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Annelid assemblages on artificial hard substrata differ from those on natural rocky shores after decades for colonization: A case study on a century old seawall in Western Mediterranean.

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Abstract

Although strong differences have been observed between the assemblages on artificial substrata and on natural hard-bottom habitats, little is known about the mechanisms that cause them. The purpose of this study was to examine the differences in Mediterranean low shore annelid assemblages dwelling on an old artificial, vertical hard substratum and a natural, horizontal one. The structure of the *Ellisolandia elongata* turfs covering the two habitats showed little divergence in terms of length and number of thalli, as well as in available space for epibionts. In this respect, colonization duration might explain the lack of significant dissimilarities in the phytal canopy. In spite of this, statistical analyses showed that the specific composition of the two annelid assemblages differed in a significant manner. Although they shared a set of constant species, their relative abundances were dissimilar and this was especially evident for several species belonging to families Syllidae and Enchytraeidae . Abundance and species richness were significantly higher on natural structures, as expected, but Shannon diversity and equitability indexes were lower. Apparently, the sciophilous condition of vertical surfaces, which do not occur naturally in the area, is the main driver of the differences in species composition and its capital importance remains after colonization processes have occurred.

Keywords

Artificial harbours; Man-induced effects; Zoobenthos; Phytobenthos; Polychaeta; Oligochaeta; Mediterranean; south-eastern Spain

Abbreviations

ANOVA: Analysis of variance

Ar: Area

AvSf: Total available surface

He: Height

IGME: Instituto Geológico y Minero de España

MS-BG: Mean Square – Between Groups

MS-WG: Mean Square – Within Groups

NF: Number of fronds

nMDS: non-Metric Multidimensional Scaling

PERMANOVA: Permutational Analysis of Variance

PNOA: Plan Nacional de Ortofotografía Aérea

SIMPER: Similarity Percentage

Vol: Total phytal volume

WHR: Width/Height ratio

Wi: Maximum width

1. Introduction

In Europe, it has been estimated that 22,000 km² of the coastal zone are occupied by artificial surfaces (Mineur et al., 2012) and that about 50% of the Mediterranean shorelines bordering southern Europe are dominated by artificial infrastructures (Airoldi and Bulleri, 2011). Due to this process of physical transformation, dramatic changes in the marine communities occur, and these modifications can alter the ecological functions of the species assemblages (Bustamante et al., 2014). The impact of the

resulting changes on the coastal habitats and the assemblages of organisms inhabiting them is not yet fully understood, but there are clues that point to it being profound. Construction of structures results in the fragmentation and destruction of natural habitats and their replacement with artificial habitats, and the human-made substrata are colonized by new assemblages of plants and animals, which can cause significant disturbances on transformed areas (Bacchiocchi and Airoidi, 2003).

Because marine artificial substrata support diverse colonizing assemblages of benthic organisms, it has been suggested that they might represent adequate mimics of natural hard-bottom habitats (Thompson et al., 2002; Pister, 2009). However, studies point out that human-made structures do not function in the same manner as natural rocky habitats, and often introduce surfaces and species that are absent from the natural environments (Airoidi and Bulleri, 2011). The communities growing on artificial structures might look similar to those on natural rocky shores but they are suspected to be in essence a poor imitation (Moschella et al., 2005) characterized by lower number of taxa (Bulleri and Chapman, 2010) and impoverished genetic diversity (Fauvelot et al., 2012). Not only is biodiversity lesser but the population structure of present species may be severely altered, as well as their reproductive success (Moreira et al., 2006).

Little is known about the mechanisms that cause these contrasting biodiversity patterns (Aguilera et al., 2014). The lower biodiversity is primarily due to the paucity of key microhabitats of artificial habitats (Firth et al., 2013), since most of them lack surface heterogeneity. In comparison, natural rocky shores generally have rougher surfaces and a variety of habitats including rock pools and crevices, which provide refuge from both biotic and abiotic stressors at all states of tide (Aguilera et al., 2014; Hall et al., 2018). Certain artificial structures may even favour colonization by alien and range-shifting species (Vaselli et al., 2008; Mineur et al., 2012) and mounting evidence

suggests the communities associated with artificial structures can support more invasive non-native species than natural habitats (Airoidi and Bulleri, 2011; Firth et al., 2013; Ulman et al., 2019).

Chapman (2006) summarized the differences between littoral stages on seawalls and natural rocky shores, and they were consistent in three ways. First, many microhabitats are absent from seawalls, as stated above. Second, seawalls are very steeply sloping or even vertical, whereas many rocky shores are only gently sloping, as is the case of the studied location. This modified orientation has been shown to be a major determinant influencing the structure of littoral assemblages (Glasby and Connell, 2001). Even if it were possible to ensure that nothing else was altered, building steeper habitats than the natural ones will nearly always cause losses of local biodiversity (Chapman and Underwood, 2011). On the other hand, vertical littoral surfaces are often under shade and thus have reduced heat and desiccation stress (Lam et al., 2009), which could be a favorable feature in dryer and hotter climates. Thirdly, changing the slope from near horizontal to near vertical considerably reduces the extent of the littoral available surface, and it alters species-area relations (Chapman and Underwood, 2011). Artificial vertical substrata may severely crowd littoral species into a limited area and species that do not usually come into contact can be forced to occupy the same area, potentially increasing the strength of interspecific interactions (Bulleri and Chapman, 2010).

