

Facilitation of macrofaunal assemblages in marinas by the habitat-forming invader *Amathia verticillata* (Bryozoa: Gymnolaemata) across a spatiotemporal scale

J.M. Guerra-García^{a,*}, S. Ruiz-Velasco^a, C. Navarro-Barranco^a, J. Moreira^b, G. Angulo^a, R. García-Domínguez^a, J. Amengual^a, P. Saenz-Arias^a, C.M. López-Fé^a, I. Martínez-Pita^c, F.J. García-García^c, M. Ros^a

^a Laboratorio de Biología Marina, Departamento de Zoología, Facultad de Biología, Universidad de Sevilla, Avda Reina Mercedes 6, 41012, Sevilla, Spain

^b Departamento de Biología (Zoología) & Centro de Investigación en Biodiversidad y Cambio Global (CIBC-UAM), Universidad Autónoma de Madrid, Cantoblanco 28049, Madrid, Spain

^c Departamento de Sistemas Físicos, Químicos y Naturales, Universidad Pablo de Olavide, Carretera de Utrera km 1, 41013, Sevilla, Spain

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ABSTRACT

Widespread habitat-forming invaders inhabiting marinas, such as the spaghetti bryozoan *Amathia verticillata*, allow exploring facilitation processes across spatiotemporal contexts. Here we investigate the role of this bryozoan as habitat for native and exotic macrofaunal assemblages across different ecoregions of Western Mediterranean and East Atlantic coasts, and a monthly variation over a year. While only 7 (all peracarid crustaceans) of the 54 associated species were NIS, they dominated macrofaunal assemblages in terms of abundance, raising the potential for invasional meltdown. NIS richness and community structure differed among marinas but not among ecoregions, highlighting the importance of marina singularities in modulating facilitation at spatial scale. Despite facilitation did not depend on bryozoan abundance fluctuations, it was affected by its deciduous pattern, peaking in summer and disappearing in late winter. Monitoring *A. verticillata* in marinas, especially in summer periods, may improve the detection and management of multiple associated NIS.

1. Introduction

Facilitative or positive interactions are encounters between organisms that benefit at least one of the participants and cause harm to neither (Bruno et al., 2003). Epibiosis provides an excellent model to understand facilitation (Lazzeri and Auker, 2022), and habitat-forming species play critical roles in facilitating epibiota, as shown by the abundance and diversity of its epibionts (Bruno et al., 2003; Thornber et al., 2016). In this sense, arborescent invaders growing on artificial habitats (e.g. marinas and vessel hulls) may facilitate the establishment and subsequent spread of their associated species, including NIS (Floerl et al., 2004). Despite this potential risk, the facilitator role of fouling basibiota has been scarcely studied and the factors affecting this process across environmental gradients are poorly understood (Firth et al., 2021). This is particularly important in hot spots for biological introductions, such as marinas.

The widespread habitat-forming species *Amathia verticillata* (delle

Chiaje, 1822) (Bryozoa: Gymnolaemata), previously named *Zoobotryon verticillatum*, is commonly known as the 'spaghetti bryozoan' because of the erect, arborescent, and stoloniferous appearance of their colonies. These consist of thick transparent stolons with a trifurcated branching pattern (Vieira et al., 2014; Waeschenbach et al., 2015). It is a generalist species, being able to survive in variable environmental conditions and in multiple habitats (Marchini et al., 2015; Humara-Gil and Cruz-Gómez, 2019). It overgrows a wide range of artificial and natural substrates, including vessel hulls, pontoons, rocky shores, macroalgae, mangroves, oysters and gorgonians (Aslam et al., 2019 and references therein). This bryozoan is a common integrant of the fouling communities where it can form extensive and massive colonies (Minchin et al., 2016). The species can rapidly colonize, cover, and dominate large areas, infesting ports, marinas, ships, pipelines and industrial marine installations (Gestoso et al., 2018; Nascimento et al., 2021). It can reach new areas via larvae or through detached colonies due to mechanical removal, reattaching and colonizing a wide variety of substrates

* Corresponding author.

E-mail address: jmguerra@us.es (J.M. Guerra-García).

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(Marchini et al., 2015). Although ballast waters can contribute to the dispersal of the species (Robinson and Walters, 2003), the lecithotrophic and short-living larvae of this bryozoan probably limits its autonomous dispersal capabilities (Minchin, 2012; Miranda et al., 2018). Alternatively, *A. verticillata* can easily spread by hull fouling (Marchini et al., 2015; Miranda et al., 2018; Humara-Gil and Cruz-Gómez, 2019). Indeed, this bryozoan is considered better adapted to hull fouling than other substrates due to the persistence of its broad and robust stolon under high hydrodynamic conditions (Marchini et al., 2015). For these reasons, *A. verticillata* is among the most recorded species in Mediterranean ports and marinas (Minchin et al., 2012; Tempesti et al., 2020) and is one of the mostly observed on boat hulls across the Central and Western Mediterranean (Ferrario et al., 2019; Ulman et al., 2019).

Amathia verticillata is widely distributed in temperate and tropical areas. Like other bryozoan species with cosmopolitan distribution, it was initially expected to represent a complex of cryptic species. Nevertheless, Nascimento et al. (2021), based on molecular data, suggested that *A. verticillata* is a single species, whose broad distribution has been mediated by humans. Its frequent occurrence on boat hulls and pontoons of harbours and marinas explains its fast dispersal worldwide (Minchin, 2012; Aslam et al., 2019). This wide distribution causes confusion about its origin area. The species has been considered cryptogenic with unknown native origin (Floerl et al., 2009; Nascimento et al., 2021), native to the Caribbean Sea (Winston, 1995), native to Atlantic Ocean (Ouni-Ben Amor et al., 2016) and even a native to the Mediterranean since the species was originally described from Naples, Italy in 1822. Some authors consider it as 'pseudo-indigenous' species in the Mediterranean (Marchini et al., 2015) based on its potential arrival there with shipping by the 18th or early 19th centuries (Cranfield et al., 1998; Carlton and Eldredge, 2009). Galil and Gevili (2014) proposed that *A. verticillata* is truly a native to the Caribbean and an exotic elsewhere (including the Mediterranean Sea). This suggestion is based on the occurrence of this bryozoan in natural habitats of the Caribbean and on its association with the native mollusc *Okenia zoobotryon* (Smallwood, 1910). This Caribbean nudibranch lives, feeds and reproduces exclusively on *A. verticillata*, so organisms exhibiting such specialized interaction are expected to have evolved closely (Galil and Gevili, 2014). According to this, *A. verticillata* would have been introduced to many areas, and presently, it should be considered as one of the most invasive NIS occurring worldwide from Mediterranean to tropical environments within the Atlantic and Indo-Pacific Oceans (Minchin et al., 2016). In fact, this species is treated as one of the most common exotic bryozoans throughout the Mediterranean (Ferrario et al., 2018).

Due to its spreading capacity and its high invasion potential, *A. verticillata* can impact biodiversity and ecosystem functioning worldwide and cause several ecological and economic impacts (Winston, 1995; Gosset et al., 2004; Molnar et al., 2008; Marchini et al., 2015; McCann et al., 2015; Minchin et al., 2016; Jebakumar et al., 2017; Kumar et al., 2022). It may cover boat hulls, structures of harbours and marinas and fishing gear (Minchin, 2012; Galil and Gevili, 2014; Marchini et al., 2015). It can also block intake pipes on vessels, industrial plants, commercial salt ponds and even turtle exclusion devices (Hogarth, 2000; McCann et al., 2015 and references therein). Regarding its ecological impacts, it can affect food web dynamics, removing large volumes of plankton (Amat and Tempera, 2009) and competing with native species. In fact, it is remarkable the mortality provoked in the seagrass *Zostera marina* by shading and biofouling leading to canopy collapse (Williams, 2007). Recently, invasion of this bryozoan over gorgonians has also been reported (Kumar et al., 2022).

Although *A. verticillata* serves as a basibiont for many organisms, including NIS, the facilitator role as host substrate for NIS has been scarcely explored (Marchini et al., 2015; Mioni and Furfaro, 2022). The information of its associated community is incomplete, and a comprehensive survey of the whole macrofaunal assemblages associated with *A. verticillata* is still lacking. The arborescent structure, massive growth and widespread distribution of *A. verticillata* make it a suitable target

species to explore facilitation processes at large scales by providing habitat for macrofaunal assemblages. In addition to increasing ecological knowledge, studying the structure and composition of associated NIS across a spatiotemporal scale can improve predictive models and management strategies to simultaneously address the spread of these NIS. The required taxonomic effort to address this issue would contribute directly to improve the baseline knowledge for the early detection of new arrivals in hot spots of species introductions. Considering all this, we aim to examine the facilitative role of *A. verticillata* in marinas by providing habitat for mobile macrofaunal assemblages, and the main abiotic drivers modulating this process across a spatiotemporal scale. Since positive interactions among non-indigenous species (NIS) may increase invasion success in various ways (Simberloff and von Holle, 1999), we also assess the potential of *A. verticillata* to trigger invasional meltdown phenomena (measured as high diversity and/or abundance of associated NIS).

