Marine Environmental Research 211 (2025) 107409



Contents lists available at ScienceDirect

Marine Environmental Research

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



Structure of sessile fouling assemblages on pontoons in marinas differs between brackish and marine salinities

Jesús Fernández-Gutiérrez [a,b,c,*], Marcos Rubal [c], Fran Ramil [d], Juan Moreira [e], Leandro Sampaio [a], Isabel Sousa-Pinto [a,b], Puri Veiga [a,b]

[a] CIIMAR/CIMAR LA, Interdisciplinary Centre of Marine and Environmental Research, University of Porto, Terminal de Cruzeiros do Porto de Leixões, 4450-208, Matosinhos, Portugal
[b] Department of Biology, Faculty of Sciences, University of Porto, Rua do Campo Alegre s/n, 4169-007, Porto, Portugal
[c] Centre of Molecular and Environmental Biology (CBMA/ARNET), Department of Biology, University of Minho, 4710-057, Braga, Portugal
[d] CIM-UVigo – Centro de Investigación Mariña, Facultade de Ciencias do Mar, Universidade de Vigo, E-36310, Vigo, Spain
[e] Departamento de Biología (Unidad de Zoología) & Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, E-28049, Madrid, Spain

ARTICLE INFO

Keywords:
Atlantic ocean
North Portugal
Artificial structures
Urban ecosystems
Invertebrates
Biodiversity

ABSTRACT

The number of recreational marinas has recently increased due to the growing demand for leisure boating. Floating pontoons of marinas provide novel habitats to fouling assemblages, specially to sessile habitat-forming species, that increase heterogeneity creating new habitats for mobile and sessile epibionts. Therefore, sessile species play a crucial role in sustaining biodiversity in urban areas. Despite the relevance of sessile fouling assemblages, the role of environmental factors in shaping the structure of these assemblages has not been comprehensively studied. In the present study, the abundance, richness and multivariate structure of sessile fouling assemblages associated with floating pontoons were studied in marinas under two different environmental conditions (brackish and marine), and the influence of environmental variables (salinity, temperature and dissolved oxygen) on fouling assemblages was tested.

Our results showed that univariate variables and assemblage composition significantly differed between environments, with lower values of abundance and richness under brackish conditions. This pattern could result from the influence of freshwater inputs in brackish marinas, that also showed a higher level of multivariate dispersion. Results also pointed out that salinity was the most important factor, explaining 46 %, 56 % and 37 % of abundance, richness and multivariate structure of sessile fouling assemblage, respectively. The sessile assemblage in marine and brackish marinas was dominated in terms of abundance by the native habitat-forming species *Mytilus galloprovincialis*, which harboured most of the collected sessile epibiont species. These findings highlight the role of floating pontoons to support sessile invertebrates in urban areas where biodiversity may be heavily impacted.

1. Introduction

Human settlements have historically concentrated near estuaries and coasts attracted by the large number of ecosystem services provided by these areas (e.g. fishing, industry, transportation, tourism, recreation) (Barbier et al., 2011). Today, more than 40 % of the global population lives within ~100 km of the coast, and this trend is expected to increase in the next years (Kummu et al., 2016; Reimann et al., 2023). This change in demography and urban distribution has significantly impacted estuarine and coastal landscapes through the addition of artificial structures to satisfy the growing commercial, recreational and residential demands (Airoldi and Beck, 2007; Bulleri and Chapman, 2010). Although artificial structures can create novel habitats for fouling taxa (Connell, 2001), species composition and ecological processes operating on these structures differ from those occurring on natural rocky reefs (Bulleri and Chapman, 2004; Moreira et al., 2006; Mayer-Pinto et al., 2018). In addition, urban areas are important sources of pollutants (e.g. heavy metals, nutrients, microplastics) derived from

* Corresponding author. CIIMAR/CIMAR LA, Interdisciplinary Centre of Marine and Environmental Research, University of Porto, Terminal de Cruzeiros do Porto de Leixões, 4450-208, Matosinhos, Portugal.
E-mail address: jgutierrez@ciimar.up.pt (J. Fernández-Gutiérrez).

https://doi.org/10.1016/j.marenvres.2025.107409
Received 13 June 2025; Received in revised form 23 July 2025; Accepted 28 July 2025
Available online 29 July 2025
0141-1136/© 2025 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

industrial discharges, wastewater effluents, and runoff that increase pollution levels in adjacent waters (Freeman et al., 2019). Consequently, coastal urbanisation is considered one of the major threats to intertidal and nearshore benthic communities (Bulleri and Chapman, 2010). Paradoxically, despite emerging legal measures to protect and sustain coastal biodiversity (EU, 2008, 2024; UN, 2015), the prevalence of submersed artificial structures will continue to grow in the future (Bugnot et al., 2021). Therefore, understanding their impacts on benthic communities is essential to guide mitigation strategies in degraded urban areas (Dafforn et al., 2015).

In recent years, recreational marinas have become one of the fastest-growing types of urban artificial structures in estuaries and coasts, driven by the expansion of the leisure boating sector (Valdor et al., 2019). Marinas introduce numerous artificial structures in the aquatic environment, ranging from pier piles and floating pontoons that facilitate boat mooring, to breakwaters and dykes to avoid hydrodynamic forces (Rivero et al., 2013). These structures hinder water circulation leading to reduced oxygen levels and increased sedimentation rates, turbidity, organic matter and pollutant concentration (e.g., biocides, heavy metals, hydrocarbons) (Floerl and Inglis, 2003; Valdor et al., 2019; Guerra-García et al., 2021a). Therefore, marinas are often dominated by opportunistic and stress-resistant species (but see Fernández-Romero et al., 2019). Moreover, as key nodes in propagule dispersal networks, marinas also contribute to the introduction and establishment of cryptogenic and non-indigenous species (NIS) (Oricchio et al., 2019; Ulman et al., 2019), which may later spread to natural surrounding habitats (Simkanin et al., 2012). Despite these disturbances, the sheltered conditions and high larval retention in marinas facilitate the colonization of submersed artificial structures by fouling organisms (Floerl and Inglis, 2003; Rivero et al., 2013). Comparisons between piles and floating pontoons have demonstrated that the latter sustain the most distinct fouling communities both in terms of species composition and functional traits (Leclerc et al., 2019; Figueroa et al., 2021). Such differences have been attributed not only to the physical properties of pontoons (e.g., homogeneous surface, limited space, orientation) (Glasby, 1999; Glasby and Connell, 2001) but also to the uncommon fact in nature of being submersed structures floating permanently near the water surface (Toh et al., 2017). Therefore, unlike subtidal communities, assemblages on pontoons are exposed to highly unstable environmental (e.g. light, temperature, salinity) and hydrodynamic conditions (e.g. swash, water motion) that shape these unique assemblages (Holloway and Connell, 2002).

Fouling assemblages on pontoons are composed of diverse sessile habitat-forming species (native or NIS) (e.g., algae, annelids, bryozoans, molluscs, sponges) that increase surface heterogeneity and provide secondary substrates for many mobile and sessile epibionts (Leclerc and Viard, 2018; Fernández-Romero et al., 2019; Guerra-García et al., 2025). In turn, small sessile epibionts enhance this three-dimensional complexity by reshaping the morphology of the secondary substrates added by habitat-forming species contributing to enhance biodiversity in impacted urban areas (Charles et al., 2018). Furthermore, by acting as both food resources and structural refuge for invertebrates and fishes, sessile species also help to improve ecosystem functionality and connectivity in urban ecosystems (Clynick et al., 2007; Ros et al., 2012; Leclerc et al., 2024). Besides, sessile assemblages on pontoons are dominated by filter-feeders (Figueroa et al., 2021; Guerra-García et al., 2021b), which are involved in water depuration and proven to be effective in the mitigation of heavily polluted urban areas (e.g., Bulleri et al., 2022; Firth et al., 2024). Sessile species thus play a crucial role in sustaining biodiversity in degraded urban areas (Toh et al., 2017), being proposed as nature-based solutions (Bulleri et al., 2022).

The ecological significance of sessile species in marinas has long been recognized (Toh et al., 2017). However, previous research has predominantly focused on the occurrence of sessile NIS (Bishop et al., 2015; Nall et al., 2015; Ulman et al., 2019) or on the colonization of substrates by native/NIS sessile taxa (Leclerc and Viard, 2018; Leclerc et al., 2019; Wrange et al., 2020; Tempesti et al., 2023). Although informative about early successional patterns, these studies have not properly explored the structure and composition of long-term established assemblages on pontoons (but see Toh et al., 2017; Guerra-García et al., 2021b; Ferrario et al., 2024; Leclerc et al., 2024), resulting in a skewed understanding of these systems. In addition, there is a lack of studies examining the abiotic and biotic factors influencing these assemblages (Toh et al., 2017; Kenworthy et al., 2018; Chebaane et al., 2023; Leclerc et al., 2024). Salinity is among the most important abiotic drivers of sessile assemblages in coastal areas worldwide (Gunter, 1961; Grabowska et al., 2015). In fact, in brackish environments, that are characterised by the transition from seawater to freshwater, salinity is the most relevant abiotic factor - often exerting a stronger effect than temperature or dissolved oxygen - in shaping the composition and distribution of benthic communities (Cognetti and Maltagliati, 2000; Charles et al., 2018; Holmes and Callaway, 2021). There is mounting evidence that the abundance and richness of sessile fouling species abruptly decreases from high to low salinity areas in natural habitats (e.g., Gunter, 1961; Hardwick-Witman and Mathieson, 1983). However, the role of salinity on the structure of fouling assemblages associated with pontoons has not yet been comprehensively studied. Thus far, some studies have examined changes in fouling assemblages of ports and marinas along brackish salinity gradients (Wrange et al., 2020), specially regarding NIS (e.g., Holmes and Callaway, 2021). Moreover, the few formal comparisons of both mobile and sessile fouling assemblages of marinas - including brackish and marine salinity conditions - have similarly focused on NIS (Jimenez et al., 2018; Afonso et al., 2020; Fernández-Gutiérrez et al., 2025). Therefore, the role of salinity on native fouling assemblages is still understudied, particularly in brackish conditions (Charles et al., 2018).