On shores with smaller tidal ranges, such as the western Mediterranean, the distribution of species is compressed into a narrow range and species live naturally in close proximity over the tidal gradient (Prusina et al., 2014), thus the effect of steeper surfaces is probably alleviated in this respect. Nevertheless, one can argue that the effect of this compression might be more radical because of the limited colonisable area

(Bonnici et al., 2018). Due to the lack of studies on microtidal seas, the subject remains unclear. It must be also taken into account that the Mediterranean littoral zone is highly stressful for organisms. Maximum habitat temperatures can reach 45–50°C in the midshore and 35–38°C during summer midday in the low-shore (Sarà et al., 2014). Moreover, changes in barometric pressure may be more important drivers than tidal forces for patterns of emersion-immersion, so organisms may remain exposed to aerial conditions for days or weeks during periods of high barometric pressure, making the littoral environment highly variable and unpredictable (Benedetti-Cecchi et al., 2006). This climatic stochasticity may emphasize the shelter provided by habitat heterogeneity (Helmuth et al., 2006), which is absent or scarce in man-made structures. On the other hand, their vertical orientation and subsequent shadowing might disfavour photophilic and more desiccation tolerant species, and favour sciophilous species that are less tolerant to dehydration and heat exposure ones.

The proliferation of defence works has caused a growing concern in mitigating their negative effect in the last decades. Nevertheless, there has been limited research as to how the marine organisms respond to these structures after construction. Little is known about the development and distribution of colonizing organisms on different types of defence structures, limiting the possibility to identify better options for the design and management of such structures (Bacchiocchi and Airoidi, 2003). In this respect, there is great interest in understanding the colonization processes in order to take measures to improve biodiversity (Aguilera et al., 2014) and assess how long the artificial substrata will take to naturalize if at all.

Photophilic algae are an important element of many nearshore communities that form diverse micro- and macro-habitats supporting epibiont fauna and epiphytic algae, as well as mobile animals, and thus they conform complex communities (Urrea et al.,

2013). In temperate waters, Fucales (Ochrophyta, Phaeophyceae) represent the dominant canopy-forming species in pristine environments (Blanfuné et al., 2016), but the short coralline algae that constitute the understory of the phytal community become dominant and form characteristic turfs when moderate disturbances happen (Bulleri et al., 2002; Mangialajo et al., 2007; Bonifazi et al., 2017). These coralline algal turfs are inhabited by a diverse and highly abundant community of small mobile invertebrates (Bussell et al., 2007; Melero et al., 2017), and their spatial structure is a most important driver regarding the organization of the assemblages (Berthelsen et al., 2015).

The purpose of this study was to examine the influence of orientation on Mediterranean low-shore communities dwelling on hard substrata by comparing the annelid assemblages inhabiting an one-century old artificial (vertical) and a natural (nearly horizontal) habitat, considering species composition and abundance of individuals. In order to detect potential sources of variation, not only the assemblage, but also the structural features of the phytal coverage were assessed. The first hypothesis is that diversity will be higher in natural habitats compared with artificial seawalls and that species composition will differ. In this respect, annelids, which are dominant in marine benthic communities of both hard and soft bottoms (Viéitez et al., 2004), can be effective surrogates for the estimation of the dynamics of benthic communities, as they play key roles in ecosystem function (Olsgard et al., 2003; Giangrande et al., 2005; Parapar et al., 2009). Secondly, it is hypothesized that small scale differences in the species composition can be detected in old structures, even though they might superficially look naturalized by substrate weathering and phytal canopy colonization.

2. Material and Methods

2.1. Study area

The study area is a cove situated in the small town of Villaricos belonging to the municipality of Cuevas de Almanzora (Almería), on the southeastern coast of Spain (Fig. 1). In spite of the proximity to important touristic and recreational areas, it has experienced little human perturbation due to its abrupt coastline consisting of a series of gently stepping cliffs interspersed with small sandy coves. Only the urban area of the village and a nearby chemical factory cause significant impact and the rest of the area remains relatively pristine. On the southern side of the studied cove, there is a stone-made wharf that was built in 1914 by the Société Minière d'Almagrera and used for iron ore shipping until circa 1950 (Broder, 2014). Its base at sea level has remained without significant modification for at least sixty years (Fig. 2 A-C), and there is no evidence of previous works having been carried out on the wall between building and this point in time. In turn, several low outcrops of schist rock lay on the northern side of the cove and both sites are covered in dense turfs of the coralline alga *Ellisolandia elongata* (Fig. 2D, E, G). The wall was built of conglomerate rock cemented with mortar (Fig. 2 F), a kind of rock which does not occur in the studied location but can be found in near areas about 10 km north and south (IGME, 1974). Due to the poor quality and the age of the mortar, several blocks of stone have fallen out leaving deep holes and enhancing spatial heterogeneity beyond the point that might be expected in a more recent man-made structure, and damage by weathering was evident along the entire base of the wall (Fig. 2 G).

2.2. Sampling methods

Sampling was conducted in August 2015, aiming to get a snapshot of the community during a time of high algal development and high faunal abundance following spring/early summer recruitment (Thrush et al., 2011). In order to compare the community inhabiting natural sub-horizontal turf habitats with that dwelling on artificial vertical ones, two stations in the same location were selected (Fig. 1), respectively on the southern side of the cove (37°14'52.07''N, 01°46'13.39''W) and on the northern one (37°14'54.77'' N, 01°46'10.10''W). In each station five randomly selected samples were collected, by scraping off a 100 cm² area of rocky bottom from depths ranging from 0.05 to 0.15 cm. Such a small sample size has been accepted as sufficient for the study of annelids in other Mediterranean locations (Fraschetti et al., 2002; Musco, 2012; Casoli et al., 2016), as well as in the study area (Melero et al., 2017). The scraped material was preserved in 70% ethanol and stored in hermetic plastic bags. In the laboratory, this material was examined under a dissecting microscope.

