Predation facilitates the abundance of biofouling non-indigenous species in estuarine marinas in NE Atlantic Portugal

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ARTICLE INFO

ABSTRACT

Harbours are highly modified habitats that differ from natural areas. They are hotspots of non-indigenous species (NIS) and act as stepping-stones in invasive processes. However, local communities can exert biotic resistance against biological invasions through trophic interactions and competition. This study assesses the biotic effects of predation on the recruitment of fouling assemblages in three marinas of NE Atlantic Portugal (Cascais, Setúbal and Sines), with particular emphasis on NIS, using predator exclusion experiments. Predation increased the relative abundance of NIS, mainly *Watersipora subatra*, in the estuarine marinas of Cascais and Setúbal, while no predation effects were registered in the coastal marina of Sines. Therefore, predation can increase the risk of NIS invasion (biotic facilitation). Furthermore, local ecosystems may have different effects and differ in vulnerability against NIS invasions. Finally, a better understanding of coastal invasive ecology and biotic effects in coastal artificial habitats will improve our capacity for NIS management.

1. Introduction

Biological invasions are among the main causes of global biodiversity loss and the ecological and socioeconomic impacts of this phenomenon are expected to increase over time (Gurevitch and Padilla, 2004; McDermott et al., 2013). The estimated costs of biological invasions exceeded 2.8 % of the world's Gross Domestic Product reported by the World Bank Group in 2017 (Zenni et al., 2021). In Europe alone, biological invasions related losses and costs have been estimated to be US$139.56 billion in 2020 (Haubrock et al., 2021), whereas global impacts of aquatic invasions are estimated to have reached US$23 billion in 2020 (Cuthbert et al., 2021). However, the impact estimations by invasive aquatic non-indigenous species (NIS) are probably underestimated due to our lack of knowledge in these systems. Consequently,

cost estimates for aquatic invasions have been increasing by one magnitude per decade as new reports are published (see Cuthbert et al., 2021). In the marine environment, coastal areas are particularly vulnerable to ecological and socio-economic impacts caused by invasive NIS (Perrings, 2002). Besides having a negative impact on native diversity, fouling NIS (e.g., barnacles, tunicates, bryozoans, sponges, molluscs) can also damage coastal infrastructure and affect industrial processes and maritime transportation (Byers, 2002; Perrings, 2002). Despite all the reported damages and costs to have resulted from marine bioinvasions, there are still not enough resources being invested in prevention, early detection and management strategies (Haubrock et al., 2021; Zenni et al., 2021). These are considered as the best strategies to fight biological invasions, and rely on inventorying and monitoring NIS and native populations, and studying the relevant ecological variables

that shape NIS introductions, establishment and invasiveness (Whitney and Gabler, 2008; Otero et al., 2013; Cook et al., 2016; Pack et al., 2022).

The main vector for the introduction of coastal NIS is maritime traffic, mainly through hull fouling and ballast water (Clarke Murray et al., 2012; Bailey et al., 2020). During the translocation journey, NIS suffer extreme conditions that vary depending on their location on the transport vessel and the duration of the trip (Chan et al., 2015). For example, organisms on vessels' hulls experience water dragging and temperature fluctuations, while organisms in ballast tanks endure limited nutrients, light and oxygen (Hewitt et al., 2009; Clarke Murray et al., 2012). At the most basic level, organisms and taxa that can survive those conditions are generally tolerant to environmental fluctuations and often exhibit plasticity to ecologically relevant conditions such as temperature or salinity, which is a common trait among invaders (Hewitt et al., 2009). The establishment and invasiveness of NIS are greatly mediated by the plasticity and tolerance to varying environmental conditions and to their ability to overcome typical ecological barriers (Freestone et al., 2013, 2021; Geburzi and McCarthy, 2018).

With marine traffic as a major vector to NIS spread and introductions, ports and marinas are highly modified habitats that are considered NIS hotspots and list among the most invaded coastal habitats (Canning-Clode et al., 2013a; Castro et al., 2020; Guerra-García et al., 2021a). Marinas can be particularly relevant, as they occur on almost every coastline, are more abundant than ports, and host communities that can be richer in NIS than ports and other artificial habitats (Ferrario et al., 2017; Chebaane et al., 2019; Tempesti et al., 2022). In addition, recreational vessels spend long periods moored in the marinas, which increases the colonisation of the hulls by fouling NIS, maximising their spread to other marinas and natural habitats, as recreational vessels visit natural areas during their trips (Mineur et al., 2012; Martínez-Laiz et al., 2019; Castro et al., 2020; Taormina et al., 2022). Consequently, marinas often play a key role in establishing and spreading marine coastal NIS and are a major pressure on biodiversity of Marine Protected Areas visited by recreational boating (Parretti et al., 2020; Letschert et al., 2021).

