Marine Pollution Bulletin 187 (2023) 114522

Contents lists available at ScienceDirect

Marine Pollution Bulletin

journal homepage: www.elsevier.com/locate/marpolbul

Location and building material determine fouling assemblages within marinas: A case study in Madeira Island (NE Atlantic, Portugal)

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A R T I C L E I N F O

Keywords:
Ecological engineering
Artificial substrata
Colonization
Fouling
Marinas

A B S T R A C T

Marinas are hubs for non-indigenous species (NIS) and constitute the nodes of a network of highly modified water bodies (HMWB) connected by recreational maritime traffic. Floating structures, such as pontoons, are often the surfaces with higher NIS abundance inside marinas and lead the risk for NIS introduction, establishment and spread. However, there is still little information on how the location within the marina and the substratum type can influence the recruitment of fouling assemblages depending on water parameters and substratum chemical composition. In this study, fouling recruitment was studied using an experimental approach with three materials (basalt, concrete and HDPE plastic) in two sites (close and far to the entrance) in two marinas of Madeira Island (NE Atlantic, Portugal). The structure of benthic assemblages after 6- and 12-months colonization, as well as biotic abundance, NIS abundance, richness, diversity, assemblages' volume, biomass and assemblages' morphology were explored. Differences between marinas were the main source of variation for both 6- and 12-month assemblages, with both marinas having different species composition and biomass. The inner and outer sites of both marinas varied in terms of structure and heterogeneity of assemblages and heterogeneity of morphological traits, but assemblages did not differ among substrata. However, basalt had a higher species richness and diversity while concrete showed a higher bioreceptivity in terms of total biotic coverage than the rest of materials. Overall, differences between and within marinas could be related to their structural morphology. This study can be valuable for management of urban ecosystems, towards an increase in the environmental and ecological status of existing marinas and their HMWB and mitigation coastal ecosystems degradation.

1. Introduction

The global physical footprint of marine-built infrastructures overpasses 32.000 km^2 (Bugnot et al., 2020). Commercial ports and marinas are among the coastal interventions with higher ecological footprint (Bugnot et al., 2020). Artificial port areas are often confined by breakwaters and seawalls, creating highly modified water bodies (HMWB), and hosting anthropogenic activities resulting in significant environmental disturbances (Tempesti et al., 2020). The number of marinas has significantly increased during the last years and is a frequent coastal feature, particularly in Europe, America and Australia (Di Franco et al., 2011; Bugnot et al., 2020). As a result, marinas are recognized as an essential environmental stressor in coastal areas (Bulleri and Chapman, 2010; Gómez et al., 2017).

Marinas are hubs for non-indigenous species (NIS) arrival, establishment and spread and constitute the nodes of a network of HMWB

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https://doi.org/10.1016/j.marpolbul.2022.114522
Received 12 October 2022; Received in revised form 16 December 2022; Accepted 19 December 2022
Available online 7 January 2023

connected by recreational maritime traffic (Wirtz and Canning-Clode, 2009; Canning-Clode et al., 2013; Gestoso et al., 2017; Ros et al., 2020). As a result, some species have colonized and dominated this artificial habitat across the globe (Bax et al., 2002; Guardiola et al., 2012; Kenworthy et al., 2018; Chebaane et al., 2019). Some of these species have shown great genetic connectivity between distant areas despite having low-range dispersal mechanisms (i.e., Pineda et al., 2011; Fehlauer-Ale et al., 2014; Wrange et al., 2016). Therefore, the NIS community inside marinas includes species adapted to the environmental conditions of their HMWBs (Megina et al., 2016; Guerra-García et al., 2021a, 2021b). For example, species that are tolerant to the environmental stress and accumulation of heavy metals experienced by the communities inhabiting artificial habitats (Rivera-Ingraham et al., 2013; Ramalhosa et al., 2019; Birch et al., 2020).

The interaction of environmental and ecological variables that determine the structure of fouling assemblages and NIS abundance inside marinas is complex and poorly understood. These include the location and shape of the HMWBs and their connectivity to adjacent water bodies, the environmental parameters of the water, such as temperature, dissolved oxygen, pollutants concentration, turbidity and siltation, and the location of the substratum inside the marina (Guerra-García and García-Gómez, 2004; Guerra-Garcia and García-Gómez, 2005; Kenworthy et al., 2018; Afonso et al., 2020; Chan et al., 2022; Saenz-Arias et al., 2022b). For example, enclosed marinas host more abundant fouling communities that increase the propagule pressure to hulls and nearby areas, increasing the risk of NIS transport (Floerl and Inglis, 2008). But also, the shape, roughness, and type of material available for colonization, the pressure of propagules received from local habitats and maritime traffic, and the vertical and horizontal ecological interactions occurring in the marina, such as predation competition and facilitation, can determine the structure of fouling assemblages in these habitats (Ros et al., 2013; Gestoso et al., 2018; Sedano et al., 2020a, 2020b; Espinosa et al., 2021; Chebaane et al., 2022; Dodds et al., 2022). Overall, the environmental variations inside marinas are related to the distance from the marina's entrance, being the furthest areas with lower environmental quality (Kenworthy et al., 2018; Rondeau et al., 2022). Nonetheless, more research is needed on the effect of different types of substrata on species coverage, diversity and NIS abundance, as well as the interaction of these with their position inside the marinas, which can be determinant of NIS success (Vaz-Pinto et al., 2014; Kenworthy et al., 2018; Firth et al., 2020; Bone et al., 2022).