In order to describe the structural features of the algae from each sample, several measurements were made. For each sample, the number of fronds (NF) was counted, and height (He), as length from the holdfast to the distal tip of the plant, and maximum width (Wi) in mm were measured for fifty randomly selected thalli. From these measurements, area (Ar) in mm² was calculated for each one assuming an approximately triangular shape of the thalli ($Ar = He \times Wi/2$) as well as the Width/Height ratio (WHR). Average values for He and WHR were computed for each sample and treated as descriptors of the phytal substratum. The total available surface (AvSf), given in cm², was obtained multiplying average Ar by the number of fronds in

the sample. Subsequently, the total phytal volume (Vol) in ml was calculated by the displacement of a known volume of water (Bussell et al., 2007).

All the collected animals were sorted into higher taxonomic groups (usually class level) while the alga fronds were stored for structural study. Annelids were identified to species using the updated regional keys provided in Fauna Ibérica series (San Martín, 2003; Viéitez et al., 2004; Parapar et al., 2012, 2015) and counted, whereas the remaining fauna were stored for further studies. Subsequently, a species abundance (as number of individuals per 1000 ml of algae) matrix was created from the actual numbers of specimens of each annelid species.

2.3. Data analyses

Differences in the phytal features of the turfs and in the annelid assemblages inhabiting the two types of surface were tested for with univariate and multivariate statistical analyses. The total abundance of annelids and the species richness, Shannon and equitability indexes for α -diversity were computed for each sample based on species abundance matrix. Mean and standard deviation values of these variables and of the morphological (thallus height and width/height ratio) and abundance (number of fronds, total available surface and volume) descriptors of the coralline algae were calculated for both stations. Significant differences were determined using one-way ANOVA test. Prior to this analysis, the Shapiro-Wilks W test was used to check the normality of residuals for each variable, and data were transformed where appropriate (Underwood, 1997; Cacabelos et al., 2016).

A second matrix was derived from the annelid abundance matrix, showing the similarity between samples by mean of the Bray-Curtiss coefficient after data were square-root transformed to limit the influence of most dominant species (Clarke and Warwick, 1994). Non-metric multidimensional scaling (nMDS) was used to visually represent the results. Differences in the composition of polychaete assemblages were tested using one-way PERMANOVA (Anderson, 2001) analysis run in Bray-Curtis similarity matrix. Significance was set at $p < 0.05$, p-values being obtained using 9999 permutations of residuals under a reduced model. A SIMPER analysis (Clarke and Warwick, 1994) was conducted aiming to establish which species were responsible for differences between assemblages. Relative abundance (the ratio between species abundance and total abundance of polychaetes) was computed in every sample for the species contributing more than 3% to dissimilarity and these values were treated as additional ecological descriptors of the annelid assemblage. These statistical analyses were made using the software package PAST 3 (Hammer et al., 2001).

To relate the environmental variables with the ecological descriptors (including the relative abundance of species contributing more than 3% to dissimilarity) that differed significantly between assemblages Generalized Linear Model (GzLM) analyses were conducted. In each model, orientation (vertical vs. horizontal) was considered as categorical predictor variable and structural features of the phytal turf (NF, He, WHR, AvSf, and Vol) were entered as predictor covariates, being the ecological descriptors of the annelid assemblages the response variables. As for ANOVA tests, normal distribution of the predictor and response variables was checked, and they were transformed when appropriated, so an identity link GzLM was performed in all the cases. Validation of the models was done using Shapiro-Wilks W test to check the normality of residuals for each model. To allow a comparison of the estimators within one model, all

predictors were standardised by their means (Greenacre & Primicerio, 2013). Results were considered significant at $p < 0.05$. The software used to perform the GzLMs was SPSS 23.0 for Windows (SPSSInc, Chicago, IL, USA).

3. Results

3.1. Phytal structure

From the point of view of the structure of the turf, it can be pointed out that on artificial vertical substrata the thalli of *Ellisolandia elongata* were more numerous, although they were wider on the natural horizontal ones resulting in higher values of width/height ratio (Fig. 3). Congruently with the higher density of vegetation on vertical substrata, both the available surface and the volume and were higher there (Fig. 3). However, the results of the one-way ANOVA analyses showed that none of these differences regarding alga structure or density of fronds was significant, except for WHR (Table 1).

3.2. Annelid assemblages

A total of 1,965 specimens of annelids, belonging to 41 species and 13 families, were collected. Seven species appeared in all the samples, namely the syllids *Syllis prolifera* (accounting for 22.44% of the specimens), *Syllis gracilis* (7.84%), and *Salvatoria vieitezi* (6.77%), the nereidids *Platynereis dumerilii* (20.66%) and *Perinereis cultrifera* (6.36%), the opheliid *Polyopthalmus pictus* (13.13%), and the enchytraeid *Lumbricillus* sp. (4.48%). With regard to the specific composition of the assemblages,

the samples collected from each type of substratum are differently placed in the nMDS plot (Fig. 4). Those collected from artificial vertical substrata (Vill-1 to Vill-5) appear on the left side of the plot, while those from horizontal natural one (Vill-6 to Vill-10) are on the right, and form a looser group, with Vill-7 located away from the rest. The described differences between the annelid assemblages were significant according the one-way PERMANOVA analysis (Pseudo- $F= 4.919$; $p= 0.008$). The SIMPER analysis detected that eight species contributed with more than 3% to the overall dissimilarity between assemblages (Table 2). Apart from the above-mentioned constant species, the syllid *Sphaerosyllis austriaca* and the sabellid *Amphicorina armandi* were relevant in terms of dissimilarity.

