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The elephant in the room: Introduced species also profit from refuge creation by artificial fish habitats

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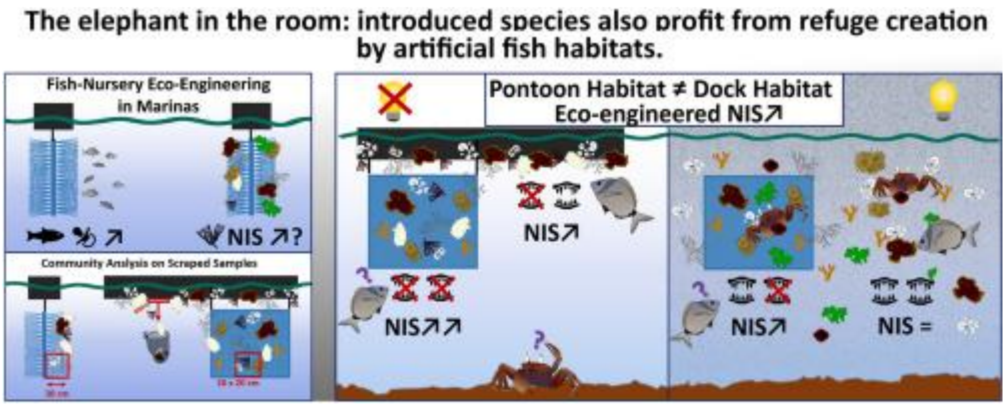
Abstract :

Increasingly, ecological rehabilitation is envisioned to mitigate and revert impacts of ocean sprawl on coastal marine biodiversity. While in the past studies have demonstrated the positive effects of artificial fish habitats in port areas on fish abundance and diversity, benthic colonization of these structures has not yet been taken into consideration. This could be problematic as they may provide suitable habitat for Non-Indigenous Species (NIS) and hence facilitate their spreading. The present study aimed to examine communities developing on artificial fish habitats and to observe if the number of NIS was higher than in surrounding equivalent habitats. The structures were colonized by communities that were significantly different compared to those surrounding the control habitat, and they were home to a greater number of NIS. As NIS can cause severe ecological and economical damages, our results imply that in conjunction with the ecosystem services provided by artificial fish habitats, an ecosystem disservice in the form of facilitated NIS colonization may be present. These effects have not been shown before and need to be considered to effectively decide in which situations artificial structures may be used for fish rehabilitation.

Graphical abstract



Highlights

► Eco-engineered artificial nurseries are increasingly used for fish restoration. ► Benthic colonization of these structures has however not yet been investigated. ► Communities on eco-engineered substrates differ from those of others in the marina. ► A higher number of introduced species was found on eco-engineered structures. ► The risk linked to introduced species must be considered when restoring urban habitats.

Keywords : Eco-engineering, Fouling, Introduced species, Rehabilitation, Artificial habitats, Community composition

1 Introduction

Urban infrastructure impacts marine coastal ecosystems in a variety of ways, including the alteration of physico-chemical conditions (Lee and Arega, 1999; Menniti et al., 2020; Schiff et al., 2007), habitat loss and fragmentation (Krauss et al., 2010), as well as the modification of ecological connectivity (Firth et al., 2016b), ecosystem functioning (Mayer-Pinto et al., 2018) and ecosystem services (Grimm et al., 2008; Vozzo et al., 2021). Therefore, this high damage to coastal marine ecosystems due to past and present ocean sprawl has led to numerous reflections for developing rehabilitation strategies to bring back biodiversity into urban habitats and to mitigate the effects of anthropogenic impacts (Airoldi et al., 2021). One way to do so is to reduce the impacts of already deployed infrastructure by 'greening' existing man-made structures (Airoldi et al., 2021; Dafforn et al., 2015; Evans et al., 2019; Hall et al., 2018; O'Shaughnessy et al., 2020). The global principle behind the proposed technical solutions consists in modifying the three-dimensional structure of the marine urban structures, either by intervening directly on their topography when a new structure is built (Ido and Shimrit, 2015; Natanzi and Mcnally, 2018), or by adding complex artificial micro-structures *a posteriori* (Bouchoucha et al., 2016; Firth et al., 2016a; Mercader et al., 2017). The objective of the structural modification differs according to the context: in some cases, it consists in promoting recolonization by local and structuring species (Strain et al., 2020; Vozzo et al., 2021) or recreating small rockpools sheltering fauna and flora that cannot withstand emersion at low tide (Firth et al., 2016a, 2013; Hall et al., 2019). In other cases, refuges are created against predators for fish juveniles (Astruch et al., 2017; Bouchoucha et al., 2016; Patranella et al., 2017; Selfati et al., 2018). All these pilot operations support the idea that harbor structures can be structurally modified to increase their attractiveness and quality for marine organisms, which allows them to contribute to the maintenance of coastal biodiversity while ensuring their primary function of coastal protection (O'Shaughnessy et al., 2020).

Even if some ecological functions within man-made habitats are definitively lost, ecological engineering has been shown to be a tool for improving the fish nursery potential of harbor areas (Astruch et al., 2017; Bouchoucha et al., 2016; Patranella et al., 2017; Selfati et al., 2018). A nursery habitat provides two important functions for fish: nutrition and protection (Beck et al., 2001; Cheminée et al., 2011; Muller, 2017; Verdiell Cubedo et al., 2007; Whitfield and Pattrick, 2015). Eco-engineered artificial habitats thus mainly aim to increase the complexity of harbor structures such as dykes, docks or pontoons in order to provide physical protection against predators (> *c.a.* 15 cm), which may not access the created narrow spaces. This subsequently increases juvenile survival (Astruch et al., 2017; Bouchoucha et al., 2016; Mercader et al., 2017; Patranella et al., 2017; Strain et al., 2018) which should mitigate the loss of some ecosystem services when replacing natural environments with artificial ones (Barbier, 2017; Liquete et al., 2016; Moberg and Rönnbäck, 2003). For these reasons government subsidies have been put in place to encourage harbor managers to increase the ecological attractivity of infrastructures, resulting in more than 30 harbors on the French Mediterranean coast being equipped with ecological rehabilitation modules (http://medtrix.fr, consulted 05.06.2022). Despite their controversial anthropocentric focus (McCauley, 2006), quantifying ecosystem services has been successful in illustrating the economic value of the environment (Barbier, 2017; Reid et al., 2006). They do however not encompass the negative impacts that may be associated to certain ecosystem functions, which are known as ecosystem disservices (Dunn, 2010; McCauley, 2006; Von Döhren and Haase, 2015). Such disservices may be unintentionally increased when aiming to restore ecosystem services (Friess et al., 2009; Handel, 2016).

