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Research Article

Macrobenthic success of non-indigenous species related to substrate features in the Mar Grande of Taranto, Italy (Mediterranean Sea)

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Abstract

The Taranto Seas of Italy, considered a hotspot of nonindigenous species (NIS) diversity, are also among the best locales in the Mediterranean to study marine fouling communities. This environment is an ideal space to study how artificial structures are utilised by NIS for further dispersion into the surrounding environment after their initial introduction. In the present study, the fouling communities found on several types of substrates (including small artificial, mobile structures and more stable, larger structures) in a quiet enclosed part of the Mar Grande of Taranto (Ionian Sea) were analysed and compared in terms of the contribution of NIS. The assemblages differed according to the age and size of the substrate, but also according to the depth and distance from a possible source of organic enrichment. As expected, NIS were abundant, especially on small ephemeral substrates, with a high number of pioneer species; by contrast, very few NIS were found on less transient substrates, which were dominated by macroalgae. This work highlights that substrate type is an important predictor of the types of NIS present, even in environments considered to be particularly vulnerable to biological invasions, such as ports and other confined environments subject to elevated human pressure.

Key words: Ionian Sea, macrofouling, artificial substrates, recipient community

Introduction

Ports and confined areas affected by intense anthropogenic activities are preferentially colonised by non-indigenous species (NIS) and can be considered hubs of diffusion of NIS into neighbouring regions. The artificial structures present in these areas can be suitable habitats for NIS and can act as potential corridors for their expansion (Bulleri and Airoldi 2005). In other words, artificial structures can be a launchpad for the introduction and further dispersion of NIS (Mineur et al. 2012), acting as a stepping stone for dispersal as well as a direct vector (e.g., Bulleri and

Airoldi 2005; Ruiz et al. 2009; McNeill et al. 2010; Bulleri et al. 2016). Indeed, the majority of NIS seem to be associated with artificial substrates, showing their prevalence in conjunction with or restriction to these structures (Ruiz et al. 2009; Ulman et al. 2017, 2019a, b).

Artificial structures are a direct consequence of human modification of the coastal environment and increase the number of habitats suitable for the settlement of many marine species. It was estimated that, in Europe, more than 22,000 km^2 of the coastal zone has been "hardened" by artificial surfaces (Airoldi et al. 2005, Airoldi and Beck 2007), increasing the connectivity of highly isolated populations (Thompson et al. 2002; Dethier et al. 2003).

The presence of several artificial substrates should, therefore, be considered a disturbance that drives invasions, even if there is little evidence that NIS perform better than native species in disturbed ecosystems (Lockwood et al. 2013; Mineur et al. 2012). As an example, fouling communities continue to form and grow even during anthropogenic disturbances, highlighting resiliency in assemblages dominated by native species with a weak contribution of NIS (Ferrario et al. 2020).

However, ecologically analogous assemblages colonising artificial structures differ from a taxonomic point of view to those found on natural rocky substrates in adjacent areas (Anderson and Underwood 1994; Connell and Glasby 1999; Glasby and Connell 1999; Connell 2001; Glasby 2001; Bacchiocchi and Airoldi 2003; Chapman 2003; Airoldi et al. 2005; Bulleri 2005; Bulleri et al. 2005; Edwards and Smith 2005; Bulleri and Chapman 2010), and the presence of NIS contributes to these differences (Bulleri and Airoldi 2005; Vaselli et al. 2008; Bulleri and Chapman 2010). In a broader context, independently of their location, the species composition of assemblages on artificial hard substrates was more similar to marinas than to natural rocky substrates of adjacent areas, so artificial structures could favour fouling NIS over native hard bottom species (Airoldi et al. 2005, Airoldi and Beck 2007). However, even if artificial structures (e.g., pontoons and pilings) represent an entry point for many NIS, their establishment seems to be almost exclusively enhanced in confined environments like ports and marinas (Glasby and Connell 1999). Therefore, artificial habitats seem to be more invaded than natural ones, and estuaries are more invaded than coastal marine habitats (Simkanin et al. 2017). The more significant invasion of artificial habitats in confined environments may also be due to a higher propagule pressure linked to the presence of vectors such as commercial, recreational and military ships as well as aquaculture facilities.

Other than propagule pressure, NIS success depends on a suite of factors such as the local conditions, environmental features, and characteristics of the surrounding communities (Catford et al. 2009). At the habitat scale, propagule pressure can be a determinant of invasion success (Lonsdale

1999; Sakai et al. 2001; Colautti et al. 2006; Simberloff 2009), but habitat qualities and local factors (e.g., characteristics of recipient assemblage) can affect invasions differently (Simkanin et al. 2017). This is probably why natural benthic habitats seem to be more resistant to invasions than artificial ones (Simkanin et al. 2012, 2013). The inherent structural features of artificial habitats such as their nature, orientation, and mobility (Glasby et al. 2007; Dafforn et al. 2009; Ruiz et al. 2009) can also influence marine invasions, so that shallow moving structures appear to be exceptionally hospitable for filter-feeding NIS (Glasby 2001; Dafforn et al. 2009). Moreover, the age of resident communities, depth, food availability, as well as the biology and physiology of single species and their interactions can influence invasibility (Cowie 2010; Lezzi and Giangrande 2018). Indeed, the succession of fouling communities can vary according to the seasonal period, primarily due to different reproductive periods and the settlement of other fouling species (Relini and Faimali 2003; Jenkins and Martins 2010; Lezzi et al. 2018; Lezzi and Giangrande 2018).

