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

Sylvain Blouet[1,2], Lorenzo Bramanti[1], Katell Guizien[1]

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

[1 2] Ville d'Agde, Aire marine protégée de la côte agathoise, 34300 Agde, France.

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

The objective of the present study was to test the hypothesis that the geographical location of ARs 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.

In each site, 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. 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 GDL 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. In the geographical sector GRU, in one of the two sites, only two sampling units could be defined given the ARs shapes, yielding a total surface of 600 m^2 (Supplementary Material Table 1). 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

Assessment of ARs colonization was carried out by autonomous scuba-diving in 2020 by counting the number of individuals of the five target species in the 44 sampling units (Supplementary Material Table1, totalling 80 ARs fully inventoried). Among the species listed in previous ARs inventories in the GDL, we selected five species that were present in most inventories, easy to identify by scuba diving 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 *Pentapora fascialis* (Pallas, 1766), one annelida *Sabella spallanzanii* (Gmelin, 1791) and one ascidian *Halocynthia papillosa* (Linnaeus, 1797) (Figure 2). The five species have a similar wide natural repartition area along European coasts ranging from 1m to 250m depth (Giangrande et al., 2005; Gori et al., 2011; Ponti et al., 2019; Turon, 1990; Weinberg and Weinberg, 1979). In addition, *S.*

spallanzanii has been recorded along the coasts of Brazil, Australia and New Zealand where it is classified as an invasive non-indigenous species (Currie et al., 2000).

The five species are present in the rocky habitat of the NW Mediterranean Sea (Laubier, 1966; True, 1970; Hong, 1980). However, in the GDL, where natural rocky habitat covers uneven surfaces within 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 five species display different spatial distributions (Dutrieux et al., 2005; Dalias et al., 2011; Padron et al., 2018; S. Blouet personal observation). *E. singularis* is frequently observed and abundant throughout the GDL (from the AGM sector to the CST sector), while *L. sarmentosa,* less abundant, is present mainly in the center of the GDL (AGD, VLR, LEU, CST). *P. fascialis* is abundant in the west of the GDL (AGD, LEU, CST, and south of CST). The distribution of *H. papillosa* is not well known, however the species has been observed in all the rocky areas of the GDL. *S. spallanzanii* is present but rare in natural rocky habitat. Nevertheless, *S. spallanzanii* is very abundant in lagoons, ports and marinas of the GDL (S. Blouet personal observation) which have been indicated as preferred habitat of the species (Currie et al., 2000).

The five species display different life-history traits. All five species reproduce once a year in different seasons and with different strategies (Table 1).

S. spallanzani reproduces in January-February, when water temperature is the coldest. The species displays multiple reproductive strategies: internal fertilization, with larvae brooded either inside or outside the mineral tube secreted around the body, and external fertilization broadcast spawning (Giangrande et al., 2000). In addition, asexual reproduction by fission has been reported (Read et al., 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 GDL (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 *Ciona 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).

Statistical analysis

We examined to which extent ARs colonization is affected by the location and timing of deployment. To do so, we tested the effect of 4 factors (geographical sector being the regional factor, site being the local factor, depth and age) on the presence/absence of the five species and on the dissimilarity between their co-occurrence assemblages. In all analyses, site was a random factor, nested either in year, age or the geographical sector factor. Due to AR deployment set up, the effect of factors age (2 levels, 1985, 2002-2009) and depth (2 levels, >20 m, <20 m depth) was tested within the AGD geographical sector only. Factor age was tested in 3 sites at <20m and factor depth was tested in 4 sites deployed in 2009. To avoid any confounding effect due to age or depth, the regional factor vs local factor were tested on the 5 geographical sectors where AR were deployed during the 2002-2009 immersion phase and at <20 m depth only (AGM, AGD, VLR, GRU, LEU: 5x2 levels). A Jaccard similarity matrix was built on presence/absence data across all pairwise sampling units. Two multivariate analyses were performed. Non-parametric multivariate analysis of variance with permutation was applied to test for the effects of age, depth and geographical sector on species assemblages (NP-manova: Anderson, 2001; Zar, 1999). Another multivariate analysis was performed to cluster most similar species assemblages in the sector of AGD (SIMPROF : Clarke et al., 2008).