In addition to the recognized and sought after effects of increasing juvenile fish abundance and diversity (Astruch et al., 2017; Bouchoucha et al., 2016; Lapinski et al., 2015; Mercader et al., 2017; Selfati et al., 2018), the eco-engineered structures also entail unintentional effects, such as providing new complex habitat for benthic organisms. To our knowledge, the unintended effects of fish-enhancing artificial habitats on marine invertebrates, and the possible disservices these provide, have received little attention. Fouling communities recruit on immerged artificial substrate (Connell, 2001; Dürr and Thomason, 2010; Sylvester et al., 2011) and harbor a great diversity and abundance of Non-Indigenous Species (NIS) (Canning-Clode et al., 2011; Ferrario et al., 2020; Leclerc and Viard, 2018; McKenzie et al., 2012; Tempesti et al., 2020). Newly immerged artificial structures may thus provide a new preferential habitat for NIS (Dafforn et al., 2012; González-Ortegón and Moreno-Andrés, 2021; Mineur et al., 2012). NIS can cause severe ecological and economical damages (Jardine and Sanchirico, 2018; Lovell et al., 2006; Pyšek et al., 2020; Vilizzi et al., 2021) through lowering biodiversity (Blum et al., 2007; Pyšek et al., 2020) and altering ecosystem trophic functioning (Pyšek et al., 2020; Walsh et al., 2016) and are therefore considered a leading cause of species extinction (Blackburn et al., 2019; Clavero and García-Berthou, 2005). A recent study has evaluated the cumulated costs generated from damages as well as investment to combat NIS as reaching well above 1.3 trillion dollars worldwide (29 billion in Europe; see Sup. Tab. 1 of Diagne et al., 2021). Moreover, NIS may constitute an even greater issue in the light of changing conditions due to climate change (Bradley et al., 2018; Spear et al., 2021; Vilizzi et al., 2021). Thus, NIS presence constitutes a major ecosystem disservice of urban habitats (Friess et al., 2009; Von Döhren and Haase, 2015), which might imply an undesired side effect of rehabilitation efforts, if these efforts benefit NIS. As early prevention may help to minimize the potential costs of NIS (Lovell et al., 2006; Olson, 2006; Pyšek et al., 2020), and since it is still necessary to assess the potential ecosystem services and disservices provided eco-engineered fish rehabilitation measures, it seems crucial to monitor the benthic communities of newly installed structures.

Here we conducted a pilot study aiming to compare the benthic community settling on eco-engineered artificial fish habitats with communities on the adjacent dock and pontoon substrata. We hypothesized that community structure would be different from the reference substrata in both cases, with some species being more prevalent on the eco-engineered structures. We tested whether among these species, NIS would be more numerous. The results obtained here may contribute towards further investigation of the question of ecological disservices of artificial restoration structures.

2 Material and Methods

2.1 Study site

The present study was conducted in the Darse Nord Marina in Toulon, located in the French Mediterranean (Fig. 1; 43°06'52.6"N 5°55'53.4"E). This marina of intermediate size (0.06 km²; 375 permanent berths; 210 visitor berths) is integrated within the larger Toulon marine urban complex which encompasses six marinas, commercial harbors, a large military port, and ferry activities over an area of approximatively 10 km². The area around the city of Toulon, including in the marine realm, constitutes a key example of ocean sprawl in the Mediterranean region (Meaille and Wald, 1990) and is subject to numerous anthropogenic pressures such as habitat modification and loss (Bouchoucha et al., 2018, 2017, 2016), pollution (Araújo et al., 2019; Mazoyer et al., 2020; Wafo et al., 2016), and NIS presence (Ruitton et al., 2005; Zibrowius, 1991). In an effort to increase biodiversity and to reduce chronic and accidental pollution in this urban region, several measures were taken in and around marinas by local decision makers and marina managers. One of these measures was the installation of a total of 33 artificial fish nurseries inside the Darse Nord marina in June 2020. As strong environmental gradients in marinas may significantly influence benthic community makeup (Gauff et al., 2022; Kenworthy et al., 2018; Rondeau et al., 2022), and to allow for a balanced experimental design (*i.e.* not all structures were present in sufficient numbers throughout the marina), we focused on the North-Western dock and North-Western pontoons (Fig. 1). The structures consist of 1 m² artificial 'seagrass beds' with 30 cm long bio-sourced plastic bristles, that were either vertically suspended 1 m below pontoons or pegged to docks for small fish to hide in (Fig. 2). Their aim is to increase juvenile fish abundance and survival.

