410.2007.00101.x

Rossi, S., Gili, J.-M., 2009. Reproductive features and gonad development cycle of the soft bottom-gravel gorgonian *Leptogorgia sarmentosa* (Esper, 1791) in the NW Mediterranean Sea. Invertebrate Reproduction & Development 53, 175–190. https://doi.org/10.1080/07924259.2009.9652304

Rossi, S., Gili, J.-M., Garrofé, X., 2011. Net negative growth detected in a population of Leptogorgia sarmentosa: quantifying the biomass loss in a benthic soft bottom-gravel gorgonian. Mar Biol 158, 1631–1643. https://doi.org/10.1007/s00227-011-1675-x

Rossi, V., Ser-Giacomi, E., López, C., Hernández-García, E., 2014. Hydrodynamic provinces and oceanic connectivity from a transport network help designing marine reserves. arXiv:1407.6920 [physics]. https://doi.org/10.1002/2014GL059540

Rouse, S., Porter, J.S., Wilding, T.A., n.d. Artificial reef design affects benthic secondary productivity and provision of functional habitat 9.

Santos, M.N., Monteiro, C.C., 2007. A fourteen-year overview of the fish assemblages and yield of the two oldest Algarve artificial reefs (southern Portugal) 7.

Seaman, W., 2007. Artificial habitats and the restoration of degraded marine ecosystems and fisheries, in: Relini, G., Ryland, J. (Eds.), Biodiversity in Enclosed Seas and Artificial Marine Habitats, Developments in Hydrobiology. Springer Netherlands, Dordrecht, pp. 143–155. https://doi.org/10.1007/978-1-4020-6156-1_13

Shanks, A., 2009. Barnacle settlement versus recruitment as indicators of larval delivery. II. Time-series analysis and hypothesized delivery mechanisms. Mar. Ecol. Prog. Ser. 385, 217–226. https://doi.org/10.3354/meps08002

Shinn, E.A., Wicklund, R.I., n.d. Artificial Reef Observations from a Manned Submersible off Southeast Florida 10.

Simpson, T.J.S., Smale, D.A., McDonald, J.I., Wernberg, T., 2017. Large scale variability in the structure of sessile invertebrate assemblages in artificial habitats reveals the importance of local-scale processes. Journal of Experimental Marine Biology and Ecology 494, 10–19. https://doi.org/10.1016/j.jembe.2017.05.003

Smale, D.A., 2012. Extreme spatial variability in sessile assemblage development in subtidal habitats off southwest Australia (southeast Indian Ocean). Journal of Experimental Marine Biology and Ecology 438, 76–83. https://doi.org/10.1016/j.jembe.2012.10.002

Spagnolo, A., Cuicchi, C., Punzo, E., Santelli, A., Scarcella, G., Fabi, G., 2014. Patterns of colonization and succession of benthic assemblages in two artificial substrates. Journal of Sea Research 88, 78–86. https://doi.org/10.1016/j.seares.2014.01.007

Stearns, S.C., n.d. Life history evolution: successes, limitations, and prospects 11.

Steimle, F., 2002. Benthic macrofauna productivity enhancement by an artificial reef in Delaware Bay, USA. ICES Journal of Marine Science 59, S100–S105. https://doi.org/10.1006/jmsc.2002.1268

Strain, E.M.A., Olabarria, C., Mayer-Pinto, M., Cumbo, V., Morris, R.L., Bugnot, A.B., Dafforn, K.A., Heery, E., Firth, L.B., Brooks, P.R., Bishop, M.J., 2018. Eco-engineering urban infrastructure for marine and coastal biodiversity: Which interventions have the greatest ecological benefit? J Appl Ecol 55, 426–441. https://doi.org/10.1111/1365-2664.12961

Svane, I., Petersen, J.K., 2001. On the Problems of Epibioses, Fouling and Artificial Reefs, a Review. Marine Ecology 22, 169–188. https://doi.org/10.1046/j.1439-0485.2001.01729.x

Tessier, A., Francour, P., Charbonnel, E., Dalias, N., Bodilis, P., Seaman, W., Lenfant, P., 2015. Assessment of French artificial reefs: due to limitations of research, trends may be misleading. Hydrobiologia 753, 1–29. https://doi.org/10.1007/s10750-015-2213-5

Tessier, A., Verdoit-Jarraya, M., Blouet, S., Dalias, N., Lenfant, P., 2014. A case study of artificial reefs as a potential tool for maintaining artisanal fisheries in the French Mediterranean Sea. Aquat. Biol. 20, 255–272. https://doi.org/10.3354/ab00563

Theodor, J., 1967. Contribution à l'études des gorgones (VII): écologie et comportement de la planula. Vie Milieu, 18 (2A): 291-301.