Artificial surfaces have a lower spatial heterogeneity than natural rocky habitats and host lower abundances of ecosystem engineers, causing an overall reduction in microhabitat complexity and heterogeneity (Seitz et al., 2006; Coombes, 2011; Lawrence et al., 2021). A higher substratum heterogeneity can increase the abundance of bioengineers and the diversity of fouling assemblages in these systems (Firth et al., 2013; Ostalé-Valriberas et al., 2018; van der Ouderaa et al., 2021). Consequently, these are essential components of ecological engineering interventions (Firth et al., 2016a, 2016b, 2016c). Nevertheless, the building material can also determine the composition of the fouling assemblages (Vaz-Pinto et al., 2014; Cacabelos et al., 2016; Sedano et al., 2020c). Concrete can have a negative effect on the early colonization of marine fouling because of its alkalinity, leaching of heavy metals and reduced surface roughness (Müllauer et al., 2015; Becker et al., 2020). As a result, an increasing number of ecological engineering projects include concrete with enhanced bioreceptivity (see review by Bone et al., 2022). Another common material inside marinas is offered by floating pontoons, which are used as moorings for recreational boating and are in direct contact with their hulls for long periods (Connell, 2000; Parretti et al., 2020). Therefore, these floating habitats receive a high propagule pressure of NIS species and provide dim surfaces underneath that host faunal communities rich in filter feeders such as bryozoans and ascidians that are often dominated by NIS (Megina et al., 2016; Ramalhosa et al., 2017, 2021; Cacabelos et al., 2022). These shadowed areas are also less visible, so they could be protected from visual predators, like fish. Therefore, the shading created by overwater and floating structures might have a negative impact on primary production, faunal behaviour and trophic interactions (Heery et al., 2017; Munsch et al., 2017). These floating structures can also host a different community of grazers, such as limpets and sea urchins, which would intervene in modifying the trophic dynamics on these surfaces (Connell, 2001; Giachetti et al., 2020; Glasby, 2001; Holloway and Connell, 2002). However, the higher abundance of filter feeders could also be explained by the physicochemical characteristics of the plastic material used in pontoons, which could promote or hinder the settlement and survival of certain fouling species (Gallo et al., 2018; Pinochet et al., 2020).

The location within the marina and the substratum type can influence the recruitment of fouling assemblages. Overall, material type can be important in early recruitment, although the shape of the marina and other environmental and chemical variables related to the distance to the entrance can be an important factor in community development (Floerl and Inglis, 2008; Vaz-Pinto et al., 2014; Kenworthy et al., 2018). In order to raise knowledge in this area, this study researches the contribution of the location in the marina and substratum type, as well as water parameters related to location and substratum chemical composition, to the structure of benthic assemblages, NIS and native species abundance and calcareous and organic biomass through an experimental approach. We hypothesize that the location in the marina has a more substantial effect on fouling development than the material available for recruitment.

2. Methodology

2.1. Study site

The study was carried out in Madeira Island, NE Atlantic Portugal (Fig. 1, A), in the marinas of Calheta (32°43′ 05.4″ N, 17°10′ 21.4″ W), with mooring capacity for 337 vessels up to 25 m in length and 3.5 m draft, and Quinta do Lorde (32°44′ 30.1″ N, 16°42′ 42.9″ W), with mooring capacity for 264 vessels up to 50 m in length and 5.2 m draft.

2.2. Experimental design

The experimental setup included 24 structures, each with a replicate of basalt, concrete, and high-density polyethylene (HDPE). These are the main materials present in the marinas of Madeira. First, because of the abundance of volcanic rocks in the island, which are widely used to construct quarry boulder breakwaters. Second, because concrete is the most important and used construction material on a global scale, due to its availability, efficiency, and low cost (Becker et al., 2020). Therefore, it is commonly used in Madeira for the construction of seawalls and concrete breakwaters (e.g., cubes and tetrapods). Finally, HDPE is widely used to build the floating pontoons found inside marinas across the globe.

First, basalt replicates were collected from a nearby beach to build the experimental structures. Then, concrete replicates were constructed as replicas of the basalt rocks using plaster casts, whereas HDPE replicas were obtained covering basalt rocks in aluminium foil and used as moulds to shape HDPE sheets using a heat gun. The inner faces of the HDPE moulded sheets were then painted in grey to imitate the colour of basalt and cement replicates and filled with concrete to increase their density and sturdiness. Therefore, each structure had a replica of each material (basalt, concrete and HDPE) with equal morphology (Fig. 2, A). All materials were sanded with 80 grit sandpaper to standardize replicates roughness.

Surface heterogeneity was measured to test possible differences in shape and roughness between materials. This was done by deploying three transects in three randomly chosen replicates of each material and measuring surface profiles at two scales: 10 cm linear transects, with 5 mm resolution, and 2 cm linear transects, with 0.5 mm resolution. For