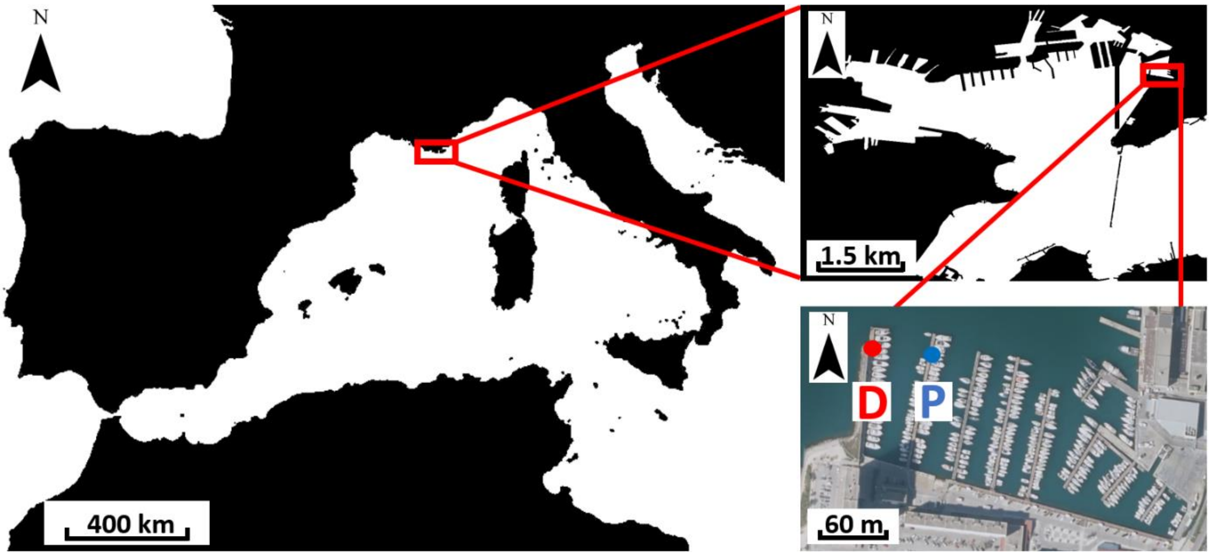


Fig. 1: Location of the Darse Nord marina in Toulon, France, Mediterranean Sea. The positions of the studied Pontoon (Blue; P) and dock (Red; D) are indicated.

2.2 Benthic assessment

Benthic communities were assessed 22 months after the structures were deployed (deployment: June 2020). This allowed for an adequate development of the community, reaching the 'dynamic maturity' inherent to marina communities, which are driven by recurring disturbances and fluctuations in populations of individual species (Rondeau et al., 2022; Sutherland, 1981). Two factors were integrated in the sampling design, comparing the eco-engineered structures with nearby unengineered patches ('degree of engineering') on pontoons and on docks ('habitats'). For each of the four treatments (Unengineered Dock, Eco-engineered Dock, Unengineered Pontoon, Eco-engineered Pontoon) we sampled five replicates (20 samples in total) on independent structures spaced at least 2 m apart over a period of three weeks between the 24th of March and 11th of April 2022. Quadrat sampling was used on the eco-engineered structures and surrounding habitats (Fig. 2). The substrate was thoroughly scraped over a surface of 20 cm x 20 cm, catching all organisms with a 1 mm mesh mosquito net. On pontoons, horizontal sciaphyllic communities close to the structures were scraped (Fig. 2A). Since the eco-engineered structures themselves were vastly shaded by the pontoons and both are made from plastic, the underside of pontoons constitute the closest habitat and the most comparable reference, even if the orientation could be considered different (horizontal *vs* vertical, although one must note that the three-dimensional bristle structure of the engineered structures has no real orientation). On the docks, vertical substrate was scraped (20 x 20 cm) at the same depth as the eco-engineered structures (Fig. 2B). Engineered structures on both docks and pontoons were sampled to reach 30cm within the plastic bristles.

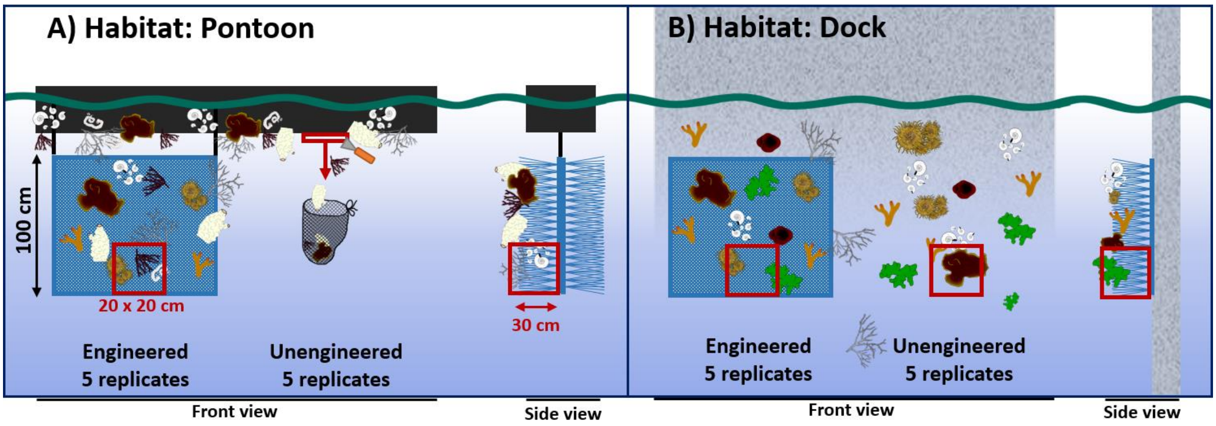


Fig. 2: Illustration of the sampling protocol on A) Pontoons and B) Docks. Communities were scraped within 20 x 20 cm quadrats (red squares) and caught in nets. On Eco-engineered structures the quadrat depth reached 30 cm within the bristles (side view).

Scrapings were brought directly to the laboratory in small batches and maintained in seawater for taxonomic identification on living communities. As the colonizable surface area of the eco-engineered structure bristles was much greater than the flat surface of unengineered habitats, we chose to conduct a qualitative community analysis. This qualitative assessment also avoids biases linked to different colonization times among substrates, as slow growth later succession organisms are identified regardless of their size or abundance (*e.g.*, Oysters were found on all substrates). All sessile species larger than 1 mm (algae, ascidians, bivalves, bryozoans, cirripedes, cnidarians, sponges, serpulids) were identified to the lowest taxonomic level possible, assessing morphological criteria with a binocular magnifier and a microscope (Bianchi, 1981; Brunetti and Mastrototaro, 2017; Harmelin, 1990, 1968; Hayward and Ryland, 1985, 1998, 1995, 1979; Langeneck et al., 2020; Licciano and Giangrande, 2008; Reverter-Gil and Souto, 2019; Riedl, 1983; Rosso and Di Martino, 2016; Tilbrook et al., 2001; Leandro M. Vieira et al., 2014; Vieira et al., 2013; Leandro M Vieira et al., 2014; Zabala and Maluquer, 1988; Zenetos et al., 2017; Zibrowius, 1971). To avoid biases linked to sampling effort within one sample, we standardized the observation/identification time per sample to 3 h, for a total of 60 h of observation time. In most cases, no new species were found within a sample during the last hour of analysis. After taxonomic analysis, the entire communities were dried for 2 weeks at 60°C and then burned at 480°C for 8 h to assess dry mass and Ash Free Dry Mass (AFDM).

