

# Ecological succession within microhabitats (tidepools) created in riprap structures hosting climax communities: An economical strategy for mitigating the negative effects of coastal defence structure on marine biodiversity

E. Ostalé-Valriberas<sup>a,b,\*</sup>, A. Martín-Zorrilla<sup>a</sup>, J. Sempere-Valverde<sup>a</sup>, J.C. García-Gómez<sup>a</sup>, F. Espinosa<sup>a</sup>

<sup>a</sup> Laboratorio de Biología Marina de la Universidad de Sevilla (LBMUS)/Área de Investigación I+D+i del Acuario de Sevilla/Estación de Biología Marina del Estrecho (Ceuta), Universidad de Sevilla, Seville, Spain

<sup>b</sup> Instituto de Estudios Ceutíes, Paseo del Revellín 30, 51001 Ceuta, Spain.

## ARTICLE INFO

### Keywords:

Coastal engineering  
Rockpools  
Functional diversity  
Population fragmentation  
Invasive species  
Artificial structure

## ABSTRACT

The substitution of natural habitats with artificial structures, such as coastal defence structures, has significantly detrimental effects on the marine biological community. In this context, the application of ecological engineering to marine ecosystems presents an opportunity to mitigate these environmental impacts and enhance ecosystem services. There are proposals aimed at mimicking structures found in the natural environment to increase topographic complexity in artificial substrates, thereby promoting biodiversity and hindering the establishment of invasive species. The present study focuses on assessing change in the biological community of intertidal pools constructed on existing coastal defence structures and their influence on a halo (5 cm) of humidity created around the pools. Using an inexpensive method, the tidepools were created at the beginning of 2014 using a pneumatic hammer (DeWalt brand D25902K), imitating the tidepools of the adjacent natural substrate. The coastal defence structures (riprap) which were selected for the study host climax communities since they were built >8 years ago. After 7.5 years of the creation of this microhabitat, the value of species richness in the tidepool was 64.2% higher than in the control, Shannon diversity 41.54% and functional diversity 6.27%. The study of the effect on a halo (5 cm) of humidity produced around the pool shows that Shannon diversity is higher than in the control treatment, demonstrating that the microhabitat created mitigates the harsh environmental (high temperature and desiccation) conditions of the intertidal zone beyond the interior of the tidepool. The results showed that the species richness in the tidepools was bigger in the high intertidal than the low, therefore it is more beneficial to create this microhabitat in high intertidal zone. The created microhabitats serve as shelter and breeding sites for animal species that were not previously observed in the studied artificial structure, as detected for species such as *Pisania striata*, *Ocenebra edwardsii*, *Stramonita haemastoma*, *Meralarhaphé neritoides*, *Siphonaria pectinata*, *Paracentrotus lividus* and *Spirorbis* sp., thus contribute to reducing the fragmentation of their populations. In terms of “ecological succession”, the current study demonstrated that typical species of a mature benthic biological community had colonised the created microhabitat 7.5 years later. These species included the Anthozoa *Anemonia sulcata*, *Actinia equina* and *Exaiptasia diaphana* or the endangered Mollusc *Dendropoma lebeche*.

## 1. Introduction

Coastal cities are rapidly expanding in response to a growing demand

for space, the protection of coastal assets and populations, aquatic tourism, and maritime traffic (Espinosa and Bazairi, 2023). The replacement of natural habitats with artificial structures, such as coastal

\* Corresponding author at: Laboratorio de Biología Marina de la Universidad de Sevilla (LBMUS)/Área de Investigación I+D+i del Acuario de Sevilla/Estación de Biología Marina del Estrecho (Ceuta), Universidad de Sevilla, Seville, Spain.

E-mail address: [enrostval@alum.us.es](mailto:enrostval@alum.us.es) (E. Ostalé-Valriberas).

<https://doi.org/10.1016/j.ecoleng.2024.107187>

Received 8 August 2023; Received in revised form 8 January 2024; Accepted 14 January 2024

Available online 28 January 2024

0925-8574/© 2024 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC license (<http://creativecommons.org/licenses/by-nc/4.0/>).



Fig. 1. The areas under study in Ceuta, located in the Strait of Gibraltar, include the following locations: A) Dock of Levante, B) Chorrillo Beach, and C) Fuente Caballo Beach. From Ostalé-Valriberas et al. (2018).

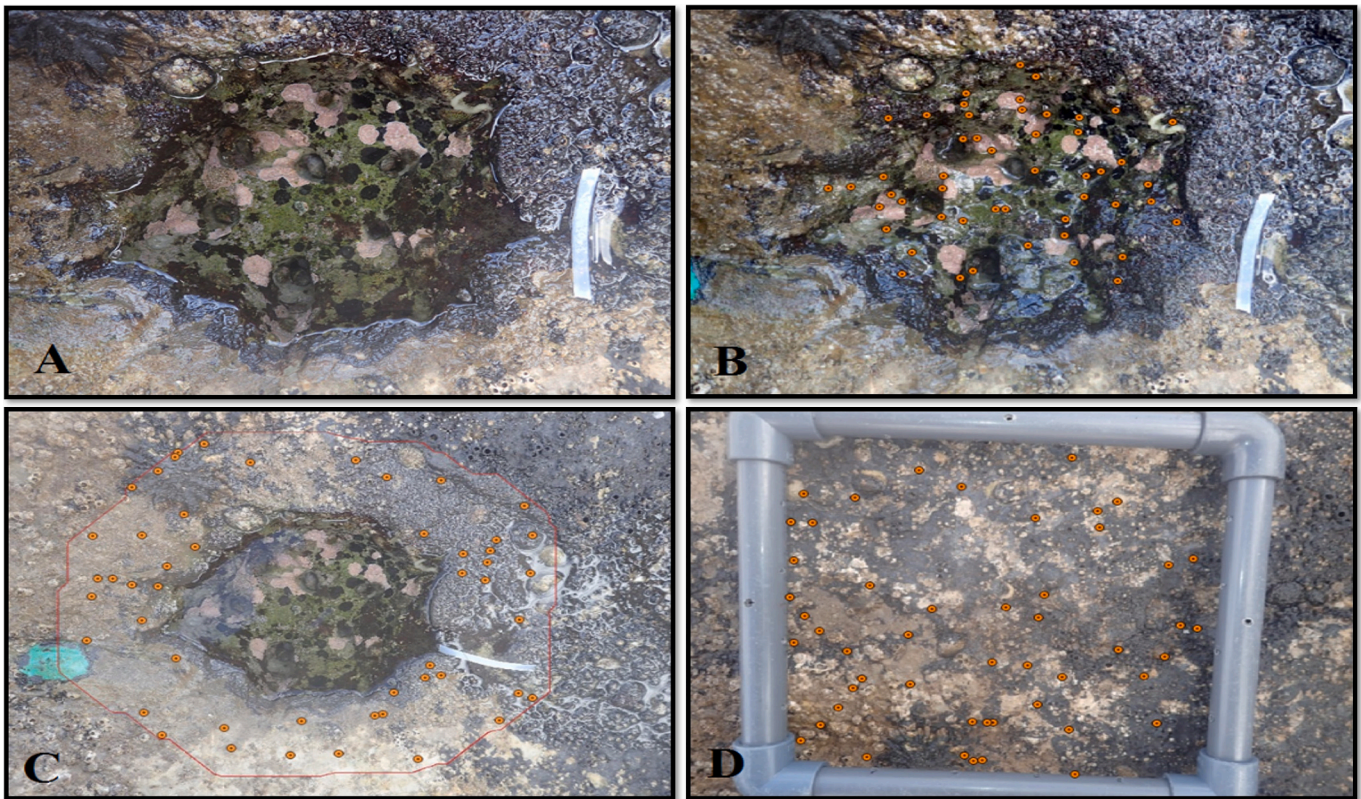


Fig. 2. Example of species coverage appraisal by random point count methodology. A: Tidepool filled with water to delimit pool edge, B: Tidepool. C: Halo with a 5 cm perimeter, D: Control (10 cm from the halo area). From Ostalé-Valriberas et al. (2018).

defence structures, has exerted a substantial adverse impact on the environment (Firth et al., 2020; Sempere-Valverde et al., 2023). This leads to the destruction and fragmentation of native species' habitats, isolating their populations and adversely affecting marine biodiversity. This, in turn, facilitates the proliferation of invasive species, carrying significant consequences at both national and international scales (Airoldi et al., 2005; Waltham and Dafforn, 2018). In this context, the application of ecological engineering in marine biology represents an opportunity to ameliorate these environmental impacts and enhance ecosystem services (Mitsch, 2012; Bishop et al., 2017). The concept of "Ecological Engineering," recently applied in the field of marine biology, integrates ecological, economic, and social considerations into the planning of artificial ecosystems. Essentially, it entails integrating ecological objectives and principles into the design of human-made structures in marine environments (Bergen et al., 2001; Schulze et al.,

1996; Firth et al., 2014).