The relative abundance of the species contributing most to dissimilarity showed conspicuous differences between types of surface, and sometimes a wide dispersion within each one (Fig. 5). Mean values of relative abundance were far higher in the natural communities for *P. dumerilii*, *S. austriaca*, *S. prolifera*, and *A. armandi*. *Polyopthalmus pictus* was also more abundant in this type of substratum, but the difference was not so notable. The rest of the species showed higher relative abundances in the turfs growing on vertical walls, more evidently for *S. gracilis* and *S. vieitezi*. Whereas the differences in the population densities of *P. cultrifera*, *P. dumerilii*, *P. pictus*, and *A. armandi* were not significant, *S. vieitezi*, *S. austriaca*, *S. gracilis*, *S. prolifera*, and *Lumbricillus* sp. showed significant differences in the mean values for each kind of substratum (Table 3).

The remaining ecological descriptors calculated from the abundance matrix are presented in Figure 6. Abundance and species richness were higher in the samples from horizontal, natural substrata. However, the Shannon index and the related equitability

were higher in artificial structures. The differences between the two types of substratum were significant for all the descriptors (Table 3).

Distribution of residuals validated all the GzLMs except that of abundance. Results for the species contributing more than 3% to dissimilarity and discriminating the assemblages (Table 4) showed in all the cases that orientation was a main influencing factor. NF, He and, AvSf were also influencing factors for *Lumbricillus* sp. and Vol influenced the relative abundance of *S. austriaca*. All the predictor variables had an effect for *S. prolifera*. Regarding ecological indexes for α -diversity (Table 5) orientation was again a main influencing factor in all the GzLMs. It was the only factor for the Shannon index, but species richness showed a significant relationship also with NF, He, and AvSf. The influence of the evaluated environmental variables on equitability is difficult to assess since all of them showed high values of correlation.

4. Discussion

At first sight, the studied vertical seawalls are good surrogates for the natural low-shore communities of the area, since no significant differences were found regarding structural features of the dominant species of alga. Cacabelos et al. (2016) found that the limited dispersal of propagules from adult plants was a more important factor than slope in limiting the species ability to colonise coastal infrastructures. Similarly, Cefali et al. (2016) found only a minor effect of slope on the distribution of habitats in the littoral communities of western Mediterranean localities. In this respect, the natural patchiness of the coast surrounding the study location, with alternating rocky outcrops and small sandy beaches, might act as a source of *Ellisolandia elongata* propagules for artificial

structures in the area and favour the presence of flourishing and complex turfs that mimic those growing on natural surfaces.

Natural habitats usually have higher species diversity and richness compared with artificial ones (Bulleri and Chapman, 2010; Aguilera et al., 2014). This was not the case regarding the annelid assemblage in the studied herein communities and the results of the analysis of biodiversity were rather confounding. In this location, abundance and species richness were significantly higher on natural structures, as expected, but Shannon and equitability indexes were lower. In any case, nMDS and PERMANOVA analyses showed that specific composition of the two assemblages was not the same. Although they shared a set of constant species, their relative abundances differed. Lam et al. (2009) for sessile invertebrate assemblages on the coast of Hong Kong, Di Franco et al. (2011) for sessile invertebrate and macroalgae in Sicily, or Megina et al. (2013) for hydroid assemblages in southern Spain and Portugal, described similar situations in which the assemblages differed in their qualitative composition but not in number of species.

Species of the family Syllidae appeared as responsible for this dissimilarity, since all the syllid species evaluated showed significant differences in abundance between assemblages, whereas the remaining polychaetes did not. Additionally, four out of the five species contributing most to dissimilarity between artificial vertical and natural horizontal surfaces in SIMPER analysis belonged to Syllidae. This family is particularly diverse and abundant in shallow rocky environments and it has demonstrate to be important in explaining dissimilarity between artificial and natural substrata (Bonnici et al., 2018). The abundances of the oligochaete *Lumbricillus* sp. were also significantly different, being higher on the wall and related to the higher available surface.

Direct and indirect effects at modified habitats can be difficult to interpret (Marzinelli et al., 2009). Frequently, the lower biodiversity of human-made structures has been related to their lack of surface heterogeneity and the inherent paucity of key microhabitats (Moreira, 2006; Firth et al., 2013; Aguilera et al., 2014; Hall et al., 2018). However, coastal structures that have been in place for many years are virtually indistinguishable from adjacent rocky shores from a purely physical point of view, due to the weathering and bioerosion processes that make rock surfaces rougher and more complex, particularly on limestone blocks (Moschella et al., 2005). More importantly, overall species diversity is coupled to the availability of biogenic microhabitats, which are usually scarce in artificial hard surfaces (Aguilera et al., 2014). The studied wall was erected more than 100 years ago and the soft nature of the building material allowed an intense degradation of its surface. It produced an array of holes, crevices and overhangs that render the spatial heterogeneity of this artificial structure equivalent to that observed in adjacent natural rocky habitats.

Additionally, benthic communities on human-made structures become more similar with age to those on natural shores, in terms of biodiversity, as succession processes take place (Pinn et al., 2005; Martins et al., 2016) and encrusting algae and other constructing organisms settle. In this respect, the duration of colonization might explain the lack of significant differences in the structure of the phytal substratum between the natural and artificial habitats studied and the subsequent similarities of accessibility to biogenic microhabitats. However, several studies reported that benthic communities were qualitatively distinct from those on natural systems, even for surfaces that had been colonised for more than a decade (Moschella et al., 2005; Gacia et al., 2007; Burt et al., 2011). The results of this study corroborate this conclusion. The dissimilarities between the two annelid assemblages were appreciable long after the building of the

wall and in spite of heavy phytal colonization. Furthermore, GzLM analyses showed that the effects of phytal traits on the relative abundance of discriminating species and on the ecological descriptors were either absent or obscure, whereas orientation was an influencing factor in all the cases, pointing out that some intrinsic features of vertical surfaces remain without changing over time.