In the present paper, we compared the fouling assemblages on different artificial substrates located in a confined environment in the Mediterranean Sea that is considered a hotspot of NIS diversity (Cecere et al. 2016; Lezzi et al. 2018). We hypothesized that even though assemblages develop in response to different local environmental features, when they are subjected to similar pre-settlement factors (e.g., larval supply), the community can have a gradient of resistance to NIS colonisation. Indeed, in an area where the propagule pressure can be assumed to be similar, colonisation of large and long-lasting artificial substrates can differ from small transient ones because the size and duration of immersion of the substrate can drive the success of fouling species, thus influencing interspecific competition (Rodriguez et al. 1993; Lozano-Cortés and Zapata 2014; Chang and Marshall 2016; Valentine et al. 2016). The contribution of NIS to species richness, considering the community on both natural and artificial structures, has never been investigated in the Taranto Seas and is poorly investigated throughout the Mediterranean Sea (e.g., Megina et al. 2013, 2016).

Materials and methods

Study area

The investigated area is located along the Apulian Ionian coast, in the southwestern part of the Mar Grande of Taranto, Italy, where there is a private aquaculture facility (Maricoltura Mar Grande Srl; Figure 1). The Mar Grande is a semi-enclosed basin covering an area of 35 km^2 with an average depth of ~ 12 m (maximum depth of ~ 42 m) and is connected to the Ionian Sea through two openings and to the Mar Piccolo by two narrow channels. The water temperature has seasonal variations typical of the coastal Ionian region, with an average annual temperature of ~ 18 °C, ranging from 14 °C to 28 °C. The salinity is ~ 38‰ and is mostly uniform

Figure 1. Map of the study area: (A) location of the site in South Italy Gulf of Taranto; (B) position of the sampling area in the Mar Grande of Taranto.

throughout the year. Hard bottom communities on both natural and artificial substrates within the basins have been widely investigated, and most of the studies were conducted in the Mar Piccolo (Parenzan 1969; Gherardi 1973; Gherardi and Lepore 1974; Tursi et al. 1977, 1978, 1979; Montanaro and Tursi 1983; Pierri et al. 2010, 2019; Lezzi et al. 2018). Phytobenthic communities, mainly seaweeds, have also been previously examined in the area (Pierpaoli 1923; Petrocelli et al. 2019). Intense anthropogenic activity characterises the whole area. In the northern portion, ~ 5 km away, there is a commercial port which hosts ships from all over the world; to the northeast, there is the city of Taranto. In the southern portion, there are two tourist harbours for small and local recreational boats (~ 300 berths), including the floating pontoon and quay investigated here, as well as a fish production facility and various structures for mussel aquaculture. The fish production facility, at present, is collaborating with public research institutes for experimental activities in integrated multi-trophic aquaculture.

Sampling site and sampling collection

Several artificial substrates present in the area were investigated. These included structures that were immersed for a long time (e.g., anchored

permanently on the bottom, such as quays and anchoring bodies), floating structures (i.e., mobile pontoons), and structures more recently immersed for experimental objectives. The present work investigated the differences in fouling communities across these structures and time points, as these communities were not in the initial stages of ecological succession and have varying degrees of maturity. Sampling was performed in the summer due to higher NIS presence during this season. The assemblage present in the summer should be considered the final stage of the community development (Lezzi and Giangrande 2018).

Fouling communities were collected in July 2018 from the following different substrates (Figure 1):

(1) Suspended collectors: artificial structures (i.e., coconut ropes placed around cages from the fish aquaculture facility) to recruit fouling organisms at ~ 2 m depth. These collectors had a small colonisable surface and were submerged in October 2017 and analysed after nine months of uninterrupted immersion in the water.

(2) Anchor concrete blocks: stable substrate with 2–10 m^2 of colonisable surface that was always submerged at 12 m depth and made of reinforced concrete, iron poles, and a chain. The structures were used to anchor the portions of the fish production equipment from the aquaculture facility, and were more than four years old at the time of observation.

(3) Perpendicular face of a quay of the marina: large, stable substrates made of concrete that have been in the water for at least 10 years. Samples were collected at 2 m depth from both the protected and exposed sides of the quay.

(4) Pontoon, floating dock: large, floating substrate made of plastic that has been in the water for three years at the time of observation. Samples were collected at ~ 3 m depth.

SCUBA divers photographed and scraped off three randomly selected 20 × 20 cm replicates from the anchor blocks, pontoon and quay. For the suspended collectors, three replicates, from 1–3 m depth, were analysed by in vivo photographs using ImageJ software (Abràmoff et al. 2004) to determine the percentage coverage of the organisms. Afterwards, samples were scraped from the ropes to identify the organisms individually. Samples from all substrates were fixed with 4% formalin then 70% alcohol. Collected materials were then transported to the laboratory for taxonomic analysis. Sessile organisms were later identified to the lowest possible taxonomic level using a binocular stereo microscope (LEICA MZ 125).