Thorson, G., 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews 25, 1–45. https://doi.org/10.1111/j.1469-185X.1950.tb00585.x

Todd, C.D., 1998. Larval supply and recruitment of benthic invertebrates: do larvae always disperse as much as we believe? Hydrobiologia 375, 1–21. https://doi.org/10.1023/A:1017007527490

Toledo, M.-I., Torres, P., Díaz, C., Zamora, V., López, J., Olivares, G., 2020. Ecological succession of benthic organisms on niche-type artificial reefs. Ecol Process 9, 38. https://doi.org/10.1186/s13717-020-00242-9

True, M.A., 1970. Étude quantitative de quatre peuplements sciaphiles sur substrat rocheux dans la région marseillaise. Bulletin Institut Océanographique Monaco, 69(1401): 1- 48.

Turner, S.J., Todd, C.D., 1993. The early development of epifaunal assemblages on artificial substrata at two intertidal sites on an exposed rocky shore in St. Andrews Bay, N.E. Scotland. Journal of Experimental Marine Biology and Ecology 166, 251–272. https://doi.org/10.1016/0022-0981(93)90223-B

Turon, X., 1990. Distribution and Abundance of Ascidians from a Locality on the Northeast Coast of Spain. Marine Ecology 11, 291–308. https://doi.org/10.1111/j.1439-0485.1990.tb00385.x

Ulses, C., Estournel, C., Durrieu de Madron, X., Palanques, A., 2008. Suspended sediment transport in the Gulf of Lions (NW Mediterranean): Impact of extreme storms and floods. Continental Shelf Research 28, 2048–2070. https://doi.org/10.1016/j.csr.2008.01.015

van der Stap, T., Coolen, J.W.P., Lindeboom, H.J., 2016. Marine Fouling Assemblages on Offshore Gas Platforms in the Southern North Sea: Effects of Depth and Distance from Shore on Biodiversity. PLoS ONE 11, e0146324. https://doi.org/10.1371/journal.pone.0146324

Vivier, B., Dauvin, J.-C., Navon, M., Rusig, A.-M., Mussio, I., Orvain, F., Boutouil, M., Claquin, P., 2021. Marine artificial reefs, a meta-analysis of their design, objectives and effectiveness. Global Ecology and Conservation e01538. https://doi.org/10.1016/j.gecco.2021.e01538

Wang, W., Wang, J., Choi, F.M.P., Ding, P., Li, X., Han, G., Ding, M., Guo, M., Huang, X., Duan, W., Cheng, Z., Chen, Z., Hawkins, S.J., Jiang, Y., Helmuth, B., Dong, Y., 2020. Global warming and artificial shorelines reshape seashore biogeography. Global Ecol Biogeogr 29, 220–231. https://doi.org/10.1111/geb.13019

Weinberg, S., Weinberg, F., 1979. The Life Cycle of a Gorgonian: Eunicella Singularis (Esper, 1794). Contributions to zoology Bijdragen tot de dierkunde 48, 127–140. https://doi.org/10.1163/26660644-04802003

Wendt, P.H., Knott, D.M., Dolah, R.F.V., n.d. COMMUNITY STRUCTURE OF THE SESSILE BIOTA ON FIVE ARTIFICIAL REEFS OF DIFFERENT AGES 18.

Whomersley, P., Picken, G.B., 2003. Long-term dynamics of fouling communities found on offshore installations in the North Sea. J. Mar. Biol. Ass. 83, 897–901. https://doi.org/10.1017/S0025315403008014h

Wilson, K., 2002. Restoration of Hong Kong fisheries through deployment of artificial reefs in marine protected areas. ICES Journal of Marine Science 59, S157–S163. https://doi.org/10.1006/jmsc.2002.1186

Zar, J., 1999. Biostatistical analysis.