To fill this knowledge gap, the present study aims to explore differences on the structure of sessile assemblages associated with floating pontoons of marinas under different environmental conditions: brackish vs marine. Specifically, we hypothesized that (i) the abundance, richness and multivariate structure of sessile fouling assemblages will differ between environments; (ii) there will be lower values of abundance and richness in brackish marinas, as it happens in natural habitats (e.g., Gunter, 1961; Hardwick-Witman and Mathieson, 1983) and (iii) salinity will be the main environmental factor explaining variability of fouling assemblages.

Understanding the influence of environmental conditions on fouling assemblages in marinas is paramount to assess the potential of floating pontoons to support biodiversity in degraded urban areas and guide ecologically sustainable practices for marina management (Dafforn et al., 2015; Toh et al., 2017; Guerra-García et al., 2021b).

2. Material and methods

2.1. Study area

Sampling was conducted in June 2023 at six marinas: three located in areas subjected to brackish conditions ("brackish" marinas, hereafter BM) and three under marine conditions ("marine" marinas, hereafter MM) along the Northern Portuguese Coast. From North to South, BM were in Viana do Castelo (VB), Esposende (ES) and Afurada (AF), while MM were in Viana do Castelo (VC), Póvoa do Varzim (PV) and Leça da Palmeira (LE) (Table 1, Fig. 1). Selected marinas were similar in terms of depth (from 2 to 7 m) and activity type (recreational boating) to avoid potential confounding effects derived from different activities on the studied assemblages.

The northern coast of Portugal represents a significant hub in the Portuguese recreational boating sector, with the second-highest number of registered leisure boats of the country (Grupo de Trabalho da Náutica de Recreio, 2012) and the third-largest number of recreational moorings on mainland Portugal (PwC, 2018). This region experiences a semi-diurnal tidal regime, with the largest spring tides of about 4.0 m. The

Table 1
Location of sampled marinas under brackish and marine environments and mean values (±SE) of surface salinity (psu), temperature (°C) and dissolved oxygen (mg/l).

Environment	Marina	Coordinates	Salinity (psu)	Temperature ((°C)	Dissolved oxygen (mg/l)
Brackish	Afurada	41°08′32.7″N 8°39′03.7″W	7.59 ± 0.18	21.40 ± 015	8.25 ± 0.05
	Esposende	41°31′37.2″N 8°46′49.1″W	4.37 ± 0.17	21.90 ± 0.31	7.18 ± 0.06
	Viana do Castelo	41°41′38.8″N 8°49′17.9″W	19.58 ± 0.31	19.47 ± 0.42	8.24 ± 0.15
Marine	Leça da Palmeira	41°11′11.5″N 8°42′18.0″W	32.17 ± 0.27	20.60 ± 0.25	8.47 ± 0.12
	Póvoa do Varzim	41°22′16.7″N 8°45′54.0″W	34.50 ± 0.06	17.77 ± 0.07	8.73 ± 0.21
	Viana do Castelo	41°41′06.4″N 8°50′18.0″W	34.00 ± 0.10	16.60 ± 0.25	9.87 ± 0.20

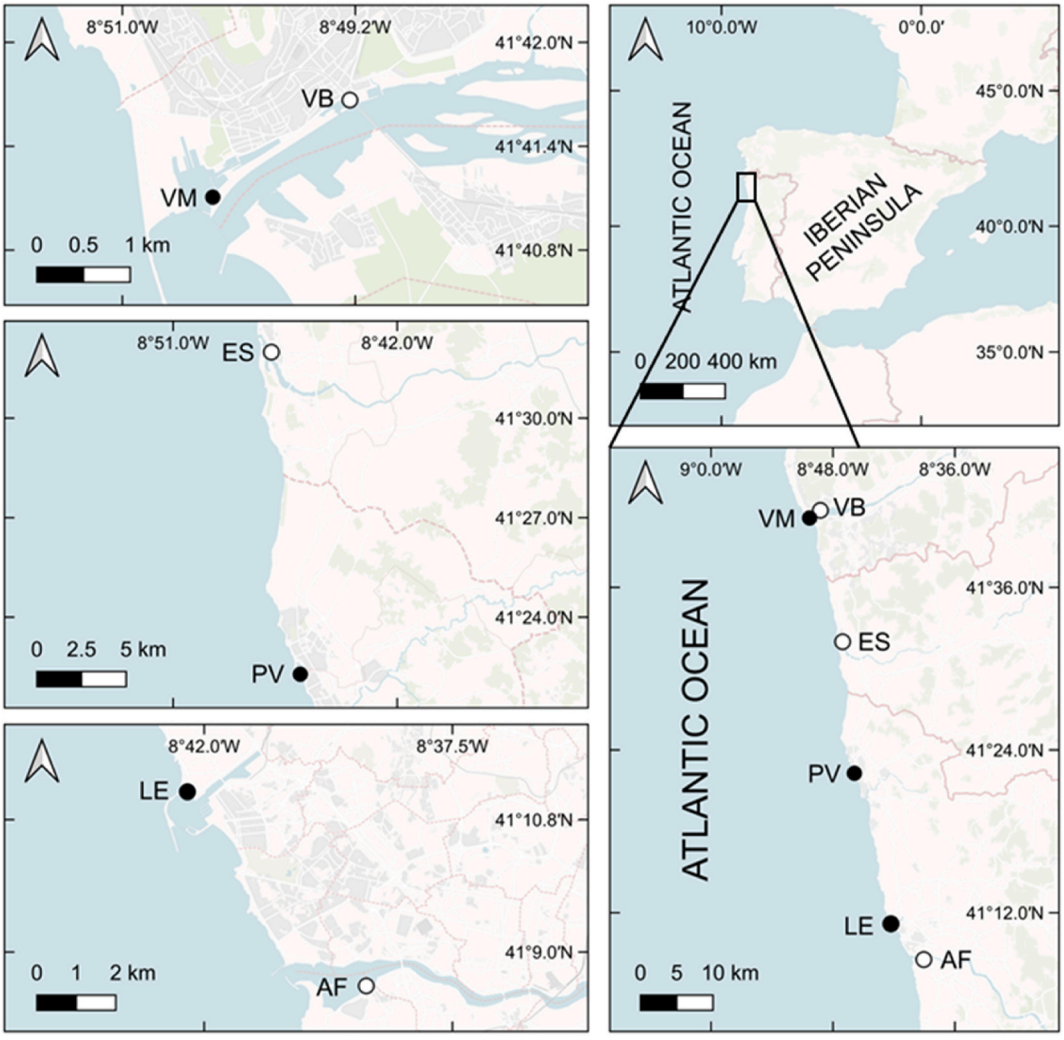


Fig. 1. Location of the studied marinas under brackish (white dots) and marine (black dots) environments in North Portugal. From North to South: Viana do Castelo (brackish, VB), Viana do Castelo (marine, VM), Esposende (ES), Póvoa do Varzim (PV), Leça da Palmeira (LE) and Afurada (AF).

coastline is predominantly straight and highly exposed to wave action, with the dominant swell coming from W and NW. Common wave heights range from 1.5 to 2.0 m, with maximum values around 7 m. Moreover, the study area is under the influence of a seasonal upwelling that provides nutrients and enhances primary productivity during the spring and summer months (Lemos and Pires, 2004). The coastline, dominated by a rocky intertidal zone, is interspersed with estuaries and strongly influenced by rivers discharge, specifically Douro, Lima and Minho rivers. Thus, salinity values may decrease in coastal areas due to heavy rainfalls during the autumn and winter seasons (Rubal et al., 2023). The studied BM are located in estuarine areas that are largely composed of sedimentary substrates while natural hard substrates are scarce. Therefore, artificial structures such as marinas are often the only hard substrate available for fouling organisms within estuaries (Marchini et al., 2007; Rubal et al., 2023).

2.2. Sampling and sample procedure

At each marina, three sites were randomly selected on floating pontoons for sampling. Selected pontoons were all made of fiberglass and, according to marina operators, none were recently cleaned nor deployed (>5 years), ensuring the sampling of undisturbed, long-term established assemblages (see Fernández-Gutiérrez et al., 2025). Measurements of surface salinity, temperature and dissolved oxygen were made *in situ* using multiparametric probes (Table 1). On the lateral submersed surface of the pontoons, just below water level, 4 quadrats

(10 × 10 cm) were randomly placed per site and the fouling assemblage was scrapped in each quadrat. Samples were washed through a 0.5 mm mesh sieve and the retained fraction was fixed in a 4 % formaldehyde solution stained with Rose Bengal. In the laboratory, animals were sorted and identified to the lowest taxonomical level possible. The abundance of solitary sessile species (i.e., anemones, annelids, barnacles, mussels, pedunculated ascidians) was quantified as number of individuals per 100 cm^2. On the other hand, encrusting, modular and/or stolonal sessile taxa (i.e., bryozoans, entoprocts, hydroids, sponges) were quantified as number of colonies per 100 cm^2. Though animals may break during scraping and sieving, colonies were still individually recognized under the dissection microscope since they were attached to different substrates: algae, ascidians, barnacles, mussel shells and byssus or even litter. Therefore, colonies were only counted when attached to the substrate thus avoiding the identification and quantification of fragments (see Fernández-Gutiérrez et al., 2025).