2. Material and methods

2.1. Study area

The study was conducted along the Atlantic and Mediterranean coasts of the Iberian Peninsula and Northern Africa. The area has remarkable biogeographical interest since encompasses three ecoregions as defined by Spalding et al. (2007): South European Atlantic Shelf, Western Mediterranean, and Alboran Sea (Fig. 1). These correspond with four of the five official demarcations of the Spanish



Fig. 1. Study area showing the location of the 68 marinas surveyed for the present study along the Iberian Peninsula and Northern Africa. White circles indicate marinas where *Amathia verticillata* was absent, while black circles indicate the marinas where it was present. The three ecoregions considered in the study (see Spalding et al., 2007) are marked in the map. FAR: Faro, CHI: Chipiona, ROT: Rota, AME: Puerto América, CEU: Ceuta, SMI: Marina-Smir, DIQ: M-Diq, ALM: Almería, BEN: Benicarló, VIL: Vilanova i la Geltrú, BAR: Barcelona, EST: L'Estartit.

jurisdictional waters for the implementation of the Marine Strategy Framework Directive: North Atlantic (NOR) and South Atlantic (SUR) (both included in the South European Atlantic Shelf of Spalding et al., 2007), Straits and Alboran (ESAL) and Eastern and Balearic demarcation (LEBA) (Gofas et al., 2017).

2.2. Sampling surveys

A spatial study was conducted along the whole Iberian Peninsula, also including several locations at Northern Africa (Fig. 1). Pontoons of 68 marinas were surveyed from May to June 2011 (late spring and early summer) (Fig. 1, Table S1). *Amathia verticillata* was present in 12 marinas belonging to Spain, Portugal and Morocco (four located in each ecoregion, Table S1, Figs. 1 and 2), which were consequently selected for this work. Three colonies of *A. verticillata* were haphazardly collected from the lateral submerged area of pontoons at each marina, close to the water surface. Each colony was directly removed by hand, kept in a plastic container, and preserved in 96% ethanol.

An additional temporal study was conducted over the period of one year in the Puerto América marina, Cádiz, which is next to the Port of Cádiz, a major international port in Southern Spain. This marina is located in the Strait of Gibraltar, considered an important region for commercial and recreational maritime traffic, and a hot spot for biological invasions (see Drake and Lodge, 2004). Indeed, Puerto América marina has been suggested as an excellent location for studying fouling communities on artificial substrates and an appropriate scenario for monitoring settlement of NIS (Ros et al., 2013a; Gavira-O'Neill et al., 2018). Field procedure was the same as that used for the spatial study, and three colonies of *A. verticillata* were haphazardly collected monthly from December 2011 to December 2012.

In the laboratory, associated epifauna of each sample were removed from *A. verticillata* by washing over a 0.5-mm sieve with fresh water.

Following the same criteria described by Sánchez-Moyano et al. (2000), all mobile epifauna was selected, as well as solitary sessile/sedentary organisms such as polychaetes and bivalves. Associated organisms were sorted, identified to species level whenever possible, and counted. Species names and systematic arrangement of taxa follows the World Register of Marine Species (WoRMS Editorial Board, 2023). Volume of *A. verticillata* samples was measured as the difference between the initial and final volume when placed into a graduated cylinder with a fixed amount of water (see Pereira et al., 2006; Ros et al., 2013a). To allow standardized comparisons, abundances of epifaunal species were expressed as number of individuals/1000 ml of substrate (*A. verticillata*).

2.3. Environmental variables

For the spatial and temporal study, three random measurements of salinity, temperature and turbidity were made *in situ* in each marina and sampling survey (see Ros et al., 2015). Salinity (psu) and temperature (°C) were measured using a conductivity meter CRISON MM40 and turbidity (ntu), using a turbidimeter WTW 335 IR. Additionally, for the spatial study, three surface seawater samples were collected in each marina and kept cold until analytical procedures in the laboratory. Analysis of major, minor and trace elements (P, S, Cd, Cr, Cu, Mn, Ni, Pb and Zn) was performed using a VARIAN ICP 720-ES (simultaneous ICP-OES with axially viewed plasma), equipped with ultrasonic nebulizer CETAC U5000AT + after filtration through Nylon filters (pore size = 0.45 µm) and acidification with 2% HNO₃ (30% v/v) (see Guerra-García et al., 2021a for more methodological details). Total organic carbon (TOC) was analysed on a Shimadzu TOC-VCSH with ASI-V auto sampler after filtration through Whatman 1 paper (pore size = 11 µm). It was obtained by the difference between total carbon (TC) and total inorganic carbon (TIC) which was removed by acidification and measured separately. Additionally, human population density (mean

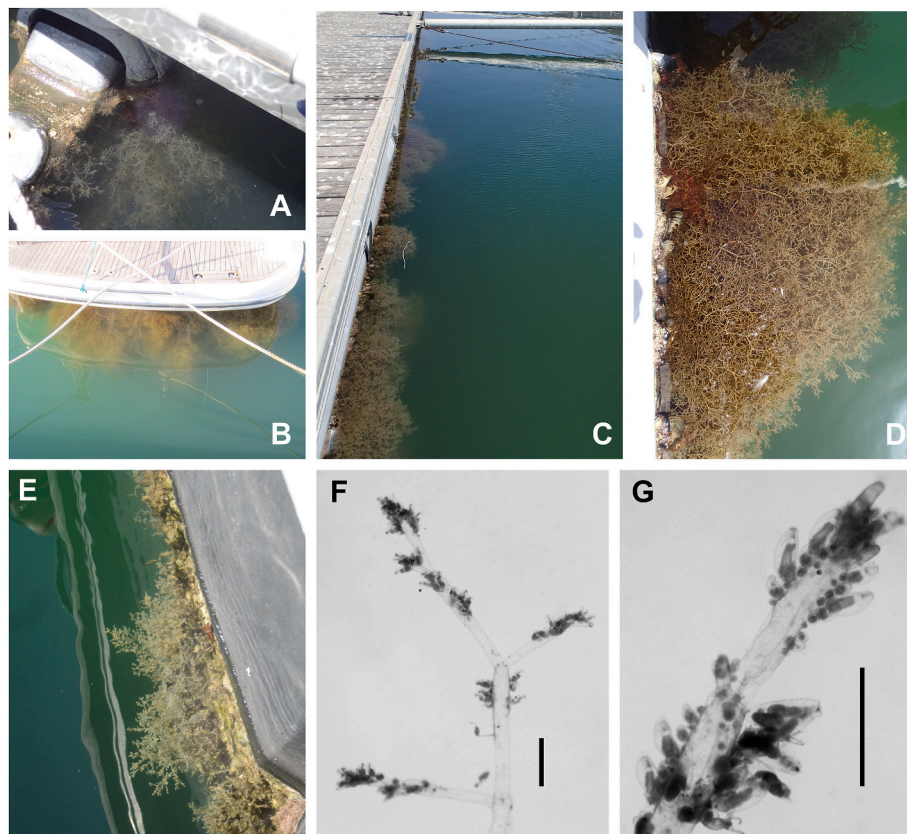


Fig. 2. Colonies of *Amathia verticillata* attached to leisure craft hulls (A,B) and floating pontoons (C–E). F,G: Details of stolon with zooids of a colony of *A. verticillata* from Puerto América marina. Scale bars: 1 mm.

number of people per km² inhabiting the locality in which each marina belongs) and number of marina berths were also included (data taken from Ros et al., 2015; Fernández-Romero et al., 2019). To explore if the abundance of *A. verticillata* could affect the epifaunal community, its frequency of occurrence was measured in each marina and sampling survey (Ros et al., 2013a, 2015; Guerra-García et al., 2015; Gaviña-O'Neill et al., 2018). This was achieved by placing 20 random 20 × 20 cm quadrats along the pontoon system. Each quadrat was placed perpendicular to the water surface, on the lateral surface of the pontoons. Presence/absence of *A. verticillata* in each quadrat was immediately recorded and data were expressed as frequency of occurrence in percentage (e.g. if *A. verticillata* was found in the 20 quadrats samples, it had a frequency of 100%, and if it only appeared in one quadrat, it had a frequency of 5%).

2.4. Statistical analyses

For the spatial study, the experimental design to compare the epifaunal assemblages (total community and NIS) in marinas from the Iberian Peninsula and Northern Africa included two factors, 'Ecoregion', a fixed factor with three levels (South European Atlantic Shelf, Alboran Sea and Western Mediterranean), and 'Marina', a random factor with four levels nested within Ec. The design for the temporal study in Puerto América marina included a single fixed factor 'Month' [Mo] with 10 levels (10 monthly sampling surveys, from December 2011 to December 2012, since *A. verticillata* was absent February, March and April 2012). The number of replicates was $n = 3$ in both studies, corresponding with the three samples of *A. verticillata* collected for each marina and sampling event.