Zelli, E., Quéré, G., Lago, N., Di Franco, G., Costantini, F., Rossi, S., Bramanti, L., 2020. Settlement dynamics and recruitment responses of Mediterranean gorgonians larvae to different crustose coralline algae species. Journal of Experimental Marine Biology and Ecology 530–531, 151427. https://doi.org/10.1016/j.jembe.2020.151427

Zhan, A., Briski, E., Bock, D.G., Ghabooli, S., MacIsaac, H.J., 2015. Ascidians as models for studying invasion success. Mar Biol 162, 2449–2470. https://doi.org/10.1007/s00227-015-2734-5

Figure captions:

Figure 1: Map showing the layout of the 6 geographical sectors and 15 sites where artificial reef sampling was carried out.

Figure 2: Photographs of the five species inventoried on AR *a) Sabella spallanzanii b) Eunicella singularis c) Leptogorgia sarmentosa d) Halocynthia papillosa* e) *Pentapora fascialis; all © Blouet sylvain*

Figure 3: Map showing the five species co-occurence assemblages inventoried on ARs in the 15 sites in the Gulf of Lion.

Figure 4: Composite showing in the upper part the diversity of species assemblage in the sampling units of the five sites (A, B, C, D, E) in AGD sector together with the type of AR, depth and years of deployment and in the lower part, the dendrogram obtained by group average clustering based on the Jaccard dissimilarity index using the presence /absence of species (P=0.04 at 62% of dissimilarity). The red dotted line delineates the two clusters identified by the analysis.

Figures :

Figure 1 :