The biota present in artificial systems varies from that found in adjacent natural systems (Glasby, 1999; Firth et al., 2013a; Farrugia Drakard et al., 2021, Thompson et al., 2023.). In natural substrates, the heterogeneity of the substrate is an essential factor for maintaining biodiversity, whereas artificial substrates tend to be smoother and more homogeneous, resulting in lower biodiversity (Evans et al., 2019). There are proposals aimed at imitating structures found in the natural environment to increase topographic complexity in artificial substrates and, consequently, enhancing biodiversity which has been termed as 'Greening of Grey Infrastructures (GGI)' (Firth et al., 2020). It could be done in several ways such as creation of textured surfaces (Strain et al., 2020; Evans et al., 2021), holes and crevices (Chapman and Underwood, 2011; Hall et al., 2019), and rock pools (Firth et al., 2014; Morris et al., 2019; Ostalé-Valriberas et al., 2018).

**Table 1**  
Biological traits with their categories for the taxa studied. Adapted from [Martini et al. \(2021\)](#).

Biological traits	Traits categories
Growth Form Algae	Articulated-arborescent Filamentous Foliose No articulated-arborescent Flattened Globose
Growth Form Animal	Tubular shell Turriculate shell Conical shell Shield shell Tentacle Sharp thorns Bivalve
Longevity	< 2 years (animals); annual (complete their life cycle in one season) (macroalgae). 2–5 years (animals); perennial (macroalgae). 5–15 years (animals); perennial long lived (macroalgae). > 15 years (animals)
Introductory potential	Yes No
Reproductive strategy	Asexual - vegetative (fragmentation) Asexual - vegetative (spores/propagules) Sexual – gonochoric Sexual – hermaphrodite
Environmental position	Epilithic Epiphytic Epizoic Vagil
Feeding strategy	Autotroph Suspension Feeder / Filter Predator Herbivore/Grazer Detritivore
Sociality	Solitary Gregarious Colonial Turf
Relative adult mobility	None Low Medium High
Development mode	Planktotrophic Lecithotrophic Direct
Maximum size	0–1 cm 1–5 cm 5–10 cm 10–25 cm > 25 cm

Tidepools are micro-habitats that host great biodiversity, as they protect against the harsh environmental conditions of the intertidal zone, such as desiccation and high temperatures when the tide goes down ([Metaxas and Scheibling, 1993](#); [Araújo et al., 2006](#); [Firth et al., 2013b](#)). Previous studies have demonstrated that the establishment of these microhabitats within coastal defence structures enhances the biodiversity of these man-made constructions, including the facilitation of new species' establishment of the natural adjacent zone ([Sempere-Valverde et al., 2023](#)). As a consequence, the inclusion of tidepools enhances ecological stability by increasing biodiversity on artificial structures, complicating the colonization by potential invasive species not previously established in the environment ([McCann, 2000](#); [Glasby et al., 2007](#); [Dafforn et al., 2015](#)). The present study focuses on the work of [Ostalé-Valriberas et al. \(2018\)](#), whose objectives were to investigate

the ecological benefits of constructing intertidal pools in coastal defence structures and their effect on a halo of humidity produced around the pool. In conclusion, after one year of monitoring the created micro-habitat, the biological community was more complex in terms of biodiversity, serving as a refuge for species not present in the original artificial substrate in its first year of creation ([Ostalé-Valriberas et al., 2018](#)). However, most of the studies have not undergone long-term changes and critical assessment, hindering the adoption of GGI as a mainstream solution ([Firth et al., 2020](#)). Consequently, this study places particular emphasis on the long-term monitoring of the biological community within the established microhabitat. Changes have been studied in two different intertidal heights to elucidate whether the new microhabitats contributed differently to the overall diversity depending on their tidal range. In this context, previous findings by [Bulleri and Chapman \(2010\)](#) indicated a greater contribution in the high level in seawalls from Australia, although such data is limited in other regions or for various types of artificial structures. Furthermore, the majority of studies have predominantly used taxonomic diversity as a proxy for assessing the impact of artificial substrata on marine biodiversity, while functional diversity (including different biological traits) has received notably less attention ([Sedano et al., 2020](#)).

To this end, the objectives of this study are to answer the following questions: i) does the creation of tidal pools increase local biodiversity in artificial coastal protection structures in which the biological community that had already reached its climax state was established?, ii) is the increase in diversity caused by artificial pools greater in the upper level than in the lower level of the intertidal zone?, iii) how has been the succession of the biological community in the new microhabitat created? and iv) what species have been directly benefited from the created microhabitat?

## 2. Materials and methods

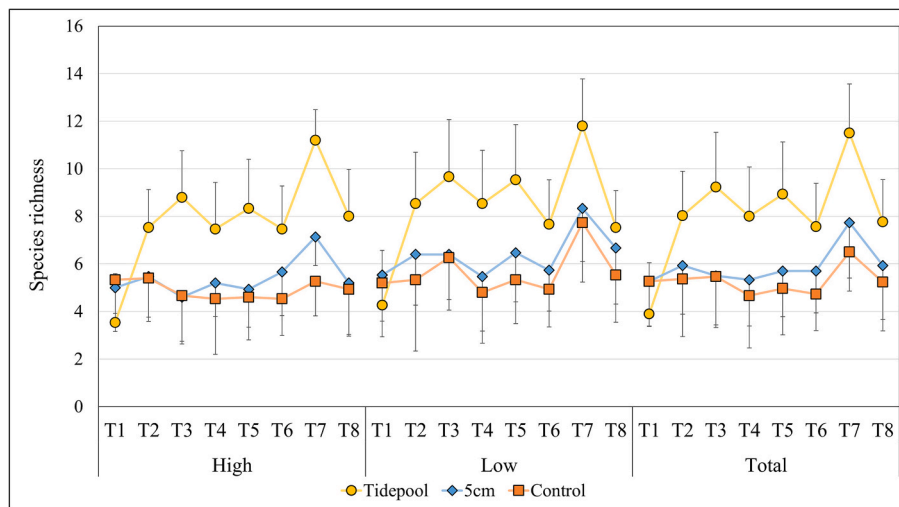
### 2.1. Study location

The study was conducted in Ceuta, a city on the southern coast of the Strait of Gibraltar (North Africa, Spain). This area is considered to be of high ecological value, since it is on the border of three biogeographical provinces: Mediterranean, Lusitanian and Mauritanian, as well as the Mediterranean Sea and the Atlantic Ocean causing its marine flora and fauna to overlap, therefore, it is a transition area with a high biodiversity ([Coll et al., 2010](#)). Its location makes it an area of special risk of disturbance since it is one of the most maritime traffic zones worldwide where many important ports are located (Algeciras, Gibraltar and Tangier Med). It makes this area a habitat with a high risk of disturbances, impacts or possible environmental disasters ([Ostalé-Valriberas et al., 2022](#)).