Once overcome their journey and multiple ecological barriers, most successfully established NIS exhibit a high resistance to abiotic stressors which often puts them at competitive advantage towards their native counterparts (Shea and Chesson, 2002; Geburzi and McCarthy, 2018). For instance, invasive fouling NIS often have allelochemicals that improve their competitive capacity against local fouling species (horizontal interactions) or protection against potential consumers such as foragers and predators (vertical interactions) (Mackenzie et al., 2001). These interactions can have a negative or positive biotic effect on NIS populations. Negative impacts (biotic resistance) occur when local consumers such as fish and benthic grazers prey on NIS and decrease NIS abundance and spread (DeRivera et al., 2005; Forrest et al., 2013; Santamaría et al., 2018; Simkanin et al., 2013; Tiralongo et al., 2021). In contrast, positive effects (biotic facilitation) may occur when consumers selectively feed on native species over NIS, increasing NIS abundance and spread, a mechanism known as the Enemy Release Hypothesis (Keane and Crawley, 2002; Colautti et al., 2004). Therefore, the trophic effects of local consumers, such as foraging fish and grazing vagile fauna, are important elements in structuring fouling assemblages in artificial habitats (Leclerc et al., 2019; Janiak and Branson, 2021). Both biotic resistance and biotic facilitation of NIS by predation/grazing have been previously reported in artificial areas (Rogers et al., 2016; Gestoso et al., 2018; Leclerc et al., 2019; Janiak and Branson, 2021). However, our knowledge and understanding of where and why these opposing effects occur is still greatly limited.

Understanding the trophic effects of consumers inside different marinas over different geographic areas is crucial for improving management strategies against NIS invasions. However, the current available information is low and geographically scattered, and a higher research effort over broad geographical areas is needed to understand the biotic effects of consumers on fouling assemblages' dynamics. In this context, this study was designed to investigate the effect of the exclusion of predators on the recruitment of fouling assemblages in several marinas of mainland Portugal region, testing the hypotheses: (H1) exposure to predation determines fouling assemblages' abundance, structure and the overall abundance and dominance of NIS in fouling; and (H2) the intensity and direction of the biotic effects by predators on fouling assemblages' recruitment and NIS abundance are site specific depending on the particularities of each marina, rather than homogeneous across marinas.

2. Materials and methods

2.1. Study site

The study was carried out in three marinas of mainland Portugal: Sines, Setúbal and Cascais (Fig. 1) for 12 weeks, from June to September 2012. The marina of Cascais is located at the end of the Tagus estuary, west of Estoril in the great Lisbon area, and has a capacity for 650 vessels up to 25 m. The marina of Setúbal is located in the Sado estuary, next to the third-largest commercial port in Portugal, and can host 150 vessels up to 15 m. Finally, the marina of Sines is located in the vicinity of a fishing harbour and the second largest Portuguese commercial port and has a capacity for 230 vessels up to 15 m in length (APPA, 2022).

2.2. Experimental design

Predator exclusion effects were tested with a caging experiment, which is a widely used method for the detection of predation effects on epifauna (Virnstein, 1978; Como et al., 2006; Anderson et al., 2008; Gestoso et al., 2018; Chebaane et al., 2022). The 12-week experiment (June–September 2012) relied on the use of a deployment raft setup (Fig. 2) with three 10×10 cm PVC settlement plates (previously sanded) haphazardly arranged under three experimental conditions: a predation exclusion treatment (T: caged), a procedural control (Cp: open cages) and a control for the experiment (Ce: uncaged). The mesh size used in this experiment is ¼ in. In each marina, a total of 5 deployment raft setups (i.e., replicates) were hung from the fixed docks at 0.5 m from the seafloor, with cages ($14 \times 14 \times 9$ cm) being cleaned, for both T and Cp, from fouling or replaced every two weeks. Non-swimmer predators and grazers' physical accessibility from the seafloor to the plates was ensured by lines (i.e., ropes) and plastic meshes (see Fig. 2).

The main predators in these studied areas that could access to the plates are the mesopredators such as the decapods *Alpheus macrocheles* (Hailstone, 1835) and *Pagurus anachoretus* (Risso, 1827), the sea urchin *Paracentrotus lividus* (Lamarck, 1816) and small fish such as *Coris julis* (Linnaeus, 1758) (Neves, 1967; Instituto de Oceanografia, 2010; Jacinto et al., 2013).

Water temperature in each marina was recorded every 4 h using a temperature logger (Onset HOBO UA-001-64) for the duration of the experiment.