Solar radiation influences the altitudinal distribution patterns of littoral organisms (Prusina et al., 2014). Vertical habitats are more likely to be shaded and therefore protected from solar radiation than horizontal ones (Firth et al., 2014). Thus, physical stress is most likely reduced on artificial seawalls, which are inherently vertical, compared to natural rocky shores that usually have gentler slopes. The Mediterranean littoral environment is very harsh for organisms regarding thermal stress, especially in summer (Sarà et al., 2014), and the amelioration of these extreme climatic circumstances might explain the differences between the assemblages. The sciophilous preference and the lack of relationship of the annelid species that are more abundant in the artificial vertical substratum (San Martín, 2003 for *S. vieitezi*; Abbiati et al., 1987 for *S. gracilis*) to structural features of the turf reinforce the idea of the key importance of shadowing in vertical littoral surfaces under hot climates.

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Conflicts of interest

The author declare that he has no competing interests

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FIGURE AND TABLE CAPTIONS.

Fig. 1. Map of south-eastern Spain showing the collection sites of this study. Aerial photograph by PNOA ceded © Instituto Geográfico Nacional, Spain

Fig. 2. Aerial photographs of the sampling area (A) in 1956, (B) circa 1980 and (C) 2017. (D) Detail of the *Ellisolandia elongata* turfs growing on natural, horizontal surfaces in the studied locality. (E) General view of the seawall studied. (F) Detail of the same showing the conglomerate rock and the mortar used. (G) Detail of the *Ellisolandia elongata* turfs growing on man-made, vertical surfaces in the studied locality: Aerial photographs by PNOA ceded © Instituto Geográfico Nacional, Spain

Fig. 3. Structural features of *Ellisolandia elongata* turfs; box-and-whisker plots for mean values and standard deviations from vertical (blue) and horizontal (purple) substrata. *: significant difference ($p < 0.05$), **: significant difference ($p < 0.01$), n.s.: not significant difference. Abbreviations.- NF: number of fronds, He: height of fronds, WHR: Width/Height ratio, AvSf: total available surface, Vol: total phytal volume.

Fig. 4. Non-metric multidimensional scaling (nMDS) ordination plot comparing assemblages from the sampling stations. Blue circles: samples from vertical substrata. Purple circles: samples from horizontal substrata.

Fig. 5. Relative abundance (%) of the constant species; box-and-whisker plots for mean values and standard deviations from vertical (blue) and horizontal (purple) substrata. *: significant difference ($p < 0.05$), **: significant difference ($p < 0.01$), n.s.: not significant difference.

Figure 6. Ecological descriptors; box-and-whisker plots for mean values and standard deviations from vertical (blue) and horizontal (purple) substrata. *: significant difference ($p < 0.05$), **: significant difference ($p < 0.01$), n.s.: not significant difference.

Table 1. Results of the one-way ANOVA test for the structural features of *Ellisolandia elongata* turfs in the samples. Degrees of freedom: 1 (between groups), 8 (within groups). *: $p < 0.05$, **: $p < 0.01$, n.s.: not significant. Abbreviations.- MS-BG: mean square (between groups), MS-WG: mean square (within groups), NF: number of fronds, He: height of fronds, WHR: W/H ratio, AvSf: total available surface, Vol: total phytal volume.

Table 2. Results of SIMPER analysis showing annelid species contributing more than 3% to dissimilarity between artificial vertical and natural horizontal surfaces. Abbreviations.- AvDissim: Average dissimilitude, Contr: contribution of the species to dissimilitude, Mean Vert: mean abundance of the species on vertical substrata, Mean Horiz: mean abundance of the species on horizontal substrata.

Table 3. Results of the one-way ANOVA test for relative abundance of species contributing more than 3% to dissimilarity between types of substratum and for ecological descriptors. Degrees of freedom: 1 (between groups), 8 (within groups). *: $p < 0.05$, **: $p < 0.01$, n.s.: not significant. Abbreviations.- MS-BG: mean square (between groups), MS-WG: mean square (within groups).

Table 4. Values of χ^2 from the GzLM testing the effects of orientation and the structural features of the phytal substratum on relative abundance of species contributing more than 3% to dissimilarity between types of substratum. *: $p < 0.05$, **: $p < 0.01$, n.s.: not significant.

Table 5. Values of χ^2 from the GzLM testing the effects of orientation and the structural features of the phytal substratum on total abundance of annelids and on α -diversity indexes. *: $p < 0.05$, **: $p < 0.01$, n.s.: not significant.

	Transformation	MS-BG	MS-WG	F
NF	Log(x+1)	0.10	0.003	3.48 ^{n.s.}
He	None	0.001	3.33	0.0003 ^{n.s.}
WHR	None	0.05	0.01	8.44*
AvSf	None	1.61x10 ⁻⁹	1.47x10 ⁻¹⁰	1.10 ^{n.s.}
Vol	None	51.98	39.56	1.31 ^{n.s.}

Table 1

	AvDissim	Contr	Mean Vert	Mean Horiz
<i>Syllis prolifera</i>	4.91	12.04	19.20	43.60
<i>Sphaerosyllis austriaca</i>	3.22	7.88	4.07	20.20
<i>Polyopthalmus pictus</i>	2.99	7.33	16.80	29.40
<i>Salvatoria vieitezi</i>	2.54	6.22	23.30	10.70
<i>Syllis gracilis</i>	2.43	5.95	24.20	12.40
<i>Platynereis dumerilii</i>	1.87	4.60	28.30	35.90
<i>Amphicorina armandi</i>	1.86	4.55	9.25	15.70
<i>Perinereis cultrifera</i>	1.84	1.50	17.20	16.20
<i>Lumbricillus sp.</i>	1.31	3.22	17.30	11.60

