Artificial reefs geographical location matters more than shape, 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. While most studies focused on short term colonization by pioneer species, we propose to test the relevance of geographic location, shape, duration of immersion and depth on the ARs long term colonization by species found in natural stable communities in the Gulf of Lion. We recorded the presence of five sessile invertebrates species, with contrasting life history traits and regional distribution in the natural rocky habitat, on ARs with different shapes deployed during two immersion time periods (1985 and the 2000s) and in two depth ranges (<20m and >20m). At the local level (~5kms), neither shape, depth nor immersion duration differentiated ARs assemblages. At the regional scale (>30kms), colonization patterns differed between species, resulting in diverse assemblages. This study highlights the primacy of geographical positioning over shape, immersion duration and depth in ARs colonization, suggesting it should be accounted for in maritime spatial planning.

KEY WORDS: ARTIFICIAL REEF, BENTHIC INVERTEBRATES, SHAPE, 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 such as recreational and traditional fishing and scuba diving (Chen et al., 2013). Beneficial effects such as increase in fish biomass and capture efficiency near ARs have been reported (reviewed by Bohnsack and Sutherland, 1985; Tessier et al., 2014) but led to a debate on the effects of ARs fishery, opposing attraction vs production (Grossman et al., 1997). The fish attraction argument is based on the quick colonization by fish and mobile invertebrates (Powers et al., 2003; Relini, 2002; Santos and Monteiro, 2007). 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, 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, data on colonization by benthic invertebrates in the long-term (Svane and Petersen, 2001). Indeed, 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 change over time in a succession

53 between pioneer and specialist species (Connell and Slatyer, 1977). In contrast with pioneer species,
54 specialist ones have slower colonization dynamics, because of their lower fecundity (Fava et al., 2016).
55 However, after colonization, specialists are expected to outcompete pioneer species due to their more
56 efficient use of environmental resources (Connell and Slatyer, 1977). Among these, light availability is
57 an essential factor shaping marine benthic communities across the water depth gradient (Odum,
58 1971). Several studies have shown a decrease in the density of benthic invertebrates with depth on
59 ARs (Lewbel et al., 1986.; Moura et al., 2007; Shinn and Wicklund, 1989; van der Stap et al., 2016)
60 explained by the decrease in light intensity (Relini et al., 1994). The structural complexity has also
61 been put forward as important characteristics linked to ARs efficiency in ecological restoration (Strain
62 et al., 2018). Structural complexity increases available surface for colonization and niches diversity with
63 various shelter and light exposure conditions, the latter being related to different benthic assemblage
64 compositions (Glasby, 2000; Glasby, 1999) and higher productivity (Vivier et al., 2021). The recent 3D
65 printing techniques using concrete, allow the design of ARs mimicking natural habitats (Ly et al., 2021).
66 However, those studies concerned short-term colonization (<3.5 years) (Wendt et al., 1989) hence
67 based on pioneer species with high dispersal capacities which colonization is likely mainly regulated
68 by post-settlement processes such as competition, predation and physical disturbance (Todd, 1998).
69 In contrast to mobile species, sessile benthic invertebrates can only colonize reefs after larval dispersal
70 which is limited by reproduction frequency (Thorson, 1950). Colonization implies thus an effective
71 dispersal between natural areas and ARs, which depends on source population spatial distribution,
72 species fecundity, dispersive larval traits and ocean circulation. Nevertheless, until now dispersal
73 drivers have been disregarded while colonization disparities among ARs may result from differences in
74 both larval connectivity (which in turn depends on fecundity, dispersal capacities and adult distribution
75 in the natural habitat) and post-recruitment processes.
76 The objective of the present study was to test the hypothesis that the geographical location of ARs
77 deployment with respect to the natural habitat can condition ARs colonization after more than 10
78 years. To this aim we investigated the effects of local (shape, depth and immersion duration) and

regional (geographic area) factors on the presence of five species of sessile invertebrates with different life history traits, endemic to the Gulf of Lion (GoL) (Northwestern Mediterranean Sea) and frequently found on natural hard substrates.

MATERIALS AND METHODS

Study area and spatially stratified sampling design

The study area extended along 160 km of the GoL coastline (Figure 1). The GoL 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 GoL 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 GoL 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 GoL represent 40% of the total AR volume in France (Tessier et al., 2015).

In the present study we examined the oldest (in the 80s) and the youngest (in the 2000s) ARs with the most common shapes (namely pipe, steel cage, Bonna, Comin, pyramid, heap of telegraph poles, and concrete box, Figure 1). For the analysis of data, we followed a stratified sampling design. To this aim, the GoL 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 referring to Aigues-Mortes, AGD to Agde, VLR to Valras, GRU to Gruissan, LEU to Leucate, CST to Canet/Saint-Cyprien sectors, Figure 1). Each sector included ARs deployed during either the first (1985, CST geographical sector), the last (2002-2009, AGM, VLR, GRU, LEU geographical sectors) or both periods of immersion (AGD), and of different shapes. In each geographical sector, two sites were defined except in AGD (5 sites, AGD1, AGD2, AGD3, AGD4, AGD5) and GRU (3 sites, GRU1, GRU2, GRU3). To test for location effect, sites were separated by a distance ranging from 2.1 to 11.7 km (median value of 7.5 km) except in GRU, where two of the

three sites (GRU1 and GRU2) were defined in the same location to account for different shapes. Hence, depending on the geographical sector, sites may differ either by AR shape, immersion depth or timing of deployment (Figure 1). Due to this set up, the effect of these three factors was only tested locally (see Statistical analysis). In each site (except in the geographical sector GRU), three sampling units separated by a distance between 4m and 3.6 Km (median distance of 251 m) were set out by pooling neighboring ARs reaching a minimum surface of 89 m^2 per sampling unit and totalling a minimum developed surface of 306 m^2 per site (Table 1: Supplementary Material). In the geographical sector GRU, GRU2 and GRU3 included only one sampling unit because the surface of a single AR in these sites already yielded 459 m2 (heap of telegraph poles; Table 1: Supplementary Material). Such large continuous sampling units in each site aimed at limiting the effect of recruitment spatial variability over distances from 100s meters to kilometers arising from the non-uniformity of the flow of larvae (Daigle et al., 2014; Glasby, 2000; Simpson et al., 2017; Smale, 2012). Such a spatial scale is consistent with the spatial scale of flow homogeneity obtained in simulations over GoL soft-bottom habitat (Briton et al., 2018). This inventory methodology enabled us to test for the existence of structuring factors at the local and regional scale. Developed reef surface was calculated on the basis of technical specifications data present in the state concession documents taking into account only the colonizable surface (surfaces in contact with the sediment were excluded).

Colonization assessment and species selection

Assessment of ARs colonization was carried out by autonomous scuba-diving in 2020 by direct visual census counting the number of individuals of the five target species on the entire surface of ARs (7295 m^2; Table1: Supplementary Material). On the ARs, all individuals older than one year (size > 2 cm) have been recorded. Among the species listed in previous ARs inventories in the GoL, we selected five species that were present in most inventories, easy to identify by direct visual census and spanning different phyla with contrasting life-history traits (Créocean, 2003 & 2004; Table 1). We selected two gorgonians *Eunicella singularis* (Esper, 1791) and *Leptogorgia sarmentosa* (Esper, 1789), one bryozoan