2.3. Data analysis

Univariate and multivariate analyses were done to test the hypothesis that the structure of fouling assemblages differed between the two different environmental conditions (i.e. brackish vs marine). For these analyses, total abundance (N) and total taxa richness (S) were calculated per replicate. Analyses of variance (ANOVA) were done to explore significant differences on N and S between environmental conditions considering the following three-way design: Environment (En), a fixed orthogonal factor with two levels (marine and brackish); Marina (Ma), a random factor nested in Environment, with three levels; and Site (Si), a random factor nested in Marina and Environment, with three levels and four replicates. Before ANOVA, Cochran's tests were done to check for homogeneity of variances; when significant, data were square root transformed to achieve homogeneity.

To explore differences on the structure of sessile fouling assemblages between environmental conditions, a permutational multivariate analysis of variance (PERMANOVA) was used following the aforementioned three-way design. To reduce the influence of numerically dominant species and increase the contribution of less abundant ones, abundance values of each species were fourth-root transformed for the calculation of the Bray-Curtis similarity matrix by permutation of residuals under a reduced model (Anderson, 2001a). When the number of unique permutations for a factor was lower than 30, Monte Carlo P-values were considered (Anderson et al., 2008). The PERMDISP procedure was used to test whether differences in the multivariate assemblage structure between environmental conditions were due to varying multivariate dispersion (Anderson, 2006). Multivariate patterns were illustrated by non-metric multidimensional scaling (nMDS) ordination based on centroids per marina.

The SIMPER procedure was used to determine the percentage contribution (δi%) of each taxon to the Bray-Curtis dissimilarity between assemblages from marine and brackish environments (δi) (Clarke, 1993). A taxon was considered important when its contribution to the total percentage dissimilarity was ≥4 %. The ratio δi/SD(δi) was used to quantify the consistency of a particular taxon contribution to the average dissimilarity in all pair-wise comparisons of samples between salinity conditions. Values ≥ 1 indicated a high degree of consistency.

The relationship between univariate and multivariate sessile fouling assemblage data and environmental variables of surface water (salinity, temperature and dissolved oxygen) was analysed using nonparametric multivariate multiple regression (McArdle and Anderson, 2001). A stepwise forward-selection procedure was applied to environmental variables to develop a model of the sessile fouling assemblage data (i.e., N, S and the multivariate structure). Analyses were based on Euclidean similarity matrices for N and S, and Bray-Curtis similarity matrix for multivariate data, which were fourth-root transformed. P-values were calculated using 9999 permutations of residuals under the reduced model (Anderson, 2001b). All non-parametric multivariate multiple regressions were done using the program DISTLM (Anderson, 2002). Previously, Draftsman plots were done to check the skewness of environmental variables and data were log (x+1) transformed. Additionally, constrained ordination, a distance-based redundancy analysis (dbRDA, Legendre and Anderson, 1999), was done to explicitly investigate the relationship between environmental variables and sessile fouling assemblages.

3. Results

3.1. Sessile fouling assemblages

A total of 76 480 individuals and 89 taxa were found. Of these, 68 species were exclusive to MM, 12 to BM and 9 occurred in both. In terms of richness, Cnidaria was the most diverse phylum (23 species) followed by Bryozoa (19 species) and Chordata (12 species) (Table S1). Of the collected taxa, 73 were native, 8 cryptogenic and 8 NIS (Table S2); further details on cryptogenic and NIS in the sampled marinas are provided by Fernández-Gutiérrez et al. (2025). In MM, the most dominant taxa in terms of abundance were the mussel *M. galloprovincialis* (71.66 %), Actiniaria (7.83 %) and the annelid *Spirobranchus triqueter* (Linnaeus, 1758) (2.92 %). BM were also dominated by *M. galloprovincialis* (78.69 %) followed by the entoproct *Barentsia benedeni* (Foettinger, 1887) (10.64 %) and the non-indigenous hydrozoan *Cordylophora caspia* (Pallas, 1771) (3.57 %) (Table S2).

N and S values were significantly lower in BM than in MM (Table 2; Fig. 2A and B). The multivariate structure of sessile assemblages also showed significant differences between environmental conditions (Table 3). PERMDISP analysis suggested that dispersion of samples could contribute to these differences ($F = 57.124$, $p = 0.001$); samples from BM showed a greater dispersion than samples from MM (Fig. 3). However, the nMDS ordination showed a clear separation between MM and BM (Fig. 4).

SIMPER analysis indicated an average dissimilarity of assemblages of ~84 % between salinity conditions. In total, 47 species were identified as the main responsible for differences, of which 42 were exclusive or more abundant in MM (Table S3). Collectively, these taxa contributed with more than 90 % to the total explained dissimilarity between assemblages, but only 6 of them contributed with ≥4 % (Table S3). Among these, only *M. galloprovincialis* and the NIS bryozoan *Watersipora subatra* (Ortmann, 1890) were found both in BM and MM. On the other hand, the annelid *Spirobranchus lamarcki* (Quatrefages, 1866), the barnacle *Perforatus perforatus* (Bruguière, 1789), the bivalve *Anomia ephippium* Linnaeus, 1758, and the bryozoan *Amathia gracillima* (Hincks, 1877) were exclusively found in MM.

3.2. Influence of environmental variables on sessile fouling assemblages

Results of DISTLM showed that environmental variables explained 46.43 % of the variability in N. Salinity was the variable that explained the greatest amount of variation (46.42 %). However, after the inclusion of salinity, the p-values associated with the conditional test to add

Table 2
Summary of ANOVAs testing significant differences on the abundance (N) and richness (S) between brackish and marine environments. Significant differences indicated in bold. *: $p < 0.05$; **: $p < 0.01$, ***: $p < 0.001$. ns: non-significant.

Source of variation	df	N		S	
		MS	F	MS	F
Environment (En)	1	12758.82	**26.24****	6981.68	**12.05***
Marina (Ma)(En)	4	486.15	**4.93***	579.26	**37.88*****
Site (Si) (En x Ma)	12	98.67	1.21	15.29	1.93
Residual	54	81.60		7.94	
Total	71				
Transformation		sqrt(x+1)		none	
Cochran's test		C = 0.2437	ns	C = 0.2163	ns

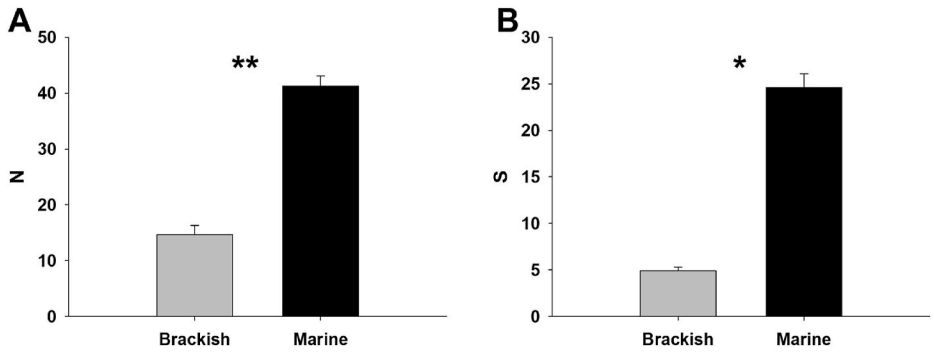


Fig. 2. Mean values (+SE) of (A) Abundance (N, number of individuals, square root transformed) and (B) richness (S, number of taxa) in brackish and marine environments. Asterisks indicate significant differences between conditions: *: $p < 0.05$; **: $p < 0.01$.

Table 3
Results of PERMANOVA testing significant differences in the multivariate structure of fouling assemblages between marine and brackish environments. All tests used 999 random permutations; Monte Carlo p-values were considered when the number of unique permutations were lower than 30. Significant differences indicated in bold. *: $p < 0.05$; **: $p < 0.01$.

Source of variation	df	MS	Pseudo-F	Unique permutations
Environment (En)	1	72107	**4.75***	10
Marina (Ma)(En)	4	15170	**23.67****	998
Site (Si) (En x Ma)	12	641.06	**1.49****	995
Residual	54	430.39		
Total	71			

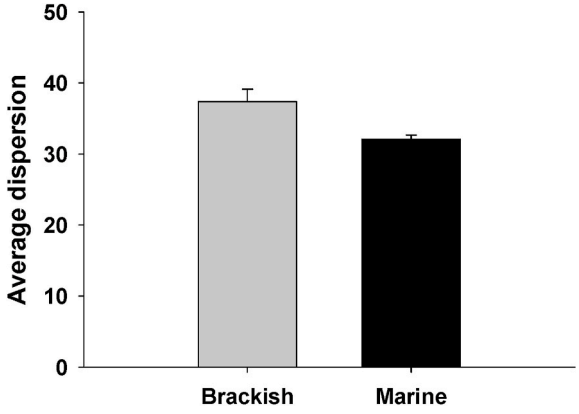


Fig. 3. Average sample dispersion (+SE) in marinas under brackish and marine environments.

dissolved oxygen and temperature were not statistically significant ($p > 0.05$) (Table 4). In this way, the best model to explain N would include only salinity.