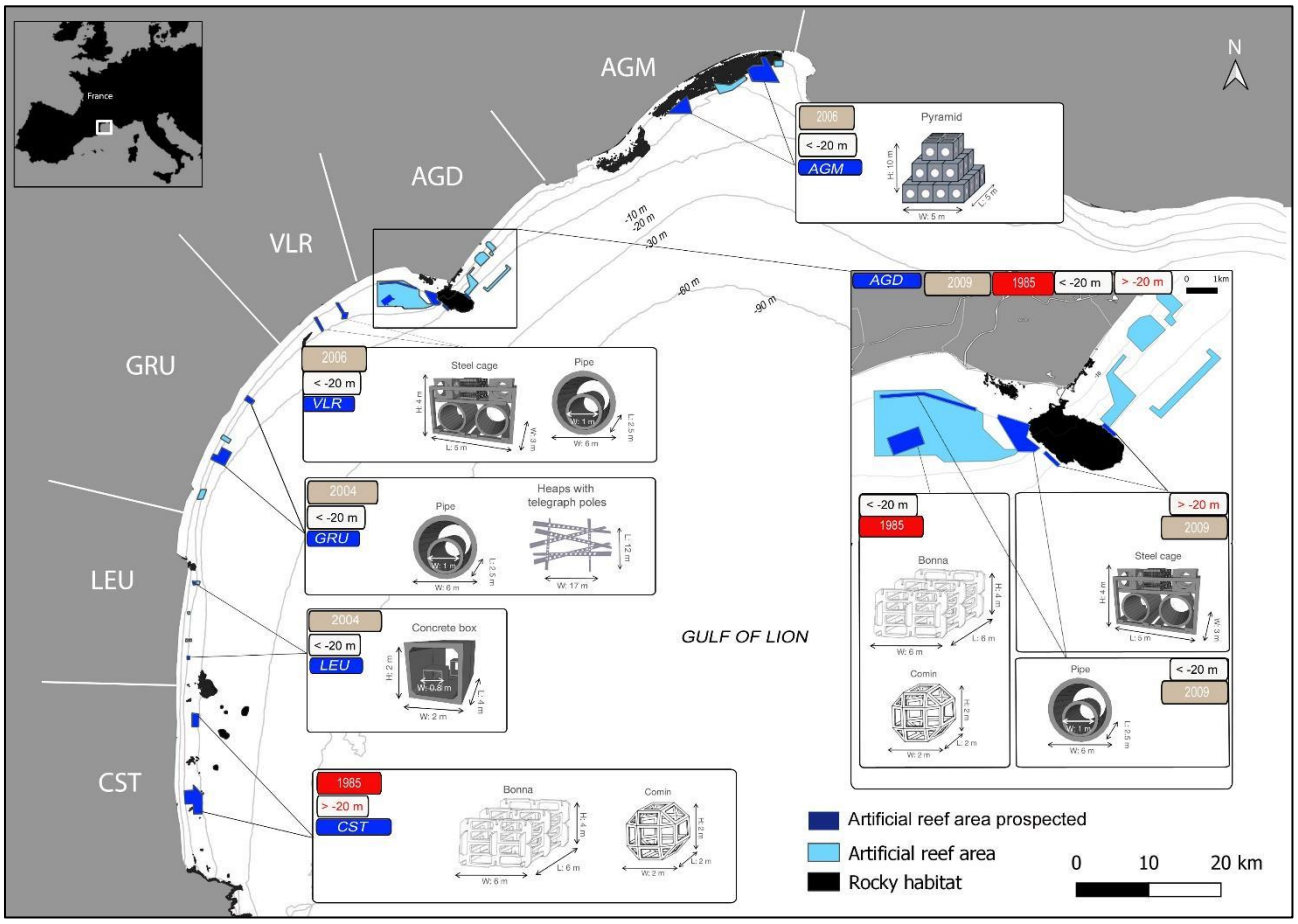


Figure 2 :

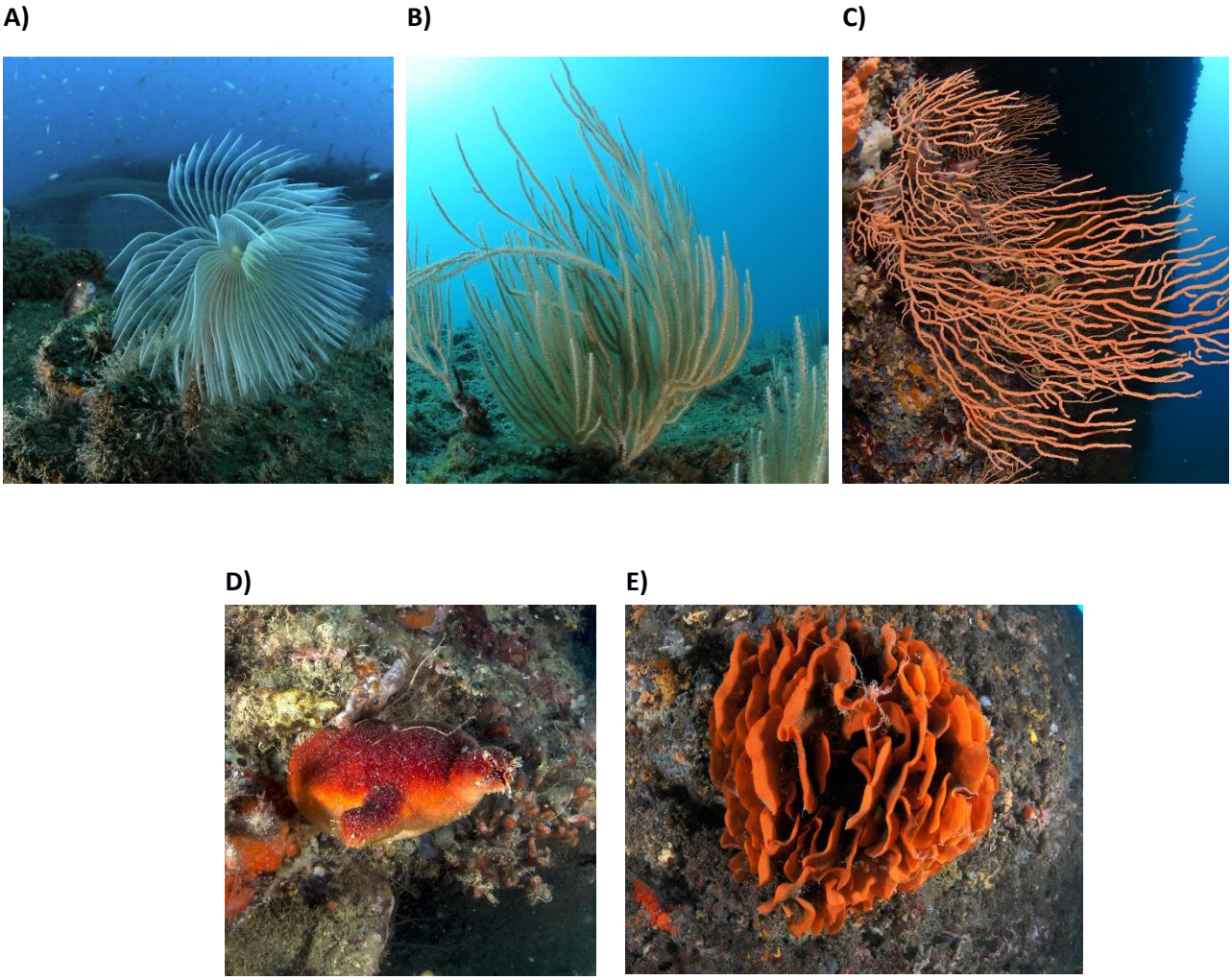


Figure 3 :