131 *Pentapora fascialis* (Pallas, 1766), one annelida *Sabella spallanzanii* (Gmelin, 1791) and one ascidian
132 *Halocynthia papillosa* (Linnaeus, 1797) (Figure 2). The five species have a similar wide natural
133 repartition area along European coasts ranging from 1m to 250m depth (Giangrande et al., 2005; Gori
134 et al., 2011; Ponti et al., 2019; Turon, 1990; Weinberg and Weinberg, 1979). In addition, *S. spallanzanii*
135 has been recorded along the coasts of Brazil, Australia and New Zealand where it is classified as an
136 invasive non-indigenous species (Currie et al., 2000).
137 The five species are present in the rocky habitat of the NW Mediterranean Sea (Laubier, 1966; True,
138 1970; Hong, 1980). However, in the GoL, where natural rocky habitat covers uneven surfaces within
139 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
140 five species display different spatial distributions (Dutrieux et al., 2005; Dalias et al., 2011; Guizien et
141 al., 2022; S. Blouet personal observation). *E. singularis* is frequently observed and abundant
142 throughout the GoL (from the AGM sector to the CST sector), while *L. sarmentosa,* less abundant, is
143 present mainly in the center of the GoL (AGD, VLR, LEU, CST). *P. fascialis* is abundant in the west of the
144 GoL (AGD, LEU, CST, and south of CST). The distribution of *H. papillosa* is not well known, however the
145 species has been observed in all the rocky areas of the GoL.
146 *S. spallanzanii* is present but rare in natural rocky habitat. Nevertheless, *S. spallanzanii* is very abundant
147 in lagoons, ports and marinas of the GoL (S. Blouet personal observation) which have been indicated
148 as preferred habitat of the species (Currie et al., 2000).
149
150 The five species display different life-history traits. All five species reproduce once a year in different
151 seasons and with different strategies (Table 1).
152 *S. spallanzani* reproduces in January-February, when water temperature is the coldest. The species
153 displays multiple reproductive strategies: internal fertilization, with larvae brooded either inside or
154 outside the mineral tube secreted around the body, and external fertilization broadcast spawning
155 (Giangrande et al., 2000). In addition, asexual reproduction by fission has been reported (Read et al.,
156 2011). *S. spallanzani* releases lecithotrophic larvae with a planktonic larval duration (PLD) of about 4

weeks (Giangrande et al., 2000). It's life span can exceed 5 years, with sexual maturity after one year (Giangrande and Petraroli 1994; Giangrande et al., 2000). Like most gorgonians, *E. singularis* releases lecithotrophic larvae in early summer (June to August). Even though larval competency period can reach up to 2 months (Guizien et al., 2020; Zelli et al., 2020), PLDs ranging from 7 to 14 days best explain gene flow among *E. singularis* natural populations dwelling in the fragmented rocky habitat of the GoL (Padron et al. 2018). *E. singularis* life span can reach 25-30 years with sexual maturity before 6 years (Gori et al., 2007; Weinberg and Weinberg, 1979) (Weinberg and Weinberg 1979, Gori et al. 2007).

The other gorgonian, *L. sarmentosa* also releases lecithotrophic larvae but in the late summer (September to October) and the PLD is unknown (Rossi and Gili 2009). *L. sarmentosa* life span can reach 20 years with female sexual maturity within 2-3 years after settlement (Rossi and Gili 2009).

H. papillosa is a simultaneous hermaphrodite which releases larvae in late summer (September-October; Becerro and Turon, 1992), presumably lecithotrophic. The PLD of *H. papillosa* larvae is unknown but PLD shorter than 12 hours has been consistently reported for other solitary ascidian species (Ayre et al., 1997). We did not find any data about the age at sexual maturity and the life span of *H. papillosa*. However, the ascidians are considered as highly invasive, particularly because of their rapid growth and early sexual maturity (Zhan et al., 2015), with some species such as C*iona intestionalis* complex and *Ciona savigniy,* reaching sexual maturity at the age of 2 months (Zhan et al., 2015) and continuous spawning (Carver et al. 2003).

P. fascialis displays both sexual and asexual reproduction. During sexual reproduction, most bryozoans release lecithotrophic larvae which settle after a few minutes or a few hours, rarely beyond several days (Keough, 1983). *P. fascialis* larval release has been inferred to happen in June based on recruitment observations (Cocito et al., 1998a). Asexual reproduction happens by colony fragmentation or budding extension (Cocito et al., 1998b). Individual life span is estimated to be about 10 years with early sexual maturity after 2 years (Cocito et al., 1998b).

183 **Statistical analysis**

184 We examined to which extent ARs colonization measured by the presence/absence of the five species
185 and on the dissimilarity between their co-occurrence assemblages is affected by the AR shape, location
186 and timing of deployment (age). Due to the GoL AR deployment set up, the effect of some factors was
187 tested only locally. We first verified that shape was not affecting colonization, by testing the effect of
188 shape in one geographical sector where different shapes were deployed at same depth and time
189 (VLR1/VLR2, Table 1: Supplementary Material). Second, the effect of factors age (2 levels: 1985 and
190 the 2000s) and depth (2 levels, >20 m, <20 m depth) was tested within the AGD geographical sector
191 only. Factor age was tested in 3 sites at <20m (AGD1/ AGD2 & AGD3) and factor depth was tested in 4
192 sites deployed in 2009 (AGD2&AGD3 / AGD4&AGD5). Third, factor location was tested both at
193 regional and local level (geographical sector being the regional factor, site being the local factor). To
194 avoid any confounding effect due to age or depth, the regional factor vs local factor were tested on
195 the 5 geographical sectors where AR were deployed during the 2000s immersion phase and at <20 m
196 depth only (AGM, AGD, VLR, GRU, LEU: 5x2 levels). A Jaccard similarity matrix was built on
197 presence/absence data across all pairwise sampling units used in each test (Table 2: supplementary
198 material). Two multivariate analyses were performed. Non-parametric multivariate analysis of
199 variance with permutation was applied to test for the effects of shape, age, depth and geographical
200 sector on species assemblages (NP-manova: Anderson, 2001; Zar, 1999). Site was considered as a
201 random factor, nested either in depth, age or the geographical sector. Another multivariate analysis
202 was performed to cluster most similar species assemblages in the sector of AGD (SIMPROF : Clarke et
203 al., 2008) (Table 2 : supplementary material).

204 When significant differences between the five species co-occurrence assemblages were detected for
205 a factor, a non-parametric univariate analysis (Kruskall-Wallis) was performed for each species
206 independently to detect the species driving the difference (Table 2 : supplementary material). Fisher
207 post-hoc test was used to identify the site where the difference arose. A same p-value of 0.05 was
208 taken for detecting significant differences. Analyses were performed with Matlab software using the

Fathom package for multivariate analyses (Jones, 2014) and the Matlab statistics toolbox for univariate analyses.

RESULTS

Artificial reefs colonization by the five target species at regional scale

Among the five target species, *S. spallanzanii* was the only one whose presence was recorded in all the sampling units and geographical sectors (Figure 3). In only one out of 16 sites, it was the only species detected. *H. papillosa* and *L. sarmentosa* were detected in five of the six geographical sectors (not present in GRU and AGM, respectively). *P. fascialis* and *E. singularis* were detected in 3 of the 6 geographical sectors (CST, LEU, and AGD for *P. fascialis* and AGM, AGD and LEU, for *E. singularis*). Finally, *E. singularis* was the least frequently observed species, being detected in only 5 out of the 16 sites. In all geographical sectors, at least three of the five target species were detected, except GRU where only two of the five species were detected. Assemblages of two species were found in two sites out of 16 (sector AGD and GRU), assemblages of three species were found in 7 sites, assemblages of four species were found in 2 sites and assemblages of five species were found in 3 sites.

Shape effect on five target species at local scale

No differences in species assemblages were found in VLR between pipe and steel cage (NP-MANOVA, $F=9.08\ e\text{-}19$, $P>0.05$; Table 2).

Similarly, in the geographical sector GRU, the same assemblages were detected on sites differing by ARs shape (pipes and a heap of telegraphical poles) in the same location (GRU1 and GRU2). Conversely, different assemblages were detected between two sites (GRU2 and GRU3) separated by 9 km although ARs shape was the same (heaps of telegraphical poles). Due to the absence of replication in unit samplings, it was not possible to perform a statistical test on the effect of shape in this geographical sector.

235 **Age and depth effects on five target species at local scale**

236 Despite all five target species being detected on ARs in the AGD sector, assemblage composition
237 among sites differed (Figure 3). Clustering of sampling units within the 5 sites (AGD1, AGD2, AGD3,
238 AGD4, AGD5) in AGD identified 2 clusters (SIMPROF: $P < 0.05$; Figure 4). The two sites (AGD2 and AGD3)
239 with same age (2009), depth range (less than 20 m) and reef shape (pipe) were attributed to different
240 clusters.