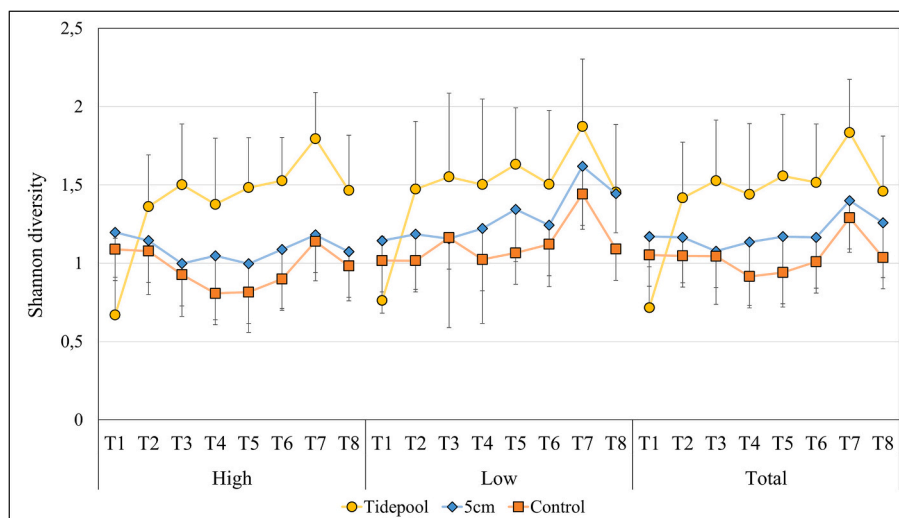
The present study extends the ongoing monitoring of the artificial rock pools, previously created and studied during the first year by [Ostalé-Valriberas et al. \(2018\)](#). As it was originally described in such study, it was conducted on three artificial substrates made with dolomite limestone rock: the ripraps of the Chorrillo and Fuente Caballos beaches, and the Levante breakwater that belongs to the port of Ceuta ([Fig. 2](#)). For the study, coastal defence structures were selected that had been built for more than eight years, so it could be stated that the established (control) biological community had already reached the climax phase of ecological succession in intertidal rocky habitats ([Coombes, 2011](#); [Dong, 2016](#)). (See [Fig. 1.](#))

### 2.2. Experimental design and sampling

The experimental design included the same three factors as in [Ostalé-Valriberas et al. \(2018\)](#): time, height at the intertidal fringe, and treatment. However, the “Time” factor was considerably expanded from one to seven years of monitoring, and now consisted of eight levels covering different seasons and years: T1 (summer 2014), T2 (winter 2015), T3



**Fig. 3.** Species richness results in treatments (Tidepool, 5 cm, and Control) over time (in T1, T2, T3, T4, T5, T6, T7, and T8) at two intertidal levels (High and Low) and overall (mean  $\pm$  SD).



**Fig. 4.** Shannon diversity results in treatments (Tidepool, 5 cm, and Control) over time (in T1, T2, T3, T4, T5, T6, T7, and T8) at two intertidal levels (High and Low) and overall (mean  $\pm$  SD).

(winter 2016), T4 (summer 2016), T5 (winter 2017), T6 (summer 2017), T7 (winter 2021), and T8 (summer 2021). The intertidal height factor had two levels: ‘High’ (at +0.75 m height from zero tide level) and ‘Low’ (at +0.25 m height from zero tide level). Finally, the treatment factor had three levels: “Pool” (the interior of the pool), “Halo” (the area surrounding each pool with a width of 5 cm) and “Control” (a 20  $\times$  20 cm quadrant adjacent to each pool, 10 cm from the halo area) (Fig. 2).

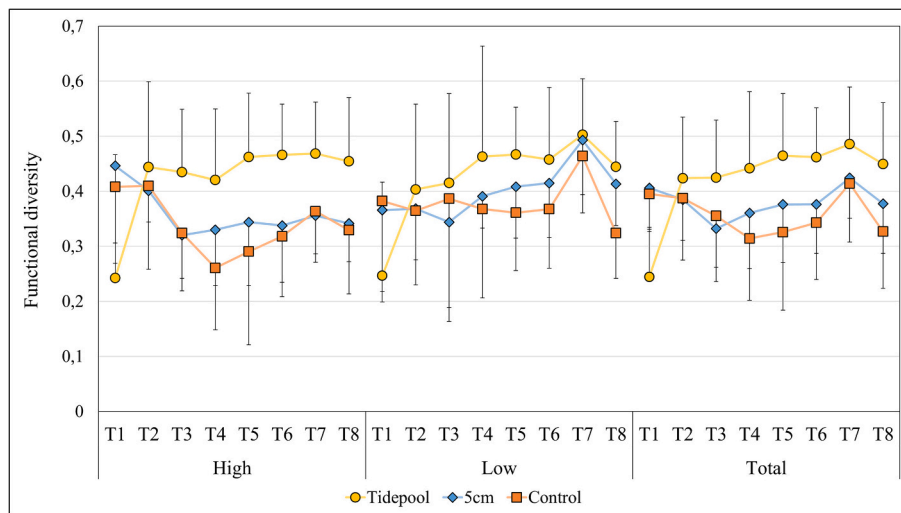
In each of the three artificial substrates, 5 pools were made per height (High and Low). During two weeks in January 2014, these tidepools were created using a pneumatic hammer (DeWalt D25902K), imitating the tidepools of the adjacent natural substrate. To rule out significant differences between their dimensions that could affect the results, an ANOVA was performed on the surface-volume relationship of the tide pools. The mean dimensions of the pools were 16.56  $\times$  14.1 cm, 376.48 cm<sup>2</sup> surface area and 319.34 cm<sup>3</sup> volume. Small pools were created because the size of the rocks on which the pools were created was 1.5 m<sup>2</sup>, although larger and deeper tide pools are known to show higher biodiversity (Martins et al., 2007).

In February 2014, this study began by burning the artificial tidepools and their adjacent halo perimeter (5 cm) with a propane gas torch (T0).

Sampling campaigns were conducted in summer and winter of 2014–2015, 2016, 2017 and 2021. Sampling was carried out by imaging with an Olympus TG-1 camera, by random overlap of 50 points to obtain the species coverage (Dumas et al., 2009). Photoshop was used to delimit the area of the pools, the 5 cm halo and the control, and Photoquad was used to superimpose the points (Fig. 2). Choosing 50 as the optimal number of dots was calculated using 5 randomly taken images of each treatment and overlapping 5, 10, 20, 30, 50, 60 and 70 dots. The result was that with 50 points 95% of the species were represented in each treatment, for species present without representation in the analysis a symbolic coverage value of 0.5% was assigned. To account for the abundance of vagile fauna that may not be represented by the photographic method, their numbers were quantified in situ during photographic sampling.

### 2.3. Functional diversity

To analyse the functional diversity of each sample, we calculated the “functional dispersion” index, which describes the abundance-weighted mean distance of individual species to their group centroid (community



**Fig. 5.** Functional dispersion results in treatments (Tidepool, 5 cm, and Control) over time (in T1, T2, T3, T4, T5, T6, T7, and T8) at two intertidal levels (High and Low) and overall (mean ± SD).

of all species) in a multivariate trait space (Laliberté and Legendre, 2010). Eleven important functional traits were selected following physiological and ecological factors, attribute selection was based on the ability of these attributes to demonstrate changes in ecosystem functioning and benthic responses (Martini et al., 2021). Information on biological attributes was collected from a variety of sources, including identification guides, scientific articles, attribute databases and data provided by local experts (García-Gómez, 2015; Hofrichter, 2004; Prieto, 2013; WoRMS Editorial Board, 2023). When reliable data were not available, expert opinion and data from a phylogenetically close species were used. Fuzzy annotation was performed, i.e. each level of the functional trait was scored from 0 to 3 according to the affinity of the

species to different functional traits (Table 1).

The FD package (<https://cran.r-project.org/package=FD>) within the R statistical software was employed to compute the functional dispersion index, adhering to the recommended procedure (Magneville et al., 2022). Initially, the dissimilarity matrix between species in each sample was computed. Subsequently, a principal component analysis (PCO) was conducted, and ultimately, the functional dispersion index was determined. This index reflects the distribution of species within the multivariate functional trait space. It was selected due to it does not require that the number of species must exceed the number of functional traits (Nasi et al., 2018).

**Table 2**

Three-way RM-ANOVA results for species richness, Shannon diversity and functional dispersion. T1 (Summer 2014), T2 (Winter 2015), T3 (Winter 2016), T4 (Summer 2016), T5 (Winter 2017), T6 (Summer 2017), T7 (Winter 2021), and T8 (Summer 2021). Le: level. Tr: treatment. 5 cm: halo perimeter. Con: control. Bold font:  $p < 0.005$  and interaction between different factors.