After the 12-weeks settlement period, plates were individually removed, tagged, photographed and examined under a stereomicroscope to identify fouling species to the highest taxonomic resolution possible. The assemblages were then dried in a stove and weighted using a precision scale to obtain dry biomass. Taxa relative abundance was estimated from pictures by overlaying 49 points on a 7×7 stratified random grid covering the whole plate. All identified species were also classified based on their biogeographic status (NIS, native, cryptogenic) according to the most recent databases and literature (Saldanha, 1974; Dexter, 1992; Southward et al., 2004; Marchini et al., 2007; Nagar et al., 2010; Canning-Clode et al., 2013b; Chainho, 2014; Chainho et al., 2015; Reverter-Gil and Souto, 2019). Cryptogenic status was considered in the absence of evidence that the recorded species were native or introduced in the studied region (Carlton et al., 2011). However, taxa could not be identified at the species level and were classified as unresolved.
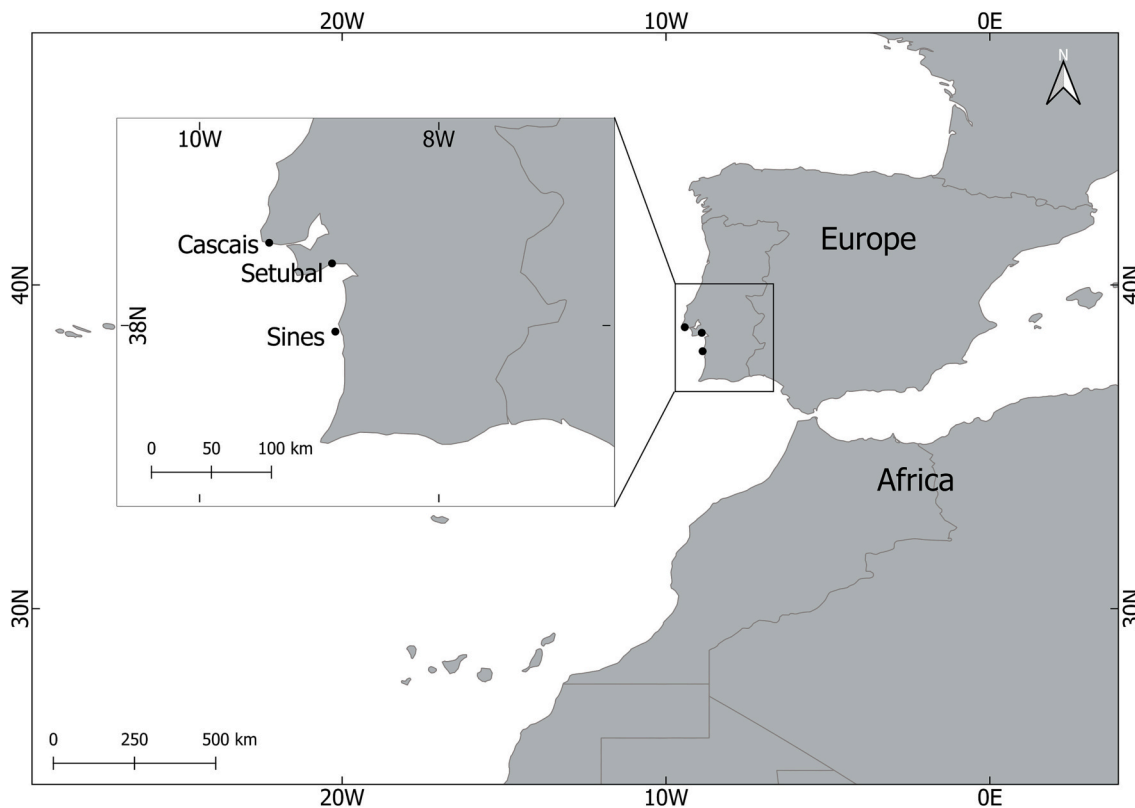
Fig. 1. Location of the studied marinas in Portugal (NE Atlantic): Sines (37°57′N, 8°51′W), Setúbal (38°31′N, 8°53′W) and Cascais (38°41′N, 9°25′W).

2.3. Data analysis

Species relative abundance was standardised and fourth-root transformed before calculating Bray–Curtis similarity matrix. Then, similarity values were tested using PERMANOVA on a randomised complete blocks design with the factors Marina (random, 3 levels), Treatment (Fixed, 3 levels) and Rack (Random, 5 levels, nested in Marina). However, PERMANOVA does not unveil specific patterns for each marina nor does it identify significant groups of samples based on taxonomic composition. Therefore, a follow-up cluster analysis was applied to species relative abundance data using the Bray–Curtis similarity matrices and the significance of the clustered branches was tested using the Similarity Profile (SIMPROF, $p < 0.005$) routine to identify significantly different groups of samples (i.e., SIMPROF-Groups (SFG) and thus identify organism assemblages (Clarke et al., 2008; Monteiro et al., 2021). Principal Coordinates Ordination (PCO), adding correlation vectors to identify the species' contribution to the variability among samples.

Univariate PERMANOVAs were carried out using the same design than multivariate analysis, using the relative abundance of the species highlighted in the PCO ordination with a relative mean abundance higher than 5 %. These analyses were also carried out with square-root transformed dry biomass (gr), NIS and native species relative abundances, total species richness, and NIS and native species richness. Statistical analyses and plots were computed in Primer-e v6 and v7 + PERMANOVA add-on (Anderson et al., 2008; Clarke and Gorley, 2015) and IBM SPSS Statistics 27.

3. Results

Based on temperature logger data the warmest water temperatures registered during the experiment occurred in the marina of Setúbal (22.6 °C), while the coldest temperature was registered in the coastal marina of Sines (13 °C in July) (see Fig. S1). Temperatures were always

higher in the marina of Setúbal, although showing the same fluctuations than those observed in the other marinas. Regarding the experiment, the cages of two replicates in Cascais (caged treatment) were lost during the experiment and these replicates had to be discarded from the experiment. Overall, no differences between the procedural and experimental controls (Cp and Ce) were detected in Setúbal and Cascais, which indicates the absence of artefact effects caused by caging on the fouling assemblages (Table 1). Moreover, the absence of differences among racks indicates that the experiment was not affected by an excessive heterogeneity of the assemblages within marinas (Table 1).

A total of 43 taxa, included in 8 major taxa (Annelida, Arthropoda, Bryozoa, Chlorophyta, Cnidaria, Mollusca, Porifera and Tunicata) were identified on the settlement plates over the course of the experiment (Table S1). The most represented in number of species were Bryozoa, with 16 species, and Tunicata, with 7 species. Bryozoa and Annelida were the most abundant phyla. Overall, 22 species were classified as native, 8 as non-indigenous (NIS) and 2 as cryptogenic. However, 11 taxa could not be identified at the species level and were tagged as unresolved.