When significant differences between the five species co-occurrence assemblages were detected for a factor, a non-parametric univariate analysis (ANOVA Kruskall-Wallis) was performed for each species independently to detect the species driving the difference. Fisher post-hoc test was used to identify the site where the difference arose. A same p-value of 0.05 was 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 4). In only one out of 15 sites, it was the only species detected. *H. papillosa* was detected in all geographic sectors but not in all the sampling units. *L. sarmentosa* was detected in five of the six geographical sectors (not present in AGM) and *P. fascialis* was detected in 3 of the 6 geographical sectors (CST, LEU and AGD). Finally, *E.singularis* was the least frequently observed species, being detected in only three geographical sectors (AGM, AGD and LEU). In all geographical sectors, at least three of the five target species were detected. Assemblages of two species were found in only one site out of 15 (sector AGD), assemblages of three species were found in 8 sites, assemblages of four species were found in 2 sites and assemblages of five species were found in 3 sites.

Age and depth effects on five target species at local scale

Despite all five target species being detected on ARs in the AGD sector, assemblage composition among sites differed (Figure 3). Clustering of sampling units within the 5 sites (A, B, C, D, E) in AGD identified 2 clusters (SIMPROF: P <0.05; Figure 4). The two sites (B and C) with same age (2009), depth range (less than 20 m) and reef shape (pipe) were attributed to different clusters. In fact, one cluster grouped ARs of different age at a same depth (1985 in site A and 2009 in site B) while the other cluster grouped ARs of the same age but at different depths (less than 20 m in site C and more than 20 m in sites D and E). In both clusters, different AR shapes were found (steel cage and pipes in one cluster, pipes, Comin and Bonna in the other cluster, Figure 4). The geographic distance between the two clusters (A-B) and (C-D-E) was 7.5 km and the median value of the intra-cluster geographic distance was 3 km.

Multivariate analysis of variance confirmed that neither age (NP-MANOVA, F=1.43 P<0.05 ; Table 2) nor depth (NP-MANOVA, F=1.37 P<0.05 ; Table 3) explained site differences in the five species assemblages found on ARs in AGD (P<0.05 ; Tables 2 and 3). Differences among the five sites in AGD were due to different ARs colonization by three species (Kruskall-wallis: *E. singularis*, *P. fascialis*, *H. papillosa*: all P<0.05; Table 4). Site C differed from other sites by the presence of *E. singularis*, and sites D and E differed from sites A and B due to the presence of *P. fascialis* and *H. papillosa* (Post-hoc tests).

Geographical effect on five target species at local and regional scales

The five species co-occurrence assemblages on ARs deployed in the same period and at same depth were significantly different at both regional and local scales (NP-MANOVA : geographical sector F=3.19 P<0.05; site (geographical sector) F=3.64 P<0.05; Table 5). These differences were due to different 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=0.003 for *P. fascialis*; Table 6). Both species were not detected in the north of the GDL (AGM). In contrast, for *E. singularis*, local differences (Kruskall-wallis: site P=0.01) were more significant than regional ones (geographical sector P=0.036; Table 6), the species being detected in geographical sectors in the north, center and south of GDL.

DISCUSSION

The study of effective integration of ARs into the rocky habitat network through their colonization by species building up their natural biodiversity is essential to assess their ecosystem functions, prior and after deployment. In the present study, we showed that ARs spread along the GDL coastline had been colonized by five species found in the natural rocky habitat of the region, ten years after their deployment. However, spatial colonization patterns differed among species, resulting in diverse assemblages in different geographical sectors of the GDL. Locally, neither age, immersion depth or reef shape 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). 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 to be an important factor structuring benthic assemblages, along a depth gradient in natural and artificial environments (T. Glasby, 1999a; T. M. Glasby, 1999b; Svane and Petersen, 2001)–. Absence of depth effect in the present study, although in the GDL light intensity strongly attenuates within the upper 30 m of the water column (Durrieu de Madron et al., 2011) was potentially a bias due to the five species selected in the present study whose distributions are not strongly structured by light intensity. Another factor which has been shown to drive the intensity of ARs colonization is structural complexity (see Bohnsack and Sutherland, 1985 for a review). Nevertheless, there is no consensus about the relationship between complexity and subtidal benthic invertebrates abundance, due to potential bias in controlling the surface and scale in ARs of different complexity (Rouse et al., 2019; Strain et al., 2018). The similarity in the 5 species co-occurrence between different reef shapes at the same depth found in the present study suggests structural complexity is less important than the geographical location in AR colonization by benthic invertebrates.