Source	Df	Species richness			Df	Shannon diversity index			Df	Functional diversity		
		F	P	Pairwise comparisons		F	P	Pairwise comparisons		F	P	Pairwise comparisons
<b>WITHIN-SUBJECTS VARIATION</b>												
Time	3	33.92	<b>&lt; 0.001</b>		6.09	21.99	<b>&lt; 0.001</b>		6.09	6.41	<b>&lt; 0.001</b>	
Ti x Le	3	1.84	0.076457		6.09	2.5	<b>&lt; 0.05</b>	Up: T1 < T2 = T3 = T4 = T5 = T6 < T7 > T8	6.09	4.63	<b>&lt; 0.001</b>	Up: T1 = T2 = T3 = T4 = T5 = T6 = T7 = T8
Ti x Tr	6	1.14	<b>&lt; 0.001</b>	Pool: T1 < T2 = T3 = T4 = T5 = T6 < T7 > T8 5 cm: T1 = T2 = T3 = T4 = T5 = T6 < T7 > T8 Con: T1 = T2 = T3 = T4 = T5 = T6 = T7 = T8	12.19	10.79	<b>&lt; 0.001</b>	Down: T1 < T2 = T3 > T4 = T5 = T6 < T7 > T8 Pool: T1 < T2 = T3 = T4 = T5 = T6 < T7 > T8 5 cm: T1 = T2 = T3 = T4 = T5 = T6 < T7 = T8 Con: T1 = T2 = T3 = T4 = T5 = T6 < T7 > T8	12.19	8.34	<b>&lt; 0.001</b>	Down: T1 = T2 = T3 = T4 = T5 = T6 < T7 > T8 Pool: T1 = T2 = T3 = T4 = T5 = T6 < T7 = T8 5 cm: T1 = T2 = T3 = T4 = T5 = T6 = T7 = T8 Con: T1 < T2 = T3 = T4 = T5 = T6 < T7 > T8
Ti x Le x Tr	3	0.21	0.312461		12.19	1.11	0.34		12.19	0.91	0.52	
Residuals	588				512.04				512.04			
<b>BETWEEN-SUBJECTS VARIATION</b>												
Level	1	10.22	<b>&lt; 0.001</b>	Up < Down	1	3.61	<b>&lt; 0.001</b>	Up < Down	1	3.72	0.056	
Treatment	2	55.83	<b>&lt; 0.001</b>	Pool > (5 cm = Con)	2	18.67	<b>&lt; 0.001</b>	Pool > 5 cm > Con	2	8.08	<b>&lt; 0.001</b>	Pool > (5 cm = Con)
Le x Tr	2	0.095	0.909		2	0.53	0.52		2	0.87	0.41	
Residuals	84				84				84			

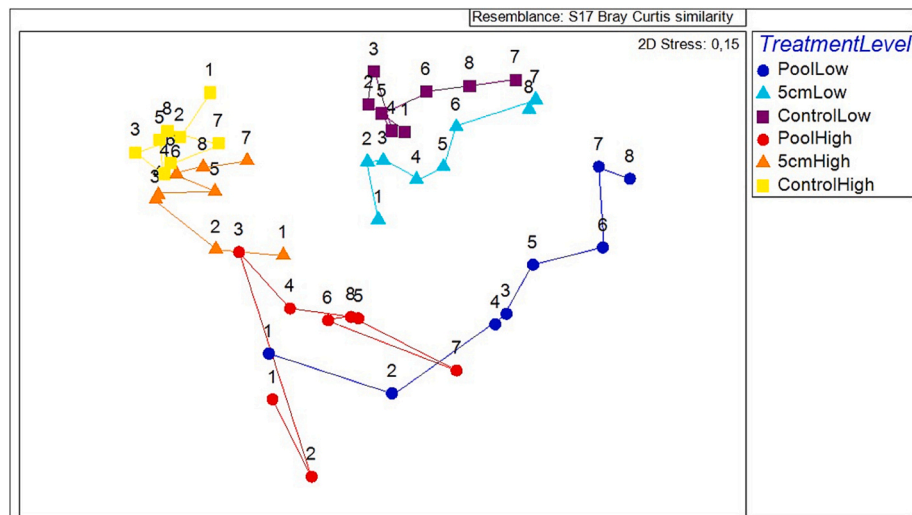


Fig. 6. nMDS showing PCO centroids for level and treatment factors combination according to each studied time. Results were plotted separately for natural and artificial surfaces.

## 2.4. Statistical analysis

### 2.4.1. Univariate statistical analysis

To check for homogeneity of variance, a Levene's test was performed for each treatment (tidepool, 5 cm halo and control). The Student-Newman-Keuls (SNK) test was used to perform post-hoc analyses for each treatment.

To test the effects of the factors on the values of species richness (S), Shannon diversity (H') and functional diversity calculated from the cover data, a repeated measures ANOVA analysis (RM-ANOVA) was performed. The orthogonal factors fixed under 6 considerations were time (four levels: T1, T2, T3, T4, T5, T6, T7 and T8; repeated measures), level (two levels: high and low) and treatment (three levels: Tid: tidepool; 5 cm: halo perimeter; Con: control). For the study of functional diversity, the same analysis was carried out with the functional trait values for each species. To check the homogeneity of variances of the time factor, Mauchly's test of sphericity was carried out for the biological parameters; in the absence of sphericity, the Greenhouse-Geisser test was used. The Bonferroni test was performed as a post hoc test to obtain a pairwise comparison of the different levels of the factors.

To assess the effect of microhabitat creation at the upper and lower intertidal level, a one-way ANOVA was performed for each biological parameter (species richness, Shannon diversity and functional diversity) based on the results obtained in the final year of the study (T7 and T8). SPSS software was used for this analysis (IBM Corp. Published in 2012. IBM SPSS Statistics for Windows, version 21.0. Armonk, NY: IBM Corp.).

### 2.4.2. Multivariate statistical analysis

Species coverage data was used to calculate a Bray Curtis dissimilarity matrix. These were used to test the same orthogonal design as the RM-ANOVA with repeated measures distance-based permutational multivariate analyses of variance (RM-PERMANOVA). Finally, a SIMPER was carried out to assess the percentage contribution of each taxon to the dissimilarity among treatments (Clarke, 1993), and a nMDS ordination was performed to look descriptively at differences between samples and over time. PRIMER v.6 (Clarke and Gorley, 2006) was used to perform these analyses.

## 3. Results

### 3.1. Results of biological parameters 7.5 years after the creation of the tidepools

An average value of T7 (Winter 2021) and T8 (Summer 2021) was used as representative at the end of the monitoring period to avoid the seasonal effect. The results of the three biological parameters studied, species richness (F: 42.57;  $p < 0.001$ ; SNK: Tidepool > 5 cm > control), Shannon diversity (F: 23.24;  $p < 0.001$ ; SNK: Tidepool > 5 cm > control) and functional diversity (F: 10.71;  $p < 0.001$ ; SNK: Tidepool > (5 cm = control)), show that the values of the tidepool were significantly higher than those of the control 7.5 years after its creation (Figs. 3, 4 and 5). 7.5 years after the creation of the tidepools, the value of species richness in the tidepool was 64.2% higher than the adjacent control treatment, Shannon diversity 41.54% and functional diversity 6.27%.

### 3.2. Change of the biological parameters in the upper and lower level of the intertidal zone

The results of the comparison between the tidepool and control treatments in the last year (T7 and T8), including species richness, Shannon diversity, and functional diversity, exhibited significant differences at both upper and lower levels. The differences between the tidepool and control were more pronounced in the upper level of the intertidal zone than in the lower level (see results of column Tid. Vs C (%) on Table 3).

### 3.3. Ecological succession

The results show that there are significant differences for the time factor in the biological parameters studied (Table 2, Figs. 3, 4 and 5). In the same sense, the interaction between time and treatment factors has a significant impact on Shannon diversity, species richness and functional diversity. Analysing pairwise comparisons of tidepools, an increase in species richness and Shannon diversity was observed between T1 and T2 (first year) and between T6 and T7 (seventh year), with a decrease observed between T7 and T8. As for functional diversity, an increase was observed between T6 and T7, followed by a significant decrease in T8 (Table 2). The temporal trend in the 5 cm treatment reveals that there was a significant increase in species richness and Shannon diversity between T6 and T7 (seventh year), followed by a decline observed between T7 (winter) and T8 (summer).