Regarding S, DISTLM results showed that the three studied environmental variables explained the 69.22 % of the variability (Table 4). Again, salinity was the variable that explained the greatest amount of variation (56.19 %) followed by temperature (10.74 %) and dissolved oxygen (2.30 %), which were also significant ($p < 0.05$) (Table 4). Thus, the best model to explain S would include the three studied variables.

When considering the multivariate structure of sessile fouling assemblages, the three studied environmental variables explained the 48.20 % of the variability (Table 4). Salinity was the variable that explained the greatest amount of variation (36.64 %) followed by temperature (6.76 %) and dissolved oxygen (4.81 %), which were also significant. Therefore, the best model to explain multivariate sessile fouling assemblage structure would include the three environmental variables.

The first two dbRDA axes explained 90.48 % of the fitted variation, which is about 43.61 % of the total variation in the structure of the sessile fouling assemblages (Fig. 5). All dbRDA axes together explain 100 % of the fitted variation and 48.20 % of the total variation.

4. Discussion

Salinity is one of the most important abiotic drivers affecting the composition and distribution of sessile assemblages in natural hard substrata worldwide (Gunter, 1961; Hardwick-Witman and Mathieson, 1983; Grabowska et al., 2015). In fact, in brackish environments, salinity consistently plays a dominant role in shaping the structure of sessile assemblages, overriding the influence of other key environmental variables such as temperature and dissolved oxygen (Cognetti and Maltagliati, 2000; Charles et al., 2018; Holmes and Callaway, 2021). However, its effects on sessile fouling assemblages associated with floating pontoons have been unevenly studied, with a clear bias towards NIS (e.g., Jimenez et al., 2018; Afonso et al., 2020; Fernández-Gutiérrez et al., 2025). Although these studies have generated valuable data for decision makers to develop NIS management strategies, the focus on NIS has overlooked the composition, distribution and identity of native species that compose these assemblages (Guerra-García et al., 2021b; Leclerc et al., 2024), specially in brackish waters (Charles et al., 2018). Consequently, the ability of pontoons to support sessile invertebrates on urban artificial structures under different environmental conditions remains yet to be fully understood.

In the present study, abundance (N), diversity (S) and multivariate structure of sessile fouling assemblages on pontoons were studied in marinas located at two different environmental conditions: brackish and marine. Our results fully supported the initial hypotheses since: (a) abundance, diversity and multivariate structure significantly differed between the studied environments; and (b) there were lower values of N and S in BM. Specifically, the number of colonies/individuals (N) was almost six times lower in BM than in MM. Regarding the total number of species, 23.59 % were only found in BM, while 76.41 % were present in MM. These findings align with the well-documented decrease in N and S of sessile assemblages on natural rocky reefs following a gradient from high to low salinity values (e.g. Gunter, 1961; Hardwick-Witman and Mathieson, 1983). For example, Grabowska et al. (2015) reported significantly lower N and S values in sessile communities on natural rocky substrates in the inner region of the Baltic Sea (4–7 psμ) compared to the outermost one (22–27 psμ). In the same area, lower values of sessile fouling coverage were reported by Wrange et al. (2020) on settlement plates of recreational marinas in the innermost region. Moreover, the few formal comparisons between brackish and marine salinities (focused only on fouling mobile and sessile NIS) have also found significantly lower numbers of NIS in marinas under brackish salinities (Jimenez et al., 2018; Afonso et al., 2020; Fernández-Gutiérrez et al., 2025).

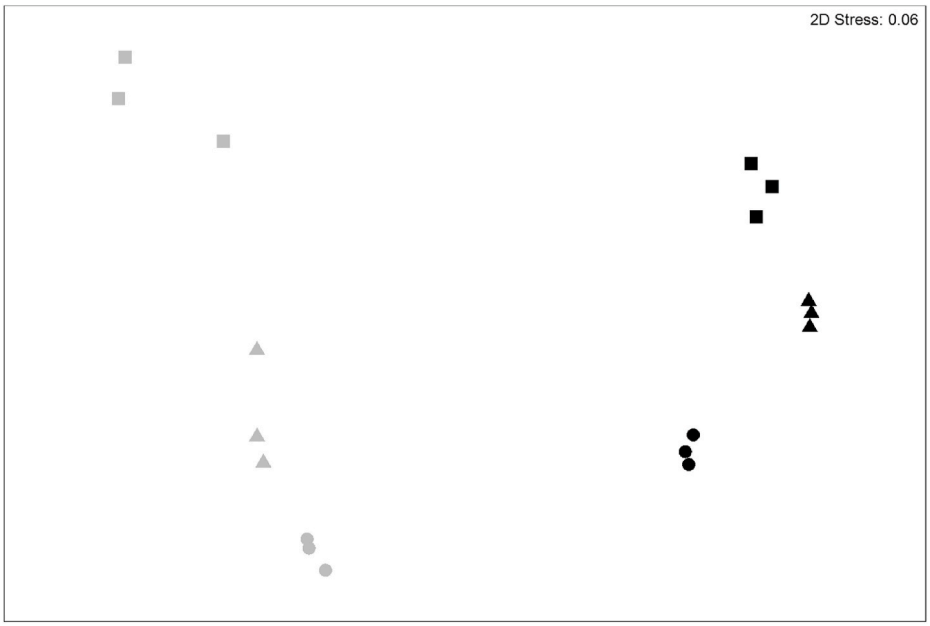


Fig. 4. nMDS plots of centroids per site and marina from brackish (grey symbols) and marine (black symbols) environments. Brackish marinas: Esposende (grey squares), Afurada (grey triangles) and Viana do Castelo (grey dots); Marine marinas: Leça da Palmeira (black squares), Póvoa do Varzim (black triangles) and Viana do Castelo (black dots).

Table 4
Results of DistLM carried out to ascertain the role of the studied surface water environmental variables (salinity, dissolved oxygen and temperature) on univariate (N and S) and multivariate data of sessile fouling assemblages. Forward-selection of variables were considered, where amount explained by each variable added to the model is conditional on variables already in the model (i.e., those variables listed above it). %Var: percentage of variance in species data explained by that variable; Cum. (%): cumulative percentage of explained variance. Variables significantly related to sessile fouling assemblages indicated in bold: *: $p < 0.05$; **: $p < 0.01$, ***: $p < 0.001$.

N				S			
Variable	Pseudo-F	%Var	Cum (%)	Variable	Pseudo-F	%Var	Cum (%)
Salinity	**60.647*****	46.421	46.421	Salinity	**89.787*****	56.192	56.192
Dissolved oxygen	0.004	0.003	46.424	Temperature	**22.396*****	10.735	66.927
Temperature	0.009	0.007	46.430	Dissolved oxygen	**5.078***	2.298	69.225

Assemblage			
Variable	Pseudo-F	%Var	Cum (%)
Salinity	**40.473*****	36.636	36.636
Temperature	**8.243*****	6.762	43.398
Dissolved oxygen	**6.308****	4.805	48.203

The third hypothesis was also supported because analyses selected salinity as the most important driver of the abundance and diversity of sessile fouling taxa associated with urban artificial structures, with significant lower values of N and S at lower salinity areas (brackish environments). These values could be explained by the location of the studied BM in estuaries subjected to high freshwater input from rivers (see Fernández-Gutiérrez et al., 2025; Veiga et al., 2025), which limits the dispersal and survival of sessile species according to each species' tolerance to low salinity (Gunter, 1961; Podbielski et al., 2022; Loiseau et al., 2024). In this line, previous studies reported a decrease in sessile fouling richness in brackish marinas under strong river inputs (Clarke Murray et al., 2014; Nall et al., 2015; Afonso et al., 2020), a pattern that has also been described in natural rocky reefs (Loiseau et al., 2024). Similarly, low salinity/freshwater inputs applied in biofouling control have shown to be useful in reducing the abundance, richness and coverage of sessile fouling invertebrates in marinas under marine salinities (Castro et al., 2018; but see Saloni and Crowe, 2015).

Concerning the multivariate structure, significant differences were detected by PERMANOVA indicating that the abundance and identity of sessile taxa differed between the studied environments. The average dissimilarity between brackish and marine assemblages was high (~84 %) and consistent with the ~94 % dissimilarity observed by Fernández-Gutiérrez et al. (2025) for NIS fouling assemblages or the 81 % dissimilarity reported by Veiga et al. (2025) for mobile fouling assemblages in the same marinas and salinity conditions. However, significant differences detected by PERMDISP suggest that the dispersion of samples could contribute to the observed differences. Warwick and Clarke (1993) hypothesized that benthic assemblages show a greater multivariate dispersion in response to different anthropogenic or natural stressors, which was empirically demonstrated in sessile communities (Roberts et al., 1998, 2006). In our study, samples from BM showed a higher dispersion, suggesting that low salinity conditions could act as an important environmental stressor shaping brackish assemblages (Van Diggelen and Montagna, 2016; Loiseau et al., 2024). Oppositely, the lower dispersion in marine conditions would be reflecting fewer variations in salinity values (Fernández-Gutiérrez et al., 2025). Despite differences on dispersion, the nMDS ordination revealed a clear separation between BM and MM according to salinity conditions and therefore a straightforward relationship between sessile fouling assemblage structure and salinity. This relationship was supported by DISTLM results,