Benthic invertebrate assemblages result from complex processes that operate at multiple spatial and temporal scales (Smale, 2012). At the regional scale, larval availability can become a major factor explaining colonization success. Change in the composition of assemblages during the early colonization of artificial substrates by benthic invertebrates has been attributed to the availability and abundance of larvae during the seasons rather than a sequence of distinct succession (Bramanti et al., 2003; Turner and Todd, 1993). The larval behaviour (buoyancy and motility) and the characteristics of the biological cycle of the species (spawning timing and PLD) can play a key role in determining the dispersal distance (Todd, 1998), and consequently the possibility to reach habitat suitable for settlement. Dispersion distance is generally correlated with PLD, thus, a species with a long PLD is supposed to colonize habitats further away than species with a shorter PLD (Shanks, 2009). In this study, the five species were chosen among different phyla known for their contrasting planktonic durations, swimming abilities and larval dispersal periods, although these larval traits are only known 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 <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.

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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 :

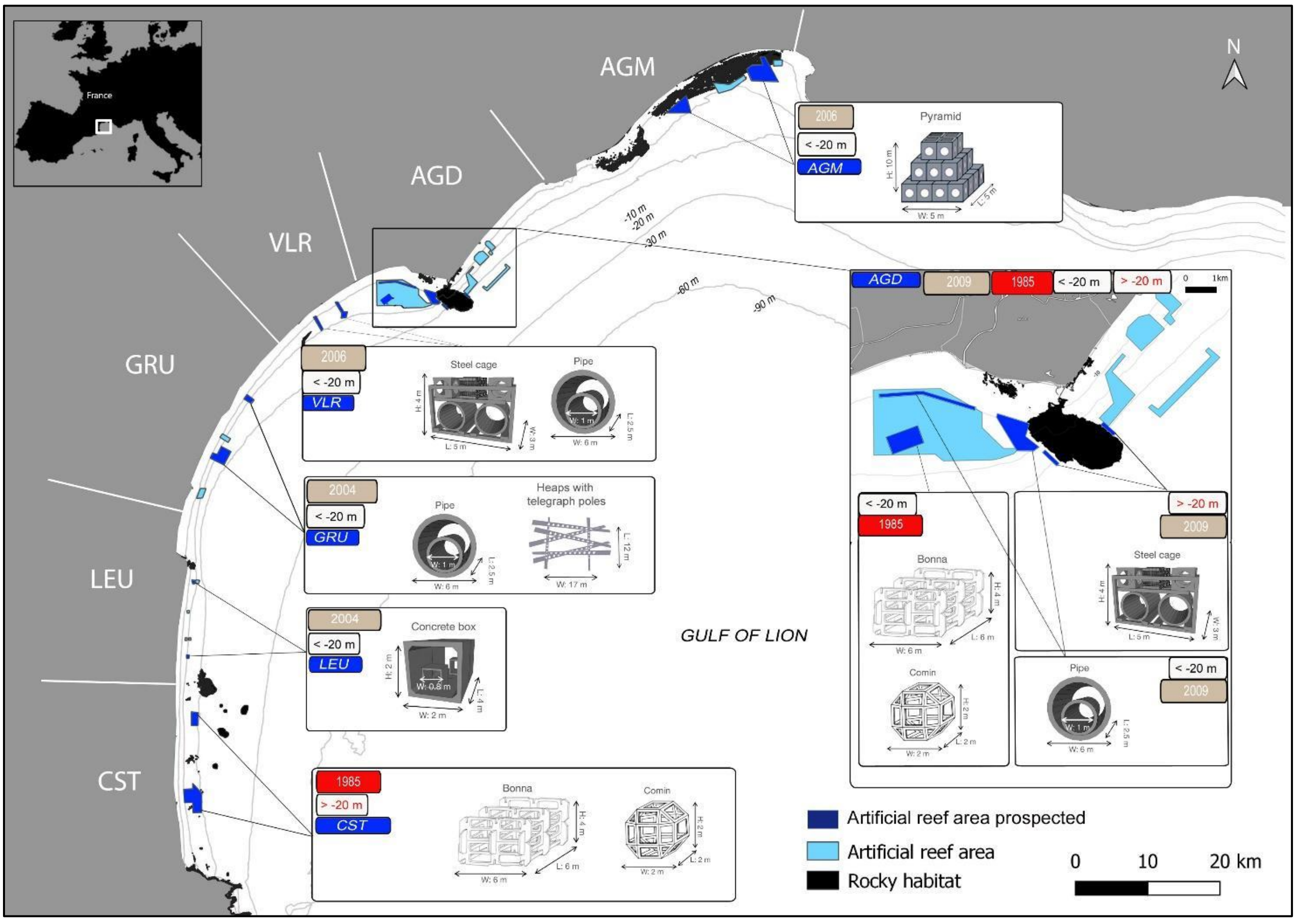

Figure 2 :