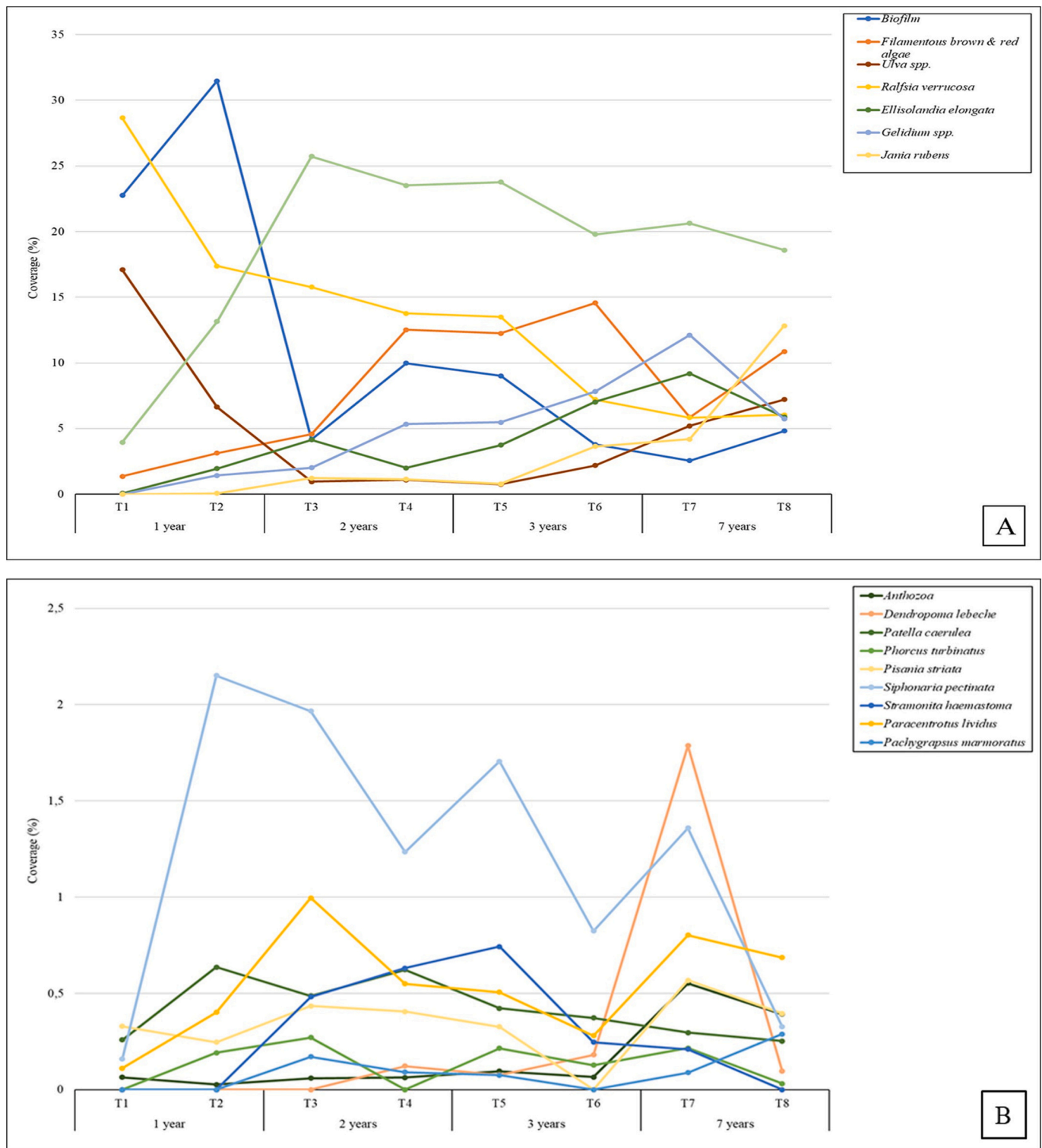


Fig. 7. Coverage of the most important species through the time within created pools. A: algae species. B: animal species, Anthozoa brings together the species *Exaiptasia diaphana*, *Actinia equina* and *Anemonia sulcata*.

The RM-PERMANOVA revealed significant differences over time \* treatment interaction (pseudo-F = 1.94;  $p < 0.001$ ; pairwise tests: Tidepool: T1 ≠ T2 ≠ T3 ≠ T4 ≠ T5 = T6 ≠ T7 ≠ T8; 5 cm: T1 = T2 ≠ T3 = T4 = T5 = T6 ≠ T7 = T8; control: T1 = T2 = T3 = T4 = T5 = T6 = T7 = T8) in the same way, SIMPER analyses show that 7.5 years (T8) after the creation of the tidepools some new species settled within the microhabitat (Table 4).

The results of the ecological succession (based on species coverage), that the created microhabitat has undergone are shown for each tidal level in the MDS (Fig. 6). Precisely, a separation between the two levels of the intertidal is observed for the 5 cm and control treatments. In the tidepool treatment, there is a noticeably change of the biological assemblages over time, being greater in the lower level of the intertidal.

Comparing the species in the high tidepools at T1 versus T8 (7.5

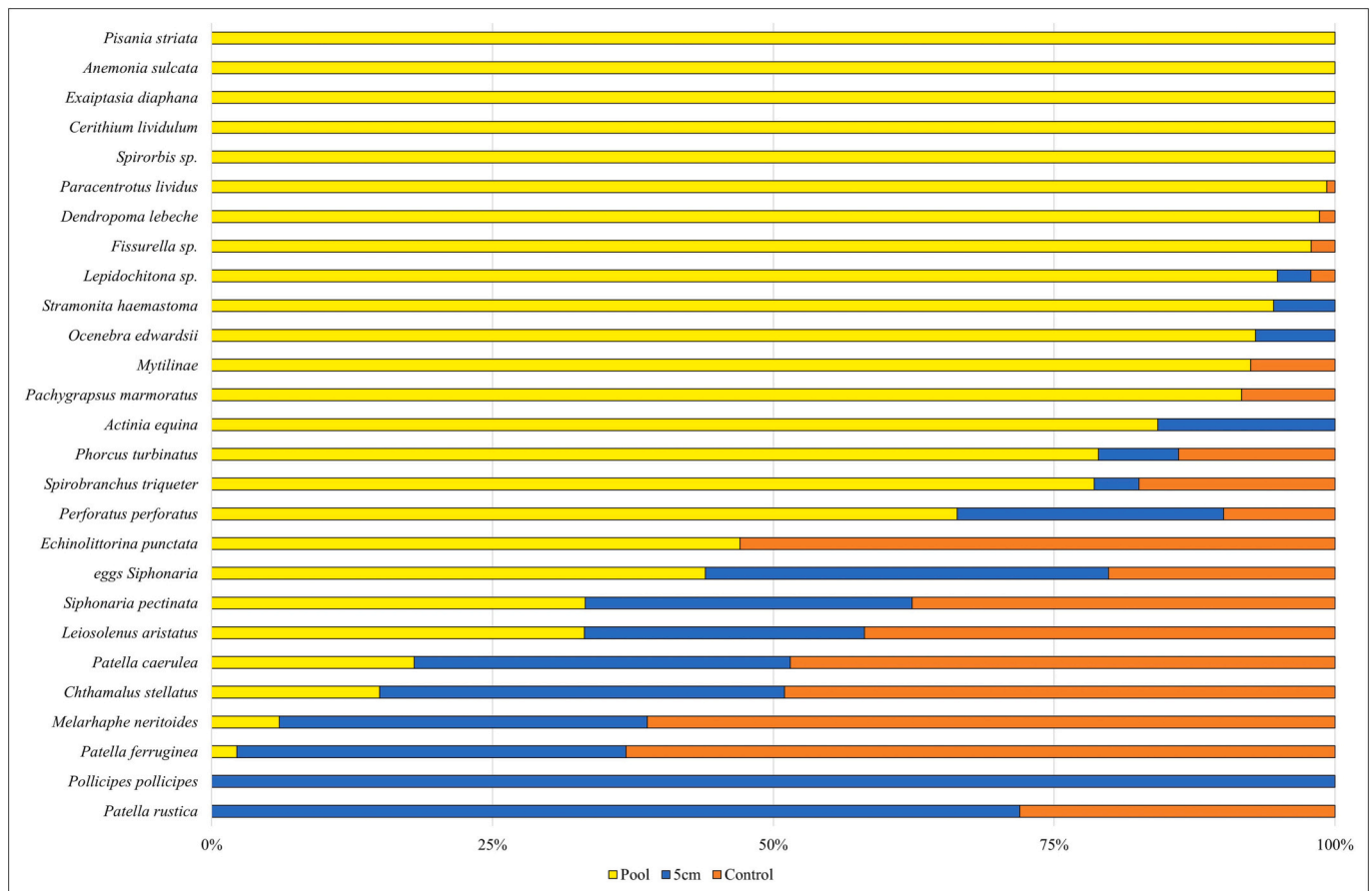


Fig. 8. Percentage of individuals of animal species and *Siphonaria pectinata* eggs observed in each treatment (tidepool, 5 cm halo and control).