For each replicate, total number of species, number of NIS, total abundance and abundance of NIS (individuals/1000 ml *A. verticillata*) were calculated. To compare these community descriptive parameters, two-way ANOVA (spatial study) and one-way ANOVA (temporal study) were conducted following the above experimental design. Homogeneity of variances was checked using Cochran's test and transformations were applied when necessary. When variances remained heterogeneous even after data transformation, untransformed data were still analysed, as ANOVA is a robust statistical test and is relatively unaffected by the heterogeneity of variances, particularly in balanced experiments (Underwood, 1997). In such cases, to reduce type I error, a significant level of $p < 0.01$ was considered.

Differences in the total and NIS community structure among ecoregions and marinas (spatial study) were tested by permutational multivariate analyses of variance (PERMANOVA), using the same experimental design explained above. Additional PERMANOVA was conducted to explore differences among months (temporal study). Analyses were based on Bray-Curtis similarities. Significant P-values were obtained by computing 9999 permutations with the method 'permutation of residuals under a reduced model' for the spatial study (two factors), and the method 'unrestricted permutation of raw data' for the temporal study (single factor) (Anderson, 2005). Additionally, to test the dispersion among samples for the factors 'Ecoregion', 'Marina' and 'Month', a permutational analysis of multivariate dispersions (PERMDISP) was also used (999 permutations). Non-parametric multidimensional scaling (MDS) was carried out to show the relationship among ecoregions and marinas, according to the total and NIS community assemblages (based on species composition and their abundance). Relative level of acceptable stress for MDS were checked following Sturrock and Rocha (2000).

Distance-based linear modelling (DistLMs) was used to assess the relative contribution of environmental parameters to the variability observed in total and in NIS community structure (Anderson et al., 2008). DistLMs were conducted for both, spatial (temperature, salinity, turbidity, TOC, P, S, Cd, Cr, Cu, Mn, Ni, Pb, Zn, frequency of occurrence of *A. verticillata*, number of berths and population density) and temporal study (temperature, salinity, turbidity and frequency of occurrence of

A. verticillata). The analyses were performed based on the matrix of square-root transformed abundance data. Abiotic data were transformed by $\log(x+1)$ and normalized to reduce the effects of differences in unit scales. The model was constructed using the best combination of predictors (Best procedure) using AIC (Akaike's Information Criteria) (Leonardi et al., 2020; Mulik et al., 2020; Wei et al., 2020; Guerra-García et al., 2021b). Prior to the DistLM analysis, multicollinearity between abiotic factors and skewness of data were evaluated using Draftsman plot based on Spearman correlations (Guerra-García et al., 2021b). Additionally, for the spatial study, distance-based Redundancy Analysis (dbrDA) was performed to provide a visual representation of the total and NIS community fitted to the significant predictor variables in the multi-dimensional space (Mulik et al., 2020; Wei et al., 2020). The BEST routine (BIO-ENV) was also employed to explore correlations between the matrix of faunal abundances (total and NIS) and environmental predictors (Anderson et al., 2008). The Bray-Curtis similarities matrix was based on faunal abundances while the Euclidean distances-based matrices derived from all the possible sequential combinations of the environmental variables. Spearman rank coefficient was used to identify the best environmental variables that explained the observed patterns on 999 permutations.

PERMANOVA, PERMDISP, MDS, DistLM, dbrDA and BIO-ENV analyses were carried out using the PRIMER v.6+PERMANOVA package (Anderson et al., 2008). ANOVA analyses were conducted on the GMAV5 software (Underwood et al., 2002).

3. Results

3.1. Spatial study

3.1.1. Macrofaunal community and NIS

Regarding associated macrofauna, 2664 individuals belonging to at least 41 species were found in *A. verticillata* during the spatial study along Iberian Peninsula and Northern Africa. Arthropoda was the dominant phylum (23 species, 95% of the total abundance, TA), followed by Annelida (13 species, 4% TA) and Mollusca (5 species, 1% TA). Within Arthropoda, Superorder Peracarida was the most abundant taxa. Three orders of peracarids comprised 99.9% of all arthropods: Amphipoda (78% TA), Tanaidacea (14% TA) and Isopoda (7.9% TA). Five NIS were found (Table 1, Table S2, Figs. 3 and 4), all of them corresponding to peracarid crustaceans: the amphipods *Caprella scaura*, *Jassa slatteryi* and *Laticorophium baconi*, and the isopods *Paracerceis sculpta* and *Paranthura japonica*.

Concerning the total number of species per marina, Marina-Smir in Morocco showed the highest species richness (14 species) followed by the Western Mediterranean marinas Benicarló, Vilanova i la Geltrú and L'Estartit (13 species) (Table 1). This pattern was also obtained for the number of species per replicate (Fig. 5). In terms of species richness, NIS represented only a fraction (usually less than the half) of the total number of species per replicate (Fig. 5). However, in terms of abundance NIS dominated the community (Fig. 5). In fact, the five NIS (representing only 12% of the total number of species) comprised 60% of the total abundance.

According to the ANOVA results, the total number of species and the number of NIS differed significantly among marinas, although no differences were obtained for the factor 'Ecoregion' (Table 2). Neither 'Ecoregion' nor 'Marina' had significant influence on the total and NIS abundances (Table 2). Based on the structure of the total and NIS community, PERMANOVA confirmed significant differences among marinas, without differences among ecoregions (Table 3). The two-dimensional MDS supported this pattern showing no clear segregation of ecoregions (Fig. 6).

3.1.2. Influence of environmental data on macrofaunal assemblages

Regarding *A. verticillata* abundance, Faro (Portugal), Marina-Smir (Morocco) and Barcelona (Spain) marinas showed the highest values

Table 1

List of macrofaunal species associated to the bryozoan *Amathia verticillata* in marinas from the Iberian Peninsula and Northern Africa. Light blue: 1–100 ind/1000 ml; medium blue: 101–1000 ind/1000 ml; dark blue: >1000 ind/1000 ml. Abundance data are included in Table S2. Relative abundance of *A. verticillata* (frequency of occurrence) in each marina is also included. Light orange: <20%; medium orange: 20–40%; dark orange: >40 %. FAR: Faro, CHI: Chipiona, ROT: Rota, AME: Puerto América, CEU: Ceuta, SMI: Marina Smir, DIQ: M-Diq, ALM: Almería, BEN: Benicarló, VIL: Vilanova i la Geltrú, BAR: Barcelona, EST: L'Estartit. NIS are indicated with an asterisk. ¹Ros et al., 2013b; ²Saenz-Arias et al., 2022a, 2022b; ³Martínez-Laiz et al., 2018.

	S.E.ATLANTIC SHELF				ALBORAN SEA				W.MEDITERRANEAN			
	FAR	CHI	ROT	AME	CEU	SMI	DIQ	ALM	BEN	VIL	BAR	EST
<i>Amathia verticillata</i> (delle Chiaje, 1822)	Dark Orange	Dark Orange	Dark Orange	Dark Orange	Dark Orange	Dark Orange	Dark Orange	Dark Orange	Dark Orange	Dark Orange	Dark Orange	Dark Orange
Phylum Annelida												
Class Polychaeta												
<i>Amphiglena mediterranea</i> (Leydig, 1851)								Dark Blue		Light Blue		
<i>Cirratulus</i> sp.					Dark Blue							Light Blue
<i>Ctenodrilus serratus</i> (Schmidt, 1857)							Dark Blue					
<i>Exogone naidina</i> Örsted, 1845							Light Blue					
<i>Hydroides</i> sp.				Dark Blue					Dark Blue	Light Blue	Dark Blue	
<i>Janua heterostropha</i> (Montagu, 1803)							Light Blue	Light Blue				Dark Blue
<i>Lumbrineris coccinea</i> (Renier, 1804)							Light Blue					
<i>Platynereis</i> sp. (juveniles)								Light Blue				
Sabellidae undet. (juveniles)										Dark Blue		
<i>Salvatoria clavata</i> (Claparède, 1863)						Dark Blue	Dark Blue	Light Blue				Dark Blue
<i>Sphaerosyllis pirifera</i> Claparède, 1868						Dark Blue	Dark Blue	Light Blue				Light Blue
<i>Spirorbis</i> sp.										Light Blue		
<i>Syllidia armata</i> Quatrefages, 1866		Light Blue		Dark Blue								
Phylum Arthropoda												
Class Malacostraca												
Order Amphipoda												
<i>Caprella equilibra</i> Say, 1818					Dark Blue		Dark Blue					
* ¹ <i>Caprella scaura</i> Templeton, 1836	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue
Corophiidae undet.	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue
<i>Coxischyrocerus inexpectatus</i> (Ruffo, 1959)	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue
<i>Elasmopus rapax</i> Costa, 1853	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue
<i>Erichthonius</i> spp.												
* ² <i>Jassa slatteryi</i> Conlan, 1990												
* ² <i>Laticorophium baconi</i> (Shoemaker, 1934)	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue
<i>Lembos websteri</i> Spence Bate, 1857	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue
<i>Monocorophium acherusicum</i> (Costa, 1853)	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue
<i>Monocorophium sextonae</i> (Crawford, 1937)	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue
<i>Phthisica marina</i> Slabber, 1769	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue
<i>Stenothoe</i> sp.	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue
Order Isopoda												
<i>Dynamene edwardsi</i> (Lucas, 1849)							Dark Blue	Dark Blue		Dark Blue		Dark Blue
<i>Ianiropsis</i> cf. <i>breviremis</i> (G.O. Sars, 1883)										Dark Blue		Dark Blue
* ³ <i>Paracerceis sculpta</i> (Holmes, 1904)	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue	Dark Blue
* ³ <i>Paranthura japonica</i> Richardson, 1909							Light Blue	Light Blue	Light Blue	Light Blue	Light Blue	Light Blue
Order Tanaidacea												
<i>Chondrochelia</i> cf. <i>savignyi</i> (Kroyer, 1842)										Light Blue		Light Blue
<i>Tanais dulongii</i> (Audouin, 1826)		Dark Blue					Dark Blue	Dark Blue		Dark Blue		Dark Blue
<i>Zeuxo</i> sp.				Light Blue			Dark Blue	Dark Blue		Dark Blue		Dark Blue
Order Decapoda												
<i>Palaemon serratus</i> (Pennant, 1777)										Light Blue		
<i>Pisidia bluteli</i> (Risso, 1816)				Light Blue								
Class Hexapoda												
Diptera undet. (larvae)		Light Blue										
Phylum Mollusca												
Class Bivalvia												
<i>Musculus subpictus</i> (Cantraine, 1835)							Dark Blue			Dark Blue	Dark Blue	
<i>Mytilus galloprovincialis</i> Lamarck, 1819										Dark Blue	Dark Blue	
Class Gastropoda												
<i>Bittium reticulatum</i> (da Costa, 1778)							Light Blue					
<i>Rissoa parva</i> (da Costa, 1778)	Dark Blue											
<i>Peringia ulvae</i> (Pennant, 1777)		Light Blue										