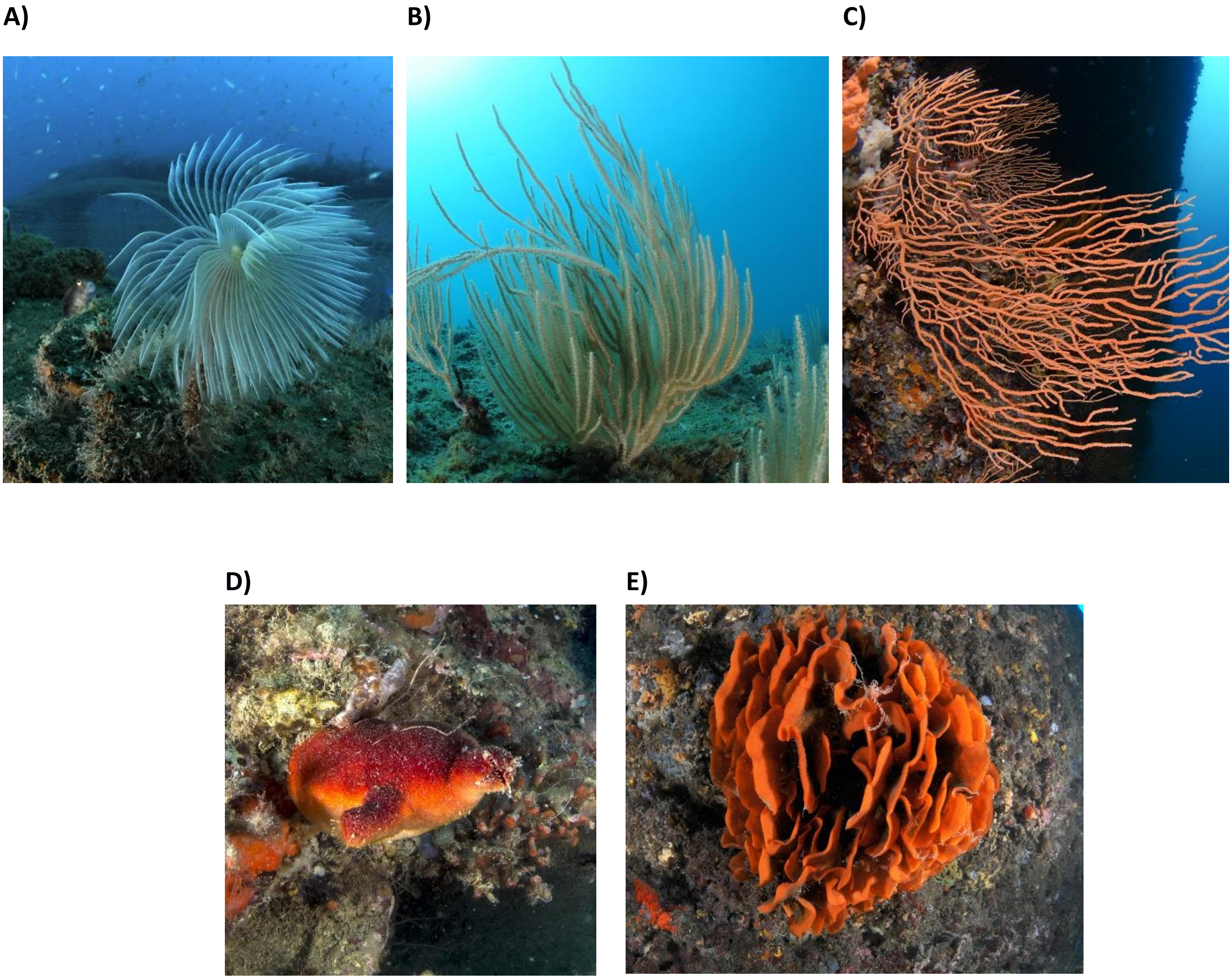

Figure 3 :