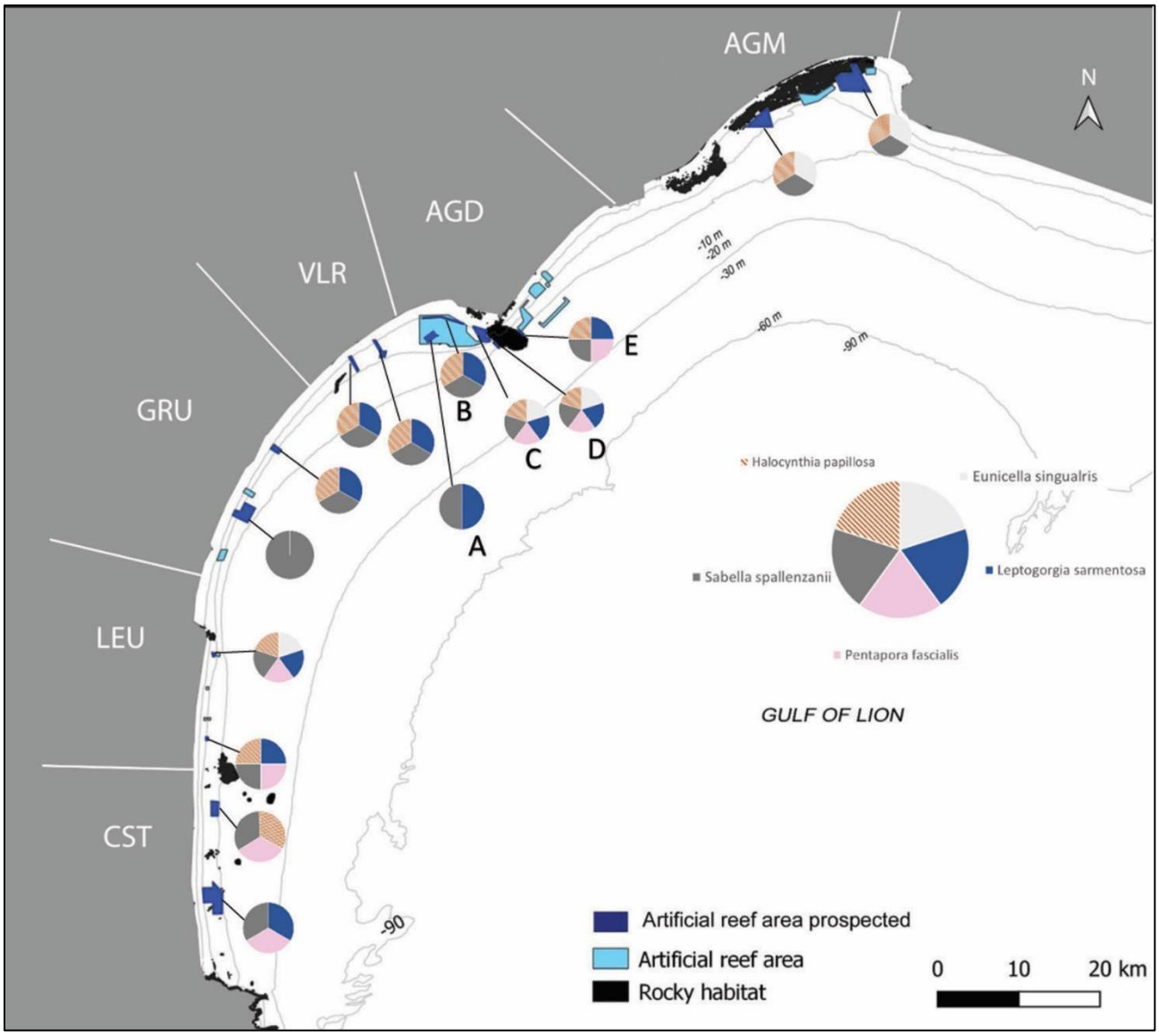