Fig. 3. NIS associated with *Amathia verticillata*. A: *Caprella scaura*, B: *Paracaprella pusilla*, C: *Jassa slatteryi*, D: *Stenothoe georgiana*, E: *Laticorophium baconi*, F: *Paracerceis sculpta*, G: *Paranthura japonica*. Five species (A,C,E,F,G) were present in the spatial study and the seven were found along the temporal study. Scale bars: 1 mm. Photos were taken of specimens collected in Puerto América marina.



Fig. 4. Specimens of *Caprella scaura* (left: male, right: female) attached to a colony of *Amathia verticillata* from Rota marina. Scale bar: 1 mm.

based on frequency of occurrence data (Table 1 above). A full dataset of environmental data measured in water of the 12 studied marinas (where *A. verticillata* was present) is provided in Table S3.

According to the DistLM, the environmental variables which significantly correlated with the whole epifaunal community were Cr (17.9% of variation explained, Pseudo-F = 2.17, p = 0.02), Ni (17.7%, Pseudo-F = 2.15, p = 0.021) and P (14.5%, Pseudo-F = 1.70, p = 0.035).

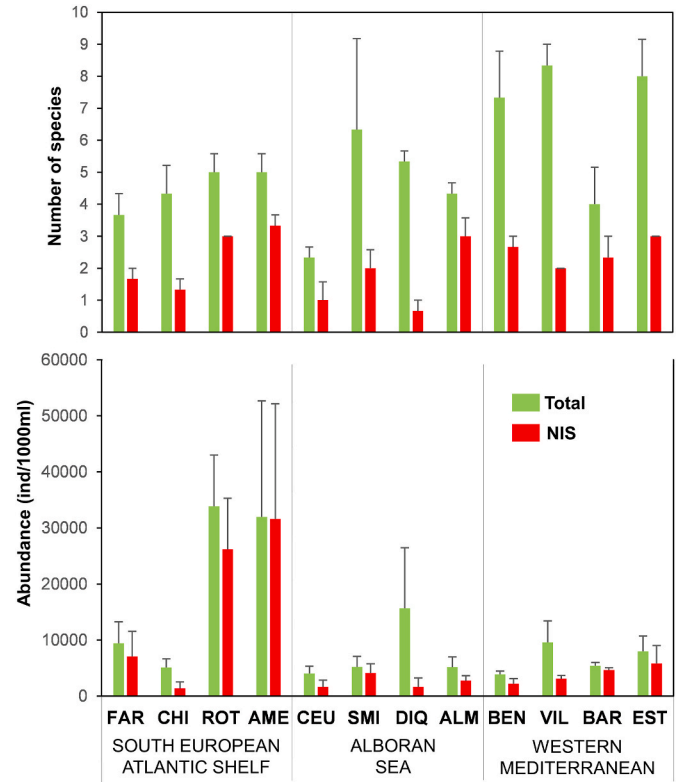


Fig. 5. Average values and standard error of the mean (n = 3) for the total number of species, number of NIS, the sum of all species abundance (total abundance) and the sum of NIS abundances (NIS abundance) in each marina sampled during the spatial study. FAR: Faro, CHI: Chipiona, ROT: Rota, AME: Puerto América, CEU: Ceuta, SMI: Marina-Smir, DIQ: M-Diq, ALM: Almería, BEN: Benicarló, VIL: Vilanova i la Geltrú, BAR: Barcelona, EST: L'Estartit.

Temperature, salinity, TOC, turbidity, and frequency of occurrence of *A. verticillata* were also correlated significantly with the first two axes of dbRDA, which explained 45.4% of the total variation (Fig. 7A). The best DistLM model (AIC = 66.81, R² = 0.983) was obtained for the combination of temperature, salinity, TOC, S, Cd, Cr, Cu, Zn, frequency of *A. verticillata* and human population density. BIO-ENV results showed that the best model (Rho = 0.426) was obtained with the combination of Cr, Ni, Cd, Mn and Pb.

When the NIS community was analysed separately, DistLM showed that P was the only variable which correlated with the epifaunal community (19% of variation explained, Pseudo-F = 2.34, p = 0.04). TOC, frequency of *A. verticillata*, Ni, Cu, Pb, Zn, number of berths and human population density were also correlated significantly with the first two axes of dbRDA, which explained 71.7% of the total variation (Fig. 7B). In this case, the best DistLM model (AIC = 26.29, R² = 0.99) was obtained for the combination of temperature, salinity, P, Cr, Ni, Zn, frequency of *A. verticillata*, number of berths and human population density. BIO-ENV showed the best model (Rho = 0.343) for the combination of Mn, Pb, Zn and number of berths.

3.2. Temporal study

3.2.1. Macrofaunal community and NIS

In relation to associated macrofauna, 1093 individuals belonging to at least 26 species were found during the temporal study (Table 4, Table S4). Similarly to the spatial study, Arthropoda was the dominant phylum (19 species, 97.4% TA), followed by Annelida (6 species, 2.5% TA) and Mollusca (1 species, 0.1% TA). Within Arthropoda, Superorder Peracarida was also the most abundant taxon: Amphipoda (83.7% TA), Isopoda (13% TA) and Tanaidacea (0.3% TA). During the temporal

Table 2

Summary of ANOVA results for total species richness, total abundance, NIS richness and NIS abundance in the spatial study throughout the Iberian Peninsula and Northern Africa (two-way ANOVA), and the temporal study from December 2011 to December 2012 in Puerto América marina, Cádiz, Southern Spain (one-way ANOVA). *p < 0.05, **p < 0.01, n.s. not significant. MS: Mean Square. Significant results in bold.

SPATIAL		TOTAL						NIS					
		Number of species			Abundance			Number of species			Abundance		
Source of variation	df	MS	F	p	MS	F	p	MS	F	p	MS	F	p
Ecoregion [Ec]	2	0.71	2.16	0.1713 n.s.	282	2.59	0.1290 n.s.	2.33	1.03	0.3946 n.s.	714874170	3.29	0.0846 n.s.
Marina [Ma (Ec)]	9	0.33	2.75	0.0230*	1.09	2.06	0.0762 n.s.	2.26	4.52	0.0015**	217224309	1.60	0.1728 n.s.
Residual	24	0.12			0.53			0.50			136105477		
Total	35												
Cochran test		C = 0.52, p < 0.01			C = 0.63, p < 0.01			C = 0.22, n.s.			C = 0.77, p < 0.01		
Transformation		ln(x)			ln(x)			None			None		

TEMPORAL		TOTAL						NIS					
		Number of species			Abundance			Number of species			Abundance		
Source of variation	df	MS	F	p	MS	F	p	MS	F	p	MS	F	p
Month [Mo]	9	8.61	2.10	0.0803 n.s.	67071144	1.87	0.1178 n.s.	5.66	3.54	0.0089**	38006488	1.88	0.1156 n.s.
Residual	20	4.10			35956042			1.60			20250779		
Total	29												
Cochran test		C = 0.46, n.s.			C = 0.27, n.s.			C = 0.33, n.s.			C = 0.41, n.s.		
Transformation		None			None			None			None		

Table 3

Summary of the PERMANOVA and PERMDISP results based on macrofaunal community (Total community and NIS community) for the spatial study throughout the Iberian Peninsula and Northern Africa (two-way PERMANOVA), and the temporal study from December 2011 to December 2012 in Puerto América marina, Cádiz, Southern Spain (one-way PERMANOVA). *p < 0.05, ***p < 0.001, n.s. not significant. MS: Mean Square. Perm.: Unique permutations. Significant results for PERMANOVA in bold.