In Setúbal and Cascais marinas, the treatments exposed to predation had a different community structure than the caged one (Table 1; Fig. 3), with the controls having a higher relative abundance of the NIS *Watersipora subatra* and *Hesperibalanus fallax* than the treatment (see SFG 2 to SFG4 in Fig. 3 and Fig. 4). On the other hand, the caged treatments in Setúbal and Cascais had a community structure like the marina of Sines (SFG 1 in Fig. 3 and Fig. 4). This group (SFG 1) was characterized by the presence of the native species *Crisia* cf. *denticulata, Janua heterostropha* and *Anomia ephippium* (see univariate PERMANOVA results for these species relative abundances at Table S2 in the supplementary materials).

Unlike Setúbal and Cascais, caging did not affect the assemblages' structure in Sines, where the procedural control and the treatment differed but were similar to the experimental control (uncaged) (see Table 1). These differences may resemble a procedural effect, but the homogeneous composition of Sines assemblage, combined to their
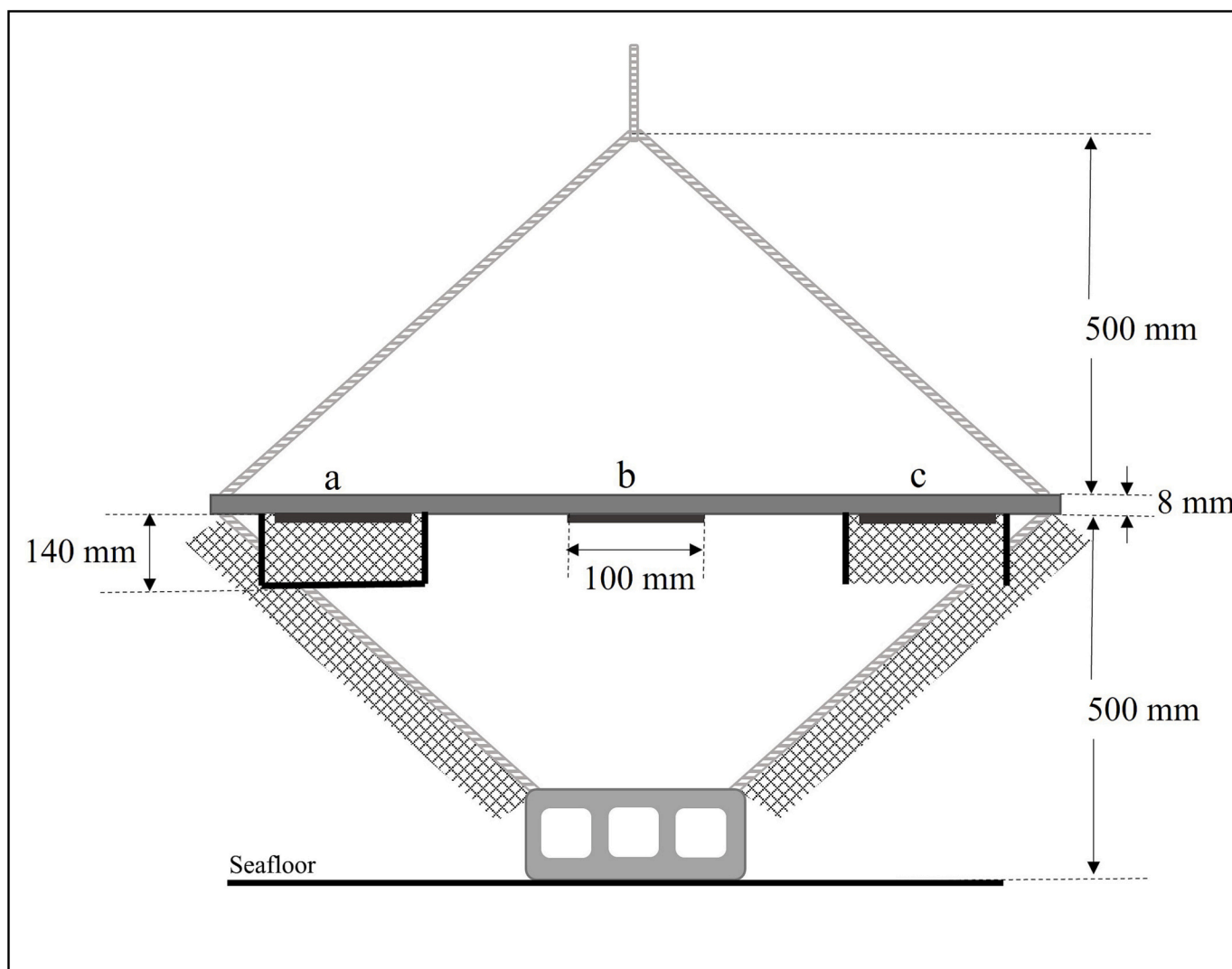
Fig. 2. Schematic representation of the rack and the three experimental plates: (a) caged, (b) uncaged, and (c) open cage. In each studied marina, 5 racks were deployed.

Table 1
Multivariate PERMANOVA results for species relative abundance and pairwise comparisons. Bold font indicates statistical significance, P(perm) < 0.05. Df: degree of freedom; MS: mean square sum; Ce: control for the experiment (unc-aged); Cp: control for the procedure (partially caged); T: Treatment (caged); ≠ indicates differences between groups, P(perm) < 0.05; =: indicates the absence of differences between groups, P(perm) > 0.05.