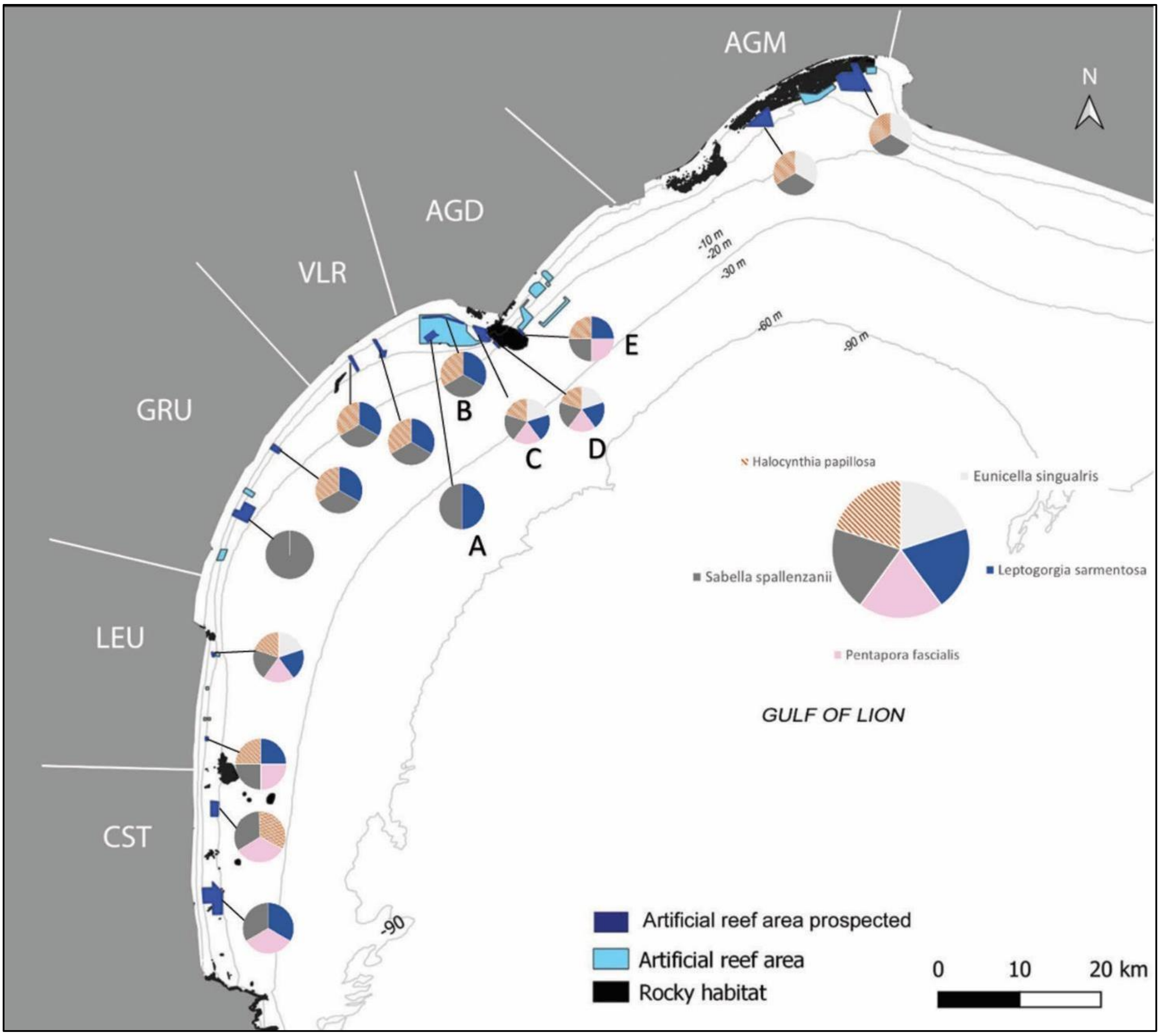
AGM
N
AGD
VLR
GRU
LEU
CST
-10 m
-20 m
-30 m
-60 m
-90 m
-90
A
B
C
D
E
Halocynthia papillosa
Eunicella singualris
Sabella spallenzanii
Leptogorgia sarmentosa
Pentapora fascialis
GULF OF LION
Artificial reef area prospected
Artificial reef area
Rocky habitat
0
10
20 km

Figure 4:

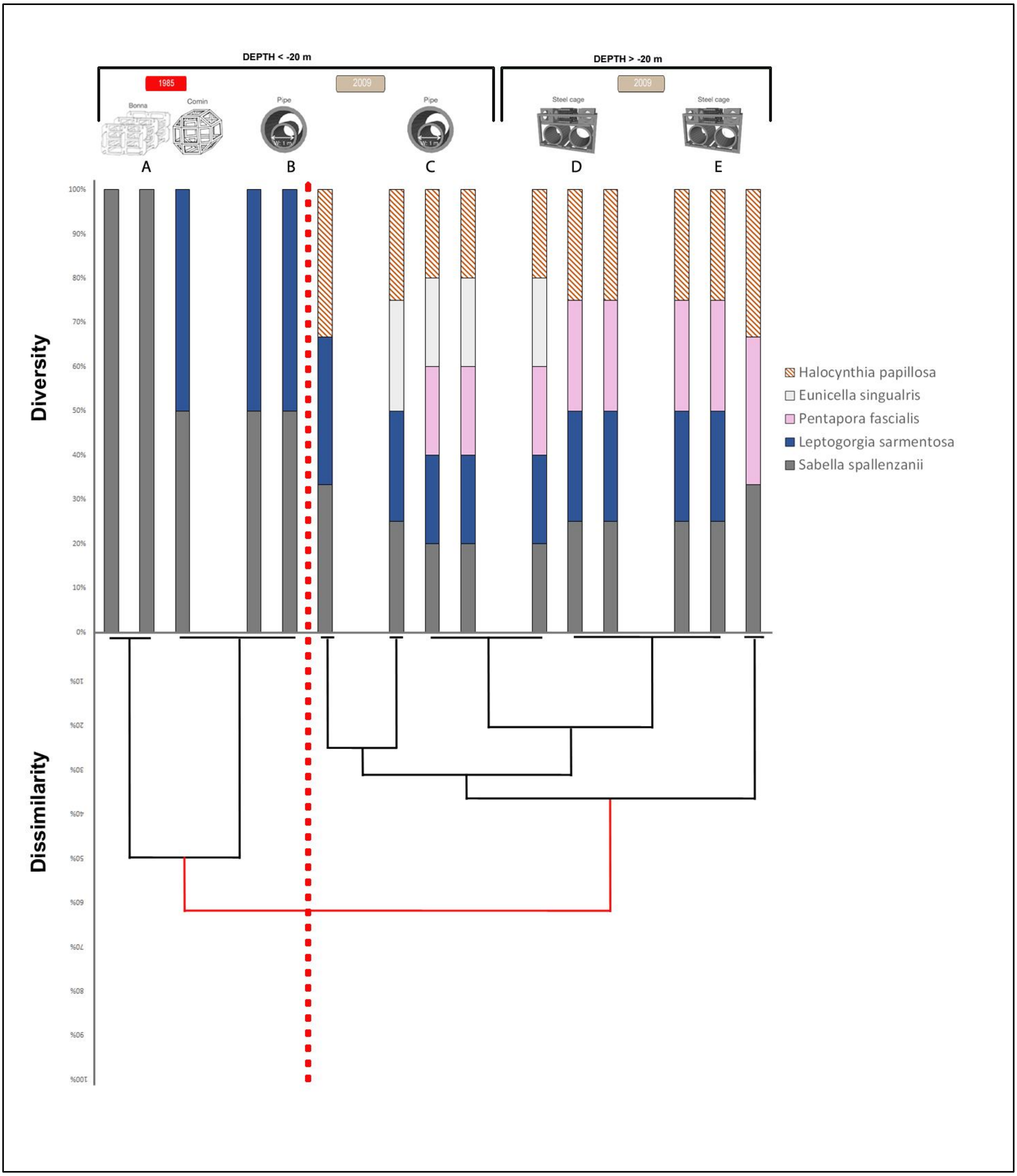
DEPTH < -20 m
DEPTH > -20 m
1985
2009
2009
Bonna
Comin
Pipe
Pipe
Steel cage
Steel cage
A
B
C
D
E
Diversity
Dissimilarity
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
10%
20%
30%
40%
50%
60%
70%
80%
90%
100%
▨ Halocynthia papillosa
☐ Eunicella singualris
■ Pentapora fascialis
■ Leptogorgia sarmentosa
■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

Table captions

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

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

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

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

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

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

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