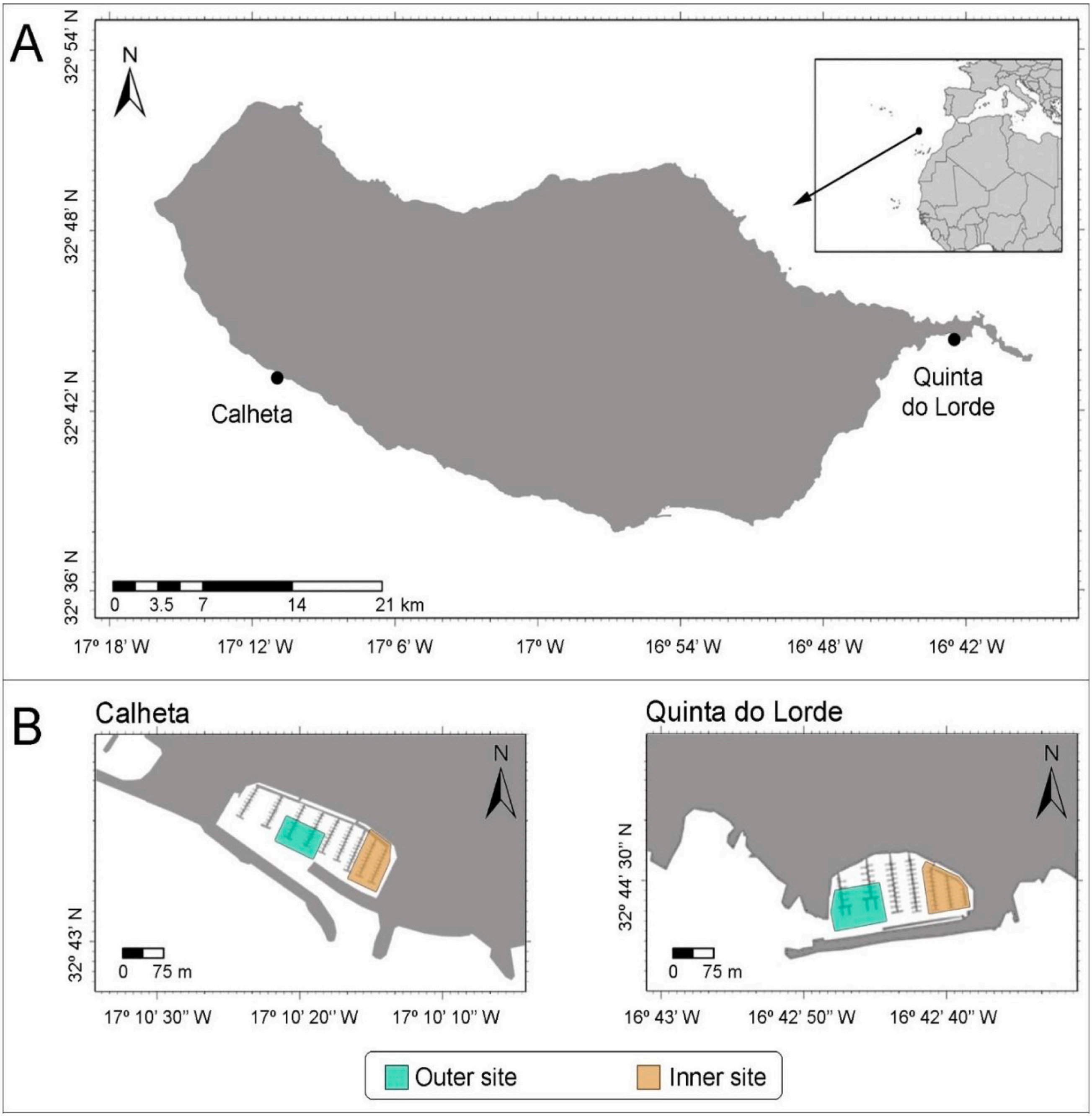

Fig. 1. Study site. A: Location of the marinas on the Island of Madeira (NE Atlantic, Portugal). B: Sites include the pontoons in which the experimental structures were deployed in the marinas of Calheta and Quinta do Lorde.

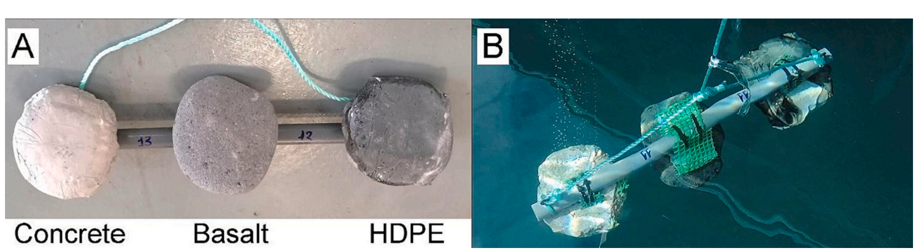

Fig. 2. Two of the 24 structures deployed in this study. A: structure before deployment, showing the concrete, basalt and plastic HDPE replicates surfaces. The order of substratum replicates differed among structures. B: Structure hanging at 1.5 m depth from a pontoon in Quinta do Lorde right after deployment.

the smallest transects, the measurements were taken using slices of negative latex-rubber profiles from the replicates' surfaces (see Sempere-Valverde et al., 2018). These profile-length measures were then used to calculate the Wright coefficient of heterogeneity for each transect (Wright, 1983; Espinosa et al., 2011).

Three samples of each substratum material were collected to assess their chemical composition and toxicity. The chemical composition of rocky materials (basalt and cement) was obtained as semiquantitative major elements measurements using X-ray fluorescence (XRF). For rocky materials, trace elements measurements using XRF Pro-Trace calibration. The plastic HDPE material was analysed for toxic elements using TOXEL standards. All chemical composition analyses were carried out using a ZETIUM spectrometer.

Structures were deployed on January 18th, 2021, 12 in Caleta and 12 in Quinta do Lorde, by hanging them from the pontoons, with the replicates surfaces facing downwards at 1.5 m depth (Fig. 2, B). In each marina 6 structures were located close to the entrance of the marina (outer site), and 6 in the innermost area (inner site) (Fig. 1, B). Structures were revisited and photographed 6 and 12 months after deployment. Species relative coverage on replicates was obtained by deploying a 10 × 10 cm quadrat over the replicates and overlaying 100 points in a random-stratified arrangement (5 × 5 grid with 4 points per cell) using CPCe software (Kohler and Gill, 2006). Twelve months after deployment, structures were retrieved and inspected under a binocular microscope to confirm species ID. All identified species were assigned to one of three categories based on their biogeographical distribution: native, NIS, cryptogenic (unknown origin) or unresolved (based on an inability to identify to species level) in accordance with literature and several current databases (e.g., Castro et al., 2022 and references therein). After retrieving the structures and identifying the species, the fouling community was scratched away from the replicates, sieved using a 0.5 mm mesh and submerged in a graduated cylinder to calculate their volume using a burette. Finally, samples were dried on a stove at 80 °C for 16 h and weighted to obtain the dry biomass.

Water temperature was monitored by installing one iButton™ temperature data logger in each marina. These were hanged from the pontoons at 1 m depth, located in an area between the inner and outer sites, and set to record temperature each 4 h. Temperature data was then used to calculate the average daily temperature and daily variation (daily standard deviation) in each marina. The hydrodynamic exposition in each site was estimated using chalk flow blocks (Doty, 1971). Three chalk blocks of 51 g (±2) were weighted and deployed in each site and marina in July 2021 for three days. Three additional chalk blocks were submerged in stagnant seawater in the same period to estimate the basal dissolution rate (control). The average tidal flushing time was calculated for each marina using the volume of the marina and the tidal prism, which is the volume between the average high and low tide marks (see Monsen et al., 2002 for more details).

2.3. Statistical analyses

Taxa relative abundance was down-weighted and square root transformed before calculating Bray-Curtis similarity among replicates (Clarke et al., 2006). A Principal Coordinates Ordination (PCO) with Pearson correlations overlays using taxa relative coverage was carried out using 6- and 12-month replicates to highlight those species with higher contribution to overall multivariate variation. In addition, replicates variation in the multivariate space were displayed separately for each time (6 and 12 months) using non-Metric Multidimensional Scaling (nMDS). For multivariate analyses, two randomized-blocks PERMANOVA tests were carried out separately for 6 and 12 months. The design tested included the fixed factors Marina (2 levels), Site (2 levels) and Material (3 levels), and the blocking factor Structure (random, 24 levels), which was nested in Marina and Site (see Anderson et al., 2008). These factors were also tested for multivariate dispersions were tested using PERMDISP.

Differences in substratum roughness (factor: Material) and chalk blocks dissolution (factors: Marina and Site) were tested using univariate PERMANOVA on Euclidean Distances (Anderson et al., 2008). In addition, the variables of volume, biomass, species richness, Shannon diversity, total biotic abundance, and NIS and native species abundances were square root transformed and analysed using univariate PERMANOVA on the same test design as multivariate data (see Anderson et al., 2008). All these variables, along with the relative abundance of assemblages' morphological traits (encrusting-prostrate, massive-erect and branched) were also used to carry out distance-based Redundance Analysis (db-RDA) to model and visualize the relationship between these variables and 12-months assemblages' composition. Statistical analyses were carried out using Primer-e v6 + PERMANOVA software (Clarke and Gorley, 2006; Anderson et al., 2008).