Source	Df	MS	Pseudo-F	P(perm)
Marina	2	12,965	15.311	**0.0001**
Treatment	2	4241.5	3.4378	**0.0019**
Rack (Marina)	12	837.48	1.2908	0.0542
Marina × Treatment	4	1117.3	1.7221	**0.0105**
Residual variation	22	648.79		
Pairwise comparison (Marina × Treatment)			Setubal and Cascais: T ≠ (Ce = Cp)	
			Sines: (T ≠ Cp) = Ce	

similarity to the caged treatments of Setúbal and Cascais, indicates different predation effects in this marina, whether due to a lower pre-dation intensity or a different predators' assemblages in this marina. Either way, predation had a lower influence on fouling structure in Sines, as assemblages were similar across treatments (Fig. 3 and Fig. 4).

Fouling dry biomass and NIS relative abundance were generally higher in the assemblages exposed to predation in Setúbal and Cascais (Table 2; Figs. 5 and 6). Given that no artefacts by racks or procedure were detected for these variables, it can be concluded that predation facilitated the recruitment of assemblages with higher biomass and NIS in these marinas. However, predation did not affect the recruitment of assemblages in Sines. Overall, no biotic effects by predation on native species abundance could be confirmed, except for Sines, where the open caged treatment had a higher native abundance than Ce and T (Table 2; Fig. 6).

Total species richness did not differ among marinas and treatments (Table S3). However, NIS and native species richness did vary between marinas and substrata. For native species, richness was higher in the treatment (caged) than the controls (Ce and Cp) in all the marinas, while NIS richness was higher in the procedural controls (Cp) than the treat-ment (T) in all marinas.

4. Discussion and conclusions

Predation exclusion promoted significant differences in fouling spe-cies composition in all three marinas. However, SIMPROF-routine did not identify different assemblages shaped by predator exclusion in Sines, as was the case for marinas in river basins (Setúbal and Cascais). In fact, estuarine marinas had higher dry biomass and higher NIS relative abundance when exposed to predation, suggesting that existing
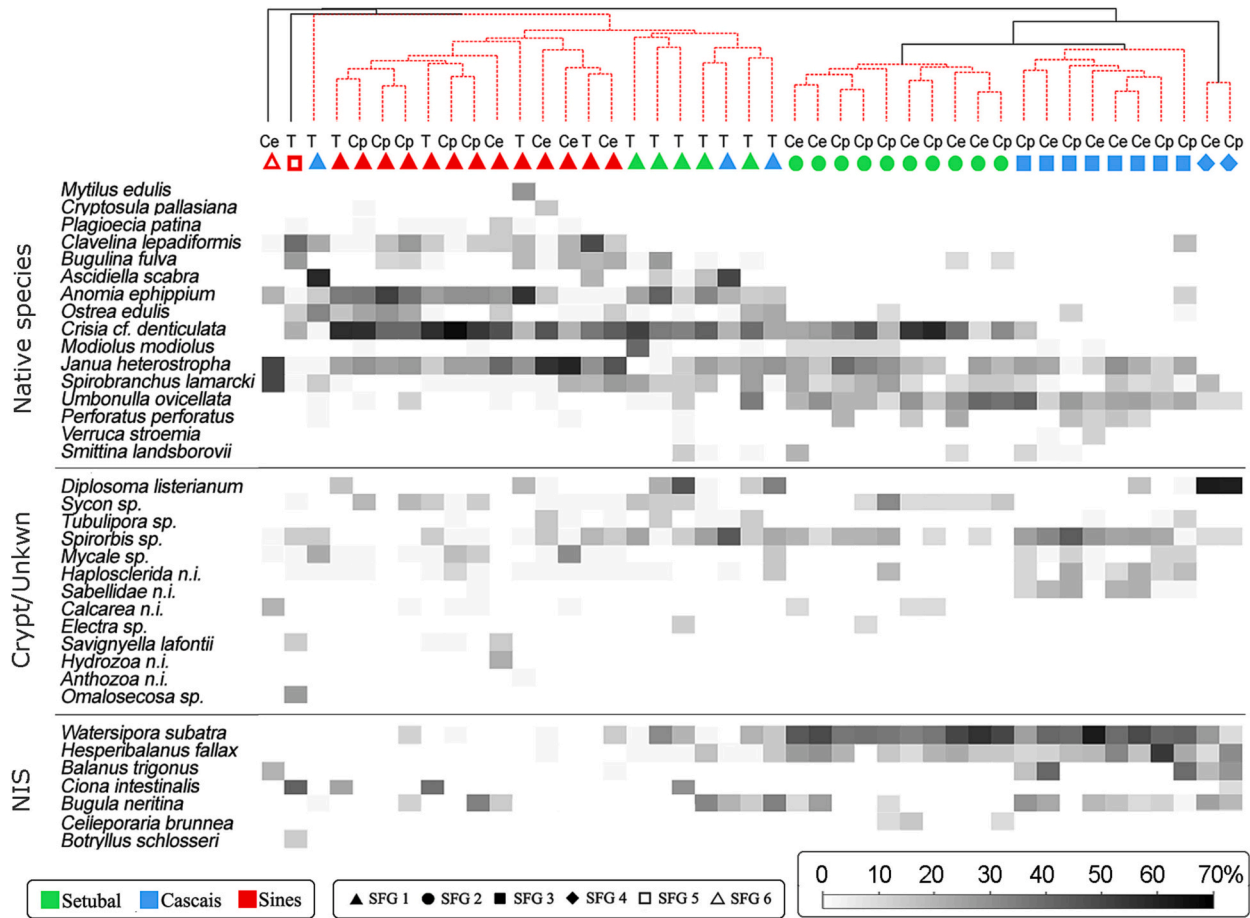
Fig. 3. CLUSTER ordination and SIMPROF grouping of samples, and shade plot illustrating the fouling species relative abundances (%) across marinas (colour) and experimental treatments (Ce: Control for experiment; Cp: Control for the procedure; T: predation-exclusion Treatment). Species are grouped by their biogeographic status: native, cryptogenic and unknown (Crypt/Unknown) and non-indigenous species. Those species that did not reach a 5 % coverage in any replicate were excluded from the plot. SFG: six statistically homogeneous SIMPROF-groups were detected among samples (SFG alpha threshold = 0.05): SFG1, SFG2, SFG3, SFG4, SFG5 and SFG6.
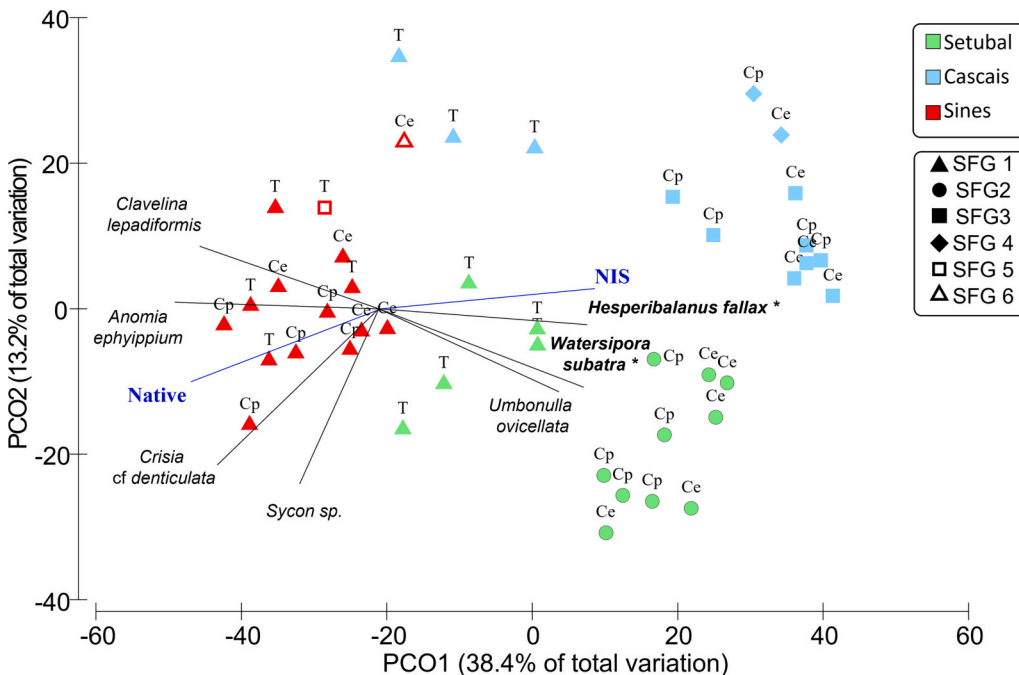