2.3 Statistical analysis

For each treatment the total number of species, exclusive species (*i.e.,* species only present in this treatment) and total number of NIS was calculated. A linear model was fitted in ‘R’ (version 4.1.3; R Core Team, 2020), testing the effect of ‘degree of engineering’, ‘habitat’, as well as their interaction on the number of NIS in a sample. Validity and applicability of the model was graphically assessed and further validated with a Shapiro test and Bartlett test. A Tukey Honest Significant Difference test (Tukey HSD) was used to identify differences between individual treatments (Tukey, 1949). The presence/absence community data was transformed into a Bray-Curtis dissimilarity matrix using the ‘vegan’ R-package (version 2.6-2; Oksanen et al., 2018). This matrix was used to generate a Principal Coordinate Analysis (PCoA) to graphically represent communities via ‘ggplot2’ (version 3.3.5; Wickham, 2016). Species vectors significantly correlating ($R^2 > 0.5$, $p < 0.05$) with the PCoA axes were projected via the ‘envfit’ function from ‘vegan’. A PERMANOVA (10^4 permutations) testing for the effect of habitat (dock *vs.* pontoon), degree of engineering (eco-engineered *vs.* unengineered), as well as their interaction (treatment) was performed after validating homogeneity of group dispersions. Further, a pairwise PERMANOVA (10^4 permutations) from the ‘pairwiseAdonis’ package (version 0.4; Martinez Arbizu, 2019) with a Benjamini-Hochberg correction (Benjamini and Hochberg, 1995) tested for individual differences between the four treatments. To identify indicator species associated with treatments, we conducted a multipattern analysis (10^4 permutations) from the ‘indicspecies’ package (version 1.7.12; Cáceres et al., 2011; De Cáceres, 2013). We allowed the analysis to test for indicator species in individual treatments, but also within a habitat or a degree of engineering (ex.: Eco-engineered Pontoon + Unengineered Pontoon). As AFDM data was slightly heteroscedastic, we applied a Kruskal-Wallis test followed by a Dunn test from the ‘FSA’ package (version 0.8.32; Ogle et al., 2021).

3 Results

The benthic fauna analysis revealed a total of 104 species (Sup. Tab. 1) on the studied structures, with 64 (8 exclusive) species on the unengineered dock, 67 (5 excl.) on the eco-engineered dock, 50 (2 excl.) on the unengineered pontoon, and 70 (12 excl.) on the eco-engineered pontoon. 23 species were common to all treatments. The total number of NIS per treatment varied between 6 NIS on the dock, 9 on the engineered dock, 8 on the pontoon, and 11 on the engineered pontoon. The linear model showed that number of NIS per sample was affected by ‘degree of engineering’ (Df = 1; F = 22.35; $p < 0.001$), ‘habitat’ (Df = 1; F = 39.72; $p > 0.001$), but not their interaction. A post-hoc analysis showed that on both habitats, NIS number per sample was higher in the eco-engineered treatment (Tukey HSD; $p.adj < 0.05$; Fig. 3). The number of NIS per sample was also higher on pontoons for both degrees of engineering (Tukey HSD; $p.adj < 0.009$; Fig. 3).

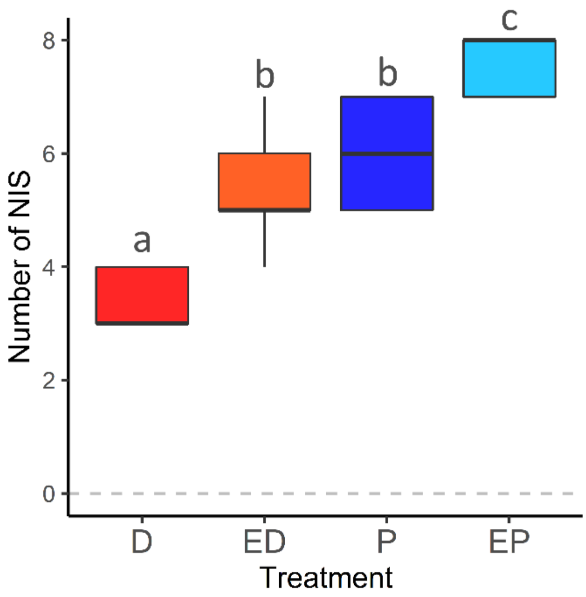


Fig. 3: Boxplot of the number of Non-Indigenous Species (NIS) in each treatment. D: Unengineered Dock, ED: Eco-engineered Dock, P: Unengineered Pontoon, EP: Eco-engineered Pontoon. Letter groups indicate significant differences assessed by Tuckey HSD on linear model.

Tab. 1: List of NIS in the marina and number of occurrences in each treatment (out of 5). Total number of NIS spp. is given below. A detailed species list with references to their status (Native, NIS, Cryptogenic) is available in the supplementary material.

Taxon	**NIS**	**Dock**	**Eng. Dock**	**Pontoon**	**Eng. Pontoon**
Mollusca	*Magallana gigas*	5	5		5
Annelida	*Branchiomma luctuosum*			3	5
Annelida	*Hydroides elegans*		3	5	5
Annelida	*Pileolaria berkeleyana*		1		1
Annelida	*Spirorbis marioni*	2	5	4	5
Bryozoa	*Bugula neritina*		1	5	2
Bryozoa	*Bugulina fulva*	2	3	5	
Bryozoa	*Bugulina stolonifera*			1	1
Bryozoa	*Tricellaria inopinata*			5	
Bryozoa	*Watersipora subatra*	5	5		3
Bryozoa	*Watersipora subtorquata*	1	1		
Urochordata	*Ascidiella aspersa*	2	3	2	5
Urochordata	*Ciona robusta*				1
Urochordata	*Styela plicata*				5
Total		6 spp.	9 spp.	8 spp.	11 spp.