3. Results

3.1. Environmental parameters

The average tidal flushing time was similar in Calheta and Quinta do Lorde (see Table 1). However, the marinas had different entrance length-width ratios, with the entrance channel of Calheta being longer and narrower (length-width ratio = 5.87) than Quinta do Lorde (length-width ratio = 1.64). Chalk blocks were dissolved at higher rates in the outer than the inner sites of both marinas (Site: pseudo-$F_{1,71}$ = 119.13; P (perm) = 0.001), with the differences in chalk dissolution between sites being greater in Calheta than Quinta do Lorde (Fig. S.1). Finally, the water masses of both marinas had similar water temperatures from early winter to summer, but from late summer to winter, the water temperature was up to 1 °C higher in Calheta than in Quinta do Lorde (Fig. 3).

Regarding the studied materials, surface heterogeneity was similar among materials at both studied scales: 10 cm transects (Material: pseudo-$F_{2,14}$ = 0.366; P(perm) = 0.719), and 1 cm transects (Material:

Table 1
Average values and standard error (±SE) for the biotic and environmental variables at the inner and outer sites of the marinas of Calheta and Quinta do Lorde (QLorde). Cov: relative coverage; spp.: species; Enc/pro: encrusting and prostrate; CB: chalk blocks.

Indicators	Predictor variables	Average (Calheta)		Average (QLorde)	
		Inner site	Outer site	Inner site	Outer site
Assemblages abundance	Volume (ml)	14.28 (±1.27)	15.44 (±1.07)	10.56 (±4.49)	6.83 (±0.47)
	Biomass (gr)	6.55 (±0.85)	6.88 (±0.68)	4.38 (±0.75)	4.66 (±0.30)
	NIS cov (%)	40.22 (±5.96)	43.89 (±5.58)	43.56 (±6.14)	59.39 (±4.22)
	Native spp. cov (%)	23.78 (±4.16)	22.72 (±3.52)	27.83 (±3.47)	15.67 (±2.72)
	Biotic cov (%)	89.78 (±3.08)	96.22 (±0.77)	86.06 (±3.73)	96.50 (±1.13)
Assemblages richness	Taxonomic richness	11.56 (±0.38)	11.56 (±0.55)	10.61 (±0.57)	13.50 (±0.63)
	Shannon diversity	1.85 (±0.06)	1.77 (±0.08)	1.61 (±0.09)	1.94 (±0.09)
Assemblages morphology	Enc/pro cov (%)	76.39 (±3.83)	72.00 (±4.44)	76.61 (±3.17)	75.17 (±2.91)
	Erect cov (%)	2.06 (±0.61)	5.44 (±1.47)	1.50 (±0.27)	2.72 (±0.61)
	Branched cov (%)	11.33 (±2.96)	18.78 (±3.97)	7.94 (±1.45)	18.28 (±2.81)
Environment	CB dissolution (%)	59.00 (±0.94)	79.67 (±1.70)	63.83 (±0.17)	70.50 (±1.57)
	Distance from entrance (m)	30.90 (±0.24)	20.00 (±0.10)	30.5 (±0.12)	9.8 (±0.22)
	Flushing time (h)	25.6 h		27.6 h	

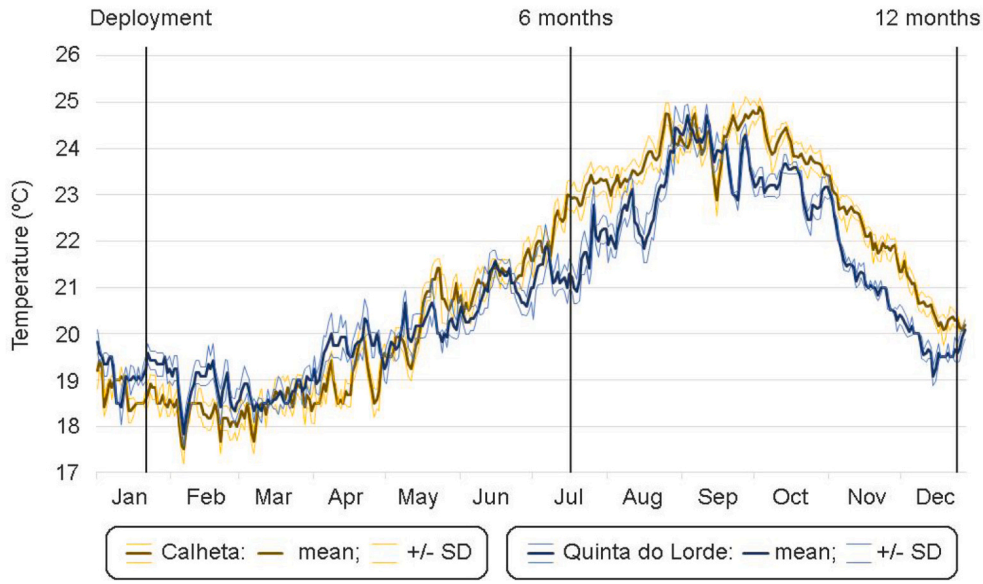

Fig. 3. Average daily temperature (°C) and daily variation, added as the daily standard deviation (SD) in the marinas of Calheta and Quinta do Lorde for the duration of the study (2021), indicating the dates for the beginning of the experiment (deployment), first sampling (6 months) and final sampling (12 months).

pseudo-$F_{2,14}$ = 3.389; P(perm) = 0.094). On chemical composition, major elements ratios were similar for both rocky materials, although concrete had a higher ratio of CaO and organic compounds than basalt; while basalt had a higher ratio of SiO_2 and Fe_2O_3 than concrete (see Table S.1 in supplementary materials). Nevertheless, minor elements varied from plastic (HDPE) to rocky substrata, with the later having generally higher concentrations of trace elements, particularly V, Cr, Ba and W (Table 2).

3.2. Fouling assemblages

Fifty-four taxa were quantified over plates, including 52 taxa and two functional groups: filamentous algae and biofilm (see full species list and mean relative coverages at Table S.2). The most abundant and well-represented groups were bryozoans, with 29.2 % relative coverage and 15 taxa, and ascidians, with 24.9 % relative coverage and 16 taxa. In terms of relative coverage, these were followed by annelids (18.7 %) and macrophytes (10.4 %). As expected for a developing fouling community, the groups of replicates were segregated by Time: 6- and 12-months, but also Marina: Calheta and Quinta do Lorde (see Fig. 4). Regarding the direction of the variation, *Diplosoma listerianum* and *Spirobranchus triqueter* were more abundant at 6 months replicates in Quinta do Lorde,

Table 2
Mean trace element concentration in parts per million (ppm) and Standard Deviation (±) for the three studied materials. HDPE: high density polyethylene; N.D.: not detected; Blank: not measured due to the use of different techniques for rocky materials (basalt and concrete) and HDPE.