Classification of substrates

Following the classification of Mineur et al. (2012), artificial structures can be divided into immobile artificial structures (i.e., coastal defences and harbours, artificial reefs and submerged wrecks, marine renewable energy devices, and static associated structures of marinas) and mobile artificial

Table 1. Features of the substrates. Immersion time: 1 = < 1 year; 2 = >3 years; 3 = > 10 years. Colonizable space: 1 = small ($\leq$ 2 m^2); 2 = medium (2–10 m^2); 3 = large ($\geq$ 10 m^2). Type of substrate: 1 = mobile; 2 = stable. Depth of immersion: 1 = shallow ($\sim$ 2 m); 2 = deep ($\sim$ 8 m). Distance from the cages: 1 = close ($\sim$ 10 m); 2 = far ($\sim$ 150 m).

	Collectors	Anchoring block	Quay Exposed	Quay Protected	Pontoon
Immersion time	1	2	3	3	2
Colonizable space	1	1	3	3	2
Nature of substrate	1	2	2	2	2
Depth of immersion	1	2	1	1	1
Distance	1	1	2	2	2

structures (i.e., all ship types, offshore platforms, buoyage and floating debris, and floating structures of marinas). Across all artificial structures, the assemblage composition was determined by the size of the substratum, immersion time, distance from an aquaculture facility (as a source of organic matter), salinity, water temperature, and even the configuration of the structure itself (Mineur et al. 2012). Indeed, constant submersion provides a suitable environment for mainly subtidal biota, which is confined to a narrow region close to the surface of the water. Moreover, the static structures and floating structures of marinas differ in the communities that develop on them (Rocha et al. 2009). Pontoon sections also have variable levels of light intensity and shade, so they provide a wide range of opportunities for both macroalgae and invertebrates to become established. Environmental parameters, such as the type, size, depth and maturity of the substrates and the distance from the aquaculture facility (as a proxy of water quality), for each structure are summarised in Table 1.

Data Analysis

The species richness and presence of NIS from each analysed substrate were compared to data from previous studies conducted in the area on artificial panel colonisation in 2014 (Lezzi et al. 2018; Lezzi and Giangrande 2018). Cryptogenic forms were not considered NIS.

In order to describe the different assemblages, the percent cover of the dominant species was determined. Due to the inherent differences in the sampled substrates, especially the coconut ropes, a qualitative comparison was performed. A PERMANOVA analysis was carried out on a Sørensen similarity matrix with 9999 permutation (Anderson 2001). Substrate (6 levels: PVC panels, coconut ropes, Anchoring blocks, Pontoon, QuayP, QuayE) was used as factor to test for differences in species assemblages between different types of substrate. When significant effects were detected ($p < 0.05$), differences between levels were identified with post-hoc pairwise comparisons. Multidimensional scaling (MDS) was performed using the software PRIMER v6 + PERMANOVA (Anderson et al. 2008) to understand the distribution of NIS according to the different substrates. The set of NIS was added as a vector overlay on the MDS plot to increase its clarity. Before the analysis, a similarity matrix was constructed using the Sørensen similarity

index. The relationship between the environmental features characterising different types of substrate and the fouling assemblages was analysed by BIO-ENV (Clarke and Ainsworth 1993) and DistLM (Distance-Based Linear Model) (Clarke and Ainsworth 1993). In BIO-ENV analysis, the similarity matrix obtained through Euclidean distances (environmental features) was matched with biotic Sorensen similarity matrices. DistLM was used to determine the best-fitting environmental characteristics and to measure the percentage of variation they were able to explain.

Results

Diversity of the sampled assemblages

In this analysis, 82 taxa were identified across all substrates, 10 of which were NIS (Supplementary material Table S1). This value is lower than the total number of species found by Lezzi and Giangrande (2018), who examined fouling assemblages on PVC panels in the same area (Table S1). The largest number of taxa was found on the anchor blocks. By contrast, the smallest number of taxa was found on the exposed side of the quay, which also showed the lowest number of NIS. The highest number of NIS was found on the suspended coconut fiber collectors. The number of NIS present in the different floating assemblages seemed, therefore, proportional to the total number of species present and ranged between 7% (on the exposed side of the quay) and 26.5% (on the suspended coconut fiber collectors) (Figure 2A, B). However, the trend was less evident when comparing assemblages from the coconut fibers and the anchor blocks under the aquaculture outplants. The total number of NIS on floating collectors mirrored that found by Lezzi and Giangrande (2018) on PVC panels. Non-indigenous species contributed the most to the communities on the suspended coconut fiber collectors and least to the quay communities, suggesting a gradient from a more sheltered environment with more NIS to a less sheltered environment composed of more native species.