SPATIAL		TOTAL					NIS				
Source of variation	df	MS	Pseudo-F	p	Perm.	MS	Pseudo-F	p	Perm.		
Ecoregion [Ec]	2	7422.5	12.746	0.1993 n.s.	4741	4822.3	0.865	0.5638 n.s.	4736		
Marina [Ma (Ec)]	9	5823.5	3.192	0.0001***	9831	5575.0	5.811	0.0001***	9924		
Residual	24	1824.4				959.3					
Total	35										
PERMDISP	Ec	F = 4.8609, p = 0.032*				F = 1.4405, p = 0.200 n.s.					
	Ma	F = 6.5105, p = 0.032*				F = 1.9024, p = 0.524 n.s.					

TEMPORAL		TOTAL					NIS				
Source of variation	df	MS	Pseudo-F	p	Perm.	MS	Pseudo-F	p	Perm.		
Month [Mo]	9	5101.8	3.634	0.0001***	9854	4307.3	5.029	0.0001***	9923		
Residual	20	1407.9				856.3					
Total	29										
PERMDISP	Mo	F = 1.1733, p = 0.812 n.s.				F = 2.3942, p = 0.295 n.s.					

study, seven NIS were found (Table 4, Table S4, Fig. 3); these corresponded to the same five taxa detected during the spatial study plus the amphipods *Paracaprella pusilla* and *Stenothoe georgiana*.

Regarding the total number of species per month, the highest value (14 species) was measured in September 2012, followed by October 2012 (12 species) and December 2011 (11 species) (Table 4). A similar pattern was also obtained for the number of species per replicate (Fig. 8). The seven NIS represented the 27% of the total number of species and comprised 56.3% of the total abundance.

Factor 'Month' did not have significant influence on the total number of species, total abundance and NIS abundance. However, the number of NIS differed significantly among months (Table 2). Regarding community structure, PERMANOVA showed significant differences among months for total and NIS community (Table 3).

3.2.2. Influence of environmental data on macrofaunal assemblages

In Puerto América marina, *A. verticillata* was not found during February, March and April 2012, and the highest abundances of the

bryozoan were measured in warmer months (Table 4 above). Highest water temperature values were measured from June to October (Fig. 9), coinciding with the maximum abundances of the bryozoan (Table 4). Salinity decreased in autumn months (October to December) and turbidity fluctuated throughout the year with a maximum in April and December 2012 (Fig. 9).

Of the four variables measured throughout the year (temperature, salinity, turbidity and frequency of *A. verticillata*), only temperature was correlated with the whole associated community in the DistLM (20.3% of variation explained, Pseudo-F = 2.03, p = 0.04). The best model (AIC = 75.33, R² = 0.380) included the combination of salinity and temperature and the BIO-ENV best model (Rho = 0.263) was obtained with the combination of salinity and frequency. For NIS community, only salinity was correlated significantly according to the DistLM (29.1% of variation explained, Pseudo-F = 3.27, p = 0.03). The best DistLM model (AIC = 71.84, R² = 0.221) was obtained for salinity, and BIO-ENV showed the best model (Rho = 0.254) also for salinity.

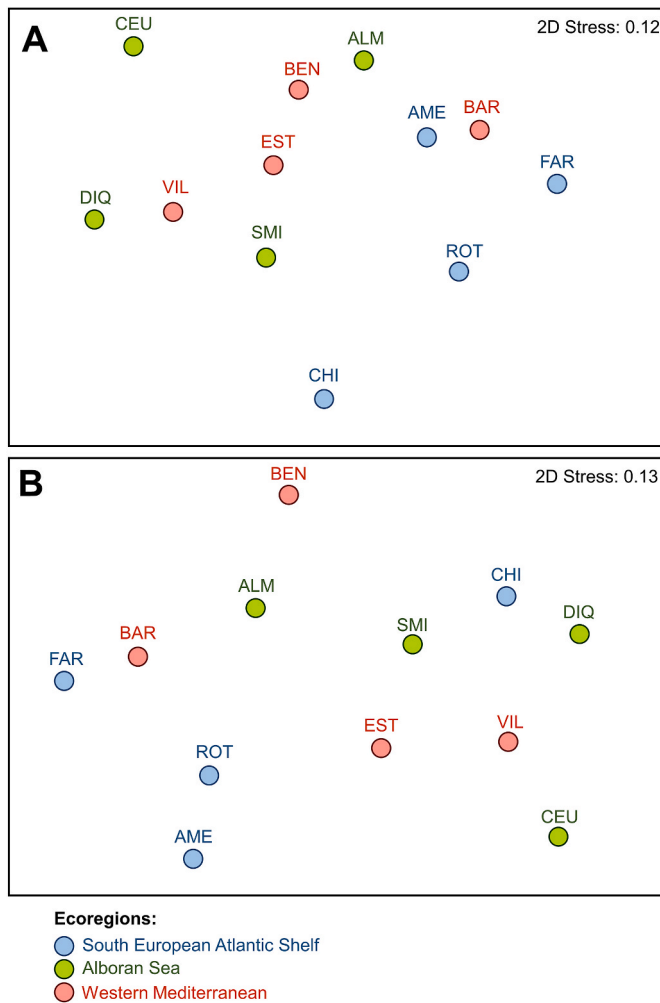


Fig. 6. Non-parametric multidimensional scaling (MDS) based on the whole community (A) and NIS community (B). FAR: Faro, CHI: Chipiona, ROT: Rota, AME: Puerto América, CEU: Ceuta, SMI: Marina-Smir, DIQ: M-Diq, ALM: Almería, BEN: Benicarló, VIL: Vilanova i la Geltrú, BAR: Barcelona, EST: L'Estartit.

4. Discussion

4.1. *Amathia verticillata* as habitat for native and non-native mobile macrofaunal assemblages

Positive interactions of habitat-forming invaders inhabiting marinas on mobile epifaunal assemblages and their potential to trigger invasional meltdown dynamics are poorly understood. Here we found that the spaghetti bryozoan, *A. verticillata*, provides habitat for a rich assemblage of macrofaunal species in marinas from the Iberian Peninsula and Northern Africa. Most of them were native (or cryptogenic), but the seven NIS recorded accounted for more than 50% of the total abundance. Despite community composition varied between marinas and months, NIS dominance was consistent across the spatiotemporal gradient surveyed, independently of factors such as the temporal fluctuations of *A. verticillata* occurrence and the ecoregion considered. These findings reinforce the growing body of research that suggests that artificial habitats promote invader dominance (Glasby et al., 2007; Castro et al., 2022).

Although some taxa associated to *A. verticillata* have been reported in previous research (Farrapeira, 2011; Minchin et al., 2012; Ros et al., 2013a; Ferrario et al., 2014; Marchini et al., 2015; Martínez-Laiz et al., 2018, 2020), the composition of the whole epifaunal community

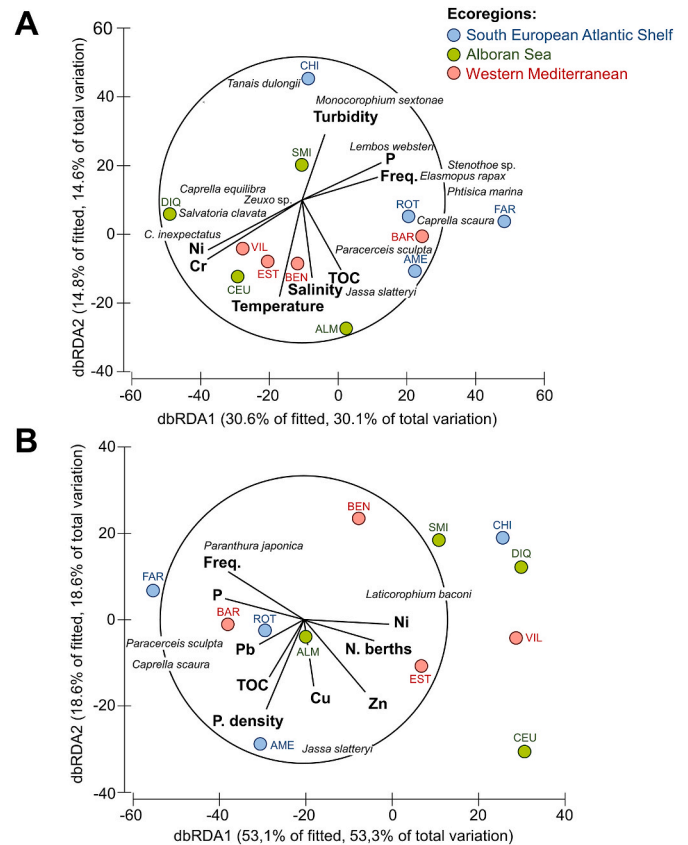


Fig. 7. Graphic representation of the dbRDA showing ordination of marinas and variables of the spatial study, based on the whole community (A) and NIS community (B), with respect to the first two axes. Only variables which significantly ($p < 0.05$) correlated with axes were included. Freq.: Frequency of occurrence, P. density: Population density, N. berths: Number of berths.