	Basalt	Concrete	HDPE
V	288.9 (±55.2)	189.5 (±7.5)	
Cr	352.7 (±487.1)	187.7 (±28.8)	2.54 (±0.23)
Co	137.6 (±25.3)	198.7 (±39.0)	
Ni	204.4 (±242.5)	107.3 (±13.1)	N.D.
Cu	55.4 (±57.9)	66.5 (±5.9)	N.D.
Zn	140.0 (±20.1)	135.9 (±21.6)	N.D.
As	9.4 (±1.1)	10.3 (±0.4)	N.D.
Br	2.2 (±1.8)	26.0 (±2.3)	1.21 (±0.10)
Cd	2.8 (±1.1)	2.1 (±0.3)	1.68 (±0.16)
Ba	497.7 (±157.5)	205.4 (±20.6)	N.D.
W	1271.3 (±517.6)	224.8 (±45.0)	
Hg			0.20 (±0.03)
Pb	N.D.	7.1 (±0.5)	0.33 (±0.05)

while *Parasmitina alba* was more abundant in 12-months replicates. Finally, *Botryllus schlosseri*, *Trididemnum cereum* and *Spirorbis* sp. were abundant at 6-months replicates in Calheta.

The factor Marina was the main source of variation for both 6- and 12-month assemblages (Table 3). In both times, there were no differences in assemblages' structure among different materials, but there were differences between each marina's inner and outer sites, except for 12-months Calheta (see Mar × Si interaction in Table 3). At 6 months, the effect of Site had a different direction in each marina (Fig. 5). At 12 months, the sites in Quinta do Lorde differed in structure, while the sites in Calheta had a similar structure but differed in multivariate dispersions (Figs. 5; 6). Overall, small-scale variations among structures (blocks) were significant, although the variation at the site and structure levels had sizes one degree of magnitude smaller than the variation among marinas (see MS values in Table 3).

Contrary to fouling assemblages' structure, species richness and Shannon diversity did not differ between marinas or sites, except for species richness, which was higher in the outer than the inner site in Quinta do Lorde (Table 4). However, they differed among materials, with basalt having a higher species richness than the other materials in Quinta do Lorde and with Shannon diversity being higher on basalt than concrete and plastic HDPE in both marinas. These differences among materials were higher than the small-scale variation among structures (MS values in Table 4).

Fouling assemblages' volume (ml) and dry biomass (gr) were similar among sites and substrata but were generally higher in Calheta than Quinta do Lorde (Table S.3). Biotic coverage was higher in the outer than inner sites and on concrete than the rest of materials in both marinas (Table S.4). However, native species only differed among materials in Quinta do Lorde, with a higher relative abundance on basalt and concrete than plastic. For its part, NIS relative abundance showed a similar coverage across marinas, sites and materials. Nonetheless, NIS and native species relative abundances were correlated with the structure of assemblages, contributing to the variation among replicates (see Fig. 7). Finally, the morphology of fouling assemblages was correlated to the multivariate variation among replicates, indicating a more morphologically heterogeneous community in the outer than inner sites of both marinas. Furthermore, the diversity measures of richness and diversity had the same direction than the relative abundances of erect and branched morphologies (Fig. 7).

The presence of variation among structures (factor Structure =

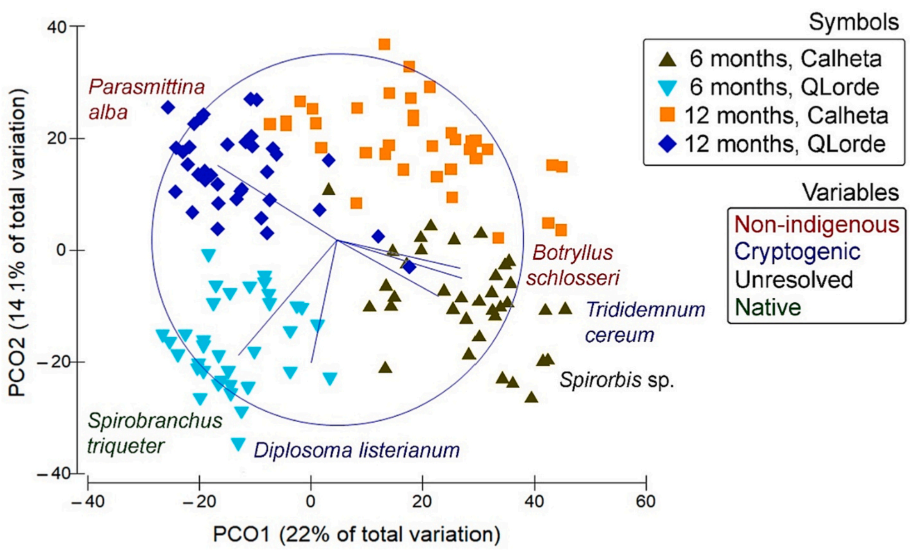

Fig. 4. Principal Coordinates Ordination (PCO) displaying 36.1 % of the total multivariate variation and those variables with a Pearson correlation higher than 0.6 with PCO1 or PCO, indicating their status with text colours. Vector length indicates the size of the Pearson correlation, and the blue circle is the maximum correlation (1). Samples are grouped by the interaction of Time: 6 and 12 months, and Marina: Calheta and Quinta do Lorde. QLorde = Quinta do Lorde. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Multivariate PERMANOVA results for taxa relative coverage at 6- and 12-months and pairwise comparisons. Bold text: significant differences (threshold: P(perm) <0.05); Mar: Marina; Si: Site; Mat: Material; In: Inner site; Out: Outer site; =: absence of significant differences; ≠: significantly different.