Description of assemblages

Assemblages of suspended coconut fiber collectors

A total of 36 taxa were present, nine of which were NIS (Table S1). The assemblage was composed almost entirely of macroinvertebrates, with a species dominance of Ascidiacea, represented by 15 taxa, while Porifera were the least represented with only the NIS *Paraleucilla magna* present. The only macroalga present was *Spyridia filamentosa*, a red alga seasonally present in the area and superficially abundant. The most abundant invertebrate species was *Mytilus galloprovincialis*, which also covered > 50% of the substrate. Other abundant species were the ascidians *Phallusia mammillata*, *Styela plicata*, and *Didemnum coriaceum* (9.5%, 12.7%, and 2.8% cover, respectively), *S. filamentosa* (12%), and the polychaetes *Sabella*
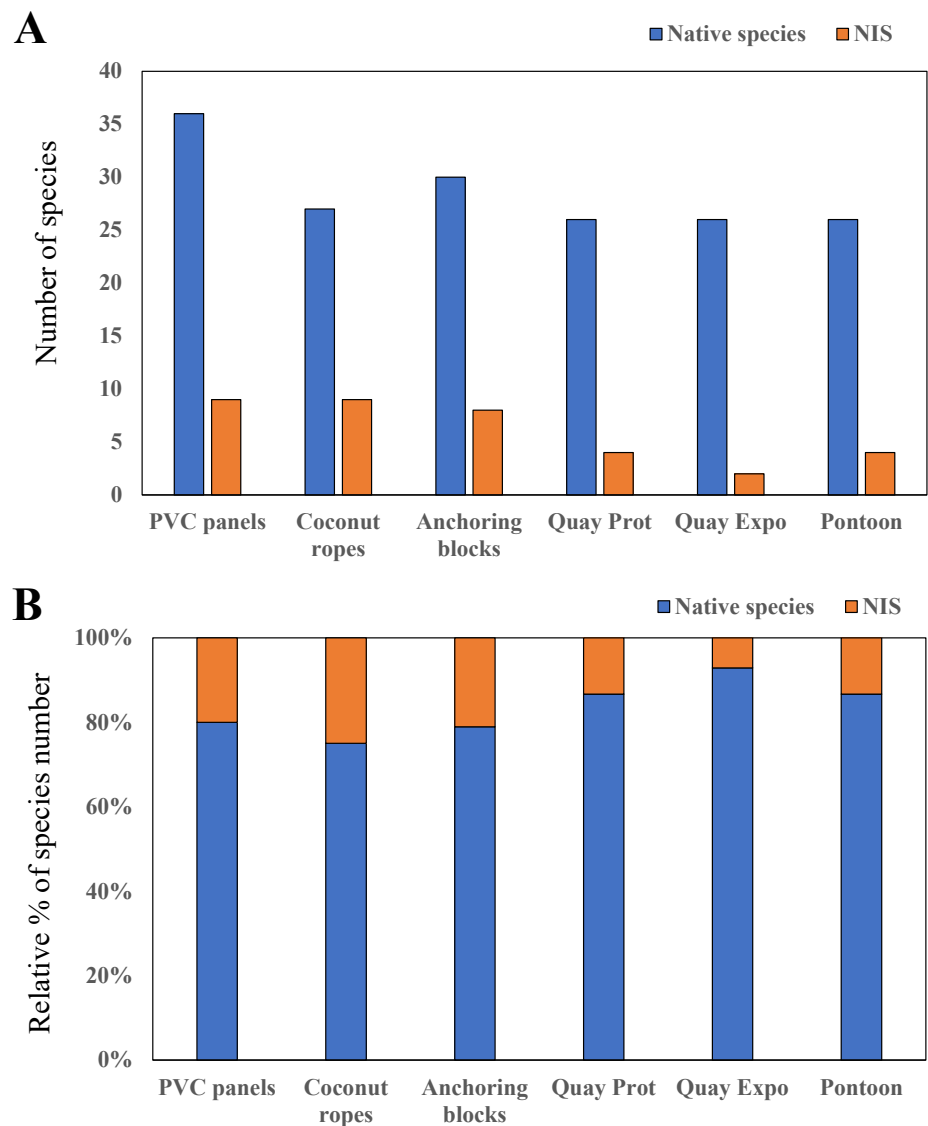
A

B

Figure 2. (A) Relative number of NIS in the examined assemblages; (B) the same, as a percentage.

spallanzanii (10%) and *P. magna* (4.5%) (Figure 3A). This composition was for the shallower assemblage, but the assemblage changed with depth with an inversion of dominance between *M. galloprovincialis* and *S. spallanzanii*; at deeper depths, *S. spallanzanii* became dominant and covered 64.2% of the substrate (Figure 3B).