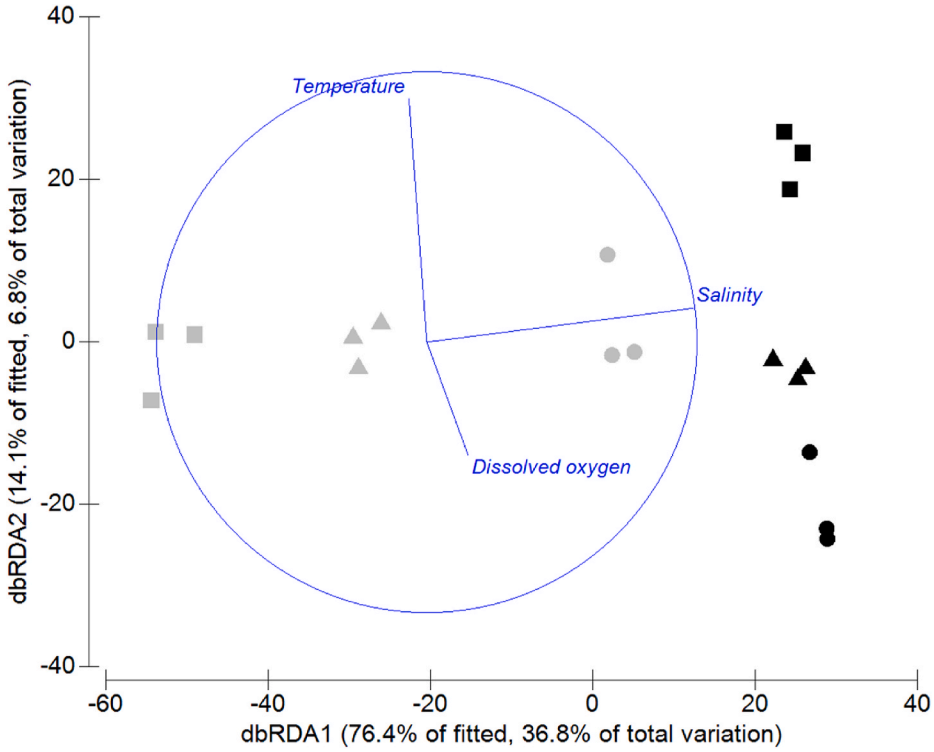


Fig. 5. Distance-based redundancy (dbRDA) plot illustrating the DISTLM model based on the sessile fouling assemblage structure of brackish (grey symbols) and marine (black symbols) environments and the fitted surface water environmental variables (salinity, temperature and dissolved oxygen) as vectors using DISTLM analysis in Table 4. Brackish marinas: Esposende (grey squares), Afurada (grey triangles) and Viana do Castelo (grey dots); Marine marinas: Leça da Palmeira (black squares), Póvoa do Varzim (black triangles) and Viana do Castelo (black dots).

which identified salinity as the only significant factor for N and the primary factor influencing S and multivariate sessile fouling assemblage structure, while temperature and dissolved oxygen contributed to a lesser extent; these results are also consistent with previous studies (Charles et al., 2018; Holmes and Callaway, 2021). Regarding the main taxa responsible for differences between BM and MM, only 2 out of 6 species were found in both environmental conditions, whereas the other 4 species were exclusively marine. The native mussel *M. galloprovincialis* was the most abundant species in both environmental conditions and was three times more abundant in MM than in BM. This pattern agrees with previous studies conducted on natural habitats and marinas in marine environments, which reported significant fewer abundances of *Mytilus* spp. under the influence of low salinity/freshwater inputs (Saloni and Crowe, 2015; Loiseau et al., 2024; Veiga et al., 2025). Despite its lower abundance in BM, *M. galloprovincialis* accounted for nearly 74 % of the total abundance. This dominance has also been reported in fouling assemblages of marinas from NW France (Leclerc et al., 2024) as well as in the northern and southern Iberian Peninsula (Fernández-Rodríguez et al., 2022; Guerra-García et al., 2021b, respectively). These findings contrast with the general pattern of NIS dominance in sessile fouling communities of pontoons described almost elsewhere (e.g. Glasby et al., 2007; Charles et al., 2018; Oricchio et al., 2019; Saenz-Arias et al., 2022; Guerra-García et al., 2025), suggesting that pontoons may serve as alternative substrates for native habitat-formers in degraded urban areas (Toh et al., 2017). In the case of mussels (but see Bulleri et al., 2022), several studies have underscored their use as nature-based solutions in ports and marinas (Firth et al., 2024 and references therein), since they can ameliorate water quality due to filtration and enhance biodiversity by increasing habitat complexity (Adams et al., 2021). Besides, most of the species found in the present study were collected as epibionts of mussels, giving account of the capacity of this habitat-forming species to sustain sessile biota in artificial structures of urban areas where biodiversity may be heavily impacted (Fernández-Rodríguez et al., 2022).

Similar to mussels, the NIS bryozoan *W. subatra* was more abundant in MM than in BM. This NIS has a great ability to colonise artificial substrates, including pontoons, and in recent years it has successfully spread along western Iberian Peninsula (Reverter-Gil and Souto, 2019). Recently, Chebaane et al. (2023) and Fernández-Gutiérrez et al. (2025) have reported this species as one of the most abundant taxa in fouling communities in North and Central Portuguese marinas under marine environmental conditions. Besides, *W. subatra* has also been recorded in brackish marinas with salinities between 20 and 30 psμ (Bishop et al., 2015; Porter et al., 2017; Fernández-Gutiérrez et al., 2025), which is in line with our observations. Nevertheless, *W. subatra* appears to be sensitive to low salinity conditions; Castro et al. (2018) reported significant mortalities at 20 psμ and 100 % mortality after exposures to 7 psμ, indicating limited tolerance of *W. subatra* to salinities below 20 psμ. Conversely, colonies of the ctenostome bryozoan *A. gracillima* were exclusively found in MM. In North and Central Portugal, it has been previously reported always in marinas under marine environmental conditions (Marchini et al., 2007; Reverter-Gil et al., 2014; Fernández-Gutiérrez et al., 2025). In natural habitats, *A. gracillima* seems to be restricted to areas with salinities above 30 psμ (Occhipinti-Ambrogi, 1985), similarly to our findings. In the same way, the serpulid worm *S. lamarcki* was found exclusively in MM. Serpulids dominate in fouling assemblages on piles and floating pontoons since early successional stages (Glasby, 1999; Connell, 2001). In general, low salinities reduces gamete production of serpulids (Gibson et al., 2001) and Castro et al. (2018) reported large mortalities of *Spirobranchus* sp. in fouling plates exposed to salinity of 7 psμ. Therefore, low salinity values may be responsible for the absence of *S. lamarcki* in BM. Indeed, greater abundances of this species have been found in estuarine areas with weak freshwater input and salinities over 30 psμ (Afonso et al., 2020; Wawrzynkowski et al., 2023). Regarding the barnacle *P. perforatus*, this species is frequent in natural and artificial hard substrata along the

Eastern Atlantic and Mediterranean Sea (Herbert et al., 2003) and was exclusively found in MM. This species can potentially cope with fluctuating salinities being however rapidly replaced towards brackish areas by more euryhaline barnacles such as *Amphibalanus* spp. or *Austrominius modestus* (Darwin, 1854) (see Saiz-Salinas and Urkiaga-Alberdi, 1999; Macho et al., 2010). In fact, salinities of about 11 psμ caused detrimental effects in *P. perforatus* larvae (Barnes and Barnes, 1974). Finally, the saddle oyster *A. ephippium* was also only present in MM. This bivalve is highly competitive in the early successional stages of the fouling communities reaching high abundances in artificial substrates (Maughan and Barnes, 2000). In Central Portugal, Chebaane et al. (2023) found a large abundance of the species on marinas under marine environmental conditions. There is few experimental work testing salinity tolerance of species of the genus *Anomia* but, *A. peruviana* d'Orbigny, 1846 experiences great mortality (75 %) under freshwater input (Schlöder et al., 2013). Moreover, Cadée (1968) reported the presence of *A. ephippium* only in the euryhaline (~33 psμ) region of the Ria of Arousa (NW Spain) and did not find this species in freshwater and brackish areas, which agrees with our results.

Our results underscore the relevant role of salinity in shaping both N and S as well as the multivariate structure of sessile fouling assemblages in urban artificial structures under brackish and marine environments. Results of multivariate regression analyses highlighted that the environmental variables here considered explained a substantial proportion of sessile fouling assemblage variability, between 46 % for the N and 69 % for the S. However, some variation remains unexplained (between 31 and 54 %) suggesting that other abiotic or biological variables did not consider in the present study may play a significant role. According to previous studies and our findings, the interplay of salinity with other relevant factors such as dissolved organic matter, dissolved oxygen, temperature, pollutants or predation may also affect the composition and diversity of sessile fouling assemblages (Charles et al., 2018; Kenworthy et al., 2018; Holmes and Callaway, 2021; Jurgens et al., 2022). Therefore, further studies are needed to fully understand the role of other environmental variables in marinas subjected to different environmental conditions. In addition, it is remarkable the great dominance of the native habitat-forming mussel *M. galloprovincialis* both in BM and MM, also hosting many epibiont species (see Veiga et al., 2025 for further details on mobile fouling invertebrates associated to mussels in the sampled marinas); this highlights the role of this species in supporting sessile epibiota in urban artificial structures (Adams et al., 2021; Fernández-Rodríguez et al., 2022; Veiga et al., 2025). Given the recent implementation of the Nature Restoration Law (EU, 2024), our data provide critical insights for habitat-specific mitigation strategies in damaged urban ecosystems such as marinas. Therefore, floating pontoons should be considered in the study area as important reservoirs of biodiversity in urban environments where species diversity is heavily impacted and natural hard bottom substrates are lack.