Table 3

One-way ANOVA results for species richness, Shannon diversity and functional dispersion for the different intertidal levels (Up and Down) in the last year (T7 and T8). Tid: Tidepool; C: Control; Tid vs C (%): ((Tid mean/C mean)-1)x100.

Biological parameters	Treatment	Mean	SD	Tid vs C (%)	F	P
<b>Up</b>						
Species richness	C	5.10	1.442	88.24	84.71	<0.001
	Tid	9.60	1.228			
Shannon diversity	C	1.06	0.296	53.68	35.76	<0.001
	Tid	1.63	0.220			
Functional diversity	C	0.35	0.091	33.16	17.65	<0.001
	Tid	0.46	0.054			
<b>Down</b>						
Species richness	C	6.63	1.433			
	Tid	9.67	2.076	45.73	21.69	<0.001
Shannon diversity	C	1.27	0.305			
	Tid	1.66	0.208	31.38	17.39	<0.001
Functional diversity	C	0.39	0.086			
	Tid	0.47	0.076	20.19	7.22	<0.05

years later), several species emerged over the years, such as *Lithophyllum incrustans*, *Gelidium* sp., brown and red filamentous algae, *Siphonaria pectinata*, *Chthamalus stellatus* and *Lepidochitona* sp. In the low tidepools, species such as *Ellisolandia elongata*, *Jania rubens*, *Gelidium* sp., *Gymnogongrus crenulatus*, *Caulacanthus ustulatus*, *Hildenbrandia rubra* and brown and red filamentous algae could be observed at T8 versus T1 (Table 4 and Fig. 7).

### 3.4. New species

The results of the RM-PERMANOVA indicated that the species composition (species coverage) differed among the treatments (pseudo-F = 33.36; p < 0.001; pairwise tests: tidepool ≠ 5 cm ≠ control).

During the study, sixty-five species were found, which 30 were animals and 35 algae, being six endangered (*Ericaria selaginoides*, *Cystoseira compressa*, *G. crenulatus*, *Lithophyllum byssoides*, *Dendropoma lebeche* and *Patella ferruginea*). Two invasive macroalgae were observed, *Rugulopteryx okamurae* and *Asparagopsis armata*, which can also be found in the adjacent natural substrate. Comparing the percentages of animals vagile and sessile observed over artificial substrate in each treatment 7.5 years after pool burning reveals that certain species mostly settled in the tidepool or 5 cm treatment. Among these species were *Paracentrotus lividus*, *Fissurella* sp., *Pisania striata*, *Stramonita haemastoma*, *Lepidochitona* sp., and *Ocenebra edwardsii* (Fig. 8).

## 4. Discussion

The present study was conducted in coastal defence structures that were constructed more than eight years before the beginning of the sampling, at the time of the creation of the pools the biota on artificial riprap had largely completed its colonization phase and was firmly established in terms of species composition (see Coombes, 2011; DELOS project: D46-DELOAS project; Dong et al., 2016). Furthermore, the assemblages found in these artificial structures are mostly similar to those found in natural or artificial substrates in this geographical area, indicating the absence of any recent environmental impact on the intertidal that could have re-established the final climax phase (see Ruiz-Tabares et al., 2003).

Previous works about tidepools created on artificial structures (see

**Table 4**

SIMPER analysis showing contribution of different taxa to similarity within treatments at different substrates and levels (breakdown: 90%) in two different moments six months (T1) and 7.5 years (T8) after pool burning. Results include average abundance of each taxa (Avg) and its relative contribution to the overall group similarity (%).

	T1												T8											
	High						Low						High						Low					
	Poza		5 cm		Control		Poza		5 cm		Control		Poza		5 cm		Control		Poza		5 cm		Control	
	Avg	%	Avg	%	Avg	%	Avg	%	Avg	%	Avg	%	Avg	%	Avg	%	Avg	%	Avg	%	Avg	%	Avg	%
Filamentous brown & red algae	0	0	0,94	6,18	0,76	2,38	0	0	0	0	0	0	1,45	3,81	0	0	0	0	3,36	25,64	1,81	9,35	1,15	5,28
<i>Ellisolandia elongata</i>	0	0	0	0	0	0	0	0	2,23	10,97	3,01	28,21	0	0	0	0	0	0	2,82	21,08	4,16	33,86	3,29	33,22
<i>Jania</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3,55	18,62	2,64	9,96	3,08	16,78
<i>Lithophyllum incrustans</i>	0	0	0	0	0	0	1,46	7,83	0	0	0	0	4,63	36,37	1,61	3,14	0	0	2,37	12,48	1,37	5,54	2,09	12,79
<i>Gelidium</i> sp.	0	0	0	0	1,02	2,66	0	0	1,57	4,64	2,38	13,61	1,28	2,84	0	0	0	0	1,59	6,53	2,83	19,42	0	0
Biofilm	4,51	49,68	2,2	19,43	0	0	2,97	19,19	3,46	24,42	1,53	7,28	2,05	11,33	1,98	12,28	0	0	0,96	3,96	1,37	3,48	0,95	4,37
<i>Caulacanthus ustulatus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1,31	3,34	0	0	0	0
<i>Hildenbrandia rubra</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,97	1,83	0	0	0	0
<i>Pseudoralfsia verrucosa</i>	4,13	44,84	3,79	47,99	1,92	17,43	5,25	60,98	5,35	50,34	3,03	30,63	2,62	15,85	4,52	35,69	4,09	38,37	0	0	2,37	8,77	2,79	17,97
<i>Ulva</i> sp.	0	0	0	0	0	0	2,12	7,04	0	0	1,05	4,14	0	0	0	0	0	0	0	0	1,11	2,39	0	0
<i>Siphonaria pectinata</i>	0	0	0,55	4,67	0,81	6,2	0	0	0	0	0,65	3,24	0,54	2,61	0	0	0,66	4,83	0	0	0	0	0,64	2,66
<i>Patella caerulea</i>	0	0	0	0	0,75	4,71	0	0	0,62	2,41	0,67	3,57	0	0	0	0	0,82	3,81	0	0	0	0	0	0
<i>Chthamalus stellatus</i>	0	0	1,34	12,03	3,54	55,09	0	0	0	0	0,87	4	2,8	18,17	4,5	42,36	5,19	47,5	0	0	0	0	0	0
<i>Perforatus perforatus</i>	0	0	0,72	2,98	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lythophyllum byssoides</i>	0	0	0	0	1,18	3,85	0	0	0	0	0	0	0	0	1,61	3,14	0	0	0	0	0	0	0	0
<i>Lepidochitona</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0,73	2,25	0	0	0	0	0	0	0	0	0	0

for example, Evans et al., 2015; Ostalé-Valriberas et al., 2018; Farrugia-Drakard et al., 2023), typically involving short-term temporal monitoring (maximum 2 years) showed substantial improvements in biological parameters within tidepools, suggesting positive ecological trends within these artificial habitats. The relevance of the current study lies in showing the persistence of these patterns over a long-term period (7.5 years) for artificial tidepools built within old coastal defence structures. During the initial three years (T5), the biological community was largely established and exhibited significantly higher 7.5 years after its establishment. Therefore, these types of solutions have been proven to be useful in the context of greening of grey infrastructure (GGI).

Previous studies have shown a decrease in diversity in pools with increasing intertidal height, because the high intertidal zone is subject to a higher environmental stress (Firth et al., 2013b). Same results have been observed in the control treatment of the present study. However, in contrast, the number of species within tidepools has been similar between the different heights. Therefore, artificial tidepools increased higher the biological diversity within upper when compared to the lower intertidal (Table 3). Similarly, Bulleri and Chapman (2010) observed that the number of 'new' species provided by artificial tidepools (compared to those existing in the surrounding area) was greater in the high intertidal compared to the low intertidal.

The ecological succession that takes place within the tidepools adheres to the model of "succession by inhibition" (Rodríguez-Martínez, 2016). During the initial stage, pioneer species, in this case, opportunistic or r-strategist species such as biofilm, *Ulva* sp., *Ralfsia verrucosa*, colonize the area, favoring the possibility of settlement of herbivorous r-strategist species such as *S. pectinata*, *P. lividus* or *P. caerulea* inhibiting their growth as a disruptive agent (Espinosa, 2006) (Table 4-T1 and Fig. 7). In this succession, the second stage is driven by herbivore pressure on species dominating the first stage (Laure et al., 2009). In the intermediate stage, red algae with complex thalli, low growth and low net productivity, such as *E. elongata*, *J. rubens* or *Gelidium* sp. experience an increase in biomass (Littler and Littler, 1980). In the model, the species controlling the initial phase remain present in the community, although with reduced coverage (Rodríguez-Martínez, 2016) (Fig. 7-A). In the present study, species such as *D. lebeche*, *A. equina* or *A. sulcata* with a more complex life cycle settle in the mature phase of the succession (Fig. 7-B).