Table 2

Species	Transformation	MS-BG	MS-WG	F
<i>Perinereis cultrifera</i>	None	30.45	16.15	1.88 ^{n.s.}
<i>Platynereis dumerilii</i>	None	10.96	81.72	0.13 ^{n.s.}
<i>Salvatoria vietzei</i>	None	373.93	7.43	50.35**
<i>Sphaerosyllis austriaca</i>	None	74.36	1.79	41.43**
<i>Syllis gracilis</i>	Log (x+1)	1.19	0.02	47.85**
<i>Syllis prolifera</i>	None	982.08	44.60	22.02**
<i>Polyopthalmus pictus</i>	None	70.97	59.04	1.20 ^{n.s.}
<i>Amphicorina armandi</i>	None	7.02	10.60	0.66 ^{n.s.}
<i>Lumbricillus sp.</i>	None	87.97	5.16	17.06**
Ecological descriptors				
Abundance	None	1.82x10 ⁻⁷	2.87x10 ⁻⁶	6.34*
Species richness	None	40.00	4.55	8.80*
Shannon index	None	0.09	0.01	7.91*
Equitability	None	0.04	0.002	19.90**

Table 3

Factor	df	<i>Salvatoria vieitezi</i>	<i>Sphaerosyllis austriaca</i>	<i>Syllis gracilis</i>	<i>Syllis prolif</i>
Orientation	1	10.384**	5.306*	8.201**	20.421**
NF(log x+1)	1	1.311 ^{n.s.}	2.348 ^{n.s.}	0.200 ^{n.s.}	10.954**
He	1	0.579 ^{n.s.}	2.203 ^{n.s.}	0.513 ^{n.s.}	9.350**
WHR	1	1.491 ^{n.s.}	0.221 ^{n.s.}	0.262 ^{n.s.}	4.514*
AvSf	1	1.947 ^{n.s.}	1.894 ^{n.s.}	0.152 ^{n.s.}	11.222**
Vol	1	2.331 ^{n.s.}	8.855**	2.893 ^{n.s.}	7.680**

Table 4

Factor	df	Species richness	Shannon index	Equitability
Orientation	1	11.850**	12.757**	50.155**
NF(log x+1)	1	6.546*	2.283 ^{n.s.}	35.869**
He	1	8.217**	2.809 ^{n.s.}	38.730**
WHR	1	2.389 ^{n.s.}	0.074 ^{n.s.}	14.155**
AvSf	1	5.730*	1.288 ^{n.s.}	33.306**
Vol	1	2.417 ^{n.s.}	0.132 ^{n.s.}	17.946**