CRediT authorship contribution statement

Jesús Fernández-Gutiérrez: Writing – original draft, Visualization, Methodology, Investigation, Data curation. **Marcos Rubal:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Fran Ramil:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Data curation. **Juan Moreira:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Data curation. **Leandro Sampaio:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Data curation. **Isabel Sousa-Pinto:** Writing – review & editing, Visualization, Resources. **Puri Veiga:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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.

Acknowledgements

Authors would like to thank the staff of the sampled marinas for kindly providing access to their facilities and Fundação Calouste Gulbenkian for its support to the program MarUMinho. Comments by two anonymous reviewers have contributed to improving the final version of the paper. This research was funded by the project Marina-Forests (https://doi.org/10.54499/2022.06806.PTDC) funded by the Foundation for Science and Technology (FCT) and partially through national funds within the scope of UIDB/04423/2020 and UIDP/04423/2020 granted to CIIMAR and LA/P/0069/2020 (and to the Associate Laboratory ARNET and (UID/04050 – Centro de Biologia Molecular e Ambiental) to CBMA. P. Veiga (https://doi.org/10.54499/2023.08939.CEECIND/CP2848/CT0002) and M. Rubal (https://doi.org/10.54499/CEECINST/00018/2021/CP2806/CT0021) were hired through the 'Regulamento do Emprego Científico e Tecnológico—RJEC' and J. Fernández-Gutiérrez was supported by a PhD scholarship from the Portuguese Foundation for Science and Technology (FCT) with reference 2023.04100.BD and DOI identifier https://doi.org/10.54499/2023.04100.BD.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107409.

Data availability

Data of this study are included in the Supplementary Material.

References

Adams, L.W., Morris, R.L., Hull, R.B., Dempster, T., Strain, E.M.A., 2021. Making marinas bivalve friendly for enhanced biodiversity outcomes. Mar. Pollut. Bull. 169, 112464. https://doi.org/10.1016/j.marpolbul.2021.112464.

Afonso, I., Berecibar, E., Castro, N., Costa, J.L., Frias, P., Henriques, F., Moreira, P., Oliveira, P.M., Silva, G., Chainho, P., 2020. Assessment of the colonization and dispersal success of non-indigenous species introduced in recreational marinas along the estuarine gradient. Ecol. Indic. 113, 106147. https://doi.org/10.1016/j.ecolind.2020.106147.

Airoldi, L., Beck, M.W., 2007. Loss, status and trends for coastal marine habitats of Europe. Oceanogr. Mar. Biol. Annu. Rev. 45, 345–405.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, England, pp. 1–214.

Anderson, M.J., 2001a. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26 (1), 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

Anderson, M.J., 2001b. Permutation tests for univariate or multivariate analysis of variance and regression. Can. J. Fish. Aquat. Sci. 58, 626–639. https://doi.org/10.1139/f01-004.

Anderson, M.J., 2002. DISTLM v.2: a FORTRAN Computer Program to Calculate a Distance-based Multivariate Analysis for a Linear Model. Department of Statistics, University of Auckland.

Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62 (1), 245–253. https://doi.org/10.1111/j.1541-0420.2005.00440.x.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. Ecol. Monogr. 81 (2), 169–193. https://doi.org/10.1890/10-1510.1.

Barnes, H., Barnes, M., 1974. The responses during development of the embryos of some common cirripedes to wide changes in salinity. J. Exp. Mar. Biol. Ecol. 15 (2), 197–202. https://doi.org/10.1016/0022-0981(74)90045-8.

Bishop, J.D.D., Wood, C.A., Lévêque, L., Yunnie, A.L.E., Viard, F., 2015. Repeated rapid assessment surveys reveal contrasting trends in occupancy of marinas by non-indigenous species on opposite sides of the western English Channel. Mar. Pollut. Bull. 95 (2), 699–706. https://doi.org/10.1016/j.marpolbul.2014.11.043.

Bugnot, A.B., Mayer-Pinto, M., Airoldi, L., Heery, E.C., Johnston, E.L., Critchley, L.P., Strain, E.M.A., Morris, R.L., Loke, L.H.L., Bishop, M.J., Sheehan, E.V., Coleman, R.A.,