Fig. 4. Principal Coordinates Analysis (PCO) on fouling species relative abundances, indicating the three studied marinas (colours), SFGs (shapes) obtained using SIMPROF (SFG alpha = 0.05), and experimental treatment and controls. Black vectors represent species with a Spearman correlation coefficient higher than 0.75 with any PCO axes, with non-indigenous species (NIS) indicated asterisks (*). Blue vectors show the direction of correlation with respect to the PCO axes for NIS and Native species sums of abundance. Ce: control for experiment; Cp: control for the procedure; T: treatment; SFG: SIMPROF-groups. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Univariate PERMANOVA results for assemblages' dry biomass (g), native species relative abundance and non-indigenous species (NIS) relative abundance. Bold font indicates statistical significance, P(perm) < 0.005. See pairwise comparison for Marina x Treatment in Fig. 5 (dry biomass) and Fig. 6 (native and NIS) abundances. Df: degrees of freedom; MS: mean square sum.

| Source	Df	Dry biomass			Native spp. abundance			NIS abundance		
		MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Marina	2	2.66	32.62	**0.001**	19.75	17.54	**0.002**	50.28	50.92	**0.001**
Treatment	2	1.80	4.18	0.101	2.69	0.76	0.519	21.99	1.90	0.246
Rack (Marina)	12	0.08	1.16	0.357	1.85	3.27	**0.007**	0.965	0.62	0.799
Marina × Treatment	4	0.44	6.21	**0.001**	3.59	6.35	**0.001**	11.69	7.56	**0.001**
Residual variation	22	0.07			0.57			1.90		
Pairwise comparisons		See Fig. 5			See Fig. 6			See Fig. 6		
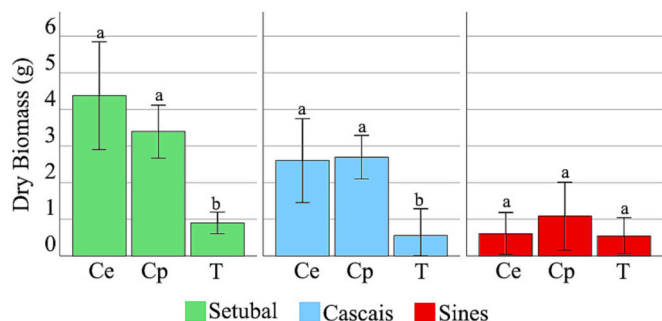
Fig. 5. Mean dry biomass in grams (g) and standard deviation error bars for the studied assemblages in each treatment and marina. Ce: control for experiment; Cp: control for the procedure; T: predation-exclusion Treatment. Letters indicate significant differences (P(perm) < 0.05) between treatments within each marina (pairwise comparison to PERMANOVA in Table 2).

predators may be targeting native species over NIS in these marinas. Contrastingly, Sines marina, which is in a coastal setting away from river basins, presented lower biomass (overall), less NIS abundance and a homogeneous, dominating assemblage (i.e., SFG1), regardless of treatment. Findings in Sines suggest that there may be lower predation pressure overall with no selectivity and/or lower overall recruitment and colonisation by fouling taxa, with higher proportion of native species.