The community structure was significantly affected by degree of engineering (PERMANOVA; $R^2 = 0.14$; $p < 0.001$), habitat (PERMANOVA; $R^2 = 0.32$; $p < 0.001$), as well as their interaction (PERMANOVA; $R^2 = 0.14$; $p < 0.001$). Habitat seemed to be the strongest driver of differences between the community structures, which was visible in the PCoA, distinguishing the dock and pontoon habitat along the PCo1 axis (34.2 %; Fig. 4). The PCo2 axis (18.8 %) corresponded to the difference between the engineered and unengineered treatment of the pontoon. The engineered and unengineered treatment of the dock were closer on the projection with overall more similar communities. The pairwise PERMANOVA revealed that all treatments had significantly different communities from each other (Pairwise PERMANOVA; $R^2 > 0.3$; $p < 0.01$), with however a notably lower R^2 for the engineered vs unengineered dock comparison ($R^2 = 0.31$ as opposed to $R^2 > 0.5$ for all other comparisons). Some species vector projections were strongly associated with the PCo1 axis, with *Umbonula ovicellata* Hastings, 1944, *Chaetomorpha sp.* Kützing, 1845, *Jania squamata* (Linnaeus) J.H.Kim, Guiry & H.-G.Choi, 2007, *Watersipora subatra* (Ortmann, 1890) and *Dictyota sp.* J.V.Lamouroux, 1809 being anticorrelated with PCo1, while *Hydroides elegans* (Haswell, 1883), *Mytilus galloprovincialis* Linnaeus, 1758 and *Branchiomma luctuosum* (Grube, 1870) were correlated. However, numerous species were associated with the PCo2 axis, corresponding to species present on the pontoon treatment such as *Bugula neritina* (Linnaeus, 1758) and *Tricellaria inopinata* d'Hondt & Occhipinti Ambrogi, 1985 or on the engineered pontoon such as *Phallusia mamillata* (Cuvier, 1815), *Phallusia fumigata* (Grube, 1864), *Styela plicata* (Lesueur, 1823) or *Limaria hians* (Gmelin, 1791).

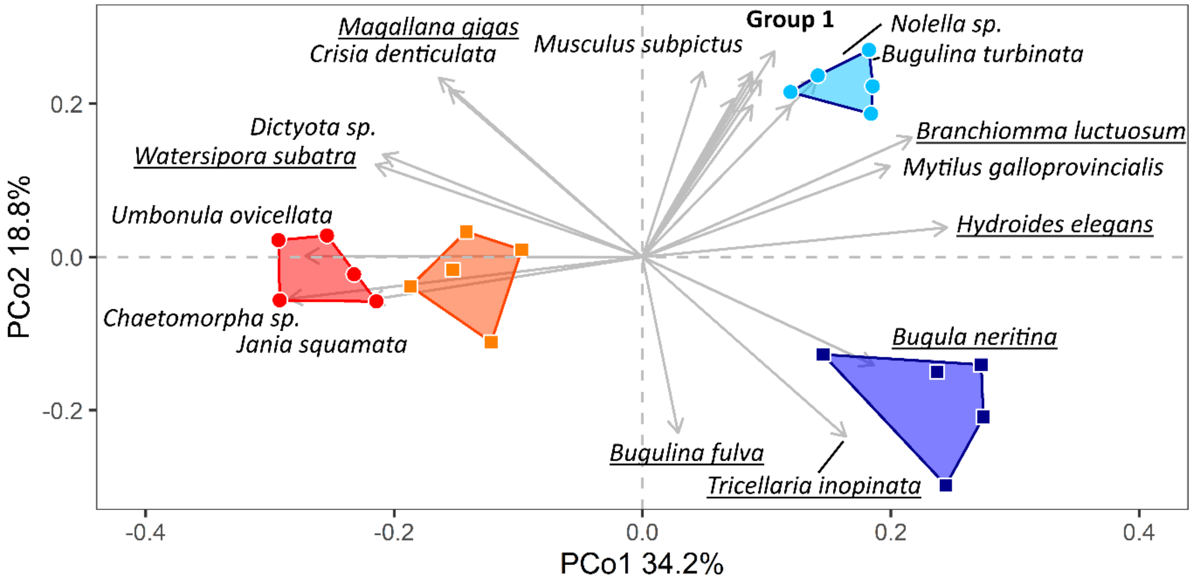
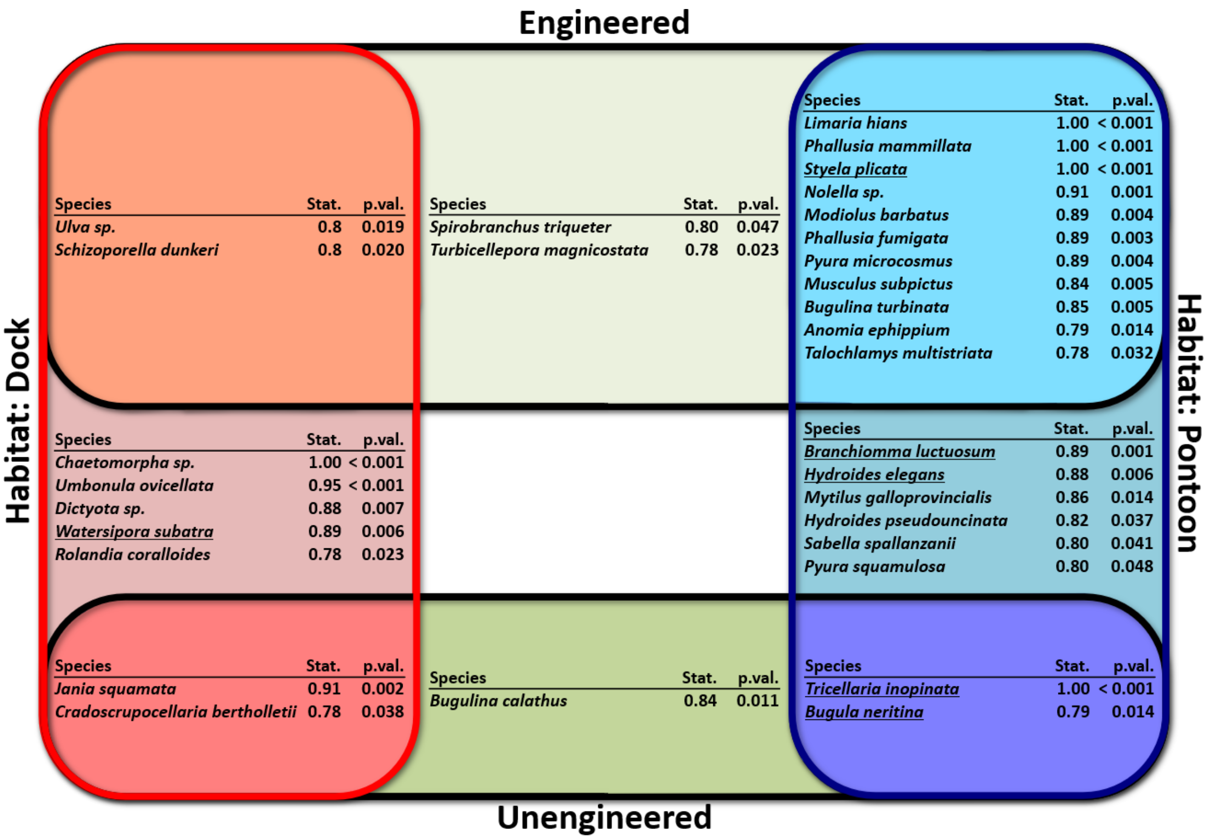