Assemblages of anchor concrete blocks

The seabed under the fish aquaculture cages was muddy with very limited or absent vegetation cover, and the fouling community was collected from artificial hard substrates, mainly concrete blocks, which were always immersed (Figure 3C). A total of 38 taxa were collected, eight of which were NIS (Table S1). Once again, the ascidians were the most abundance taxa, with 11 taxa recorded. Also well represented were molluscs and annelids with 10 and seven taxa, respectively, and sponges with three species. Overall, the assemblages were mainly composed of large-body filter feeder
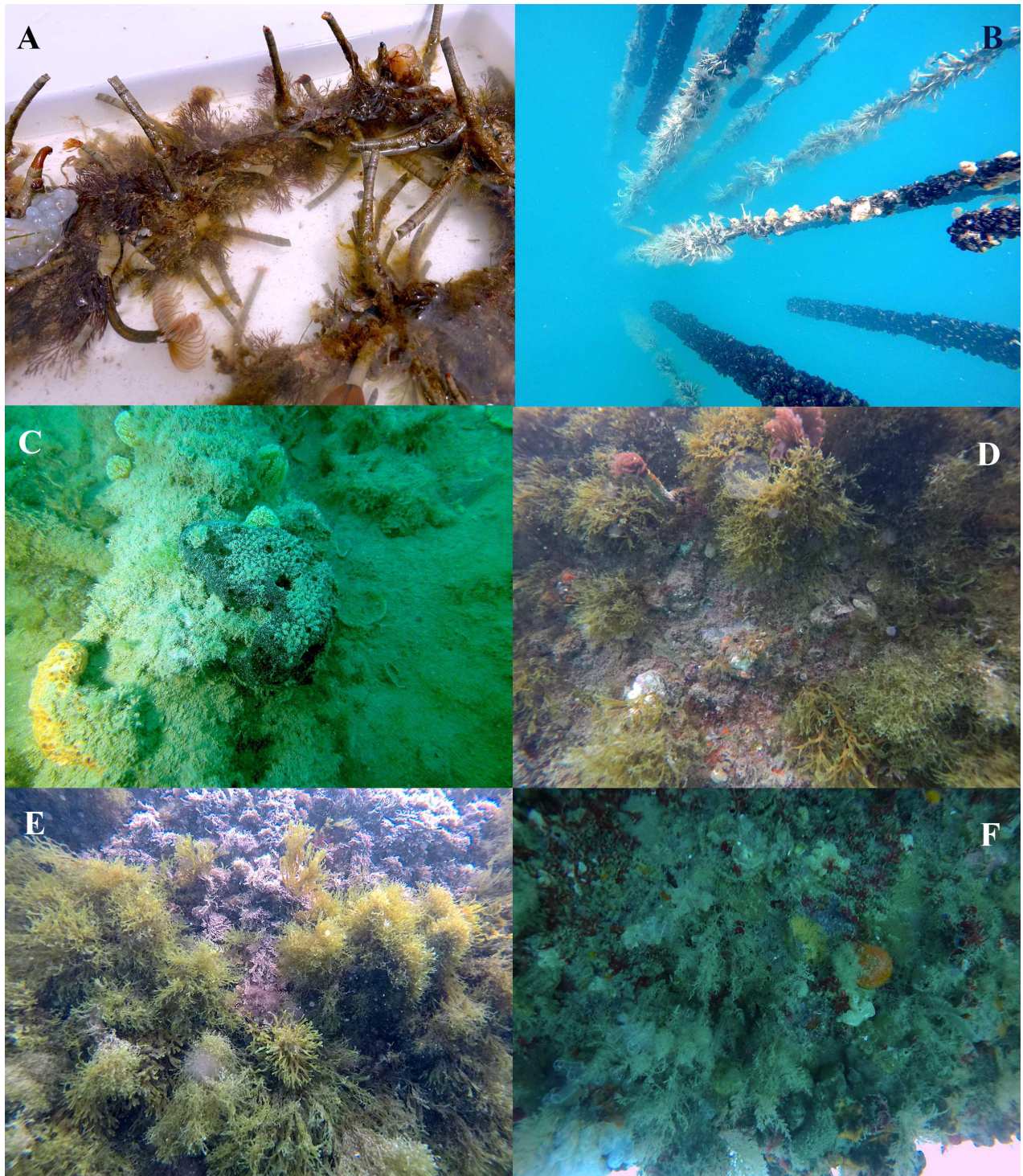
Figure 3. Photographs from the sampled assemblages: (A) coconut rope, suspended collector around the fish aquaculture cages; (B) some collectors photographed underwater in July 2019, showing the inversion of dominance between *Mytilus galloprovincialis* and *S. spallanzanii*, which covered 64.2% of the substrate after 3–4 m depth; (C) anchor concrete blocks; (D) assemblage of the exposed side of the quay; (E) assemblage of the protected side of the quay; (F) assemblage of the floating pontoon. Photographs by authors: AG, DA, JB, MDP, CL, CP.

invertebrates, with a conspicuous presence of the polychaete *S. spallanzanii* and the ascidians *Microcosmus* spp. Most of the species were typical of the fouling community except for the poriferans *Clathrina coriacea*, *Haliclona* (*Reniera*) *cinerea*, and *Oceanapia isodictyiformi*s. As for coverage, the community was dominated by two species, the polychaete *S. spallanzanii*

(30.7%) and the mollusc *M. galloprovincialis* (42.5%). The alien bivalve *Pinctada imbricata radiata* was well represented, covering up to 10% of the available surface. The ascidians of the genus *Microcosmus* contributed 10.2%, and the rest was covered by bryozoans and other ascidians.