241 In fact, one cluster grouped ARs of different age at a same depth (1985 in site AGD1 and 2009 in site
242 AGD2) while the other cluster grouped ARs of the same age but at different depths (less than 20 m in
243 site AGD3 and more than 20 m in sites AGD4 and AGD5). In both clusters, different AR shapes were
244 found (steel cage and pipes in one cluster, pipes, Comin and Bonna in the other cluster) (Figure 4). The
245 geographic distance between the two clusters (AGD4-AGD5) and (AGD3-AGD4-AGD5) was 7.5 km and
246 the median value of the intra-cluster geographic distance was 3 km.

247 Multivariate analysis of variance confirmed that neither age (NP-MANOVA, $F=1.43$ $P<0.05$; Table 3) nor
248 depth (NP-MANOVA, $F=1.37$ $P<0.05$; Table 4) explained site differences in the five species assemblages
249 found on ARs in AGD ($P<0.05$; Tables 3 and 4). Differences among the five sites in AGD were due to
250 different ARs colonization by three species (Kruskall-wallis: *E. singularis*, *P. fascialis*, *H. papillosa*: all
251 $P<0.05$; Table 5). Site AGD3 differed from sites AGD5, AGD1 and AGD2 by the presence of E. singularis,
252 the sites AGD4 and AGD5 differed from sites AGD1 and AGD2 due to the presence of P. fascialis and
253 the site AGD1 differed from sites AGD5, AGD3 and AGD4 to the presence of H. papillosa (Post-hoc
254 tests, Table 3: supplementary material).

255

256 **Geographical effect on five target species at local and regional scales**

257 The five species co-occurrence assemblages on ARs deployed in the same period and at same depth
258 were significantly different at both regional and local scales (NP-MANOVA : geographical sector $F=5.09$
259 $P<0.05$; site (geographical sector) $F=2.78$ $P<0.05$; Table 6). These differences were due to different
260 colonization of ARs by three of the five species, *E. singularis*, *L. sarmentosa* and *P. fascialis*. For the

latter two species, regional differences (Kruskall-wallis: geographical sector P=0.0002) were more significant than local differences (Kruskall-wallis: site P=0.001 for *L. sarmentosa* and P=0.005 for *P. fascialis*; Table 7). Both species were not detected in the north of the GoL (AGM). In contrast, for *E. singularis*, local differences (Kruskall-wallis: site P=0.017) were more significant than regional ones (geographical sector P=0.036; Table 7), the species being detected in geographical sectors in the north, center and south of GoL.

DISCUSSION

The resilience of marine natural biodiversity, including benthic invertebrates, is essential to ensure the sustainability of ecosystem functions. Increasing habitat is key to support the natural biodiversity resilience, which in the case of rocky habitats can be achieved by effectively integrated ARs. The effective integration of ARs into the rocky habitat network starts with their colonization by species from the natural habitat. In the present study the five species selected from the natural rocky habitat of the GoL colonized differently the ARs spread along the GoL coastline ten years after their deployment. Locally, neither age, immersion depth or shape of the ARs significantly affected colonization patterns.

Colonization of ARs are expected to evolve toward a stable state comparable to that of the natural environment, through the succession of opportunistic species (wide dispersal, high fertility, low tolerance of reduced resource levels, short life-spans, minimal dietary specialisation) followed by specialized species (limited dispersal, slow growth to a large size at maturity, delayed and limited reproduction, optimization to reduced resources and long life-spans; (Platt and Connell, 2003; Faurie et al., 2003). Monitoring of ARs short-term colonization (<3 years) have indeed shown a dominance of 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).

286 Long-term studies confirmed successions in ARs colonization (Burt et al., 2011; Nicoletti et al., 2007;
287 Perkol-Finkel and Benayahu, 2005; Whomersley and Picken, 2003), but none have described saturation
288 (Svane and Petersen, 2001). In the Tyrrhenian Sea, Nicolleti et al., (2007) described colonization in 5
289 distinct phases: (i) A first recruitment by pioneer species (hydroids, serpulids, barnacles and bivalves)
290 during the first months after immersion, followed by phases of (ii) cover dominance, (iii) regression
291 and (iv) absence of *Mytilus galloprovincialis* for more than 10 years. The installation of diverse bio-
292 builders bryozoans characteristic of the natural environment was recorded after 20 years only (v). Our
293 study shows that bio-builder engineering species such as bryozoans (*P. fascialis*) and gorgonians (*E.*
294 *singularis, L. sarmentosa*) colonized ARs as early as 10 years after their deployment, without significant
295 difference between 10 years and 35 years old ARs. However, the presence of *S. spallanzanii* described
296 as an opportunistic species (sexual precocity, various reproduction modes, rapid growth, short lived;
297 Giangrande et al., 2000) on all ARs independently of their age of deployment suggests that ARs did not
298 yet reach a stable state comparable to the natural environment. Thus, the presence of bio-builders is
299 not a sufficient indicator of the ARs naturalization to the local biodiversity.
300 The GoL's ARs being located in the sandy coastal zone are likely regularly disturbed by sediment
301 deposits due to river delivery or/and their resuspension by either trawling activities or the mechanical
302 action of the swell (Dufois et al., 2014; Durrieu de Madron et al., 2005; Ulses et al., 2008). Testing the
303 impact of swell and sediment deposit on ARs requires exploring the colonization of ARs along a
304 gradient of depth and distance from the coast (van der Stap et al., 2016). However, current ARs
305 deployment in the GoL ranged from 15 to 30 m depth and within 3 miles from the coast and did not
306 allow testing for differential effect of sediment disturbances as swell impact occurs every year in this
307 area (Guizien, 2009). Testing the impact of sediment disturbance on ARs colonization would require
308 exploring reefs deployed deeper than 50 m, such as the anchorages of the floating wind farm that will
309 be placed in the GoL in the next future (https://info-efgl.fr/le-projet/le-parc/#). Light is also expected
310 to be an important factor structuring benthic assemblages, along a depth gradient in natural and
311 artificial environments (T. Glasby, 1999a; T. M. Glasby, 1999b; Svane and Petersen, 2001) . Absence

312 of depth effect in the present study, although in the GoL light intensity strongly attenuates within the
313 upper 30 m of the water column (Durrieu de Madron et al., 2011) was potentially a bias due to the five
314 species selected in the present study whose distributions are not strongly structured by light intensity.
315 Another factor which has been shown to drive the intensity of ARs colonization is structural complexity
316 (see Bohnsack and Sutherland, 1985 for a review). Nevertheless, there is no consensus about the
317 relationship between complexity and subtidal benthic invertebrates abundance, due to potential bias
318 in controlling the surface and scale in ARs of different complexity (Rouse et al., 2019; Strain et al.,
319 2018). The similarity in the 5 species co-occurrence between different reef shapes at the same depth
320 and of the same age found in the present study suggests that shape is less important than the
321 geographical location in AR colonization by benthic invertebrates when controlling the colonized
322 surface. However, shape is an imprecise measure of structural complexity. The latter is rarely assessed
323 quantitatively and can be described by different metrics which may be similar for apparently different
324 shapes (such as steel cages and pipes, (Riera, 2020).
325 Benthic invertebrate assemblages result from complex processes that operate at multiple spatial and
326 temporal scales (Smale, 2012). At the regional scale, larval availability can become a major factor
327 explaining colonization success (Padron et al., 2018). Change in the composition of assemblages during
328 the early colonization of artificial substrates by benthic invertebrates has been attributed to the
329 availability and abundance of larvae during the seasons rather than a sequence of distinct succession
330 (Bramanti et al., 2003; Turner and Todd, 1993). The larval behaviour (buoyancy and motility) and the
331 characteristics of the biological cycle of the species (spawning timing and PLD) can play a key role in
332 determining the dispersal distance (Todd, 1998), and consequently the possibility to reach habitat
333 suitable for settlement. Dispersion distance is generally correlated with PLD, thus, a species with a long
334 PLD is supposed to colonize habitats further away than species with a shorter PLD (Shanks, 2009). In
335 this study, the five species were chosen among different phyla known for their contrasting planktonic
336 durations, swimming abilities and larval dispersal periods, although these larval traits are only known
337 accurately for *E. singularis* (Guizien et al., 2020; Zelli et al., 2020). *P. fascialis* and *H. papillosa*, the two

species with short PLD (<24h and <12h, 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 GoL 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 GoL. 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 GoL, 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 GoL, 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 extend the habitat of hard bottom benthic invertebrate natural populations.