Table 5

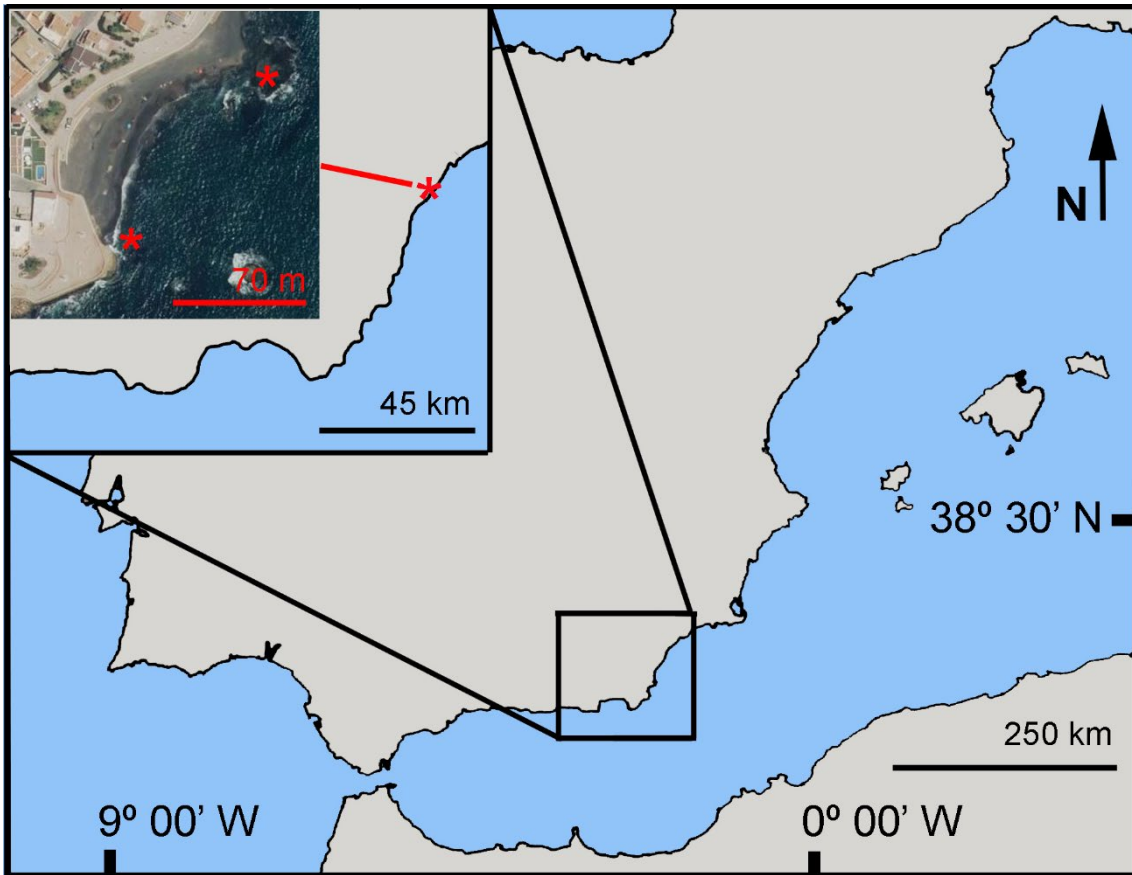


Figure 1

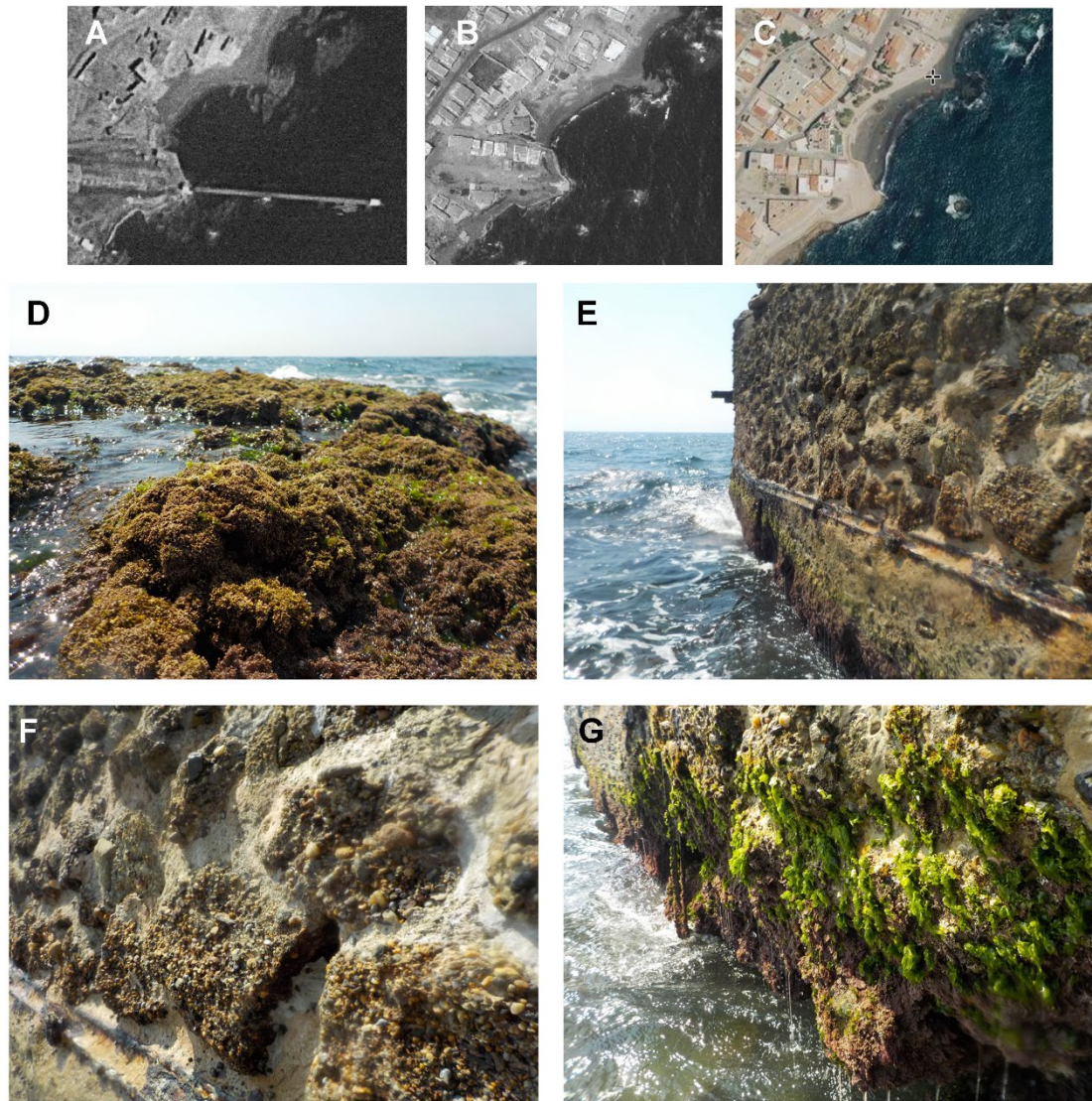


Figure 2

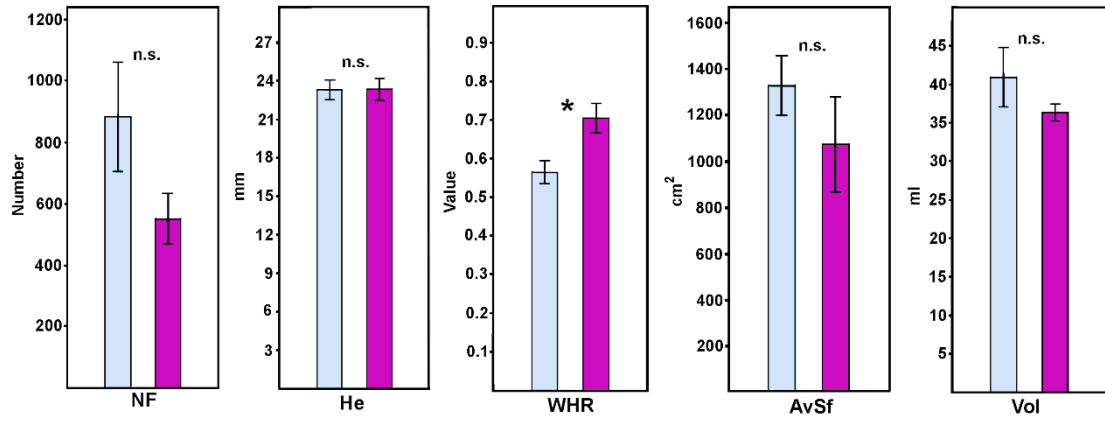