Dafforn, K.A., 2021. Current and projected global extent of marine built structures. Nat. Sustain. 4, 33–41. https://doi.org/10.1038/s41893-020-00595-1.
Bulleri, F., Chapman, M.G., 2004. Intertidal assemblages on artificial and natural habitats in marinas on the north-west coast of Italy. Mar. Biol. 145, 381–391. https://doi.org/10.1007/s00227-004-1316-8.
Bulleri, F., Chapman, M.G., 2010. The introduction of coastal infrastructure as a driver of change in marine environments. J. Appl. Ecol. 47 (1), 26–35. https://doi.org/10.1111/j.1365-2664.2009.01751.x.
Bulleri, F., Pretti, C., Bertolino, M., Magri, M., Pittaluga, G.B., Sicurrelli, D., Tardelli, F., Manzini, C., Vannini, C., Verani, M., Federigi, I., Zampieri, G., De, Marchi, 2022. Adding functions to marine infrastructure: pollutant accumulation, physiological and microbiome changes in sponges attached to floating pontoons inside marinas. Sci. Total Environ. 848, 157773. https://doi.org/10.1016/j.scitotenv.2022.157773.
Cadée, G.C., 1968. Molluscan biocoenoses and thanatocoenoses in the Ria de Arosa, Galicia, Spain. Zool. Verhandel. 95 (1), 1–121.
Castro, M.C.T., Vance, T., Yunnie, A.L.E., Fileman, T.W., Hall-Spencer, J.M., 2018. Low salinity as a biosecurity tool for minimizing biofouling on ship sea chests. Ocean Sci. 14 (4), 661–667. https://doi.org/10.5194/os-14-661-2018.
Charles, M., Faillettaz, R., Desroy, N., Fournier, J., Costil, K., 2018. Distribution, associated species and extent of biofouling "reefs" formed by the alien species *Ficopomatus enigmaticus* (Annelida, Polychaeta) in marinas. Estuarine. Coastal and Shelf Science 212, 164–175. https://doi.org/10.1016/j.ecss.2018.07.007.
Chebaane, S., Freestone, A.L., Des Pérez, A., Sempere-Valverde, J., Chainho, P., Gama Monteiro, J., Canning-Clode, J., 2023. Predation facilitates the abundance of biofouling non-indigenous species in estuarine marinas in NE Atlantic Portugal. Mar. Pollut. Bull. 188, 114724. https://doi.org/10.1016/j.marpolbul.2023.114724.
Clarke, K.R., 1993. Nonparametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x.
Clarke Murray, C., Gartner, H., Gregr, E.J., Chan, K., Pakhomov, E., Therriault, T.W., 2014. Spatial distribution of marine invasive species: environmental, demographic and vector drivers. Divers. Distrib. 20 (7), 824–836. https://doi.org/10.1111/ddi.12215.
Clynick, B.G., Chapman, M.G., Underwood, A.J., 2007. Effects of epibiota on assemblages of fish associated with urban structures. Mar. Ecol. Prog. Ser. 332, 201–210. https://doi.org/10.3354/meps332201.
Cognetti, G., Maltagliati, F., 2000. Biodiversity and adaptive mechanisms in brackish water fauna. Mar. Pollut. Bull. 40 (1), 7–14. https://doi.org/10.1016/S0025-326X(99)00173-2.
Connell, S.D., 2001. Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs. Mar. Environ. Res. 52 (2), 115–125. https://doi.org/10.1016/S0141-1136(00)00266-X.
Dafforn, K.A., Glasby, T.M., Airoldi, L., Rivero, N.K., Mayer-Pinto, M., Johnston, E.L., 2015. Marine urbanization: an ecological framework for designing multifunctional artificial structures. Front. Ecol. Environ. 13 (2), 82–90. https://doi.org/10.1890/140050.
EU. 2008, 2008. Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework directive). Orkesterjournalen L 164 (25.6), 19–40. http://data.europa.eu/eli/dir/2008/56/oj.
EU. 2024, 2024. Regulation (EU) 2024/1991 (2024) of the European Parliament and of the Council of 24 June 2024 on nature restoration and amending Regulation (EU) 2022/869. Orkesterjournalen L 2024/1991, 1–93. http://data.europa.eu/eli/reg/2024/1991/oj.
Fernández-Gutiérrez, J., Rubal, M., Sampaio, L., Moreira, J., Ramil, F., Sousa-Pinto, I., Veiga, P., 2025. Structure of non-indigenous fouling assemblages and biocontamination levels in Portuguese recreational marinas under different salinity conditions. Diversity 17 (4), 245. https://doi.org/10.3390/d17040245.
Fernández-Rodríguez, I., López-Alonso, R., Sánchez, O., Suárez-Turienzo, I., Gutiérrez-Martínez, R., Arias, A., 2022. Detection and prevention of biological invasions in marinas and ports: epibionts and associated fauna of *Mytilus galloprovincialis* revisited. Estuar. Coast Shelf Sci. 274, 107943. https://doi.org/10.1016/j.ecss.2022.107943.
Fernández-Romero, A., Moreira, J., Guerra-García, J.M., 2019. Marinas: an overlooked habitat for exploring the relation among polychaete assemblages and environmental factors. Mar. Pollut. Bull. 138, 584–597. https://doi.org/10.1016/j.marpolbul.2018.11.064.
Ferrario, J., Marchini, A., Gazzola, F., Occhipinti-Ambrogi, A., 2024. The influence of recreational boat traffic in the introduction of non-indigenous fouling species in three Ligurian marinas (Mediterranean Sea, Italy). Estuar. Coast Shelf Sci. 303, 108810. https://doi.org/10.1016/j.ecss.2024.108810.
Figueroa, N.N., Brante, A., Viard, F., Leclerc, J.C., 2021. Greater functional similarity in mobile compared to sessile assemblages colonizing artificial coastal habitats. Mar. Pollut. Bull. 172, 112844. https://doi.org/10.1016/j.marpolbul.2021.112844.
Firth, L.B., Forbes, A., Knights, A.M., O'Shaughnessy, K.A., Mahmood-Brown, W., Struthers, L., Hawcutt, E., Bohn, K., Sayer, M.D.J., Quinn, J., Allen, J., Dürr, S., Guerra, M.T., Leeper, A., Mieszkowska, N., Reid, G., Wilkinson, S., Williams, A.E., Hawkins, S.J., 2024. Ecosystem engineers enhance the multifunctionality of an urban novel ecosystem: population persistence and ecosystem resilience since the 1980s. Sci. Total Environ. 952, 175675. https://doi.org/10.1016/j.scitotenv.2024.175675.
Floerl, O., Inglis, G.J., 2003. Boat harbour design can exacerbate hull fouling. Austral Ecol. 28 (2), 116–127. https://doi.org/10.1046/j.1442-9993.2003.01254.x.
Freeman, L.A., Corbett, D.R., Fitzgerald, A.M., Lemley, D.A., Quigg, A., Steppe, C.N., 2019. Impacts of urbanization and development on estuarine ecosystems and water quality. Estuaries Coasts 42, 1821–1838. https://doi.org/10.1007/s12237-019-00597-z.
Gibson, R.N., Barnes, M., Atkinson, R.J.A., 2001. Life-History patterns in serpulimorph polychaetes: ecological and evolutionary perspectives. Oceanogr. Mar. Biol. Annu. Rev. 39, 1–101.
Glasby, T.M., 1999. Differences between subtidal epibiota on pier pilings and rocky reefs at marinas in Sydney, Australia. Estuar. Coast Shelf Sci. 48 (2), 281–290. https://doi.org/10.1006/ecss.1998.0417.
Glasby, T.M., Connell, S.D., Holloway, M.G., Hewitt, C.L., 2007. Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? Mar. Biol. 151 (3), 887–895. https://doi.org/10.1007/s00227-006-0552-5.
Glasby, T.M., Connell, S.D., 2001. Orientation and position of substrata have large effects on epibiotic assemblages. Mar. Ecol. Prog. Ser. 214, 127–135. https://doi.org/10.3354/meps214127.
Grabowska, M., Grzelak, K., Kukliński, P., 2015. Rock encrusting assemblages: structure and distribution along the Baltic Sea. J. Sea Res. 103, 24–31. https://doi.org/10.1016/j.seares.2015.05.003.
Grupo de Trabalho da Náutica de Recreio, 2012. Náutica De Recreio Em Portugal. Um Pilar do Desenvolvimento Local E Da Economia do Mar. Sinapsis Editores, Óbidos, Portugal, pp. 1–133.
Guerra-García, J.M., Martínez-Pita, I., García-García, F.J., Moreira, J., 2021b. Diversity, community structure and habitat use of molluscs in marinas from the Iberian Peninsula and Northern Africa. Ocean Coast Manag. 212, 105795. https://doi.org/10.1016/j.ocecoaman.2021.105795.
Guerra-García, J.M., Navarro-Barranco, C., Martínez-Laiz, G., Moreira, J., Giráldez, I., Morales, E., Fernández-Romero, A., Florido, M., Ros, M., 2021a. Assessing environmental pollution levels in marinas. Sci. Total Environ. 762, 144169. https://doi.org/10.1016/j.scitotenv.2020.144169.
Guerra-García, J.M., Navarro-Barranco, C., Vázquez-Luis, M., Moreira, J., César, M., Márquez, M.E., Saenz-Arias, P., Ros, M., 2025. The role of the hydroid *Eudendrium racemosum* (Cavolini, 1785) (Cnidaria: hydrozoa) as basibiont for exotic species in marinas. Estuar. Coast Shelf Sci. 315, 109180. https://doi.org/10.1016/j.ecss.2025.109180.
Gunter, G., 1961. Some relations of estuarine organisms to salinity. Limnol. Oceanogr. 6 (2), 182–190. https://doi.org/10.4319/lo.1961.6.2.0182.
Hardwick-Witman, M.N., Mathieson, C., 1983. Intertidal macroalgae and macroinvertebrates: seasonal and spatial abundance patterns along an estuarine gradient. Estuar. Coast Shelf Sci. 16 (2), 113–129. https://doi.org/10.1016/0272-7714(83)90134-8.
Herbert, R.J.H., Hawkins, S.J., Sheader, M., Southward, A.J., 2003. Range extension and reproduction of the barnacle *Balanus perforatus* in the eastern English Channel. J. Mar. Biol. Assoc. U. K. 83 (1), 73–82. https://doi.org/10.1017/S002531540300682 9h.
Holloway, M.G., Connell, S.D., 2002. Why do floating structures create novel habitats for subtidal epibiota? Mar. Ecol. Prog. Ser. 235, 43–52. https://doi.org/10.3354/meps235043.
Holmes, S., Callaway, R., 2021. Fouling communities and non-native species within five ports along the Bristol Channel, South Wales, UK. Estuarine. Coastal and Shelf Science 252, 107295. https://doi.org/10.1016/j.ecss.2021.107295.
Jimenez, H., Keppel, E., Chang, A.L., Ruiz, J.M., 2018. Invasions in marine communities: contrasting species richness and community composition across habitats and salinity. Estuaries Coasts 41, 484–494. https://doi.org/10.1007/s12237-017-0292-4.
Jurgens, L.J., Ciesielski, M., Agrawal, A., Hubbard, E., 2022. Low salinity weakens predator effects on community assembly in a sub-tropical Estuary. Estuaries Coasts 45, 2070–2081. https://doi.org/10.1007/s12237-022-01084-8.
Kenworthy, J.M., Rolland, G., Samadi, S., Lejeusne, C., 2018. Local variation within marinas: effects of pollutants and implications for invasive species. Mar. Pollut. Bull. 133, 96–106. https://doi.org/10.1016/j.marpolbul.2018.05.001.
Kummu, M., De Moel, H., Salvucci, G., Viviroli, D., Ward, P.J., Varis, O., 2016. Over the hills and further away from coast: global geospatial patterns of human and environment over the 20th–21st centuries. Environ. Res. Lett. 11 (3), 034010. https://doi.org/10.1088/1748-9326/11/3/034010.
Leclerc, J.C., Gonzalez, M., Pezy, J.P., Raoux, A., Crec'hriou, R., Broudin, C., Houbin, C., Migné, A., Loisel, S., Sevin, L., Coudret, J., Davoult, D., Charbonnelle, M., Valerdi, J. B., Schlicklin, F., Van Paemelen, R., Humbert, S., Massé, C., Viard, F., Filbee-Dexter, K., Wernberg, T., Thiébaut, E., 2024. Multi-scale patterns in the structure of fish and fouling communities associated with seaweeds in marinas. Mar. Ecol. Prog. Ser. 742, 1–19. https://doi.org/10.3354/meps14641.
Leclerc, J.C., Viard, F., 2018. Habitat formation prevails over predation in influencing fouling communities. Ecol. Evol. 8 (1), 477–492. https://doi.org/10.1002/ece3.3654.
Leclerc, J.C., Viard, F., González Sepúlveda, E., Díaz, C., Neira Hinojosa, J., Pérez Araneda, K., Silva, F., Brante, A., 2019. Habitat type drives the distribution of non-indigenous species in fouling communities regardless of associated maritime traffic. Divers. Distrib. 26 (1), 62–75. https://doi.org/10.1111/ddi.12997.
Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. Ecol. Monogr. 69, 1–24. https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2.
Lemos, R.T., Pires, H.O., 2004. The upwelling regime off the west Portuguese coast, 1941–2000. Int. J. Climatol. 24, 511–524. https://doi.org/10.1002/joc.1009.
Loiseau, V., Gendreau, Y., Calosi, P., Cusson, M., 2024. Freshwater input significantly reduces specific and functional diversity of small subarctic estuaries. Estuar. Coast Shelf Sci. 305, 108856. https://doi.org/10.1016/j.ecss.2024.108856.

Macho, G., Vázquez, E., Giráldez, R., Molares, J., 2010. Spatial and temporal distribution of barnacle larvae in the partially mixed estuary of the Ría de Arousa (Spain). J. Exp. Mar. Biol. Ecol. 392, 129–139. https://doi.org/10.1016/j.jembe.2010.04.017.

Marchini, A., Cunha, M.R., Occhipinti-Ambrogi, A., 2007. First observations on bryozoans and entoprocts in the Ria de Aveiro (NW Portugal) including the first record of the Pacific invasive cheilostome *Tricellaria inopinata*. Mar. Ecol. 28 (1), 154–160. https://doi.org/10.1111/j.1439-0485.2007.00173.x.

Maughan, B.C., Barnes, D.K.A., 2000. Seasonality of competition in early development of subtidal encrusting communities. Mar. Ecol. 21 (3–4), 205–220. https://doi.org/10.1046/j.1439-0485.2000.00703.x.