associated with this bryozoan was unknown. Simultaneously considering the spatial and temporal studies, at least 54 species belonging to the phyla Arthropoda (32 species), Annelida (16) and Mollusca (6) were found. Peracarid crustaceans, especially amphipods, were clearly dominant in terms of species richness and abundance. Moreover, all NIS associated to *A. verticillata* in this study were peracarid crustaceans, which advises for considering them in NIS monitoring programmes, as proposed by Saenz-Arias et al. (2022b). Indeed, the introduced amphipods *Caprella scaura* and *Laticorophium baconi* were the most abundant species of the study. They were found throughout the whole year in Puerto América marina and were present in most of marinas sampled along the Iberian Peninsula and Northern Africa. In fact, both exotic amphipods are quickly spreading throughout the Mediterranean and other world areas (Cabezas et al., 2014; Guerra-García et al., in press). In marinas, although polychaetes are dominant in soft bottoms (Guerra-García et al., 2021b), vagile epifauna inhabiting arborescent substrates of pontoons is mainly represented by amphipods (Saenz-Arias et al., 2022a, 2022b). This amphipod dominance in marinas has been reported for other bryozoans (*Bugula neritina* in Fernández-Romero et al., 2017 and *Tricellaria inopinata* in Gavira-O'Neill et al., 2018), hydrozoans (*Ectopleura crocea* in Gavira-O'Neill et al., 2015), algae (*Ellisolandia elongata* in Saenz-Arias et al., 2022a) or tubes of large polychaetes (*Branchiomma luctuosum* in Fernández-Romero et al., 2021 and *Sabella spallanzanii* in Ruiz-Velasco et al., 2022). The high contribution of amphipods is also the general pattern in substrates of rocky shores from natural habitats, such as bryozoans (Conradi et al., 2000; Siqueira et al., 2018), hydrozoans (Bavestrello et al., 1996; Navarro-Barranco et al., 2014), algae (Sánchez-Moyano and García-Gómez, 1998; Guerra-García et al., 2011; Pacios et al., 2011; Navarro-Barranco et al., 2019, 2021,

Table 4

List of macrofaunal species associated to the bryozoan *Amathia verticillata* in Puerto América marina over the period of one year. Light blue: 1–100 ind/1000 ml; medium blue: 101–1000 ind/1000 ml; dark blue: >1000 ind/1000 ml. Abundance data are included in Table S4. Relative abundance of *A. verticillata* (frequency of occurrence) in each marina is also included. White: absent; light orange: <20%; medium orange: 20–40%; dark orange: >40%. NIS are indicated with an asterisk. ¹Ros et al., 2013b; ²Saenz-Arias et al., 2022a, 2022b; ³Martínez-Laiz et al., 2018.

	2011		2012											
	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
<i>Amathia verticillata</i> (delle Chiaje, 1822)	Light orange	Light orange	Light orange	Light orange	Light orange	Light orange	Light orange	Light orange	Light orange	Light orange	Light orange	Light orange	Light orange	
Phylum Annelida														
Class Polychaeta														
<i>Autolytus</i> sp.	Light blue										Light blue			
<i>Hydroides</i> sp.								Light blue	Light blue		Light blue			
Nereidae undet.										Light blue	Light blue			
<i>Polyphthalmus pictus</i> (Dujardin, 1839)							Light blue	Light blue		Light blue				
<i>Salvatoria clavata</i> (Claparède, 1863)							Light blue	Light blue					Light blue	
<i>Sphaerosyllis pirifera</i> Claparède, 1868										Light blue	Light blue			
Phylum Arthropoda														
Class Malacostraca														
Order Amphipoda														
* ¹ <i>Caprella scaura</i> Templeton, 1836	Dark blue	Dark blue												
<i>Elasmopus rapax</i> Costa, 1853	Dark blue	Dark blue												
<i>Erichthonius</i> spp.	Dark blue	Dark blue												
* ² <i>Jassa slatteryi</i> Conlan, 1990	Dark blue	Dark blue												
* ² <i>Laticorophium baconi</i> (Shoemaker, 1934)	Dark blue	Dark blue												
<i>Monocorophium acherusicum</i> (Costa, 1853)	Dark blue	Dark blue												
<i>Monocorophium sextonae</i> (Crawford, 1937)	Dark blue	Dark blue												
* ¹ <i>Paracaprella pusilla</i> Mayer, 1890	Dark blue	Dark blue												
<i>Podocerus variegatus</i> Leach, 1814	Dark blue	Dark blue												
* ² <i>Stenothoe georgiana</i> Bynum & Fox, 1977	Dark blue	Dark blue												
<i>Stenothoe tergestina</i> (Nebeski, 1881)	Dark blue	Dark blue												
<i>Stenothoe valida</i> Dana, 1852	Dark blue	Dark blue												
Order Isopoda														
<i>Dynamene magnitorata</i> Holdich, 1968														
<i>Janira maculosa</i> Leach, 1814														
* ³ <i>Paracerceis sculpta</i> (Holmes, 1904)	Dark blue	Dark blue												
* ³ <i>Paranthurus japonica</i> Richardson, 1909	Dark blue	Dark blue												
Order Tanaidacea														
<i>Zeuxo</i> sp.														
Order Decapoda														
<i>Pachygrapsus marmoratus</i> (J.C. Fabricius, 1787)														
Class Pycnogonida														
Ammonotheidae undet.														
Phylum Mollusca														
Class Gastropoda														
<i>Haminoea</i> sp.														

2023), sponges (Ribeiro et al., 2003; Padua et al., 2013; Navarro-Barranco et al., 2021), ascidians (Sepúlveda et al., 2003) or corals (Terrón-Sigler et al., 2014; Cúrdia et al., 2015; Soler-Hurtado et al., 2018).

4.2. Factors affecting the facilitation role of *A. verticillata* across a spatiotemporal scale

Our results highlight the importance of the singularity of each marina in modulating the facilitator role of *A. verticillata* at spatial scale. Specifically, we found that the main differences in global and NIS community composition of macrofaunal assemblages associated to *A. verticillata* through the Iberian Peninsula and Northern Africa were due to the factor ‘marina’ and not to the biogeographical ecoregion in which the marina is located. While we measured a large set of predictor variables in each marina to understand the most relevant factors affecting epibiont patterns, the results obtained by the different models

used (DistLM, dbRDA and BIOENV) were not consistent in a spatial scale and a significant percentage of the variance associated with the data remained unexplained. This may be reflecting the difficulty of quantifying or capturing the idiosyncrasies of each marina. This agrees with other studies showing the importance of marina singularities for modulating NIS spatial patterns in ports and other artificial marine structures (Chatzinikolaou et al., 2018; Sedano et al., 2020). Guerra-García et al. (2021a) also found heterogeneity among marinas based on environmental stressors, and Guerra-García et al. (2021b) and Saenz-Arias et al. (2022a,b) highlighted the macrofaunal singularities among marinas, regardless their location (Atlantic vs Mediterranean). Spatial variations in biotic assemblages among and within marinas have been attributed to differences in the local environment as well as to the marina design (Toh et al., 2017). Indeed, the singularity of marinas, determined by environmental conditions, availability of suitable substrate or level of marine traffic, can affect several stages of the NIS invasion process (Martínez-Laiz et al., 2019). Local and small-scale

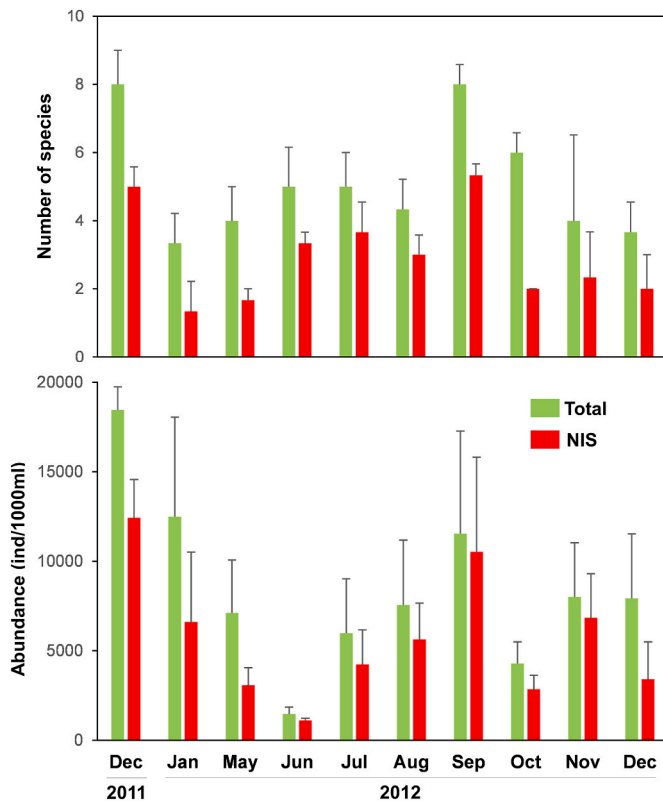


Fig. 8. Average values and standard error of the mean (bars) for the total number of species, number of NIS, the sum of all species abundance (total abundance) and the sum of NIS abundances (NIS abundance) in each survey of the temporal study in Puerto America. Three replicates (n = 3) were taken monthly from December 2011 to December 2012.

differences among and within marinas must be considered in monitoring and management strategies, including normative certifications (e.g. ISO norms, Blue Flags) (Kenworthy et al., 2018). The lack of differences in NIS richness, abundance and community structure among ecoregions may have management implications in the context of European policies such as the Marine Strategy Framework Directive (MSFD, 2008/56/EC) (Png-González et al., 2023). According to the results of the present study, NIS management must be mainly focused on the singularity of marinas rather than on their location in a particular region or demarcation throughout the Iberian Peninsula. Future studies should test for the generality of these patterns in marinas located in other world ecoregions.