Figure 3

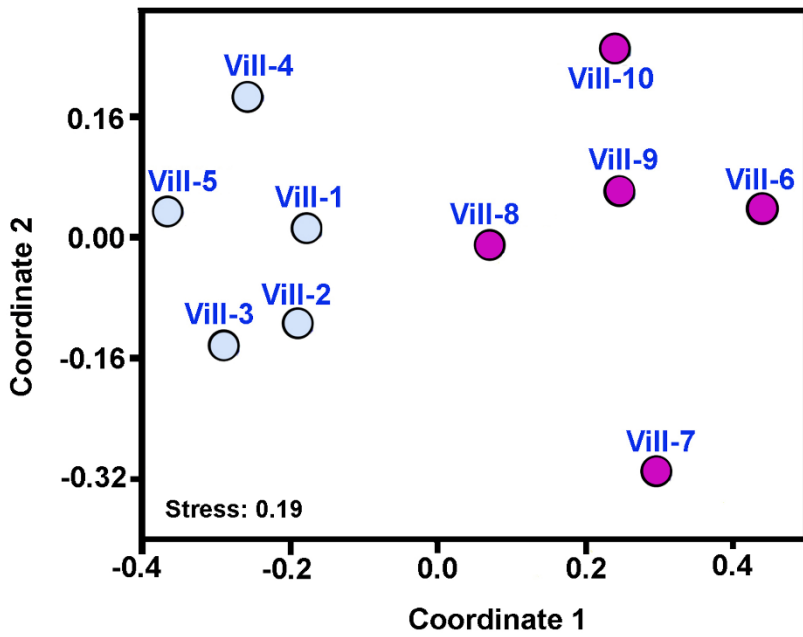


Figure 4

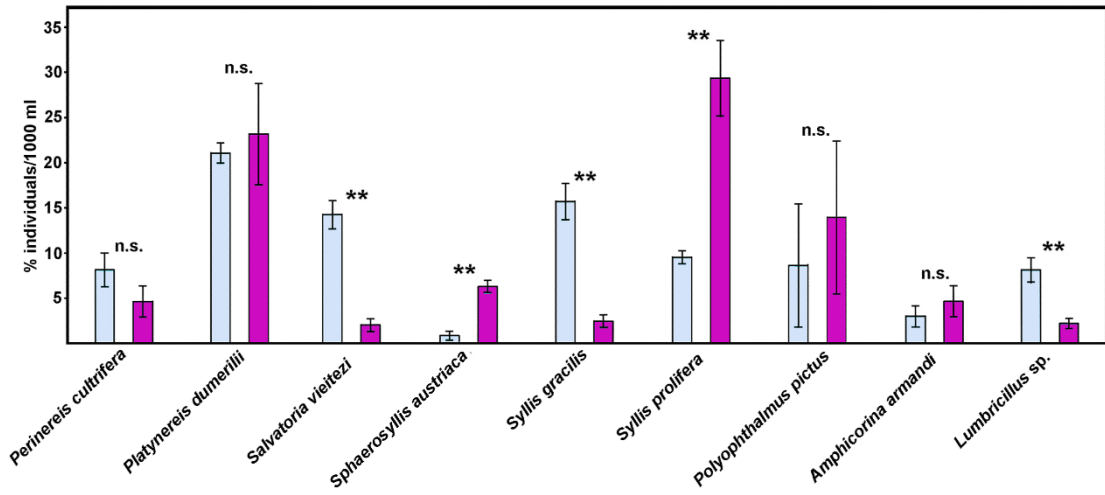


Figure 5

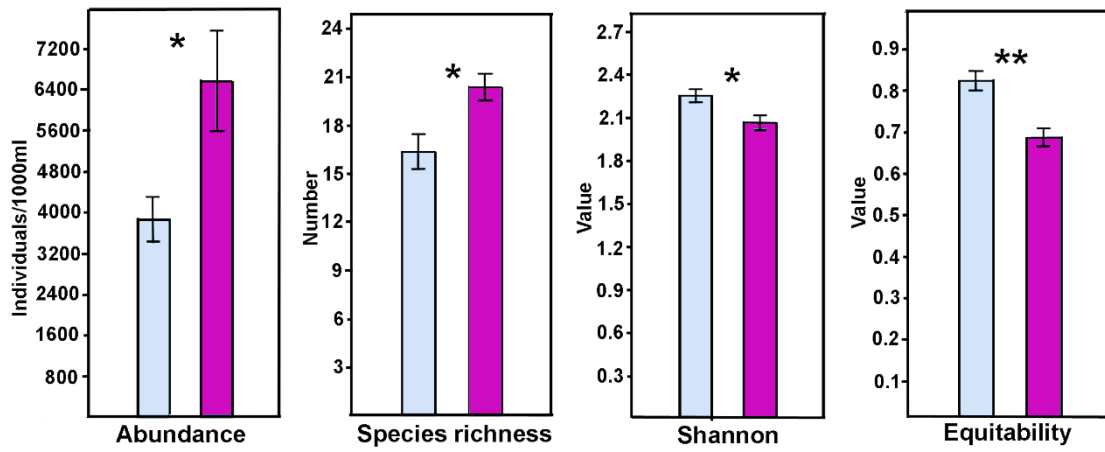


Figure 6