Mayer-Pinto, M., Cole, V.J., Johnston, E.L., Bugnot, A., Hurst, H., Airoldi, L., Glasby, T. M., Dafforn, K.A., 2018. Functional and structural responses to marine urbanisation. Environ. Res. Lett. 13 (1), 014009. https://doi.org/10.1088/1748-9326/aa98a5.

McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. Ecology 82, 290–297. https://doi.org/10.1890/0012-9658(2001)082[0290:FMMTCD]2.0.CO;2.

Moreira, J., Chapman, M.G., Underwood, A.J., 2006. Seawalls do not sustain viable populations of limpets. Mar. Ecol. Prog. Ser. 322, 179–188. https://doi.org/10.3354/meps322179.

Nall, C.R., Guerin, A.J., Cook, E.J., 2015. Rapid assessment of marine non-native species in northern Scotland and a synthesis of existing Scottish records. Aquat. Invasions 10 (1), 107–121. https://doi.org/10.3391/ai.2015.10.1.11.

Occhipinti-Ambrogi, A., 1985. The zonation of bryozoans along salinity gradients in the Venice lagoon (northern Adriatic). In: Nielsen, C., Larwood, G.P. (Eds.), Bryozoa: Ordovician to Recent. Olsen & Olsen, Vienna, Austria, pp. 221–231.

Oricchio, F.T., Marques, A.C., Hajdu, E., Pitombo, F.B., Azevedo, F., Passos, F.D., Vieira, L.M., Stampar, S.N., Rocha, R.M., Dias, G.M., 2019. Exotic species dominate marinas between the two most populated regions in the southwestern Atlantic Ocean. Mar. Pollut. Bull. 146, 884–892. https://doi.org/10.1016/j.marpolbul.2019.07.013.

Podbielski, I., Hiebenthal, C., Hajati, M.C., Bock, C., Bleich, M., Melzner, F., 2022. Capacity for cellular osmoregulation defines critical salinity of marine invertebrates at low salinity. Front. Mar. Sci. 9, 898364. https://doi.org/10.3389/fmars.2022.898364.

Porter, J., Nunn, J.D., Ryland, J.S., Minchin, D., Spencer Jones, M.E., 2017. The status of non-native bryozoans on the north coast of Ireland. BioInvasions Records 6 (4), 321–330. https://doi.org/10.3391/bir.2017.6.4.04.

PwC, 2018. Recreational boating in Portugal – a perspective on demand. PwC. In: https://www.pwc.pt/pt/publicacoes/pwc-nautica-em-portugal-uma-perspectiva-da-procura-2018.pdf.

Reimann, L., Vafeidis, A.T., Honsel, L.E., 2023. Population development as a driver of coastal risk: current trends and future pathways. Cambridge Prisms: Coastal Futures 1, e14. https://doi.org/10.1017/cft.2023.3.

Reverter-Gil, O., Souto, J., Fernández-Pulpeiro, E., 2014. Annotated checklist of recent marine Bryozoa from continental Portugal. Nova Acta Cient. Compostelana 21, 1–55.

Reverter-Gil, O., Souto, J., 2019. Watersiporidae (Bryozoa) in Iberian waters: an update on alien and native species. Mar. Biodivers. 49, 2735–2752. https://doi.org/10.1007/s12526-019-01003-4.

Rivero, N.K., Dafforn, K.A., Coleman, M.A., Johnston, E.L., 2013. Environmental and ecological changes associated with a marina. Biofouling 29 (7), 803–815. https://doi.org/10.1080/08927014.2013.805751.

Roberts, D.E., Cummins, S.P., Davis, A.R., Chapman, M.G., 2006. Structure and dynamics of sponge-dominated assemblages on exposed and sheltered temperate reefs. Mar. Ecol. Prog. Ser. 321, 19–30. https://doi.org/10.3354/meps321019.

Roberts, D.E., Smith, A., Ajani, P., Davis, A.R., 1998. Rapid changes in encrusting marine assemblages exposed to anthropogenic point-source pollution: a 'Beyond BACI' approach. Mar. Ecol. Prog. Ser. 163, 213–224. https://doi.org/10.3354/meps163213.

Ros, M., Guerra-García, J.M., González-Macías, M., Saavedra, Á., López-Fe, C.M., 2012. Influence of fouling communities on the establishment success of alien caprellids (Crustacea: amphipoda) in Southern Spain. Mar. Biol. Res. 9 (3), 261–273. https://doi.org/10.1080/17451000.2012.739695.

Rubal, M., Fernández-Gutiérrez, J., Carreira-Flores, D., Gomes, P.T., Veiga, P., 2023. Abundance and distribution of non-indigenous Calyptraeidae gastropods along north and central Atlantic shores of Portugal. Cont. Shelf Res. 269, 105138. https://doi.org/10.1016/j.csr.2023.105138.

Saenz-Arias, P., Navarro-Barranco, C., Guerra-García, J.M., 2022. Influence of environmental factors and sessile biota on vagile epibionts: the case of amphipods in marinas across a regional scale. Mediterr. Mar. Sci. 23 (1), 1–13. https://doi.org/10.12681/mms.26800.

Saiz-Salinas, J.J., Urkiaga-Alberdi, J., 1999. Faunal responses to turbidity in a man-modified bay (Bilbao, Spain). Mar. Environ. Res. 47 (4), 331–347. https://doi.org/10.1016/S0141-1136(98)00124-X.

Saloni, S., Crowe, T.P., 2015. Impacts of multiple stressors during the establishment of fouling assemblages. Mar. Pollut. Bull. 91 (1), 211–221. https://doi.org/10.1016/j.marpolbul.2014.12.003.

Schlöder, C., Canning-Clode, J., Saltonstall, K., Strong, E.E., Ruiz, G.M., Torchin, M.E., 2013. The Pacific bivalve *Anomia peruviana* in the Atlantic: a recent invasion across the Panama Canal? Aquat. Invasions 8 (4), 443–448. https://doi.org/10.3391/ai.2013.8.4.08.

Simkanin, C., Davidson, I.C., Dower, J.F., Jamieson, G., Therriault, T.W., 2012. Anthropogenic structures and the infiltration of natural benthos by invasive ascidians. Mar. Ecol. 33 (4), 499–511. https://doi.org/10.1111/j.1439-0485.2012.00516.x.

Tempesti, J., Langeneck, J., Lardicci, C., Maltagliati, F., Castelli, A., 2023. Cut the rope: Short-term colonization of mooring lines by fouling community within the port of Livorno (Northern Tyrrhenian Sea, Western Mediterranean), focusing on alien species recruitment. Mar. Environ. Res. 189, 106041. https://doi.org/10.1016/j.marenvres.2023.106041.

Toh, K.B., Ng, C.S.L., Wu, B., Toh, T.C., Cheo, P.R., Tun, K., Chou, L.M., 2017. Spatial variability of epibiotic assemblages on marina pontoons in Singapore. Urban Ecosyst. 20, 183–197. https://doi.org/10.1007/s11252-016-0589-2.

Ulman, A., Ferrario, J., Forcada, A., Seebens, H., Arvantidis, C., Occhipinti-Ambrogi, A., Marchini, A., 2019. Alien species spreading via biofouling on recreational vessels in the Mediterranean Sea. J. Appl. Ecol. 56 (12), 2620–2629. https://doi.org/10.1111/1365-2664.13502.

UN. 2015, 2015. Transforming our World: the 2030 Agenda for Sustainable Development, A/RES/70/1, pp. 1–35. https://www.refworld.org/legal/resolution/unga/2015/en/111816.

Valdor, P.F., Gómez, A.G., Juanes, J.A., Kerléguer, C., Steinberg, P., Tanner, E., MacLeod, C., Knights, A.M., Seitz, R.D., Airoldi, L., Firth, L.B., Crowe, T., Chatzinikolaou, E., Smith, A., Arvanitidis, C., Burt, J.A., Brooks, P.R., Ponti, M., Soares-Gomes, A., Ovejero, A., Méndez, G., 2019. A global atlas of the environmental risk of marinas on water quality. Mar. Pollut. Bull. 149, 110661. https://doi.org/10.1016/j.marpolbul.2019.110661.

Van Diggelen, A.D., Montagna, P.A., 2016. Is salinity variability a benthic disturbance in estuaries? Estuaries Coasts 39, 967–980. https://doi.org/10.1007/s12237-015-0058-9.

Veiga, P., Moreira, J., Sampaio, L., Fernández-Gutiérrez, J., Rubal, M., 2025. Interplay of salinity and *Mytilus galloprovincialis* abundance in vagile fouling assemblages in recreational marinas. Estuaries Coasts 48, 143. https://doi.org/10.1007/s12237-025-01586-1.

Warwick, R.M., Clarke, K.R., 1993. Increased variability as a symptom of stress in marine communities. J. Exp. Mar. Biol. Ecol. 172 (1–2), 215–226. https://doi.org/10.1016/0022-0981(93)90098-9.

Wawrzynkowski, P., Bustamante, M., Tajadura, F.J., Becerro, M.A., 2023. Evaluating ocean health and restoration success: a comprehensive study of the benthic quality index in the Bilbao estuary. Estuar. Coast Shelf Sci. 292, 108454. https://doi.org/10.1016/j.ecss.2023.108454.

Wrange, A.-L., Barboza, F.R., Ferreira, J., Eriksson-Wiklund, A.-K., Ytreberg, E., Jonsson, P.R., Watermann, B., Dahlström, M., 2020. Monitoring biofouling as a management tool for reducing toxic antifouling practices in the Baltic Sea. J. Environ. Manag. 264, 110447. https://doi.org/10.1016/j.jenvman.2020.110447.