Notably, SFG1 assemblage present in most Sines samples and those

from other marinas where predators had been excluded was mainly due to the occurrence of the native *Crisia* cf. *denticulata*, *Janua heterostropha*, and *Anomia ephippium*. In contrast, the encrusting bryozoan *Watersipora subatra* (NIS) and *Umbonula ovicellata* (Native) were particularly benefited by predation in Setúbal and Cascais. Bryozoans are widely distributed in coastal artificial habitats around the globe and form colonies that can have a very heterogeneous spatial structure (Mackie et al., 2006, 2012). Although bryozoans can have allelochemical defences to deter predation, these may play a more important role during larval recruitment, and it is more likely that the bryozoans in this study resisted predation through their calcareous skeleton and colony shape (McGovern and Hellberg, 2003).

In our study, encrusting morphologies benefited from predation pressure, while erect and branched morphologies were more abundant in the absence of predation. To this matter, erect colonies can increase fouling weight and cause economic impacts, outcompete native species, modify local habitats and facilitate the recruitment of novel species, including mobile macrofauna and other fouling NIS (Fine and Loya, 2003; Floerl et al., 2004; Davis and Marshall, 2013; Gestoso et al., 2018; Guerra-García et al., 2021c). Furthermore, the proliferation of filter feeders can have trophic effects and impact ecosystem services in closed systems, such as estuaries and lagoons (Katsanevakis et al., 2014; McQuaid and Griffiths, 2014). Therefore, predation could contribute to reducing ecological impacts on local ecosystems and socio-economic impacts on maritime traffic and coastal infrastructure by erect filter-feeding species, irrespective of whether they are native or NIS (Susick et al., 2019; Wetzel et al., 2014). As these benthic filter feeders often occur on artificial hard substrata, the management of these species in
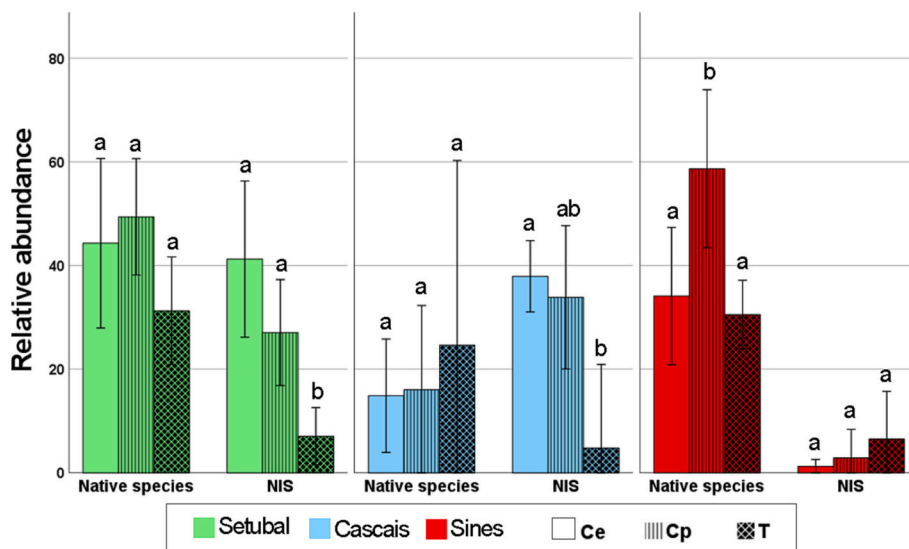

Fig. 6. Mean relative abundances and standard deviation error bars for native and NIS in each treatment and marina. Ce: control for experiment; Cp: control for the procedure; T: predation-exclusion treatment. Letters indicate significant differences (P(perm) < 0.05) on species relative abundances within treatments for each marina (pairwise comparison to PERMANOVAs in Table 2).

artificial coastlines is of great importance, particularly in sand-dominated ecosystems such as estuaries (Wetzel et al., 2014). Estuaries are vulnerable and impacted ecosystems and are among the most populated and urbanised areas of the world because of the important resource-exploitation and commerce services they provide (Vasconcelos et al., 2007; Barragán and de Andrés, 2015; Gittman et al., 2015). Therefore, it is important to understand the trophic effects and NIS dynamics in these ecosystems to inform their protection and conservation (Afonso et al., 2020).

Estuaries are highly productive ecosystems that act as nursery areas with particular mesopredator assemblages that are different from those in open coastal areas (Piko and Szedlmayer, 2007; Vasconcelos et al., 2008; França et al., 2011). Therefore, the biotic effects registered in the estuarine marinas could have been influenced by the composition and abundance of the predator community, although more research is needed to understand the trophic effects occurring in estuaries and other coastal ecosystems. Although the absence of predation exclusion effects in Sines could result from a different predation pressure in this marina (Nydam and Stachowicz, 2007), it is also possible that the higher native species richness in this marina and lower abundance of NIS could had decreased the relative importance of consumers (grazers and predators) in the assemblage's composition, with horizontal competition having a higher effect on the biotic resistance exerted by the ecosystem.