Source	Df	6 months			12 months		
		MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Marina	1	34934	20.303	**0.001**	24107	9.157	**0.001**
Site	1	6685	0.814	0.605	5839	1.176	0.420
Structure (Mar × Si)	19	1720	1.752	**0.001**	2632	3.211	**0.001**
Material	2	1490	1.019	0.470	870	1.027	0.478
Mar × Si	1	8215	4.774	**0.001**	4967	1.887	**0.045**
Mar × Mat	2	1462	1.489	0.105	847	1.033	0.451
Si × Mat	2	998	1.674	0.158	447	0.923	0.578
Mar × Si × Mat	2	596	0.607	0.864	485	0.591	0.887
Res	39	982			820		

Pairwise (Mar × Si)	6 months	12 months
Calheta	**In ≠ Out**	In = Out
Quinta do Lorde	**In ≠ Out**	**In ≠ Out**

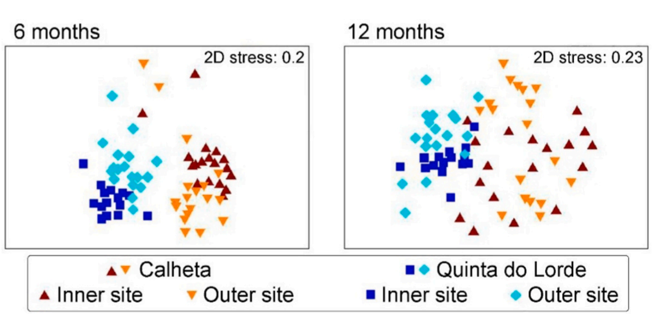

Fig. 5. nMDS ordinations for 6- and 12-months datasets. Symbols and colours represent factors Marina (Calheta, Quinta do Lorde) and Site (Inner site, Outer site).

blocks), which represents the small-scale variation within sites, was common for most analyses. These included assemblages' structure (Table 3), multivariate dispersions at 12-months (PERMDISP: $F_{23,71}$ = 4.32; P(perm) = 0.022), diversity measures (Table 4), assemblages' volume and biomass (Table S.3), and native and NIS relative abundances (Table S.4). Overall, these differences among structures indicate a high level of heterogeneity in assemblages' composition inside marinas for the studied scales.

4. Discussion and conclusions

The present study is a pioneering manipulative experiment to assess the interaction of location and type of substrata on the colonization of sessile assemblages on floating structures inside marinas. Both location and substrata influenced biotic parameters in fouling despite the particularities of each marina. For instance, Quinta do Lorde (QLorde) had a high abundance of *Spirobranchus triqueter* and *Parasmittina alba*, which are well-established NIS in this marina (Ramalhosa et al., 2019; Ferrario et al., 2020; Castro et al., 2021; Cacabelos et al., 2022). Calheta, on the contrary, is characterized by a higher abundance of native and non-indigenous ascidians (Ramalhosa et al., 2021; Png-Gonzalez et al., 2021).

The differences between marinas could have been driven by structural engineering differences, as QLorde have an ampler entrance than Calheta that would allow a higher exposition to the open sea inside its water body, creating a higher gradient between the outer and inner parts of the marina in terms of water renewal and hydrodynamic exposition (Floerl and Inglis, 2008; Vaz-Pinto et al., 2014; Rondeau et al., 2022). This gradient would influence variables such as food availability and pollutants concentration, ultimately defining the structure of the fouling

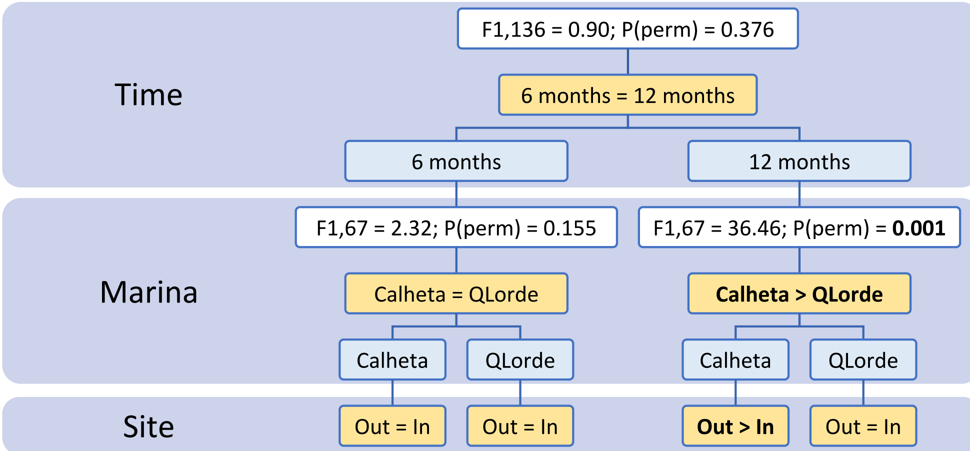

Fig. 6. PERMDISP results for variables relative coverage and the times 6 and 12 months and pairwise comparisons. Blue background = Factors and factor levels; White background: PERMDISP results; Yellow background: pairwise comparisons; Bold text: significant differences (threshold: P(perm) <0.05); QLorde: Quinta do Lorde; In: Inner site; Out: Outer site; =: absence of significant differences; >: significantly higher than. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Univariate PERMANOVA results for fouling assemblages' richness and diversity at 12-months and pairwise comparisons. Bold text: significant differences (threshold: P(perm) <0.05); Mar: Marina; Si: Site; Mat: Material; In: Inner site; Out: Outer site; HDPE: high density polyethylene; =: absence of significant differences; >: significantly higher than; <: significantly lower than.

Source	Df	Species richness			Shannon diversity		
		MS	Pseudo-F	P (perm)	MS	Pseudo-F	P (perm)
Marina	1	4.50	0.537	0.496	0.015	0.080	0.792
Site	1	37.56	4.480	0.056	0.294	1.564	0.220
Structure (Mar × Si)	20	8.38	2.676	**0.007**	0.188	3.052	**0.003**
Material	2	13.35	4.260	**0.023**	0.398	6.460	**0.001**
Mar × Si	1	37.56	4.480	**0.048**	0.756	4.022	0.051
Mar × Mat	2	11.37	3.630	**0.037**	0.098	1.594	0.210
Si × Mat	2	4.85	1.547	0.234	0.157	2.554	0.079
Mar × Si × Mat	2	1.76	0.563	0.593	0.069	1.118	0.335
Res	40	3.13			0.062		