Assemblages of the quay

In total, 35 taxa were collected, 30 from the protected side and 28 from the exposed side (Table S1). Among them were 24 macroinvertebrates (24 from the protected side and 19 from the exposed side) and 11 macroalgae (six from the protected side and nine from the exposed side). From the protected side, the macroalgae *Dictyota dichotoma* var. *intricata* covered 73.68% of the available surface area and *Ellisolandia elongata* covered 6.95% (Figure 3D); also abundant were sponges, among which the most represented was *H.* (*R.*) *cinerea* (4.07%), spreading on the rocky substrate not occupied by algae. The main differences between the protected and exposed assemblages were due to a lower macroalgal richness on the protected side. Macroalgae dominated the community on the exposed side, covering most of the substrate. Once again, the most abundant species were *D. dichotoma* var. *intricata*, covering 79.01% of the available habitat, and *E. elongata* covering 5.44%; *Jania rubens* also added to this percent coverage (Figure 3E). Among the macroinvertebrates, two polychaete sabellids, *Branchiomma luctuosum* (Grube, 1878) and *B. boholense* (Grube, 1870), were the only NIS present on the exposed side; on the protected side, these sabellids were joined by other NIS – *Hydroides elegans* and the mollusc *P. radiata*. NIS macroalgae were absent from both the protected and exposed sides.

Assemblages of the pontoon

A total of 32 taxa were collected from the pontoon (Table S1). Macroinvertebrates dominated the community, with an irrelevant quantitative contribution of macroalgae; only three species were recorded (*Corallina officinalis*, *Heterosiphonia crispella*, and *J. rubens*). During the sampling period, a bloom of the bryozoan *Crisularia plumosa* was observed. This species was the most abundant, covering about 32.15% of the surface, together with *Schizoporella errata* (27.49%) and *Clavelina lepadiformis* (20.07%). No macroalgae NIS were found, but six species of invertebrate NIS were detected (Table S1), among which the polychaete *B. luctuosum* represented 12.12% of the total cover (Figure 3F).

Community analysis between substrates

The taxonomic community composition was strongly influenced by substrate (PERMANOVA, F = 662.78, p = 0.001) that resulted significantly different from each other (PERMANOVA, Table 2). The MDS plot (Figure 4A)

Table 2. Results from PERMANOVA using Sørensen similarity matrices to test for differences between different substrates. Significant p values are given in bold.

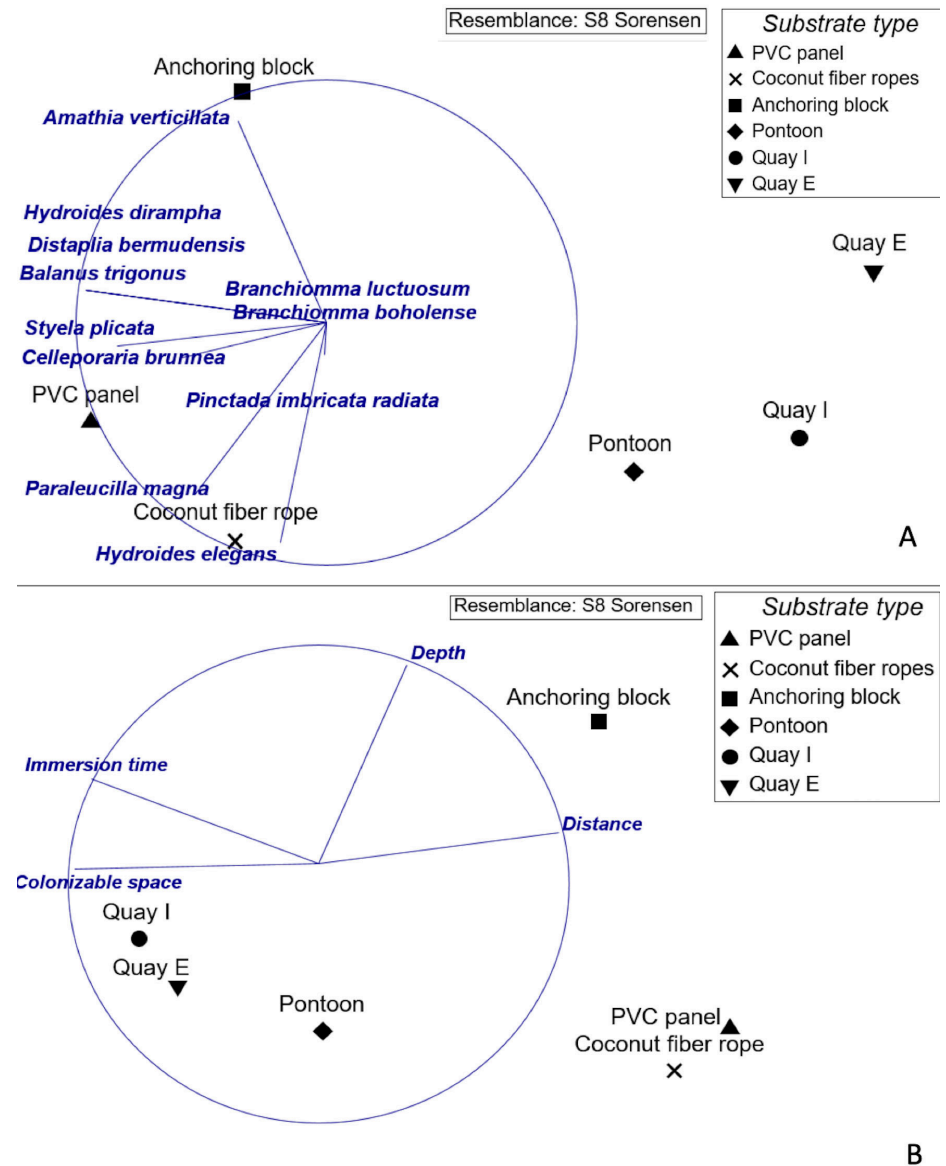| Source	df	MS	Pseudo-F	P(perm)
Substrate	5	3714.2	662.78	**0.001**
Res	12	5.6039		
Total	17			
Pairwise comparison	PVC panels ≠ coconut fiber ropes ≠ Anchoring block ≠ Pontoon ≠QP ≠QE			