Early-recruitment assemblages are mainly structured by meso-predators such as molluscs, echinoderms, crabs and small fish (Osman and Whitlatch, 2004; Nydam and Stachowicz, 2007; Lavender et al., 2014). These fouling feeders can identify assemblage patterns and express interest in specific fouling patches as well as single species, so native predators might prefer to feed from fouling assemblages rich in branched morphologies, non-calcareous bodies or native species, which would facilitate the growth of NIS (Simoncini and Miller, 2007; Caca-belos et al., 2010; López et al., 2010; Warburton and Hughes, 2011). This facilitation effect has been observed for *Watersipora subatra* in estuarine habitats (Needles et al., 2015). In this study, tunicates were more abundant in the predation exclusion treatments and bryozoans were more abundant in the predation access treatment. This pattern was more clear in the marina of Cascais and was also reported in other studies (Vieira et al., 2012). Ascidians are usually the first to be consumed by predators (Freestone et al., 2011), as these colonial organisms grow fast but lack structural defences against predators. On the other hand, calcified bryozoans can grow slower but are less vulnerable to predation, which makes them more easily overgrown by other fouling species (Oricchio and Muniz Dias, 2020). Therefore, predation could be a main driver on fouling structure, as the removal of ascidians could result in a monopolisation of space by bryozoans. Hence, predation can modify the functional traits and dominance of NIS inside marinas.

It is noteworthy to mention that other factors besides predation might influence the structure of the fouling community. For example, interspecific competition among fouling organisms can affect the dominance of species (Giachetti et al., 2020). Furthermore, assemblages recruitment and trophic effects can be influenced by temperature (Freestone et al., 2011; Lavender et al., 2014; Ashton et al., 2022). In fact, Setúbal was the marina with higher temperatures and fouling biomass. This higher temperature could be the result of higher water confinement, which has been associated with a higher fouling abundance in marinas (Monsen et al., 2002; Floerl and Inglis, 2003). Besides, these biotic and abiotic variables can interact with trophic factors. For instance, predation intensity increases with temperature (Ashton et al., 2022), so a marina with a warm water body could experience higher predation pressures or host a different predator assemblages than a colder marina. Finally, the higher fouling biomass in Setúbal could attract more mobile predators or sustain a more abundant community of consumers, which would result in different trophic pressures and effects across marinas (Freestone et al., 2011; Lavender et al., 2014; Sedano et al., 2020b; Ashton et al., 2022).

Feeding generally contributes to the heterogeneity of the consumed community at diverse geographical scales (Menge and Sutherland, 1976; Freestone et al., 2011; Lavender et al., 2014). Therefore, predation might act as a driver of heterogeneity among marinas, ultimately reducing single species and populations dominance across marinas and the genetic connectivity and spread capacity of established NIS across a coastal network of artificial habitats (Acosta and Forrest, 2009; Forrest et al., 2013; Simkanin et al., 2013; Ferrario et al., 2017). However, this was not the case in our study, which highlights the high variability of effects across geographical scales and taxonomic groups (Gittman et al., 2016; Sedano et al., 2020a, 2020b; Guerra-García et al., 2021b). Overall, our results were in consonance with the Enemy Release Hypothesis (ERH), which proposes low trophic impacts by native consumers against NIS in their introduced distribution (Keane and Crawley, 2002). From an integrated perspective, ERH can increase niche shifts (e.g., increased environmental tolerance) and evolution of invasiveness (e.g., acquisition of native allies), which will further increase the risk of invasion by NIS (Gribben and Byers, 2020). In any case, this study contrasts with a majority of studies reporting that predation on fouling NIS contributes to biotic resistance in ports and marinas (Dumont et al., 2011; Simkanin et al., 2013; Rogers et al., 2016; Leclerc et al., 2019; Janiak and Branson, 2021), while reports on facilitation effects are scarcer in the literature (e. g., Simoncini and Miller, 2007; Veiga et al., 2011; Gestoso et al., 2018). This supports previous evidence on the singularity of assemblages and biotic effects in marinas (Sedano et al., 2020b; Guerra-García et al., 2021a, 2021b; Saenz-Arias et al., 2022). Hereby, the ecological effects of coastal constructions are complex and can vary across groups of organisms and geographical scales (Gittman et al., 2016; Sedano et al., 2020a, 2020b; Guerra-García et al., 2021b). Therefore, it is reasonable that predation had different biotic effects on the fouling community in different marinas (Gestoso et al., 2018; Leclerc et al., 2019), which reveals the need of considering the uniqueness of marinas when planning action plans and management strategies. Nevertheless, a better knowledge of ecologically-relevant predators, trophic networks and biotic effects inside marinas will increase our understanding of biological invasions and improve restoration and management strategies in urban ecosystems (Geist and Hawkins, 2016; Chebaane et al., 2022).

CRediT authorship contribution statement

Sahar Chebaane: Writing – original draft, Conceptualization, Formal analysis, Visualization, Writing – review & editing. **Amy L. Freestone:** Conceptualization, Methodology, Writing – review & editing. **Antonio Des Pérez:** Investigation. **Juan Sempere-Valverde:** Formal analysis, Writing – review & editing. **Paula Chainho:** Validation, Writing – review & editing. **João Gama Monteiro:** Supervision, Formal analysis, Writing – review & editing. **João Canning-Clode:** Conceptualization, Methodology, Investigation, Validation, 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 made available on request.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2023.114724.

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