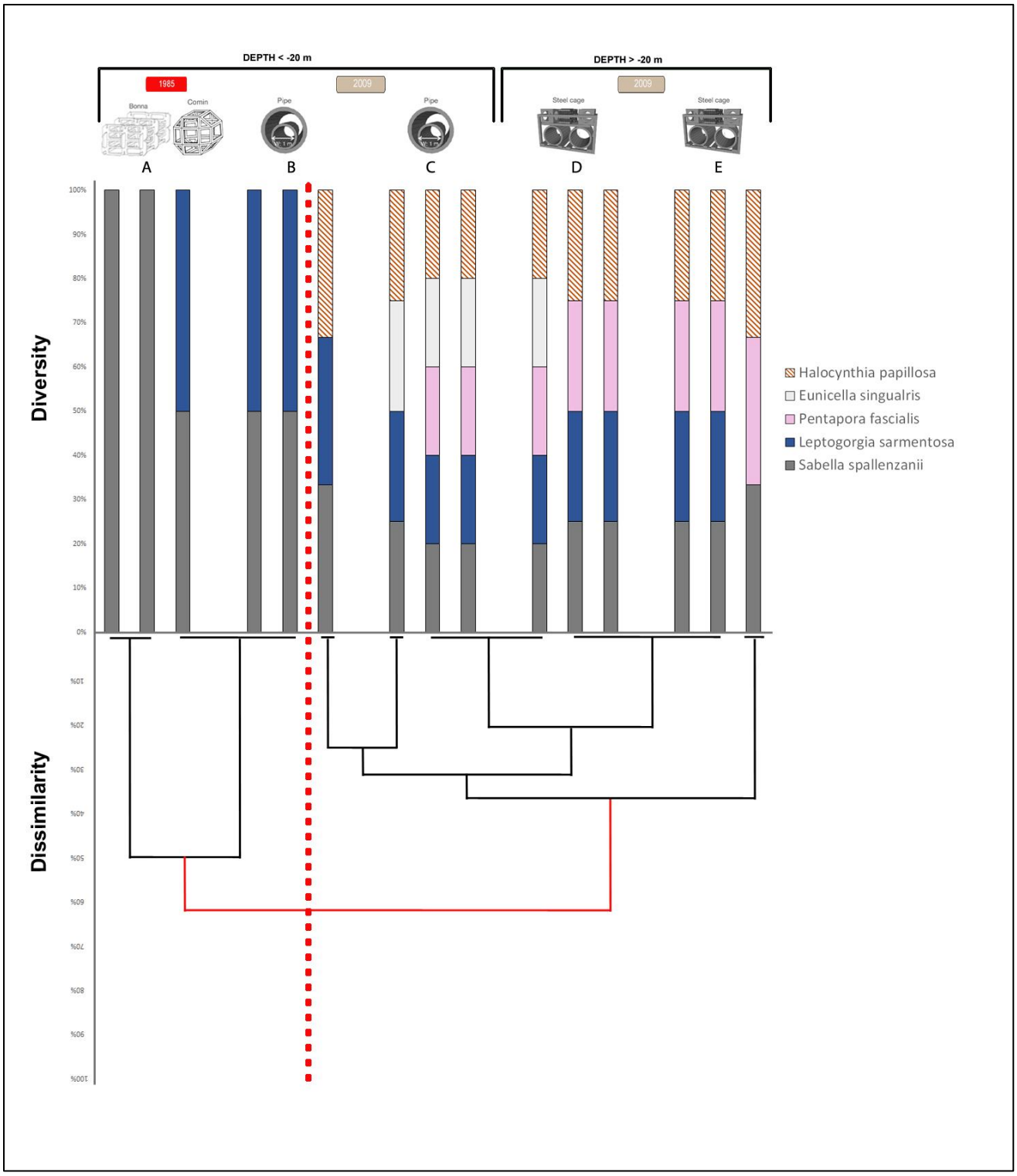