Figure 4. Non-metric multidimensional scaling plots displaying (A) taxonomic and (B) environmental similarity of fouling assemblages sampled across artificial substrates.

showed the assemblages present on the quay separated from the others, with the assemblage of the floating dock (pontoon) placed in the middle on the horizontal axis. The other sites resulted instead separated along with the vertical axis, the community on anchoring block and floating collectors (coconut fibres) at the extreme of this gradient. When the NIS are plotted, they appeared located at the right side of the model close to these more transient substrates, with the polychaetes of the genus *Branchiomma* and

in a lesser extent the mollusc *Pinctata imbricata* placed in the middle of the model, being these taxa widely distributed in most of the examined assemblages.

The results of the BIO-ENV and DistLM analyses showed a positive correlation between some environmental features and the presence–absence data matrix of fouling species. The highest rank correlations occurred with a group of three variables, i.e., immersion time, depth, and distance (BIO-ENV, r = 0.92). The DistLM analysis performed, considering the features of the substrates (Figure 4B), produced an almost identical model to that obtained by the multivariate analysis of species composition. Quay assemblages were driven by immersion time and substrate size and were characterized by a few number of NIS, while fouling assemblages of the anchor blocks were linked to water depth and to a greater presence of NIS (Figure 2A, B). Lastly, distance from the aquaculture facility (i.e., organic input) drove the assemblages of anchor blocks and coconut collectors, both of which showed a considerable number of NIS (Figure 2A).

Discussion

Determining which factors affect the establishment of newly arriving species and which habitat is more susceptible to biological invasions is a crucial goal for ecologists, conservationists, and invasion biologists (Simberloff and Wilson 1969; Sakai et al. 2001; Simberloff 2009; Corriero et al. 2015). Although many studies suggest that propagule pressure plays a vital role in biological invasions (Lonsdale 1999; Colautti et al. 2006), several authors have highlighted the ability of habitat quality to regulate the success of non-indigenous species (NIS) if propagule pressure is similar across habitats (Ruiz et al. 2009; Myan et al. 2013; Simkanin et al. 2013, 2017).

The Mar Grande of Taranto in Italy, a hotspot for NIS diversity (Occhipinti-Ambrogi et al. 2011), is an ideal field laboratory to test how habitat characteristics influence the distribution of NIS through a macroecological approach, investigating many species and habitat types (substrates) at the same time. Notwithstanding, the fouling communities observed should have similar contributions from propagule supply; thus, any differences in community composition can be attributed to post-settlement events.

There were inherent differences among the analysed artificial substrates in terms of exposure time (nine months to 10 years) and their distance from organic loading (i.e., the aquaculture facility). Even so, there were only small differences between the majority of the investigated communities, except for the floating pontoon, which showed a substantially lower number of fouling species. Greater differences were noted regarding the number of NIS and the taxonomic structure of the communities. On the whole, the richest assemblages were found on more ephemeral substrates (suspended collectors and anchor blocks), dominated by macroinvertebrates,

which also had the largest number of NIS. By contrast, the lowest number of species was found on less transient substrates (assemblages of the pontoon and quays), which were dominated by macroalgae. This dominance by macroalgae could contribute to preventing invertebrate NIS settlement. Assemblages on suspended mobile collectors yielded results qualitatively similar to those of Lezzi and Giangrande (2018), which recorded nine NIS in a similar area on PVC panels in 2014. Similar numbers of NIS were found in this study, except for the absence of *Celleporaria brunnea* and the addition of *Pinctada imbricata radiata* (Stasolla et al. 2014). However, the fouling assemblages found on the suspended mobile collectors differed slightly from Lezzi and Giangrande (2018). For example, *Spyridia filamentosa,* a floating red alga with a seasonal presence in the Mar Piccolo basin (Petrocelli et al. 2013), was abundant on the suspended mobile collectors but not on the PVC panels. However, it is possible that this could be linked to the smooth substrate of the PVC panels, which is less suitable for macroalgae attachment (Harlin and Lindbergh 1977; Anderson and Underwood 1994; Myan et al. 2013). The presence/absence of Porifera species (i.e., *Oceanapia isodictyiformis*, *Clathrina coriacea*, and *Haliclona* (*Reniera*) *cinerea*) drove differences between suspended mobile collectors and anchor blocks. These taxa are usually present on natural substrates, and their presence can indicate a high degree of maturity of the community (Griessinger 1971; de Weerdt 1985; Longo et al. 2008, Longo and Pronzato 2011). However, the algae in the pontoon assemblage gave a minimal contribution to the percent cover, compared to the quay, so that the assemblage of the pontoon was dominated by macroinvertebrates, especially the bryozoans *Schizoporella errata* and *Crisularia plumosa*. By contrast, macroalgae were a larger proportion of the cover in the exposed part of the quay.