Fig. 4: PCoA of the community structure of the four treatments: Unengineered Pontoon (dark blue), Eco-engineered Pontoon (light blue), Unengineered Dock (Red), Eco-engineered Dock (Orange). Species correlating with the projection ('envfit': $R^2 > 0.5$; $p < 0.05$) are indicated as vectors. Vector group 1 composed of: *Anomia ephippium* Linnaeus, 1758, *Limaria hians*, *Modiolus barbatus* (Linnaeus, 1758), *Phallusia fumigata*, *Phallusia*

mammillata, *Pyura microcosmus* (Savigny, 1816), *Styela plicata*, *Talochlamys multistriata* (Poli, 1795). NIS are underlined. All communities are significantly different (Pairwise PERMANOVA; $R^2 > 0.3$; $p < 0.01$).

The multipattern analysis testing the association of species to the considered explanatory variables revealed that between one and two species constituted indicator species associated with the factor 'degree of engineering' (Fig. 5). These species were associated to the eco-engineered structures, regardless of the habitat. More indicator species were associated with the 'habitat' factor, with five species characterizing to the dock habitat and six species characterizing the pontoon habitat. In general, species that were strongly correlated with the PCo1 axis, were also indicator species for the 'habitat' factor, such as *Chaetoporpha sp*., *Umbonula ovicellata* and *Dictyota sp*. for the dock or *Branchiomma luctuosum*, *Hydroides elegans* or *Mytilus galloprovincialis* for the pontoon. Certain species were more associated to a specific treatment (degree of engineering : habitat), with two indicator species per treatment, except for the engineered pontoon, which had 11 unique indicator species (Fig. 5).



Species	Stat.	p.val.
Ulva sp.	0.8	0.019
Schizoporella dunkeri	0.8	0.020

Species	Stat.	p.val.
Spirobranchus triqueter	0.80	0.047
Turbicellepora magnicostata	0.78	0.023

Species	Stat.	p.val.
Limaria hians	1.00	< 0.001
Phallusia mammillata	1.00	< 0.001
Styela plicata	1.00	< 0.001
Nolella sp.	0.91	0.001
Modiolus barbatus	0.89	0.004
Phallusia fumigata	0.89	0.003
Pyura microcosmus	0.89	0.004
Musculus subpictus	0.84	0.005
Bugulina turbinata	0.85	0.005
Anomia ephippium	0.79	0.014
Talochlamys multistriata	0.78	0.032

Species	Stat.	p.val.
Chaetomorpha sp.	1.00	< 0.001
Umbonula ovicellata	0.95	< 0.001
Dictyota sp.	0.88	0.007
Watersipora subatra	0.89	0.006
Rolandia coralloides	0.78	0.023

Species	Stat.	p.val.
Branchiomma luctuosum	0.89	0.001
Hydroides elegans	0.88	0.006
Mytilus galloprovincialis	0.86	0.014
Hydroides pseudouncinata	0.82	0.037
Sabella spallanzanii	0.80	0.041
Pyura squamulosa	0.80	0.048

Species	Stat.	p.val.
Jania squamata	0.91	0.002
Cradoscrupocellaria bertholletii	0.78	0.038

Species	Stat.	p.val.
Bugulina calathus	0.84	0.011

Species	Stat.	p.val.
Tricellaria inopinata	1.00	< 0.001
Bugula neritina	0.79	0.014

Fig. 5: Venn diagram of the indicator species (multipattern analysis) for each factor ('habitat', 'degree of engineering') and treatment. Association statistic (Stat) and p-value (p.val) are given for each indicator species. NIS are underlined.

Biomass (AFDM) was significantly higher in the engineered pontoon compared to the unengineered pontoon (Fig. 6; Dunn test; Z = 2.27, p.adj = 0.045). Despite slightly higher biomass on the engineered dock compared to the unengineered dock, no other significant differences could be identified.

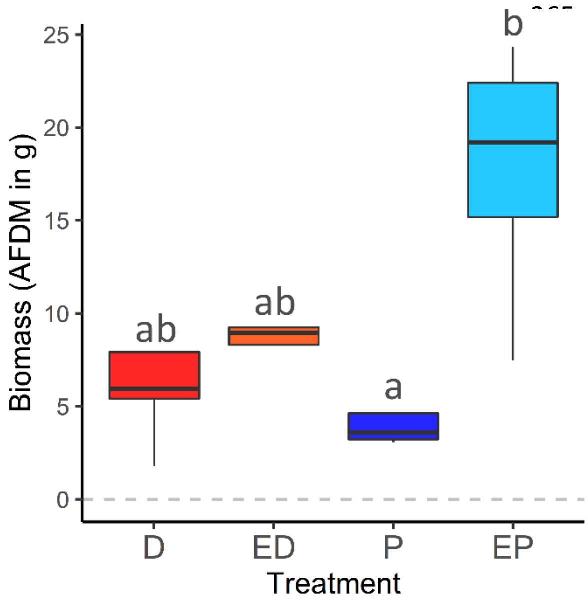


Fig. 6: Boxplot of the Ash Free Dry Mass in each treatment. D: Unengineered Dock, ED: Engineered Dock, P: Unengineered Pontoon, EP: Engineered Pontoon. Letter groups indicate significant differences assessed by Dunn test.