In particular, the created microhabitat contributed to the settlement of some vagile species such as the echinoderm *P. lividus*, the molluscs *Fissurella* sp., *P. striata*, *S. haemastoma*, *O. edwardsii* and *Phorcus turbinatus*. The persistence over time of these species demonstrates that the creation of tidepools in artificial structures could reduce habitat fragmentation for these species and improve the connectivity of their populations, considering the disruption impact caused by these structures on connectivity (Bishop et al., 2017). Furthermore, the increase in biodiversity and functional diversity over time in these types of artificial structures following the creation of these experimental microhabitats enhanced the number of functional features or niches and would therefore provide ecological resilience and, according to existing literature, make it more difficult for invasive species to settle and thus disperse, reducing invasive processes (see McCann, 2000; Glasby et al., 2007; Kennedy et al., 2002). For example, in contrast to the control treatment, herbivorous species such as *P. lividus* and *P. striata* or carnivorous species such as *S. haemastoma* have settled exclusively in the tidepools.

#### 4.1. Conclusions and management implications

As demonstrated in the present study, the topographic heterogeneity provided by artificially created tidepools within coastal defence structures mimic the microhabitats found in the adjacent natural substrates, providing refuges for various species and enhancing species richness, Shannon diversity and functional traits or biological niches over time. This feature promotes ecological stability, thus hindering the

establishment and spread of invasive species (Essink and Dekker, 2002; Paavola et al., 2005; Glasby et al., 2007). Moreover, adding shelters for native predators within such artificial structures is crucial to hinder the colonization by invasive species, considering that artificial substrates are well-known transmission vectors (Morris et al., 2019).

In addition, these created microhabitats serve as refuges and breeding sites for animal species that are not usually observed in artificial structures, such as *P. striata*, *O. edwardsii*, *S. haemastoma*, *Mel-arhaphé neritoides* and *P. turbinatus* (Ostalé-Valriberas et al., 2018, 2022). It could contribute to reducing the fragmentation of the populations of these species.

Within a coastal defence scheme, tidepools can be created at little expense, obtaining ecological benefits even in those with a climax biological community. This practice aids in mitigating the negative effects caused by low levels of biodiversity due to homogeneity caused by artificial substrates (see Naylor et al., 2023). According to previous studies, these results can be improved by increasing the size of the pool (Martins et al., 2007).

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoleng.2024.107187>.

#### Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the author(s) used ChatGPT in order to review the English grammar. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

#### CRediT authorship contribution statement

**E. Ostalé-Valriberas:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft. **A. Martín-Zorrilla:** Data curation, Formal analysis, Investigation, Software, Validation, Visualization, Writing – original draft. **J. Sempere-Valverde:** Data curation, Formal analysis, Methodology, Validation, Writing – review & editing, Visualization. **J.C. García-Gómez:** Funding acquisition, Supervision, Validation, Writing – review & editing. **F. Espinosa:** Conceptualization, Data curation, Methodology, Validation, Writing – review & editing, Formal analysis, Supervision.

#### Declaration of competing interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

#### Data availability

No data was used for the research described in the article.

#### References

- Airolidi, L., Abbiati, M., Beck, M.W., Hawkins, S.J., Jonsson, P.R., Martin, D., Åberg, P., 2005. An ecological perspective on the deployment and design of low-crested and other hard coastal defence structures. *Coast. Eng.* 52 (10–11), 1073–1087.
- Araújo, R., Sousa-Pinto, I., Bárbara, I., Quintino, V., 2006. Macroalgal communities of intertidal rock pools in the northwest coast of Portugal. *Acta Oecol.* 30 (2), 192–202.
- Bergen, S.D., Bolton, S.M., Fridley, J.L., 2001. Design principles for ecological engineering. *Ecol. Eng.* 18, 201–210.
- Bishop, M.J., Mayer-Pinto, M., Airolidi, L., Firth, L.B., Morris, R.L., Loke, L.H., Dafforn, K.A., 2017. Effects of ocean sprawl on ecological connectivity: impacts and solutions. *J. Exp. Mar. Biol. Ecol.* 492, 7–30.
- Bulleri, F., Chapman, M.G., 2010. The introduction of coastal infrastructure as a driver of change in marine environments. *J. Appl. Ecol.* 47 (1), 26–35.
- Chapman, M.G., Underwood, A.J., 2011. Evaluation of ecological engineering of "armoured" shorelines to improve their value as habitat. *J. Exp. Mar. Biol. Ecol.* 400 (1–2), 302–313.

- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18 (1), 117–143.
- Clarke, K.R., Gorley, R.N., 2006. *User manual/tutorial*. Primer-E Ltd., Plymouth, p. 93.
- Coll, M., Piroddi, C., Steenbeek, J., Kaschner, K., Ben Rais Lasram, F., Aguzzi, J., Voultsiadou, E., 2010. The biodiversity of the Mediterranean Sea: estimates, patterns, and threats. *PLoS One* 5 (8), e11842.
- Coomes, M.A., 2011. Biogeomorphology of Coastal Structures: Understanding Interactions between Hard Substrata and Colonising Organisms as a Tool for Ecological Enhancement.
- Dafforn, K.A., Glasby, T.M., Airoldi, L., Rivero, N.K., Mayer-Pinto, M., Johnston, E.L., 2015. Marine urbanization: an ecological framework for designing multifunctional artificial structures. *Front. Ecol. Environ.* 13 (2), 82–90.
- DELOS project, n.d. Environmental Design of Low Crested Coastal Defense Structure. Deliverable 46: Identification of design features to maintain biodiversity of epibiota, EVK3-CT-2000-00041. <https://cordis.europa.eu/project/id/EVK3-CT-2000-00041>.
- Dong, Y.W., Huang, X.W., Wang, W., Li, Y., Wang, J., 2016. The marine ‘great wall’ of China: local-and broad-scale ecological impacts of coastal infrastructure on intertidal macrobenthic communities. *Divers. Distrib.* 22 (7), 731–744.
- Dong, Y.W., Huang, X.W., Wang, W., Li, Y., Wang, J., 2016. The marine ‘great wall’ of China: local-and broad-scale ecological impacts of coastal infrastructure on intertidal macrobenthic communities. *Diversity and Distributions* 22 (7), 731–744.
- Drakard, V.F., Evans, A.J., Crowe, T.P., Moore, P.J., Coughlan, J., Brooks, P.R., 2023. Artificial rockpools: Seaweed colonisation and productivity vary between sites but are consistent across environmental contexts. *Mar. Environ. Res.* 188, 106022.
- Dumas, P., Bertaud, A., Peignon, C., Leopold, M., Pelletier, D., 2009. A “quick and clean” photographic method for the description of coral reef habitats. *J. Exp. Mar. Biol. Ecol.* 368 (2), 161–168.
- Espinosa, F., 2006. Caracterización biológica del molusco protegido *Patella ferruginea* Gmelin, 1791 (Gastropoda: Patellidae): bases para su gestión y conservación. PhD diss.. University of Seville.
- Espinosa, F., Bazairi, H., 2023. Impacts, evolution, and changes of pressure on marine ecosystems in recent times. Toward new emerging and unforeseen impacts within a changing world. In: *Coastal Habitat Conservation*. Academic Press, pp. 1–16.
- Evans, A.J., Firth, L.B., Hawkins, S.J., Morris, E.S., Goudge, H., Moore, P.J., 2015. Drilled rock pools: an effective method of ecological enhancement on artificial structures. *Mar. Freshw. Res.* 67 (1), 123–130.
- Evans, A.J., Firth, L.B., Hawkins, S.J., Hall, A.E., Ironside, J.E., Thompson, R.C., Moore, P.J., 2019. From ocean sprawl to blue-green infrastructure—a UK perspective on an issue of global significance. *Environ. Sci. Pol.* 91, 60–69.
- Evans, A.J., Lawrence, P.J., Natanzi, A.S., Moore, P.J., Davies, A.J., Crowe, T.P., Brooks, P.R., 2021. Replicating natural topography on marine artificial structures—a novel approach to eco-engineering. *Ecol. Eng.* 160, 106144.
- Farrugia Drakard, V., Brooks, P.R., Crowe, T.P., Earp, H.S., Thompson, B., Bourke, N., George, R., Piper, C., Moore, P.J., 2021. *Fucus vesiculosus* populations on artificial structures have potentially reduced fecundity and are dislodged at greater rates than on natural shores. *Mar. Environ. Res.* 168 <https://doi.org/10.1016/j.marenvres.2021.105324>.
- Firth, L.B., Mieszekowska, N., Thompson, R.C., Hawkins, S.J., 2013a. Climate change and adaptational impacts in coastal systems: the case of sea defences. *Environ Sci Process Impacts* 15 (9), 1665–1670.
- Firth, L.B., Thompson, R.C., White, F.J., Schofield, M., Skov, M.W., Hoggart, S.P., Hawkins, S.J., 2013b. The importance of water-retaining features for biodiversity on artificial intertidal coastal defence structures. *Divers. Distrib.* 19 (10), 1275–1283.
- Firth, L.B., Thompson, R.C., Bohn, K., Abbiati, M., Airoldi, L., Bouma, T.J., Hawkins, S.J., 2014. Between a rock and a hard place: environmental and engineering considerations when designing coastal defence structures. *Coast. Eng.* 87, 122–135.
- Firth, L.B., Airoldi, L., Bulleri, F., Challinor, S., Chee, S.Y., Evans, A.J., Hawkins, S.J., 2020. Greening of grey infrastructure should not be used as a Trojan horse to facilitate coastal development. *J. Appl. Ecol.* 57 (9), 1762–1768.
- García-Gómez, J.C., 2015. A guide on environmental monitoring of rocky seabeds in Mediterranean Marine Protected areas and surrounding zones. Marine Biology Laboratory, Department of Zoology, Faculty of Biology, University of Seville. R+D+I Biological Research Area, Seville Aquarium. Ed. RAC/SPA - MedMPAnet Project, Tunis.
- Glasby, T.M., 1999. Differences between subtidal epibiota on pier pilings and rocky reefs at marinas in Sydney, Australia. *Estuar. Coast. Shelf Sci.* 48 (2), 281–290.
- Glasby, T.M., Connell, S.D., Holloway, M.G., Hewitt, C.L., 2007. Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? *Mar. Biol.* 151, 887–895.
- Hall, A.E., Herbert, R.J., Britton, J.R., Boyd, I.M., George, N.C., 2019. Shelving the coast with vertipools: retrofitting artificial rock pools on coastal structures as mitigation for coastal squeeze. *Front. Mar. Sci.* 456.
- Hofrichter, R. (Ed.), 2004. *El mar Mediterráneo: fauna, flora. ecología*. Ed. Omega.
- Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M., Tilman, D., Reich, P., 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417 (6889), 636–638.
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91 (1), 299–305.
- Laure, M.L.N., Hawkins, S.J., Jenkins, S.R., Thompson, R.C., 2009. Grazing dynamics in intertidal rockpools: connectivity of microhabitats. *J. Exp. Mar. Biol. Ecol.* 370 (1–2), 9–17.
- Littler, M.M., Littler, D.S., 1980. The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Am. Nat.* 116 (1), 25–44.
- Magneville, C., Loiseau, N., Albouy, C., Casajus, N., Claverie, T., Escalas, A., Villéger, S., 2022. mFD: an R package to compute and illustrate the multiple facets of functional diversity. *Ecography* 2022 (1).
- Martini, S., Larras, F., Boyé, A., Faure, E., Aberle, N., Archambault, P., Ayata, S.D., 2021. Functional trait-based approaches as a common framework for aquatic ecologists. *Limnol. Oceanogr.* 66 (3), 965–994.
- Martins, G.M., Hawkins, S.J., Thompson, R.C., Jenkins, S.R., 2007. Community structure and functioning in intertidal rock pools: effects of pool size and shore height at different successional stages. *Mar. Ecol. Prog. Ser.* 329, 43–55.
- McCann, K.S., 2000. The diversity–stability debate. *Nature* 405 (6783), 228–233.
- Metaxas, A., Scheibling, R.E., 1993. Community structure and organization of tidepools. *Mar. Ecol. Prog. Ser.* 98, 187–198.
- Mitsch, W.J., 2012. What is ecological engineering? *Ecol. Eng.* 45, 5–12.
- Morris, R.L., Heery, E.C., Loke, L.H., Lau, E., Strain, E., Airoldi, L., Leung, 2019. Design options, implementation issues and evaluating success of ecologically engineered shorelines. *Oceanogr. Mar. Biol.: An Annual Review* 57, 169–228.
- Nasi, F., Nordström, M.C., Bonsdorff, E., Auriemma, R., Cibic, T., Del Negro, P., 2018. Functional biodiversity of marine soft-sediment polychaetes from two Mediterranean coastal areas in relation to environmental stress. *Mar. Environ. Res.* 137, 121–132.
- Naylor, L.A., Kosová, E., Gardiner, T., Cutts, N., Herbert, R.J., Hall, A.E., MacArthur, M., 2023. Coastal and marine blue-green infrastructure. In: *ICE Manual of Blue-Green Infrastructure*. ICE Publishing, pp. 49–65.
- Ostalé-Valriberas, E., Sempere-Valverde, J., Coppa, S., García-Gómez, J.C., Espinosa, F., 2018. Creation of microhabitats (tidepools) in ripraps with climax communities as a way to mitigate negative effects of artificial substrate on marine biodiversity. *Ecol. Eng.* 120, 522–531.
- Ostalé-Valriberas, E., Sempere-Valverde, J., Pavón-Paneque, A., Coppa, S., Espinosa, F., García-Gómez, J.C., 2022. Artificial marine micro-reserves as a new ecosystem-based management tool for marine conservation: the case of *Patella ferruginea* (Gastropoda, Patellidae), one of the most endangered marine invertebrates of the Mediterranean. *Mar. Policy* 136, 104917.
- Paavola, M., Olenin, S., Leppäkoski, E., 2005. Are invasive species most successful in habitats of low native species richness across European brackish water seas? *Estuarine. Coastal and Shelf Science* 64 (4), 738–750.
- Prieto, C.R., 2013. *Guía de las macroalgas y fanerógamas marinas del Mediterráneo occidental*. Omega.
- Rodríguez-Martínez, J., 2016. *Ecología*. Comercial Grupo ANAYA, SA.: 378–380.
- Ruiz-Tabares, A., Gordillo, I., Corzo, J.R., García-Gómez, J.C., 2003. Macrofitobentos mediterráneo y delimitación de áreas sensibles a la contaminación marina en el litoral ceutí (estrecho de Gibraltar). *Bol. Inst. Esp. Oceanogr.* 19 (1–4), 93–103, 2003.
- Schulze, P.C., Frosch, R.A., Risser, P.G., 1996. *Engineering within Ecological Constraints*. National Academy Press, Washington, D.C., pp. 111–128.
- Sedano, F., de Figueroa, J.T., Navarro-Barranco, C., Ortega, E., Guerra-García, J.M., Espinosa, F., 2020. Do artificial structures cause shifts in epifaunal communities and trophic guilds across different spatial scales? *Mar. Environ. Res.* 158, 104998.
- Sempere-Valverde, J., Guerra-García, J.M., García-Gómez, J.C., Espinosa, F., 2023. Coastal urbanization, an issue for marine conservation. In: *Coastal Habitat Conservation*. Academic Press, pp. 41–79.
- Strain, E.M.A., Cumbo, V.R., Morris, R.L., Steinberg, P.D., Bishop, M.J., 2020. Interacting effects of habitat structure and seeding with oysters on the intertidal biodiversity of seawalls. *PLoS One* 15 (7), e0230807.
- Thompson, B., Brooks, P.R., Farrugia Drakard, V., Kubin, F., Earp, H.S., Alvarez-Cienfuegos, I., Moore, P.J., Crowe, T.P., 2023. Population structure and reproductive states of the dogwhelk *Nucella lapillus* differ between artificial structures and natural shores. *Mar. Environ. Res.* 189 <https://doi.org/10.1016/j.marenvres.2023.106059>.
- Waltham, N.J., Dafforn, K.A., 2018. Ecological engineering in the coastal seascape. *Ecol. Eng.* 120, 554–559.
- WoRMS Editorial Board, 2023. *World Register of Marine Species*. <https://doi.org/10.14284/170>. Available from: <https://www.marinespecies.org>. at VLIZ. Accessed 2023-05-25.