Despite the lack of consistent patterns between environmental variables and associated macrofauna at spatial scale in the present study,

significant correlations between trace metals and associated macrofaunal communities were common in all statistical approaches. Heavy metals are relevant explanatory variables for sediment macrofaunal communities in marinas and harbours (Chatzinikolaou et al., 2018; Guerra-García et al., 2021a, 2021b) and they are also key to structure epifaunal assemblages associated with arborescent substrates in marinas (Fernández-Romero et al., 2019; Saenz-Arias et al., 2022b). Furthermore, heavy metals can be correlated with the abundance of NIS (e.g. *C. scaura* in Ros et al., 2015). In this sense, the dominance of NIS in marinas and port environments could be partially explained by a higher resistance to toxic compounds of these exotic species. Further experimental evidence based on ecotoxicological approach should be necessary to test this hypothesis.

Compared to the spatial study, the temporal study in Puerto América revealed the presence of two additional NIS (7 in total). Furthermore, we found a total of 26 species in this marina during the temporal survey while only 9 were recorded during the spatial one. Therefore, sampling on a temporal basis seems necessary for proper monitoring of NIS diversity in marinas and understanding potential impacts of habitat-former invaders. Cabezas et al. (2019) and Martínez-Laiz et al. (2021) also stressed the importance of detailed temporal studies and indicated that time series (>one year), enriched with molecular tools, are useful to identify time windows in biological invasions and properly develop management strategies. For example, we found a clear seasonal pattern in the frequency of occurrence of *A. verticillata*. The highest abundances of the bryozoan were registered during the warmer period (from June to September) while it was absent in colder months (February, March and April). This seasonal fluctuation has been observed in successive years (personal observation). Indeed, some authors (Zirpolo, 1933; Relini, 1966; Galil and Gevili, 2014) reported the occurrence of colonies only during summer, whereas a senescent phase is observed during the autumn. This deciduous pattern (Bock, 1982) directly influences its facilitating role. Interactions basibiont-epibionts will be stronger in summer than in winter periods, where the ability of *A. verticillata* to provide habitat may even disappear (as in Puerto América marina). Summer period should therefore be considered a temporal opportunity window for developing monitoring and management programmes focused on this target bryozoan. However, temporal patterns of macrofaunal assemblages, including NIS, associated to *A. verticillata* did not quite match that of the basibiont. While they varied between months and were influenced mainly by salinity, their fluctuations did not show a consistent seasonal pattern (summer vs winter). Therefore, facilitation did not depend on bryozoan abundance fluctuations. Despite facilitation of habitat-forming species are often density dependent (e.g. van Hulzen et al., 2007; Bishop et al., 2012), most mobile fouling epibionts are generalists with respect to habitat use. This is the reason why they can colonize newcomer habitat-forming species, such as *A. verticillata*. Therefore, facilitation in this case is not the result of a coevolutionary history but of a short-temporal coexistence. Although mobile epibionts

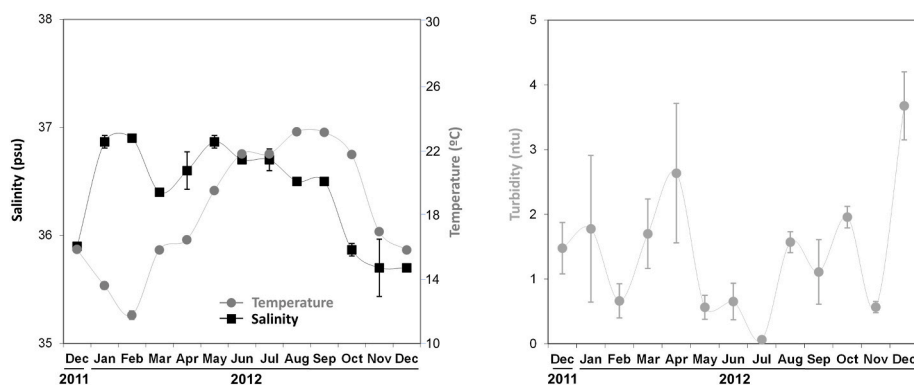


Fig. 9. Values of abiotic variables measured at each survey conducted monthly in Puerto América marina. Values are mean ± standard deviation (n = 3).

may show a preference for some type of substrate, if it is not available, they generally can colonize other available spatial niches. This habitat plasticity reflects the challenges in controlling mobile epibiont NIS once established in a particular region. Moreover, the lack of a clear seasonality is common in marinas, both in the associated fauna to fouling communities (Gavira-O'Neill et al., 2015, 2018) and in the soft-bottom benthic assemblages (Chatzinikolaou et al., 2018). For example, many of the species present in December 2011 were not found in December 2012, and species such as *Hydroides* sp., *Monocorophium acherusicum*, *M. sextonae* or *S. tergestina*, were present intermittently. Moreira et al. (2010) also found that the number of species and individuals at the sediments of Baiona harbour, Northern Spain, showed great monthly fluctuations but lacked a clear seasonal pattern of temporal evolution. Similar results have been reported for other harbour areas in temperate latitudes (Ergen et al., 2006). In addition to the quality of available spatial niches across the year (for example, presence of arborescent basibionts) and other biotic factors (such as predation and/or competition), these unstructured fluctuations may reflect the unpredictable fluctuating environmental conditions of marinas (e.g. organic inputs, heavy metal pollution, drastic changes in salinity/temperature caused by freshwater spills from the pontoons during maintenance works on recreational boats, pontoon cleaning labours, marine traffic, oil spills, etc.) (Burgin and Hardiman, 2011; Rivero et al., 2013; Murray et al., 2014; Valdor et al., 2019; Guerra-García et al., 2021a, 2021b). Populations are also susceptible to experience genetic drift over time, turning them more vulnerable to the impact of unfavourable environmental conditions (Cabezas et al., 2019; Martínez-Laiz et al., 2021). Additionally, variation in propagule pressure throughout the year can explain changes in the establishment success of invasive inoculants arriving to port environments (Hedge et al., 2012). These unpredictable drivers characteristic of each marina reinforce the importance of the marina singularity in shaping the spatiotemporal patterns of epifaunal assemblages associated to *A. verticillata*. Interestingly, salinity appeared as an important driver in structuring temporal pattern of NIS assemblages associated to *A. verticillata* using different statistical approaches. Ros et al. (2015) found that salinity was the most important factor explaining the occurrence and abundance of the exotic *C. scaura* in marinas from the Iberian Peninsula and northern Africa. These authors also pointed out the critical role of salinity and temperature in modulating the competitive interaction between *C. scaura* and the resident *C. equilibra*. In fouling communities on hard bottoms, salinity can affect the colonisation and dispersal success of NIS (Afonso et al., 2020). Salinity was also one of the parameters better correlated with soft-bottom benthic species composition and diversity in Mediterranean touristic ports (Chatzinikolaou et al., 2018). Indeed, salinity is considered one of the most significant factors modulating biological invasions (Paiva et al., 2018; Jimenez et al., 2018). In a global change context, the interaction between temperature and salinity is crucial to the NIS success (Lejeune et al., 2014; Ros et al., 2021).

In addition to the environmental matrix provided by each marina, substrate complexity and fractal dimension are known to correlate with abundance and richness of epifaunal assemblages (Veiga et al., 2014; Torres et al., 2015; Navarro-Barranco et al., 2018). The structure of *A. verticillata* (with widely separated branches and much less compact arrangement than other arborescent bryozoans such as *B. neritina* or *T. inopinata*) may provide less space suitable for refuge to epifauna. Conversely, this together with the huge size it can reach in marinas (>1 m) may reduce competition pressure among epibionts and promote the coexistence between native and non-native assemblages. Moreover, *A. verticillata* produces secondary metabolites (bromo-alkaloids), active compounds which might provide protection by discouraging predation (Marchini et al., 2015 and references therein). While this could prevent the settlement of other fouling organisms (Winston, 1995) and reduce the diversity of the associated vagile macrofauna, dos Santos et al. (2017) concluded that bromo-alkaloids do not seem to have a significant role in the chemical defense of *A. verticillata*. Interestingly, we found a

high species richness associated with *A. verticillata* compared to other arborescent substrata. For example, we found 26 associated macrofaunal species in the temporal study throughout a whole year in Puerto América marina. This is similar to the richness recorded from the same marina in other substrates, that are more three-dimensionally complex than *A. verticillata* and lack similar chemical defences, such as the bryozoan *T. inopinata* (19 species) (Gavira-O'Neill et al., 2018).