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Authors contributions

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

Conflict of interest disclosure

The authors of this manuscript declare that they have no financial conflict of interest with the content of this article.

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Figure captions:

Figure 1: Map showing the layout of the 6 geographical sectors (AGM, AGD, VLR, GRU, LEU, CST) and the 16 sites prospected (indicated in dark blue) for artificial reef sampling. Areas indicated in light blue corresponded to artificial reef deployment areas. Areas indicated in black corresponded to natural hard-substrate areas. Some of the AR shape illustrations were taken from Tessier et al., 2014.

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 16 sites (AGM1, AGM2, AGD1, AGD2, AGD3, AGD4, AGD5, VLR1, VLR2, GRU1, GRU2, GRU3, LEU1, LEU2, CST1, CST2) in the Gulf of Lion.

Figure 4: Diversity and dissimilarity. Upper part: diversity of species assemblages in the sampling units of the five sites (AGD1, AGD2, AGD3, AGD4, AGD5) in AGD sector together with the type of AR, depth and years of deployment. Lower part: 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 separates the two clusters identified by the analysis.

Figures :

Figure 1 :

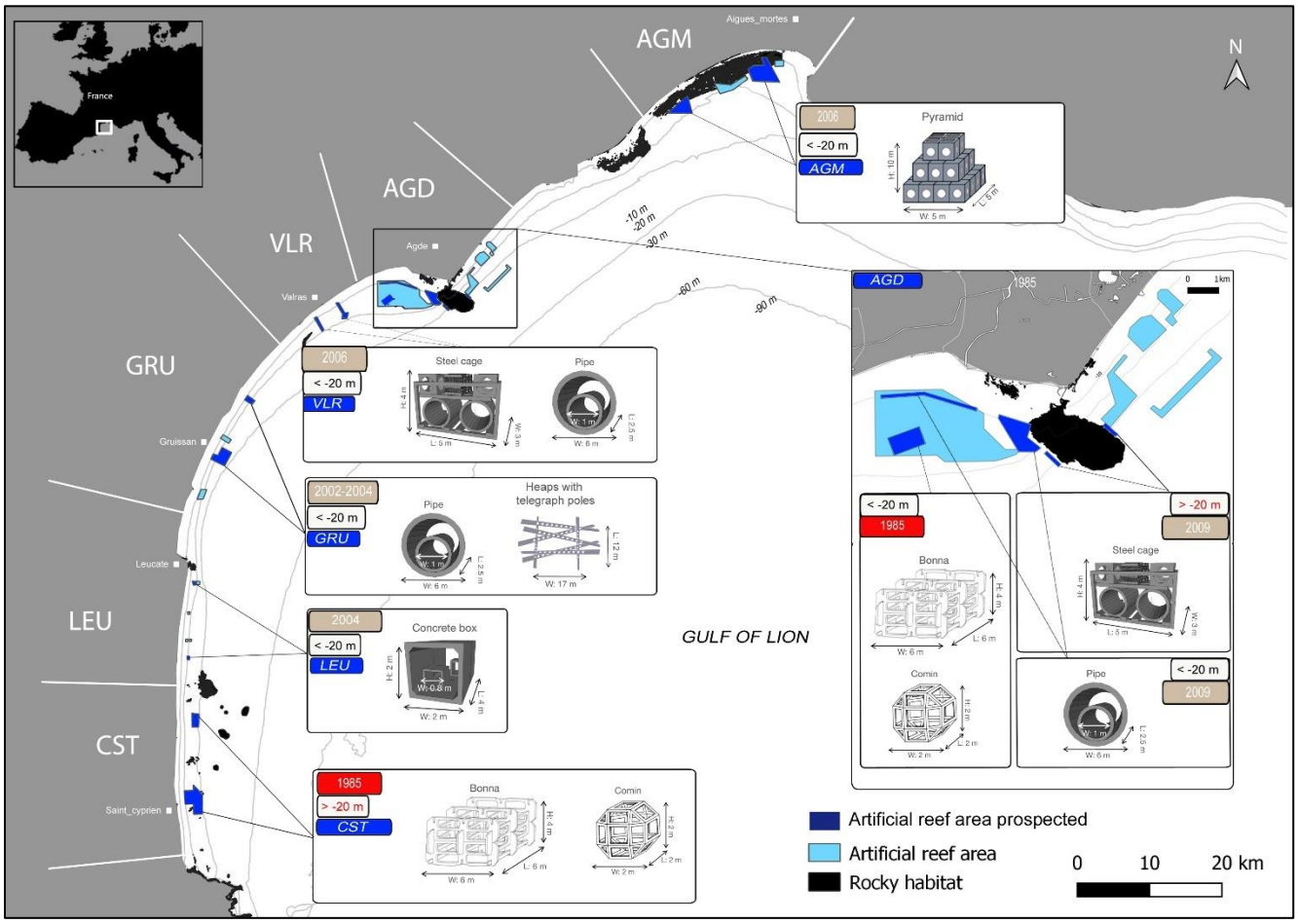
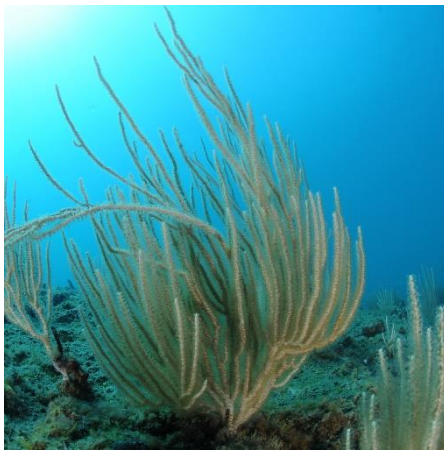


Figure 2 :

A)

B)



C)

D)

E)

Figure 3 :