4 Discussion

Increasingly, ecological rehabilitation is used to mitigate the impacts of ocean sprawl (Airoldi et al., 2021; Bouchoucha et al., 2016; Dafforn, 2017; Evans et al., 2019; Firth et al., 2016a). While several studies have demonstrated the positive effect of artificial fish habitats in marinas on fish abundance and diversity (Astruch et al., 2017; Bouchoucha et al., 2016; Lapinski et al., 2015; Mercader et al., 2017; Selfati et al., 2018), benthic colonization of these structures has rarely been taken into consideration. This may be problematic as NIS particularly privilege artificial habitats for colonization (Dafforn et al., 2012; González-Ortegón and Moreno-Andrés, 2021; Mineur et al., 2012) and may cause high ecological and economical damages in coastal ecosystems (Diagne et al., 2021; Jardine and Sanchirico, 2018; Lovell et al., 2006; Vilizzi et al., 2021; Walsh et al., 2016). Introduced species are among the major causes for global homogenization of ecosystems and species extinctions (Blackburn et al., 2019; Clavero and García-Berthou, 2005; Mckinney and Lockwood, 1999). The present study therefore aimed to understand which benthic species (macroalgae and invertebrates) develop on artificial structures designed to increase fish abundance and diversity in marinas, and whether they increase the potential threat exerted by NIS. In accordance with our hypothesis, the eco-engineered structures were colonized by different communities compared to communities on surrounding unengineered habitat and hosted a greater diversity of NIS. However, the results diverged slightly between the two considered habitats (dock and pontoon), with eco-engineered pontoons hosting the highest number of NIS.

A striking difference was observed between the docks and pontoons, with very different communities (PERMANOVA; PCo1 axis; Fig. 4) and associated indicator species (Fig. 5). This is coherent with numerous previous studies focusing on artificial structure communities in which this difference has been extensively described (Giangrande et al., 2021; Kenworthy et al., 2018; Lam and Todd, 2013; Toh et al., 2017). Numerous factors can influence the observed differences in community structure between the two habitats, such as substrate (concrete *vs*. plastic; Chase et al., 2016; Fletcher et al., 2018; Pinochet et al., 2020; Sedano et al., 2020), environmental gradients (Kenworthy et al., 2018; Rondeau et al., 2022), and hydrodynamics (Lam and Todd, 2013; Toh et al., 2017). Light availability has also been demonstrated to have a high impact on fouling communities (Dobretsov et al., 2010, 2005; Lam and Todd, 2013; Toh et al., 2017). The fact that many PCo1 correlated species and indicator species for the dock are algae (*Chaetomorpha sp.*, *Dictyota sp.*, *Jania squamata*, *Ulva sp.* Linnaeus, 1753) suggests that, in our case study, light may have been the most important factor differentiating both habitats. However, substrate may also contribute to these observations, as the eco-engineered dock treatment (plastic) slightly resembles the pontoon habitat in terms of community composition (PCo1 axis; Fig. 4).

In both habitats, communities on the eco-engineered structures were significantly different from their counterpart on the unengineered control habitat, which indicates that the added structures select species, not necessarily found in the unengineered habitat. While this is true for eco-engineered structures in general (visible for example through the indicator species associated to the 'degree of engineering'; Fig. 5), this effect is particularly intense for the eco-engineered structures suspended under the pontoon. The latter are characterized by numerous unique indicator species, with ascidians such as *Phallusia spp.* or *Styela plicata* and bivalves such as *Limaria hians* or *Talochlamys multistriata*, most of which live in crevices and interstices (Brunetti and Mastrototaro, 2017; Riedl, 1983). Conversely, the eco-engineered structures on the dock seem much closer to those of the unengineered dock, despite having significantly different communities.

Similar patterns were observed for NIS, with generally higher numbers found on the pontoon habitat compared to the dock. NIS are known to be highly prevalent in marinas, and even more so on pontoons, reaching up to 80% surface cover, which may be explained by the physical and functional properties this habitat provides (Castro et al., 2022; Connell, 2001; Dumont et al., 2011b; Glasby et al., 2007; Rondeau et al., 2022). In both studied habitats, NIS were more prevalent in the engineered treatments compared to the unengineered ones. This may be related to the materials used in the conception of the eco-engineered structure, as plastics attract fouling species and are colonized by NIS (Glasby et al., 2007; Pinochet et al., 2020). This could also be due to the shorter colonization time as NIS are often opportunistic and early colonizers (Connell, 2001; Dafforn, 2017; Giangrande et al., 2021; Glasby et al., 2007). After almost two years of immersion, the communities should however have reached their dynamic maturity (Sutherland, 1981), and species generally regarded as later succession species such as bivalves were present in all treatments. The total number of NIS and the number of NIS per sample was highest in the eco-engineered pontoon treatment (Tab. 1; Fig. 3). This includes highly prolific species such as the ascidian *Styela plicata*, the most widespread NIS in Mediterranean marinas (Ulman et al., 2019) or the tube worm *Branchiomma luctuosum* which continues its spread throughout the Mediterranean and adjacent waters (Fernández-Romero et al., 2021; Tiralongo et al., 2022). Interestingly, *Bugula neritina* and *Tricellaria inopinata*, two very common Bryozoa, were exclusive and observed to be highly abundant on the unengineered pontoon, which might be linked to substrate orientation. Aside from these two exceptions, all NIS that were present in an unengineered habitat were also present on the corresponding engineered structures, together with additional ones (Tab. 1), suggesting that these habitats potentially increase NIS diversity compared to unengineered harbor habitats.

Biomass was generally higher in the engineered treatments compared to their unengineered counterpart. However, this difference was only significant at the pontoon habitat. This increased biomass may be linked to the higher surface area available for colonization due to the increased complexity of the engineered structures.