AGM
N
AGD
VLR
GRU
LEU
CST
-10 m
-20 m
-30 m
-60 m
-90 m
-90
A
B
C
D
E
Halocynthia papillosa
Eunicella singualris
Sabella spallenzanii
Leptogorgia sarmentosa
Pentapora fascialis
GULF OF LION
Artificial reef area prospected
Artificial reef area
Rocky habitat
0
10
20 km

Figure 4:


DEPTH < -20 m
DEPTH > -20 m
1985
2009
2009
Bonna
Comin
Pipe
Pipe
Steel cage
Steel cage
A
B
C
D
E
Diversity
Dissimilarity
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Halocynthia papillosa
Eunicella singualris
Pentapora fascialis
Leptogorgia sarmentosa
Sabella spallenzanii

765 **Table captions**

766 Table 1: Larval traits (Planktonic larval duration (PLD), reproduction period, and larval trophic regime)
767 for the five species inventoried on ARs.

768

769 Table 2: Results of multivariate NP-Manova testing the interactive effects of the year (of deployment
770 and site (nested in year) on the presence/absence assemblage. Significant (P<0.05) values in bold.

771

772 Table 3: Results of multivariate NP-Manova testing the interactive effects of the depth (of
773 deployment) and site (nested in depth) on the presence/absence assemblage. Significant (P<0.05)
774 values in bold.

775

776 Table 4: Results of univariate Kruskall_wallis testing the effects of year and depth of deployment on
777 the presence/absence by species. Significant (P<0.05) values in bold.

778

779 Table 5: Results of multivariate NP-Manova testing the interactive effects of geographical sector and
780 site (nested in geographical sector) on the presence/absence assemblage. Significant (P<0.05) values
781 in bold.

782

783 Table 6: Results of univariate Kruskall_wallis testing the effects of geographical sector and site on the
784 presence/absence by species. Significant (P<0.05) values in bold.

785

786 **Tables:**

Table 1:

Species	Spawning period	Larval type	Larval duration	Ref
Leptogorgia sarmentosa	June - August	Lecithotrophic	? (supposed 1-4 weeks)	(Rossi and Gili 2009)
Eunicella singularis	July - August	Lecithotrophic	1-4 weeks (in aquarium)	(Guizien et al. 2020)
Pentapora fascialis	June	Lecithotrophic	? (supposed <1 days)	(Cocito et al. 1998)
Sabella spallanzani	January - February	Lecithotrophic	21 days (in aquarium)	(Giangrande et al. 2000)
Halocynthia papillosa	September - October	? lecithotrophic	? (supposed <2 days)	(Becerro and Turon 1992)

Table 2:

Multivariate measures					
Source	**Df**	**SS**	**Ms**	**F**	**Pvalue**
Assemblage (Presence/Absence)					
Year	1	0.4825	0.4825	1.4330	0.3330
Site(Year)	1	0.3367	0.3367	7.5551	**0.0130**
Residual	6	0.2674	0.0446		
Total	8	1.0866			

Table 3:

Multivariate measures					
Source	**Df**	**SS**	**Ms**	**F**	**Pvalue**
Assemblage (Presence/Absence)					
Depth	1	0.2491	0.2491	1.3715	0.3280
Site(Depth)	2	0.3633	0.1816	8.5969	**0.001**
Residual	8	0.1690	0.0211		
Total	11	0.7816			

Table 4:

Univariate measures					
Presence/absence					
	Df	**SS**	**Ms**	**Chi_sq**	**Pvalue**
Eunicella singularis					
	4	127.5	31.875	10.82	**0.0287**
Leptogorgia sarmentosa					
	4	60	15	6.22	0.1832
Pentapora fascialis					
	4	172.5	43.125	11.5	**0.0215**
Sabella spallazanii					
	4	0	0	nan	nan
Halocynthia papillosa					
	4	150	37.5	11.2	**0.0244**

Table 5:

Multivariate measures					
Source	**Df**	**SS**	**Ms**	**F**	**Pvalue**
Assemblage (Presence/Absence)					
Geographical sector	4	1.9921	0.4980	3.1961	0.0380
Site(Geographical sector)	5	0.7791	0.1558	3.6434	0.0010
Residual	19	0.8125	0.0427		
Total	28	3.5838			

Table 6:

Presence/absence					
Source	**Df**	**SS**	**Ms**	**Chi_sq**	**Pvalue**
Eunicella singularis					
Geographical sector	4	447.08	111.77	10.28	**0.036**
Site	9	937.66	104.18	21.56	**0.0104**
Leptogorgia sarmentosa					
Geographical sector	4	965.7	241.42	22.2	**0.0002**
Site	9	1218	135.33	28	**0.001**
Pentapora fascialis					
Geographical sector	4	937.66	234.41	21.56	**0.0002**
Site	9	1077.83	119.75	24.78	**0.0032**
Sabella spallazanii					
Geographical sector	4	0	0	nan	nan
Site	9	0	0	nan	nan
Halocynthia papillosa					
Geographical sector	4	323.59	80.89	6.01	0.1985
Site	9	561.87	62.43	10.43	0.3166