Apart from small solitary sessile/semi-sessile organisms (i.e. small polychaetes and bivalves), the present study mainly deals with vagile taxa, which dominates the associated community to *A. verticillata*. However, the bryozoan is also a suitable settlement surface for other fouling organisms. Farrapeira (2011) reported the presence of sessile encrusting animals on stolons and basal parts of *A. verticillata* colonies, such as bryozoans and tunicates. Facilitative effects of habitat-forming species will depend on the relevance of the resource it provides (Sellheim et al., 2010). Thus, the role of *A. verticillata* in providing space, refuge and/or food is likely more relevant for mobile than for sessile epibionts, as have been showed in other bryozoans such as *Watersipora subtorquata* (Sellheim et al., 2010). Nevertheless, future research should address the study of both mobile and sessile epibionts, as well as other smaller vagile associates, e.g. meiofaunal assemblages, inhabiting *A. verticillata*. This is necessary to get a global knowledge of the complete biodiversity hosted by this bryozoan. Moreover, experimental approaches to explore the relationships between the native fauna and the new arrivals in arborescent substrates are also necessary to properly understand NIS impacts at species level (Ros et al., 2013a). Despite here we show that *A. verticillata* facilitates a NIS epibiont dominance, further studies are required to explore the strength and direction of the consequences of this facilitation at community level. To do this, it should be necessary to understand how *A. verticillata* modifies the vagile community in marinas compared to other substrates (either the primary habitat provided by the marina structure, or the secondary habitat provided by other basibionts), ideally across a spatiotemporal scale. This would allow to understand the role that *A. verticillata* actually plays in shaping epibiont communities in marinas.

4.3. Potential of *A. verticillata* to trigger invasional meltdown phenomena

The widespread distribution, arborescent structure and massive growth that *A. verticillata* can reach in marinas and boat hulls turn it into a potential promoter of invasive meltdown processes. The bryozoan may facilitate the transport, establishment and subsequent spread of its NIS-dominated macrofaunal associated assemblage. Tempesti et al. (2022), based on a study conducted in different Mediterranean port systems, found that arborescent bryozoans can host a higher proportion of NIS than other sessile taxa. In this sense, the role of *A. verticillata* as a powerful vector able to introduce NIS through transport on vessel hulls, vessel fouling and mussel imports has been highlighted by other authors (Minchin et al., 2012; Marchini et al., 2015; Dailianis et al., 2016; Furfaro et al., 2018; Martínez-Laiz et al., 2018, 2020). For example, *C. scaura* has been often recorded associated to colonies of *A. verticillata* (Table S5). This amphipod can adopt the same colour of the bryozoan host, becoming cryptic and going unnoticed (Fig. 4, personal observation). This ability can let the caprellid to avoid potential predators and the bryozoan would be facilitating its establishment and subsequent spread. Regarding facilitation during transport, Martínez-Laiz et al. (2022) found that complex sessile basibionts reduced dislodgement risk in another exotic congener, *Caprella mutica*. In the same way, *A. verticillata* could increase the en-route survivorship of *C. scaura* and its other associated NIS during hull boat transport. Large mats of this uncalcified bryozoan are commonly found drifting freely in the nearshore (Pederson and Peterson, 2002), so it can also facilitate their spread from marinas to natural habitats. Mioni and Furfaro (2022) reported a NIS interaction among *A. verticillata* and two exotic sea slugs, *Polycerella emertoni* (which feeds on the diatom community associated with the bryozoan) and *Favorinus ghanensis* (which feeds mainly on the eggs laid

by the polycerid sea slug). These two nudibranchs may have entered the Mediterranean Sea travelling on this exotic bryozoan. The secondary spread along the Italian coasts of another exotic sea slug, *Polycera hedgpethi*, has also been related to its association to *A. verticillata* (Chartosia et al., 2018).

Other exotic/cryptogenic bryozoans, such as *T. inopinata*, *B. neritina*, *Calypotheca alexandriensis* and *Watersipora subtorquata*, have also been reported to host exotic associates in marinas and harbours (Table S5). NIS associated to these bryozoans are mainly peracarids and secondarily decapods, pycnogonids, polychaetes and molluscs. Gavira-O'Neill et al. (2018) suggested that the bryozoan *T. inopinata* constituted an optimal nursery habitat for juveniles of the exotic isopod *P. sculpta*, which can reach the inner zones of the colony. These authors pointed out that the compacted structure of these colonies does not provide a suitable habitat for many native species since it prevents epifauna to reach its innermost areas (Ros et al., 2013a). Therefore, *T. inopinata* could be reducing the availability of habitat for native epifauna and facilitating space for *P. sculpta*. Ros et al. (2013a) found that *B. neritina* was a suitable habitat for the establishment success of *C. scaura* based on (i) adequate complex structure of the bryozoan colonies with optimal compaction degree and less defensive structures than other erected bryozoans (e.g. frontal spines or lateral avicularia) which let caprellids penetrate to the inner parts of the colony, and (ii) similarities in physical appearance related to the caprellids ability to undergo physical colour changes and remain cryptic on the substrate. These authors suggested that this interaction between the bryozoan *B. neritina* and the caprellid *C. scaura* could be another example of 'invasional meltdown'. In Queensland (Australia), Floerl et al. (2004) found that the high tolerance of *W. subtorquata* to antifouling paints facilitates the spread of less-tolerant bryozoans settled on its surface.

Despite the potential to magnify negative impacts through invasional meltdown dynamics, our findings reflect the challenge of both assessing the impact of habitat-forming invaders on marine epifaunal communities and managing this impact. While the removal of *A. verticillata* from marinas and boat hulls would likely prevent invasional meltdown and have positive effects for boat owners and other impacted sectors, its removal may also impact the native epibionts associated. Instead, this bryozoan offers excellent opportunities for advancing ecological knowledge on facilitation processes and improving NIS management from a precautionary point of view. In this sense, monitoring arborescent bryozoans, such as *A. verticillata*, should be a priority for early detection of small mobile NIS, as well as for monitoring their establishment success (Ros et al., 2013a). Management strategies should also focus on avoiding the spread of exotic bryozoans (Gavira-O'Neill et al., 2018).

5. Conclusions

Overall, we show that the spaghetti bryozoan *Amathia verticillata* provides habitat for a rich community of macrofaunal species in marinas, most of them native and belonging to peracarid crustaceans. However, in terms of abundance, NIS dominated macrofaunal assemblages across the spatiotemporal scale considered, raising the biosecurity risk associated to this mass-growing bryozoan and the potential to trigger invasional meltdown dynamics. At spatial scale, the main factor affecting this facilitation was the marina singularity, while the ecoregion did not have a significant influence. At temporal scale, facilitation was affected by the deciduous pattern of *A. verticillata*, but it did not depend on bryozoan abundance fluctuations. Salinity was one of the main factors affecting the temporal dynamics of the associated NIS. In addition to increasing knowledge about facilitation processes in marinas, these findings have relevant implications in recommendations for detection and management of NIS in these habitats. Particularly, we propose: (1) considering facilitation processes of habitat-forming species inhabiting marinas in biosecurity risk analysis (including its potential to trigger invasive meltdown phenomena, especially when they promote

associated NIS dominance and/or high associated NIS richness); (2) prioritizing the use of erect bryozoans, such as *A. verticillata*, as target substrates to explore this issue and investigate species richness and abundances of mobile epibiont NIS in marinas; (3) within the epibionts, prioritizing the use of peracarids as target group in NIS monitoring; (4) performing temporal surveys throughout the whole year in selected marinas as a suitable complement to spatial studies for NIS detection; (5) paying attention to the singularity of marinas instead of whether they are located in a particular ecoregion. Finally, in consonance with previous work, we consider that the basis to appropriate monitoring and management guidelines is the accurate knowledge of species inhabiting hot spot for species introductions, such as marinas. Comprehensive lists of taxa are mandatory for subsequent early detection of new NIS and understanding impacts of established NIS on native communities. We encourage policy makers, governments, and funding agencies to invest in taxonomical studies to improve management strategies in biological invasions.

Credit author statements

Guerra-García JM: Conceptualization, Investigation, Methodology, Formal analysis, funding acquisition, Writing original draft.

Ruiz-Velasco S: Investigation, Writing original draft.

Navarro-Barranco C: Investigation, Methodology, Data curation, Review & editing.

Moreira J: Investigation, Methodology, Data curation, Review & editing.

Angulo G: Investigation, Methodology, Review & editing.

García-Domínguez R: Investigation, Methodology, Review & editing.

Amengual J: Investigation, Methodology, Review & editing.

Saenz-Arias P: Investigation, Data curation, Review & editing.

López-Fé, CM: Investigation, Data curation, Review & editing.

Martínez-Pita I: Investigation, Data curation, Review & editing.

García-García FJ: Investigation, Data curation, Review & editing.

Ros M: Conceptualization, Investigation, Methodology, Data curation, Writing original draft.

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.

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Appendix A. Supplementary data

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