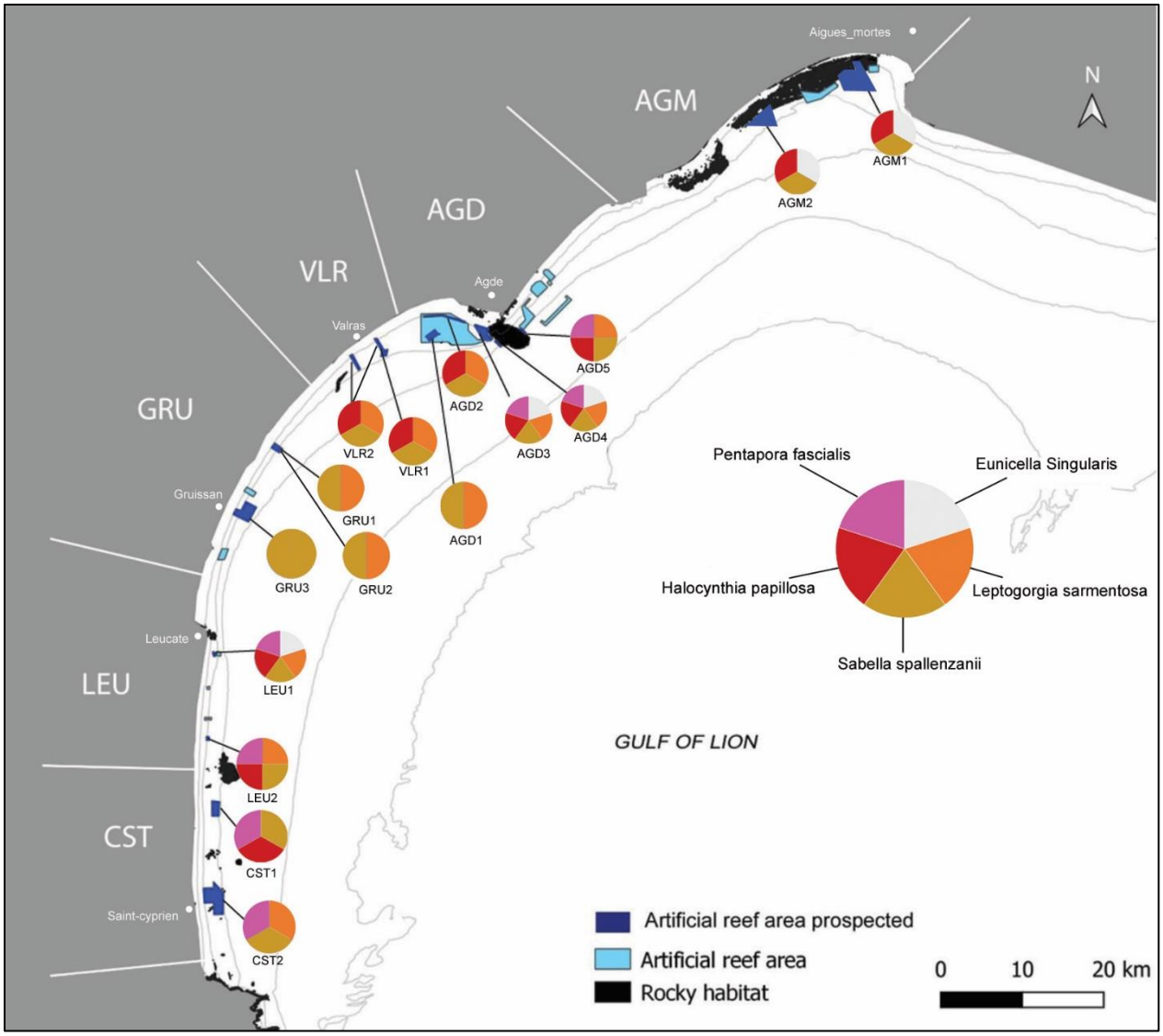
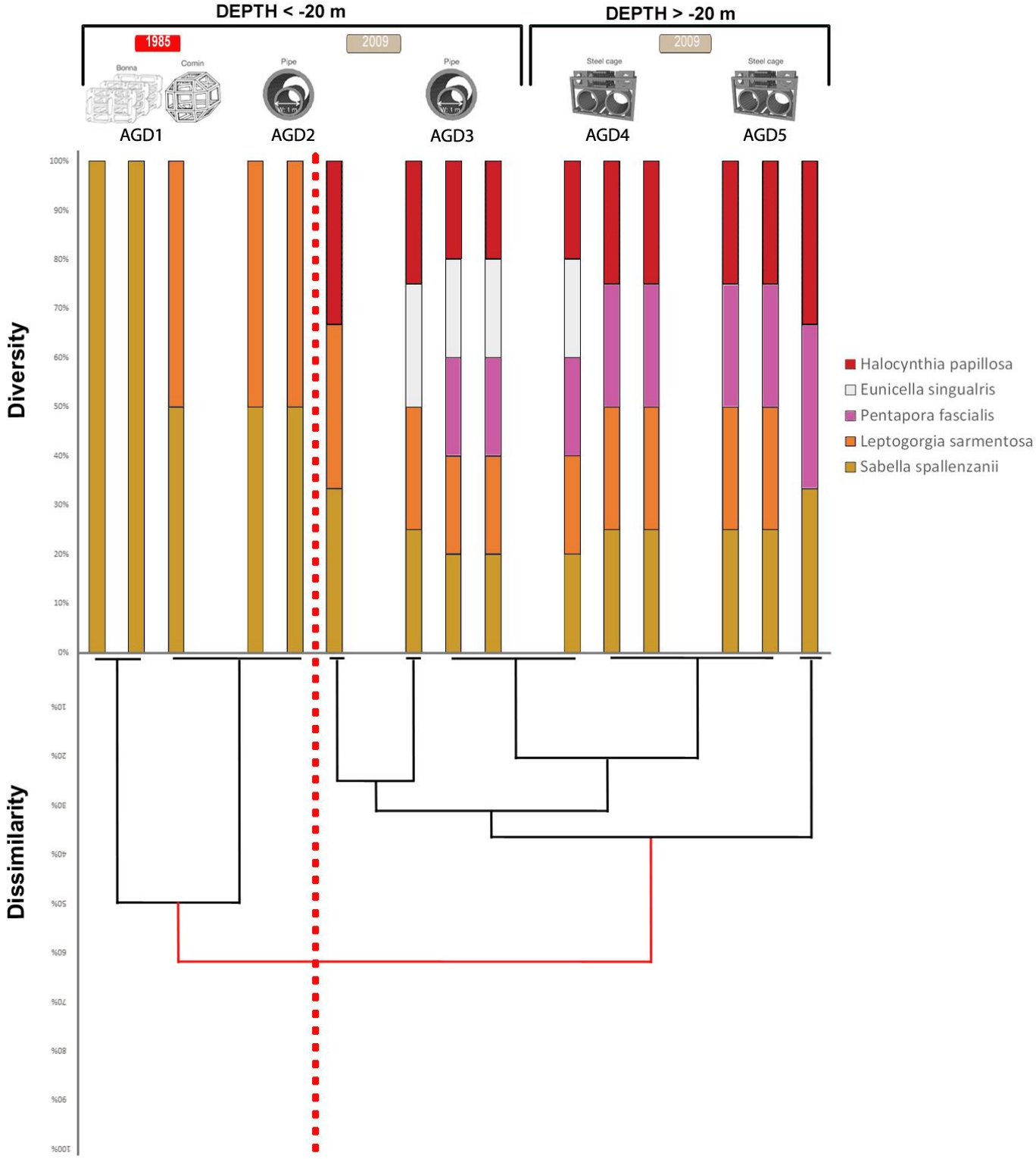

Aigues_mortes
N
AGM
AGM1
AGM2
AGD
VLR
Agde
Valras
AGD5
AGD2
AGD3
AGD4
GRU
VLR2
VLR1
Gruissan
GRU1
AGD1
GRU3
GRU2
Pentapora fascialis
Eunicella Singularis
Halocynthia papillosa
Leptogorgia sarmentosa
Sabella spallenzanii
Leucate
LEU
LEU1
GULF OF LION
LEU2
CST
CST1
Saint-cyprien
CST2
Artificial reef area 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
AGD1
AGD2
AGD3
AGD4
AGD5
Diversity
Dissimilarity
Halocynthia papillosa
Eunicella singualris
Pentapora fascialis
Leptogorgia sarmentosa
Sabella spallenzanii

755 **Table captions**

756 Table 1: Life_history traits (spawning period, relative fecundity, life expectancy, age at sexual
757 maturity, larval type, planktonic larval duration (PLD), relative abundance in the GoL) for the five
758 species inventoried on ARs.

759

760 Table 2: Results of multivariate NP-Manova testing the effect of the shape between steel cage and
761 pipe on the presence/absence assemblage. Sites tested: VLR1 vs VLR2. Significant (P<0.05) values in
762 bold.

763

764 Table 3: Results of multivariate NP-Manova testing the interactive effects of the Age (of deployment)
765 and site (nested in Age) on the presence/absence assemblage. Sites tested: AGD1 vs (AGD2 vs AGD3).
766 Significant (P<0.05) values in bold.

767

768 Table 4: Results of multivariate NP-Manova testing the interactive effects of the depth (of
769 deployment) and site (nested in depth) on the presence/absence assemblage. Sites tested: (AGD2 vs
770 AGD3) vs (AGD4 vsAGD5). Significant (P<0.05) values in bold.

771

772 Table 5: Results of univariate Kruskall_wallis testing the effect of location of deployment on the
773 presence/absence by species. Sites tested: all sites in AGD. Significant (P<0.05) values in bold.

774

775 Table 6: Results of multivariate NP-Manova testing the interactive effects of geographical sector and
776 site (nested in geographical sector) on the presence/absence assemblage. Sites tested: (AGM1 vs
777 AGM2) vs (AGD2 vs AGD3) vs (VLR1 vs VLR2) vs (GRU1 vs GRU2 vs GRU3) vs (LEU1 vs LEU2).
778 Significant (P<0.05) values in bold.