Our results indicate that in the present case, eco-engineered structures altered benthic community structure, harboring a unique taxonomic composition compared to those of other substrates, that may have benefited NIS. In general eco-engineering is regarded as mitigating NIS settlement (Perkol-Finkel et al., 2018), as it can increase native biodiversity and subsequently increase competitive biotic resistance towards NIS (Biotic Resistance Hypothesis; Elton, 1958) through the occupation of ecological niches by natives (Bishop et al., 2022; Dafforn, 2017; Firth et al., 2016a). Complex settlement plates have for instance been shown to increase biodiversity on multiple occasions (Bishop et al., 2022; Strain et al., 2020; Vozzo et al., 2021), however, these studies rarely focus on NIS prevalence. Biotic resistance in general is a disputed concept (Jeschke et al., 2012) and studies on fouling communities show varied support for competitive biotic resistance (Beshai et al., 2022; Ohayashi et al., 2022; Tamburini et al., 2022). The increased NIS prevalence in our case might result from the creation of a new niche, as for instance NIS have been shown to capitalize on habitat creation (Connell, 2001; Glasby et al., 2007), but it might also be an indirect consequence of the primary aim of the eco-engineered structures – protecting fish juveniles from predation. The structural complexity of eco-engineered structures for fish rehabilitation (here achieved by long closely packed bristles) aims to mimic natural nurseries by increasing refuge availability through physically excluding larger fish (> *c.a.* 15 cm) that could prey on juveniles, subsequently increasing juvenile fish survival (Astruch et al., 2017; Bouchoucha et al., 2016; Selfati et al., 2018). Predators however may also contribute to resistance against NIS in natural habitats (Kimbro et al., 2013; Santamaria et al., 2022; Yorisue et al., 2019), as well as in marinas (Dumont et al., 2011; Giachetti et al., 2022, 2020; Kimbro et al., 2013; Leclerc et al., 2019) and reduced predation in eco-engineered refuges may increase NIS prevalence (Dumont et al., 2011a; Forrest et al., 2013). This link between our observations and predation is supported by the high number of bivalves and ascidians present in the eco-engineered pontoon treatment, as they are, despite certain defense mechanisms, often a highly sought after prey, especially when young and/or small (Forrest et al., 2013; Giachetti et al., 2022; Koplovitz and McClintock, 2011; Seitz et al., 2001; Townsend et al., 2015). Predation might also explain why the difference in community structure between eco-engineered and unengineered treatments was lower on the dock, with overall more similar communities. Despite a certain protection of the community against generalist pelagic predators, the structures may not entirely protect against benthic predators such as crabs, gastropods etc. allowing them to access prey on the dock. As pontoons already constitute a refuge from benthic predators (Dumont et al., 2011b; Forrest et al., 2013), installing the engineered structures beneath them would constitute a double exclusion (benthic and pelagic predators), likely responsible for the much stronger differentiation of the community and the higher number of NIS (Fig. 7). NIS are regarded as a crucial biosecurity issue (Cook et al., 2016; Pyšek et al., 2020) and constitute a leading cause of species extinction worldwide (Blackburn et al., 2019; Clavero and García-Berthou, 2005). As NIS may have high impacts, even after long lag periods (Jardine and Sanchirico, 2018; Lovell et al., 2006; Walsh et al., 2016) and as their future impacts may be unpredictable in the face of climate change (Bradley et al., 2018; Spear et al., 2021; Vilizzi et al., 2021), their presence poses a potential threat. Our present observations thus reveal that associated to the ecosystem services provided by eco-engineered fish habitats, an ecosystem disservice in the form of NIS enabling might be provided. Although not all NIS may automatically be problematic species (Giangrande et al., 2020), their effect needs to be carefully considered in order to effectively decide in which situations eco-engineering should be used for fish nursery rehabilitation. Our study takes into account one zone in one marina. At present it is still difficult to establish sound experimental designs since restoration structures are not installed with scientific objectives in mind. Although more work is needed before broad-reaching conclusions can be made, further studies such as this one will help to formulate practical recommendations concerning the implementation of eco-engineered fish habitats in marinas. Based on our study results, we advise installing eco-engineered fish habitats on docks rather than below pontoons. Accounting for ecosystem disservices in ecological rehabilitation initiatives would allow for a more holistic understanding of how mitigation measures alter the environment.

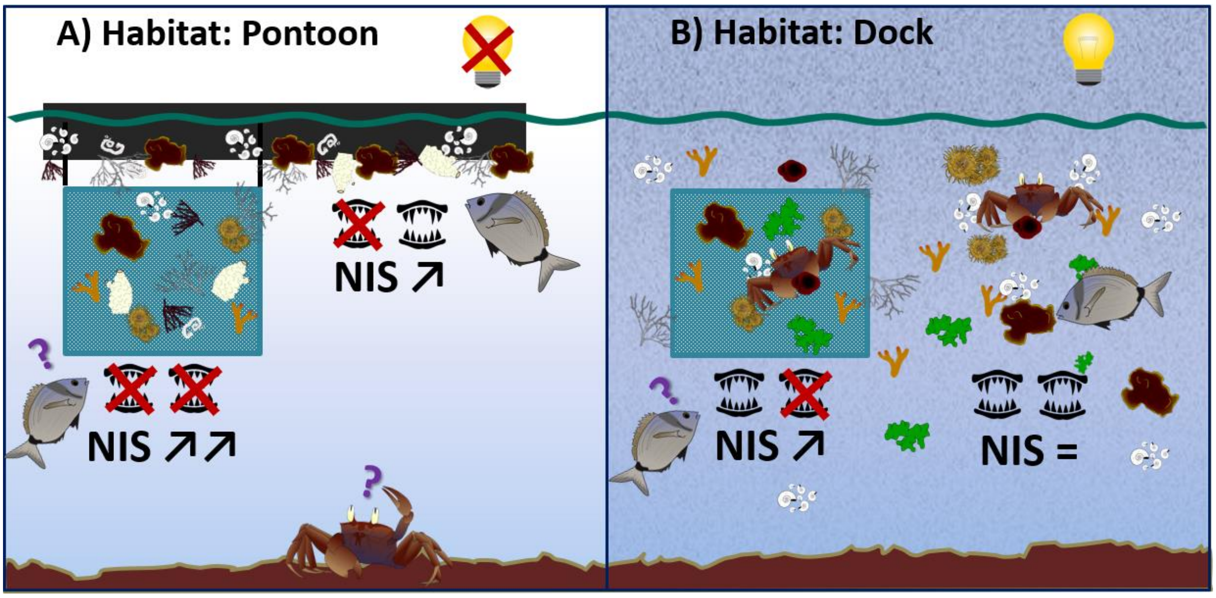


Fig. 7: Hypothesis explaining contrasted community structure and NIS number for the four treatments. While factors such as light availability explain differences between both habitats (Pontoon *vs.* Dock), a combination of exclusion of benthic predators on floating structures and the exclusion of pelagic predators on eco-engineered juvenile fish habitats might explain the higher number of NIS and exacerbated community structure difference.

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