The differences in the assemblages were highlighted by the statistical analysis on species composition, indicating the presence of two main groups. A first group (suspended mobile collectors and anchor blocks) was characterised by a typical fouling assemblage dominated by sessile macroinvertebrates, where about 20% of the species richness was due to NIS. The second one (quay assemblages and floating pontoon) was characterised by fewer NIS and the dominance of macroalgae, with a greater number of NIS on the pontoon than on the quay. The assemblages of the quay differed the most from all the other investigated substrates, mainly driven by immersion time (10 years in comparison to < 3 years for all of the other substrates) and the size of the target substrate (which is much larger than all of the other substrates). In contrast, the fouling assemblages of the anchor blocks seemed to be primarily influenced by depth linked to light attenuation, compared to the suspended mobile collectors. The differences in NIS species richness observed here across the artificial substrates is due to aspects of the substrate itself along with the

environmental characteristics of where the substrate is placed, with assemblages of large and long-lasting artificial substrates differing from those occurring on smaller transient ones. Therefore, the size and immersion time of the substrate may have driven particular species success, most likely influencing interspecific competition (Rodriguez et al. 1993; Chang and Marshall 2016; Valentine et al. 2016).

The community from both sides of the quay (i.e., exposed and protected) was a typical assemblage of organisms found from hard-bottom semi-enclosed areas (Boudouresque 1984). However, this assemblage was characterised by low species richness and cannot be defined as a fouling community in the strictest sense because it was notably different from assemblages found on submerged artificial structures (it was also different from the floating pontoon connected to the quay). Indeed, the macroalgal species composition of the quay assemblage was quite different from that reported as common in fouling communities (Fletcher 1980), with *D. dichotoma* var. *intricata* reported only occasionally on artificial structures. Moreover, the lack of Ulvales (Chlorophyta) well adapted to high nitrogen concentrations (Cecere et al. 1991) could indicate the absence of high levels of nutrients.

According to the hypothesis by Davis et al. (2000) and Stachowicz and Byrnes (2006), the community tendency to host NIS is influenced by resource availability. From this point of view, we cannot a priori exclude the possibility that the rich assemblages found on suspended mobile collectors and anchor blocks could have been influenced by organic load, indicated by the factor "distance from aquaculture facility". Indeed, the effect of aquaculture activities on fouling development, i.e., enhancing filter feeder macroinvertebrates, was already pointed out (Karakassis et al. 2000). Therefore, it is possible that the nutrients released by the aquaculture process on the immediate environment may favour the recruitment of macroinvertebrates (as well as NIS) on surrounding substrates.

Non-indigenous species were almost absent from the quay assemblage that was more similar to a "natural rocky substrate", a habitat in which macroalgae become highly competitive. The only NIS from the exposed side of the quay were two sabellid species, *B. luctuosum* and *B. boholense*, which are among the few fouling macroinvertebrates that have spread along the Italian coast and become a component of the littoral assemblage on natural rocky habitats (Giangrande *unpublished data*). These two NIS were also found as structural species in the assemblages of a previous study (Lezzi and Giangrande 2018) and were widely distributed across substrates here. The NIS mollusc *P. imbricata radiata* was absent in Lezzi and Giangrande (2018), which could be due to its recent introduction to the area (Stasolla et al. 2014).

Our results call for more experimental studies to examine NIS co-occurring in assemblages and the suitability of different types of artificial

structures for NIS (Glasby et al. 2007). Similarly, the relationship between habitat vulnerability and native species to be effective barriers to biological invasions should be investigated further (Corriero et al. 2015). The present study represents only a preliminary descriptive approach, considering the complexity of the phenomenon; however, the data reported give an important indication of the validity of the biological filter hypothesis sensu Catford et al. (2009). In this case, our study seems to suggest that species diversity does not seem to be a filter against NIS in this system. The community on the quay, which was less diverse in terms of basal encrusting species, also had the lowest number of NIS. This suggests that older communities, at least in confined and hypertrophic environments, can be an effective biological filter for NIS. Indeed, NIS are less likely to settle in well-established assemblages than in early community assemblages or bare substrates that characterise disturbed or newly created habitats (Clark and Johnston 2011). As suggested by Simkanin et al. (2012, 2013, 2017), habitat qualities and local factors (e.g., characteristic of recipient assemblage) can differentially affect invasibility. An older, established community may prevent NIS invasion as natural benthic habitats can be more resistant to invasions than artificial ones because of the increased complexity of the biogenic habitat through interactions among established community members rather than freedom from space competitors. It remains to be investigated, however, whether this filter is active on pre- or post-settlement NIS mechanisms.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Presence/absence of species collected from the different artificial substrates from the Mar Grande of Taranto in July 2019.