Pairwise:	Species richness		Shannon diversity:
	Mar × Si	Mar × Mat	Material
Calheta	In = Out	Basalt = Concrete = HDPE	**Basalt > (Concrete = HDPE)**
Quinta do Lorde	**In < Out**	**Basalt > (Concrete = HDPE)**	

assemblages (Oricchio et al., 2016; Kenworthy et al., 2018). According to this, the differences between inner and outer sites in QLorde were more pronounced than in Calheta. The marina of Calheta has a longer entrance channel than QLorde, which could reduce water renewal regardless the obtained flushing rates. This is because the water contained in the entrance channel will have a limited mix with the water outside the marina and will re-enter the water body each tidal cycle, increasing the return flow factor (see Monsen et al., 2002). This would mean a higher isolation of Calheta water body, which would be compatible with the higher water temperatures in this marina compared to other marinas in the region (Ramalhosa et al., 2021; this study). Furthermore, a higher water confinement has been associated with a higher fouling abundance in marinas, which matches with the higher assemblages' volume and biomass in Calheta (Monsen et al., 2002; Floerl and Inglis, 2008). In addition, a more confined water body would have homogenised the marina's environmental conditions, resulting in similar assemblages between sites, although the areas closer to the entrance would still have a higher environmental variability and host more heterogeneous assemblages than the inner sites (Floerl and Inglis, 2008; Kenworthy et al., 2018). Finally, the opposite orientation of Calheta and QLorde entrances could have influenced the chalk block results, as this was a punctual experiment in which westwards winds could had contribute to an increased dissolution in Calheta outer site (JS and SC pers. obs.). Overall, the differences in marinas' structural features were coincidental with differences in fouling assemblages, which raises interest on further studying the ecological implications of structural engineering choices in marinas.

Fouling assemblages inside marinas vary according to the distance to the entrance. This variation might include changes in NIS abundance, with NIS being more abundant in the inner parts of the marina than closer to the entrance (e.g., Kenworthy et al., 2018; Rondeau et al., 2022). However, NIS abundance was similar in the inner and outer parts of the marinas in this study. This could be related to the geographical conditions of oceanic islands, where the high exposition to wave action, currents and oligotrophic conditions may facilitate the elimination of pollutants inside marinas (Caldeira et al., 2002; Canning-Clode et al., 2008). As pollution gradients are responsible of establishing gradients in NIS abundance inside marinas (Gauff et al., 2022; Rondeau et al., 2022), it could be possible that these gradients were absent in oceanic islands, although more research is needed on this topic for a better understanding on the patterns found in this study. In this study, both marinas had a higher presence of erect and branched morphologies and a higher heterogeneity of morphological traits near the entrance. In general, a higher exposition to water movement promotes less erect morphologies in fouling species (i.e., Kaandorp, 1999). Nonetheless, this pattern reverses in confined environments, such as submerged caves, where a moderate exposition promotes erect and branched, and low exposition prostrate and encrusting morphologies (Nepote et al., 2017; Sempere-Valverde et al., 2019). In these cases, the low water movement in confined areas increases oligotrophy and siltation, reducing the resources available for massive sessile morphologies. However, this would not be case of Highly Modified Water Bodies (HMWB) inside marinas, which are generally more polluted than open coastal areas (Guerra-García et al., 2021a; Rondeau et al., 2022). It is unknown whether the water oligotrophy in oceanic islands is related to the patterns found in this study (Caldeira et al., 2002; Canning-Clode et al., 2008). Therefore, it would be interesting to assess fouling morphologies in future studies along with other biotic and abiotic variables to understand the factors underlying morphological differences in fouling within marinas.

Floating structures, such as pontoons, are often the surfaces with higher NIS abundance inside marinas (Connell, 1999; Dafforn et al., 2009). These surfaces increase the risk for NIS introduction, establishment and spread, so they should be prioritized when monitoring and managing port habitats (Connell, 2000). To our best knowledge, this

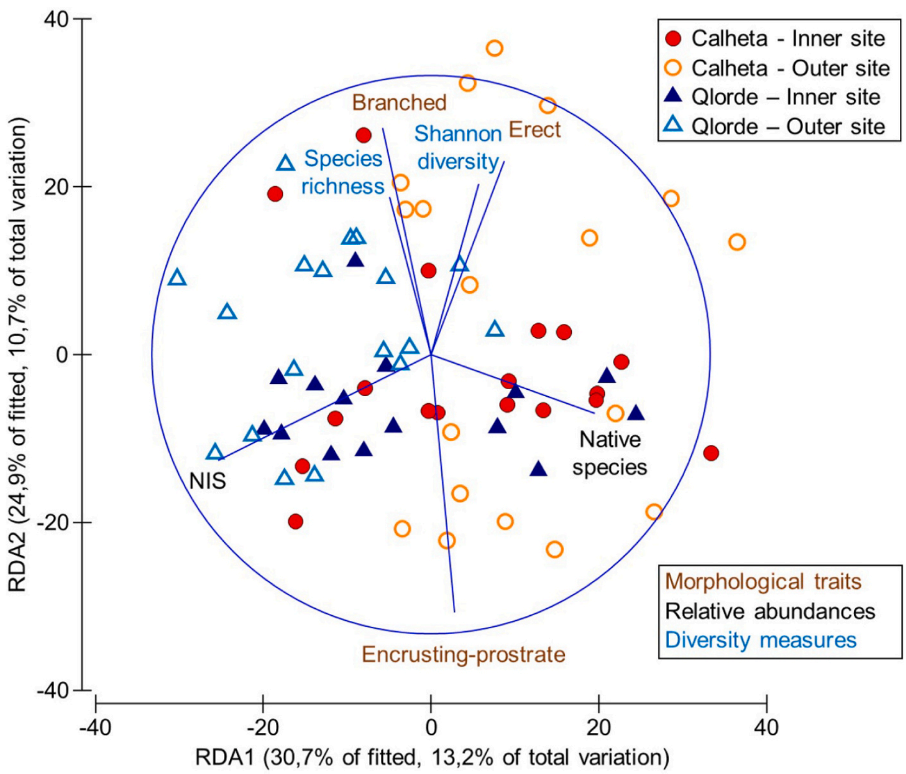

Fig. 7. Distance-based Redundance Analysis (db-RDA), including 55.6 % of the total variation. The biotic and environmental variables with a correlation higher than 0.6 with RDA1 or RDA2 axes are displayed as vectors (see Table S.3). The length of the vectors indicates the correlation index, and the blue circle indicates the correlation limit (correlation = 1). QLorde: Quinta do Lorde; NIS: non-indigenous species relative abundance. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

study is pioneering in dealing with HDPE plastic material inside marinas, despite it is used for pontoons, which are common in oceanic tidal regions. Nonetheless, substratum type can influence fouling assemblages in the studied region (Cacabelos et al., 2016; Martins et al., 2016; Png-Gonzalez et al., 2021). In contrast to floating pontoons, the moorings in microtidal regions are often fixed and constructed with concrete and quarry rock, so HDPE is less conspicuous in areas such as the Mediterranean Sea.