779

780 Table 7: Results of univariate Kruskall_wallis testing the effects of geographical sector and site on the

781 presence/absence by species. Sites tested: AGM1 vs AGM2 vs AGD2 vs AGD3 vs VLR1 vs VLR2 vs

782 GRU1 vs GRU2 vs GRU3 vs LEU1 vs LEU2. Significant (P<0.05) values in bold.

783

784 **Tables:**

785 **Table 1:**

Species	Spawning period	Fecundity	Life expectancy	Age at sexual maturity	Larval type	Planktonic larval duration (PLD)	Abundance in the GoL
Leptogorgia sarmentosa	June - August	**	20 years	2-3 years	Lecithotrophic	1-4 weeks (estimated from other gorgonians)	**
Eunicella singularis	July - August	*	25-30 years	6 years	Lecithotrophic	1-4 weeks (in aquarium)	***
Pentapora fascialis	June	**	10 years	2 years	Lecithotrophic	<1 days	**
Sabella spallanzani	January - February	***	5 years	1 years	Lecithotrophic	21 days (in aquarium)	*
Halocynthia papillosa	September - October	*** (estimated from other ascidians)	unknow	2 months (estimated from other ascidians)	lecithotrophic (estimated from other ascidians)	<12 hours (estimated from other ascidians)	**

786 Symbol legend: * = low, **=medium ***=strong

787

788 **Table 2:**

Multivariate measures					
Source	**Df**	**SS**	**Ms**	**F**	**Pvalue**
Assemblage (Presence/Absence)					
Shape	1	3.6408e-19	3.6408e-19	9.8301e-18	0.6090
Residual	4	0.1481	0.0370		
Total	5	0.1481			

789

790

791

Table 3:

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

Table 4:

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 5:

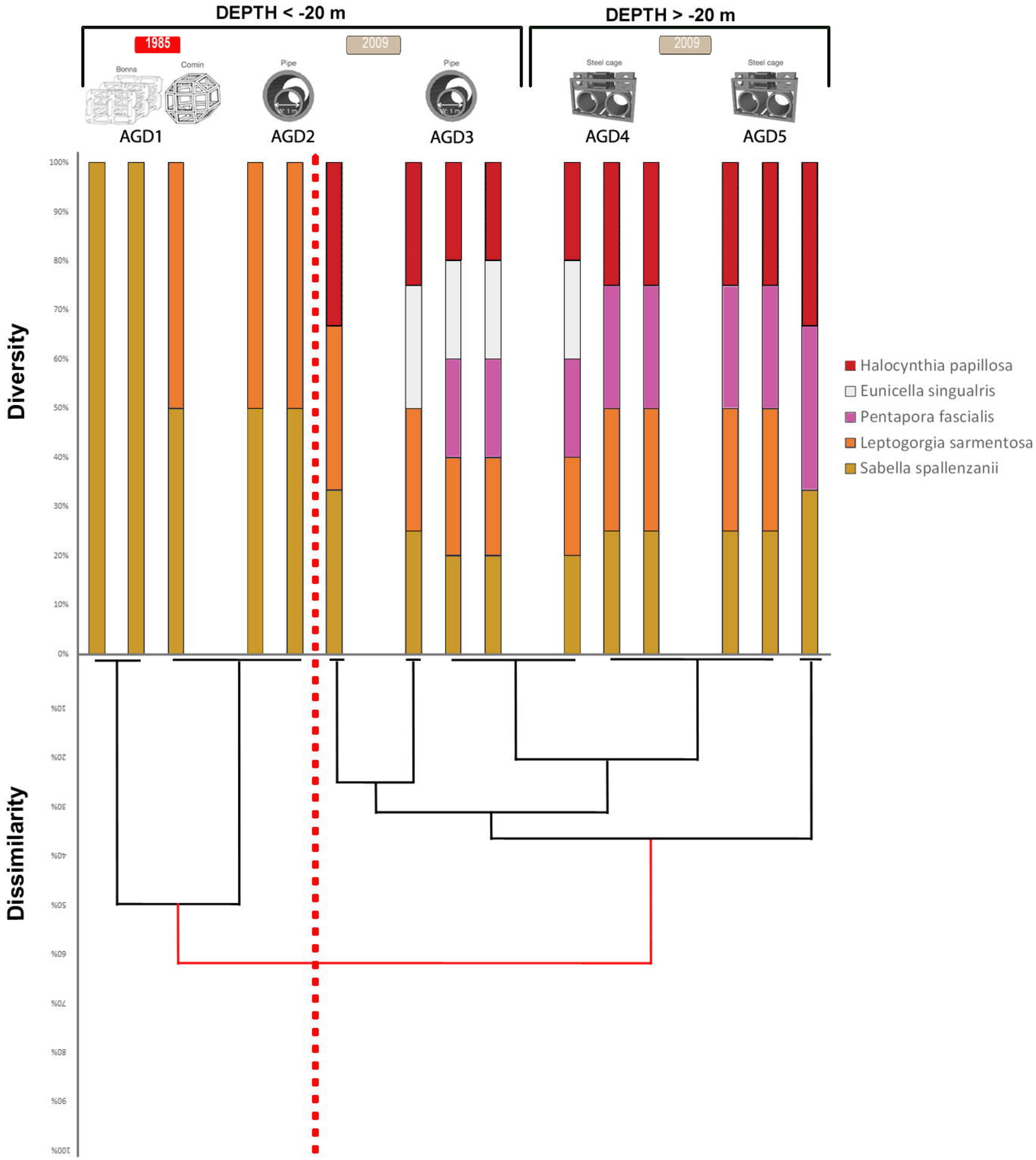
Univariate measures					
Presence/absence					
	Df	SS	Ms	Chi_sq	Pvalue
Eunicella singularis					
	4	127.5	31.875	10.82	**0.0287**
Leptogorgia sarmentosa					
	4	60	15	6.22	0.1832
Pentapora fascialis					
	4	172.5	43.125	11.5	**0.0215**
Sabella spallazanii					
	4	0	0	nan	nan
Halocynthia papillosa			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

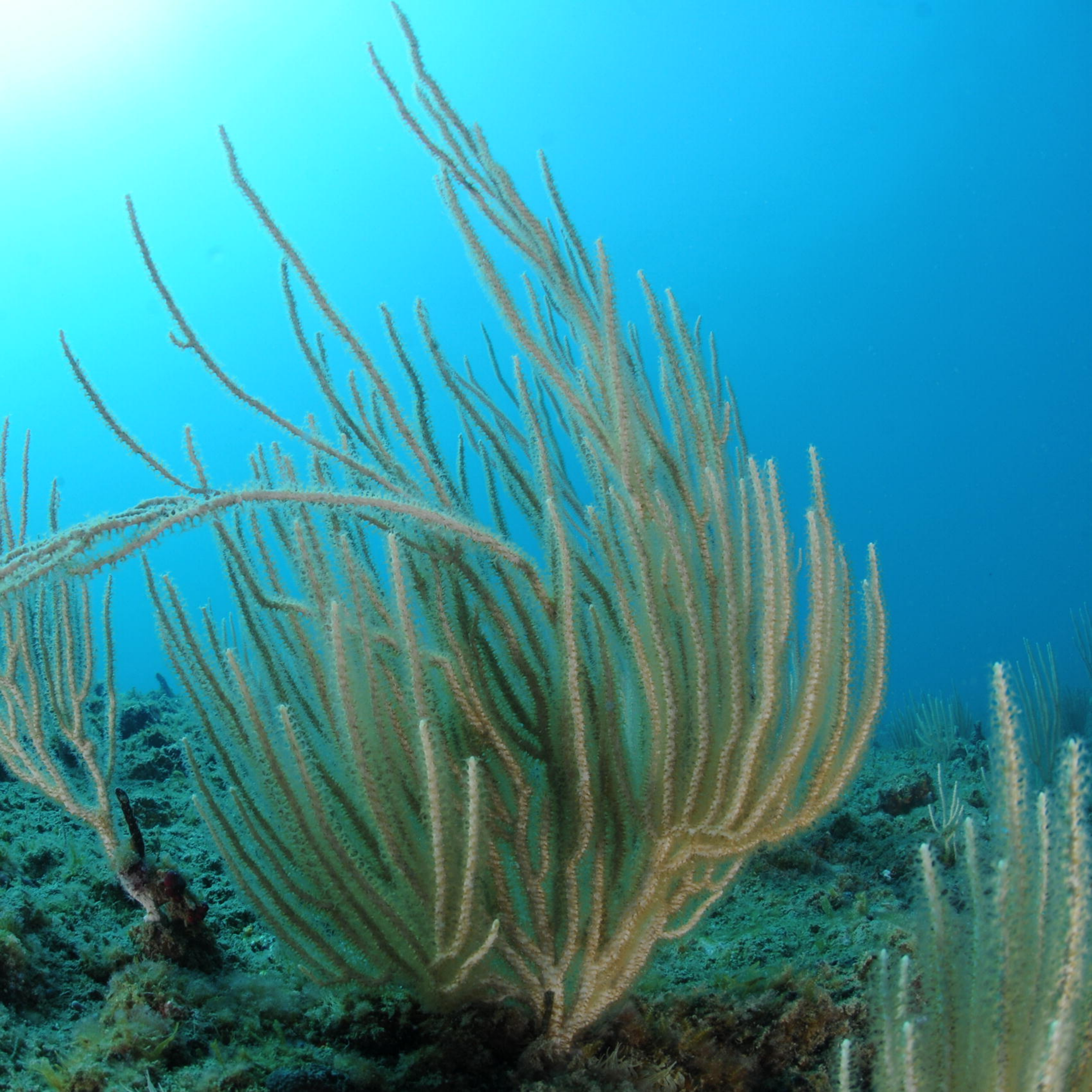
Table 6:

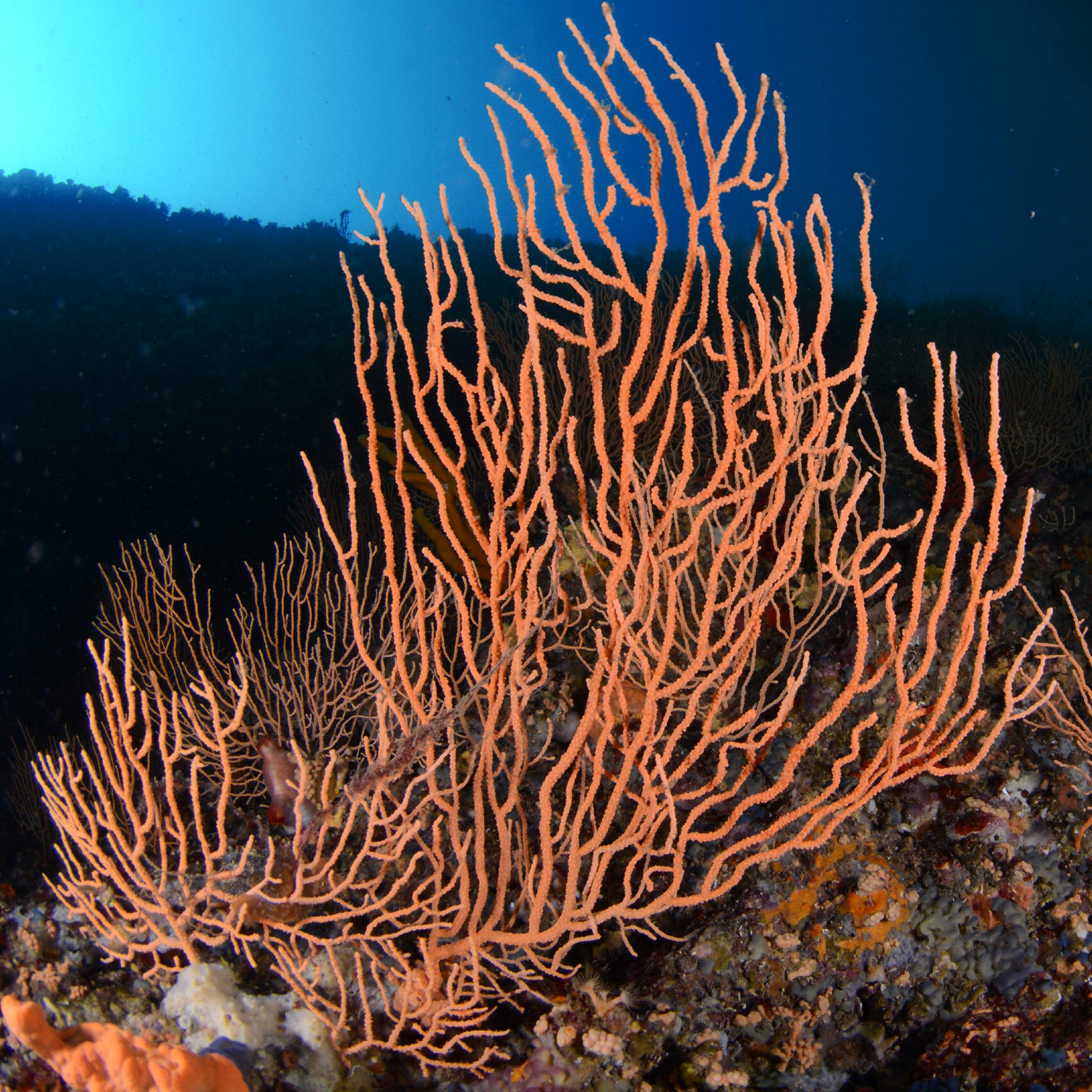
Multivariate measures					
Source	**Df**	**SS**	**Ms**	**F**	**Pvalue**
Assemblage (Presence/Absence)					
Geographical sector	4	2.1671	0.5418	5.0994	**0.005**
Site(Geographical sector)	6	0.6375	0.1062	2.7812	**0.007**
Residual	18	0.6876	0.0382		
Total	28	3.4921			

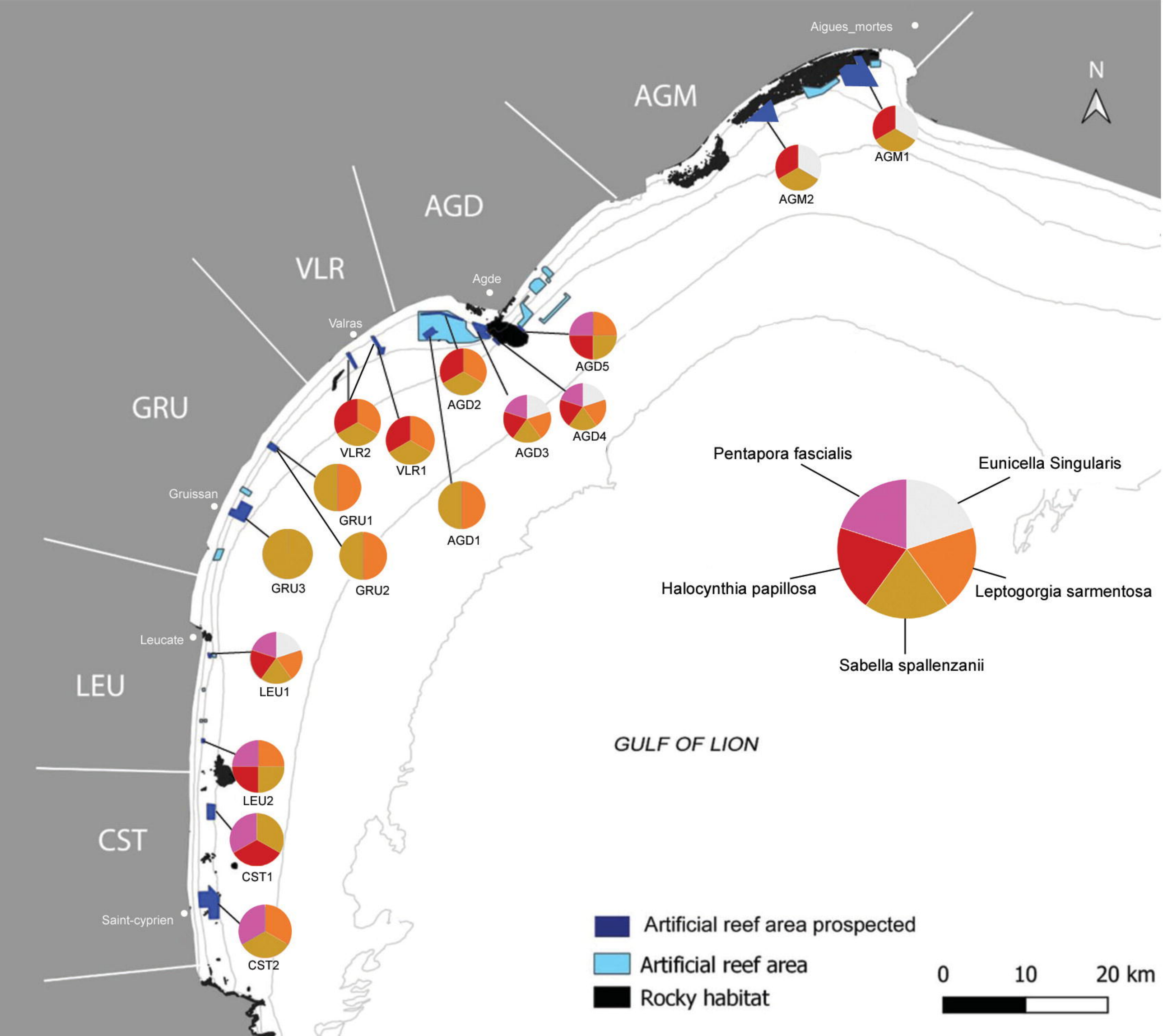
Table 7:

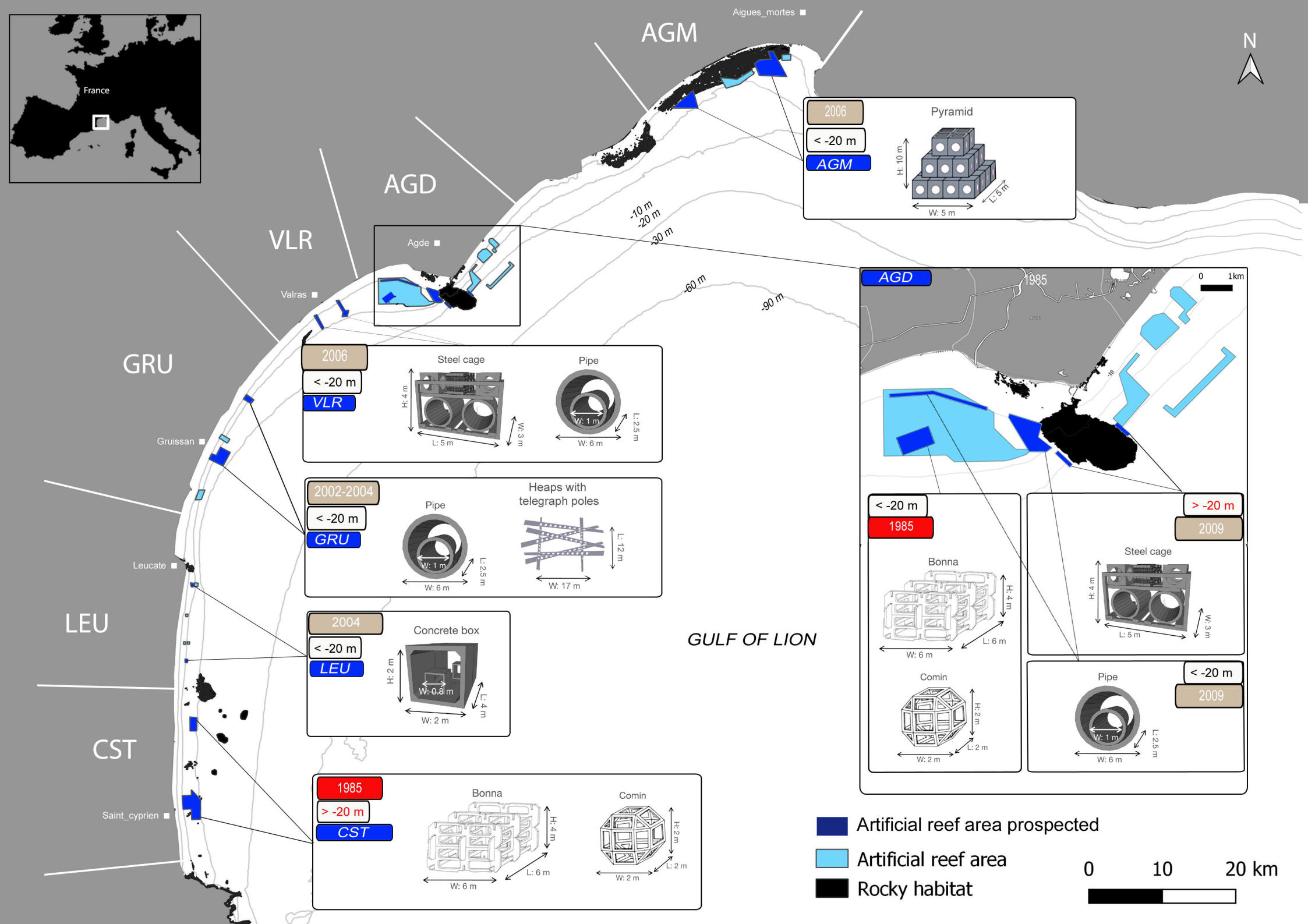
Presence/absence					
Source	**Df**	**SS**	**Ms**	**Chi_sq**	**Pvalue**
Eunicella singularis					
Geographical sector	4	447.08	111.77	10.28	**0.036**
Site	9	937.66	93.76	21.56	**0.0175**
Leptogorgia sarmentosa					
Geographical sector	4	965.7	241.42	22.2	**0.0002**
Site	9	1116.5	11.65	28	**0.0018**
Pentapora fascialis					
Geographical sector	4	937.66	234.41	21.56	**0.0002**
Site	9	1077.83	107.78	24.78	**0.0058**
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	681.5	68.15	12.53	0.2509


DEPTH < -20 m
DEPTH > -20 m
1985
2009
2009
Bonna
Comin
Pipe
Pipe
Steel cage
Steel cage
AGD1
AGD2
AGD3
AGD4
AGD5
Diversity
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Dissimilarity
10%
20%
30%
40%
50%
60%
70%
80%
90%
100%
Halocynthia papillosa
Eunicella singualris
Pentapora fascialis
Leptogorgia sarmentosa
Sabella spallenzanii






Aigues_mortes
N
AGM
AGD
VLR
GRU
LEU
CST
Agde
Valras
Gruissan
Leucate
Saint-cyprien
AGM1
AGM2
AGD5
AGD2
AGD3
AGD4
VLR2
VLR1
GRU1
AGD1
GRU3
GRU2
LEU1
LEU2
CST1
CST2
Pentapora fascialis
Eunicella Singularis
Halocynthia papillosa
Leptogorgia sarmentosa
Sabella spallenzanii
GULF OF LION
Artificial reef area prospected
Artificial reef area
Rocky habitat
0
10
20 km


France
Aigues_mortes
AGM
N
2006
< -20 m
AGM
Pyramid
H: 10 m
W: 5 m
L: 5 m
AGD
Agde
VLR
Valras
-10 m
-20 m
-30 m
-60 m
-90 m
GRU
Gruissan
2006
< -20 m
VLR
Steel cage
H: 4 m
L: 5 m
W: 3 m
Pipe
W: 1 m
W: 6 m
L: 2.5 m
2002-2004
< -20 m
GRU
Pipe
W: 1 m
W: 6 m
L: 2.5 m
Heaps with telegraph poles
L: 12 m
W: 17 m
Leucate
LEU
2004
< -20 m
LEU
Concrete box
H: 2 m
W: 0.8 m
W: 2 m
L: 4 m
GULF OF LION
CST
Saint_cyprien
1985
> -20 m
CST
Bonna
H: 4 m
W: 6 m
L: 6 m
Comin
H: 2 m
W: 2 m
L: 2 m
AGD
1985
0
1km
< -20 m
1985
Bonna
H: 4 m
W: 6 m
L: 6 m
Comin
H: 2 m
W: 2 m
L: 2 m
> -20 m
2009
Steel cage
H: 4 m
L: 5 m
W: 3 m
< -20 m
2009
Pipe
W: 1 m
W: 6 m
L: 2.5 m
Artificial reef area prospected
Artificial reef area
Rocky habitat
0
10
20 km