In this study, the type of substrata influenced diversity measures, with basalt having a higher performance than artificial materials. This is coincidental with previous studies in coastal habitats, in which rocks such as sandstone, limestone and basalt have shown better performance than concrete (Vaz-Pinto et al., 2014; Cacabelos et al., 2016; Sempere-Valverde et al., 2018; Sedano et al., 2020c). Therefore, the relatively lower diversity on concrete and HDPE could result from the artificial origin of these materials, which generate novel physicochemical conditions for marine organisms (i.e., Pinochet et al., 2020; Bone et al., 2022). For instance, the cement portion in concrete has high pH and leaches heavy metals, which is commonly associated to a lower ecological performance (Müllauer et al., 2015; Becker et al., 2020; Hayek et al., 2021). Seemingly, plastic surfaces can influence assemblages' recruitment and growth, with potential effects on assemblages' composition (Li et al., 2016; Varello et al., 2021; Pinochet et al., 2020). However, the results on substrata chemical composition did not seem to be related to the patterns found on fouling assemblages, so the differences among substrata could had been primarily influenced by the surface properties of the materials, such as porosity, hydrophobicity and albedo (Hayek et al., 2021; Bone et al., 2022). To this matter, bioreceptivity, as the ability of a material to be colonized (see Guillitte, 1995), was slightly higher for concrete, which could have resulted from a higher recruitment of larvae and propagules promoted by the high porosity of concrete surfaces (Hayek et al., 2021; Bone et al., 2022). Overall, the results of this study support that small-scale variation of environmental parameters, such as surface exposition to water movement or water temperature, are more important drivers to fouling assemblages' structure than substratum type (see also Vaz-Pinto et al., 2014). This small relevance of substratum type in marinas could be related to the singularity of this highly modified artificial habitat, in which environmental and anthropic pressures are already high (Guerra-García and García-Gómez, 2004; Guerra-Garcia and García-Gómez, 2005; Gauff et al., 2022). Nevertheless, the relevance of substratum type over assemblages' structure, richness, diversity and biomass is expected to differ at the regional scale and locally, with variation occurring among marinas in the same locality, highlighting the need to consider local particularities in management and conservation strategies (Sedano et al., 2020d; Firth et al., 2020; Saenz-Arias et al., 2022a).

The high variation registered among structures highlights high heterogeneity inside marinas due to micro-environmental variations, such as those provoked by the side of the pontoon in which the structure was installed or the presence of moored boats that can interfere with light and hydrodynamic exposure (Glasby, 1999; Connell, 2000; Kenworthy et al., 2018; Rondeau et al., 2022). Furthermore, some of the structures were hosting consumers such as *Arbacia lixula* and *Percnon gibbesi* (JS and SC pers. obs.), promoting different grazing pressures among structures. Exposure to consumers generally increases the consumed community heterogeneity, favouring or hampering NIS abundance (Simkanin et al., 2013; Gestoso et al., 2018; Chebaane et al., 2022). In general, the space left by fouling consumers can be recolonized by NIS, mainly if the consumer selectively feeds native species (Gestoso et al., 2018; Cacabelos et al., 2022). However, the homogenizing effects of feeding can also limit the dominance of NIS and exert biotic resistance (Olyarnik et al., 2009). The effect of foraging consumers, such as fish, is different on shaded surfaces, (i.e. under pontoons) than in illuminated areas and can promote the abundance of colonial organisms such as ascidians (Loureiro et al., 2021). Therefore, consumers might have played an important role in the structure of assemblages in the studied marinas. Overall, a better understanding of the biotic interactions (both lateral and vertical) inside marinas would allow the development of better ecological interventions and management plans (Leclerc and Viard, 2017; Riera et al., 2018; Cacabelos et al., 2022; Chebaane et al., 2022).

Future research should focus on understanding how the design and use of port structures influence the composition of the fouling community (e.g., Floerl and Inglis, 2008; Kenworthy et al., 2018; Saenz-Arias et al., 2022a; Rondeau et al., 2022), with special care to those aspects that can be manipulated to develop ecological engineering tools. Therefore, the environmental and ecological improvement of existing marinas and their HMWB should be a priority for coastal conservation, the mitigation of coastal ecosystem degradation and the management of NIS (Firth et al., 2020; Guerra-García et al., 2021b, 2021c; Castro et al., 2022).

Funding information

JSV was supported by a FPI Grant (PRE2018-086266) from Ministerio de Ciencia, Innovación y Universidades (Project CGL 2017-82739-P) co-financed by ERDF European Union and Agencia Estatal de Investigación, Gobierno de España. PR is funded by the project (UIDB/04292/2020) granted to MARE UI&I. AB-I and SC were financially supported by a pre-doctoral grant in the framework of the 2015 ARDITI Grant Programme Madeira 14-20 (Project M1420-09-5369-FSE-000002). JGM was supported by post-doctoral research fellowship by ARDITI (ARDITI–M1420-09-5369-FSE-000002) and by national funds through FCT – Fundação para a Ciência e a Tecnologia, I.P., under the Scientific Employment Stimulus – Institutional Calls – (CEEC-INST/00037/2021). IG is supported financially by a Maria Zambrano contract UCA under the grants call for the requalification of the Spanish university system 2021–2023, funded by the European Union – Next Generation EU. JCC is funded by national funds through FCT, I.P., under the Scientific Employment Stimulus-Institutional Call (CEECINST/00098/2018). This study had the support of FCT through the strategic project UIDB/04292/2020 awarded to MARE and through project LA/P/0069/2020 granted to the Associate Laboratory ARNET.

CRediT authorship contribution statement

Juan Sempere-Valverde: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Visualization, Project administration, Funding acquisition. **Patrício Ramalhosa:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Data curation, Writing – review & editing. **Sahar Chebaane:** Conceptualization, Methodology, Investigation, Resources, Data curation, Funding acquisition. **Free Espinosa:** Conceptualization, Methodology, Validation, Writing – review & editing, Supervision. **João Gama Monteiro:** Conceptualization, Resources. **Alejandro Bernal-Ibáñez:** Investigation, Resources. **Eva Cacabelos:** Methodology, Investigation, Writing – review & editing. **Ignacio Gestoso:** Methodology, Writing – review & editing. **José Manuel Guerra-García:** Conceptualization, Methodology, Validation, Resources, Writing – review & editing, Supervision, Funding acquisition. **João Canning-Clode:** Resources, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be available on request and publicly available on idUS.us.es.

Acknowledgements

This is contribution 113 from the Smithsonian's MarineGEO and Tennenbaum Marine Observatories Network.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2022.114522.

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