Regional Studies in Marine Science 45 (2021) 101818

Contents lists available at ScienceDirect

Regional Studies in Marine Science

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

Temporal changes of a fouling community: Colonization patterns of the benthic epifauna in the shallow northern Adriatic Sea

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ARTICLE INFO

Article history:
Received 6 January 2021
Received in revised form 19 April 2021
Accepted 1 May 2021
Available online 4 May 2021

Keywords:
Fouling community
Sessile invertebrates
Temporal patterns
Seasonal occurrence
Alien species
Placement season

ABSTRACT

Sessile benthic communities are an important element of marine ecosystems, yet their temporal patterns remain poorly understood. For this reason, the temporal changes of the fouling community on brick plates in Piran Bay, Gulf of Trieste (northern Adriatic Sea), were studied for two calendar years. The aim of this study was to identify the settlement of dominant native and alien species on artificial substrates and their temporal occurrence, both in terms of season and duration of submersion. In addition, we tried to assess the impact of the placement period on developing communities. The dominant taxonomic groups were bryozoans, which accounted for almost half of the total coverage (46%), serpulid polychaetes (25%) and bivalves (11%). Most of the species belonging to the dominant taxa occurred throughout the year, with the peak of occurrence in summer. The first settlers included serpulids and bivalves, which were constantly found on the plates together with bryozoans. Alien and cryptogenic species represented about 13% of all taxa found during the study. This highlights the importance of bare artificial structures erected outside typical hotspots for alien species; they serve as a springboard for the spread of alien fouling species. The communities that formed on plates placed in different seasons showed significant differences between them. High bryozoan coverage characterized the communities placed in winter and spring, while the plates placed in summer and autumn were dominated by serpulid polychaetes. These differences are the result of species seasonality as well as the interaction between them. The study demonstrates the importance of timing for initial colonization. It can be linked to the placement of the bare substrate for the development of the community, and provides a baseline for research and projects involving underwater constructions and the detection of alien species.

1. Introduction

Sessile suspension-feeding invertebrates dominate the Mediterranean epifaunal hard-bottom communities, also referred to as fouling communities (Gili and Coma, 1998). They play an important role in marine ecosystems as bioconstructors (reviewed in Cocito, 2004; Kružić, 2014) and as regulators of primary and secondary production of coastal food webs (reviewed in Gili and Coma, 1998).

Succession in the fouling community has been the subject of many scientific studies (e.g. Hunt and Scheibling, 1997; Kocak et al., 1999; Fava et al., 2016; Sokołowski et al., 2016). The colonization process on bare artificial structures starts with the formation of a biofilm formed by the microbial community, composed predominantly of heterotrophic bacteria and diatoms, along with their excretions, within one month after placement (Mejdandžić et al., 2015). This microfouling layer facilitates the colonization of invertebrate larvae (Wieczorek and Todd, 1998), which gradually colonize the available space. The idea of a climax in the fouling community is not as clear as in terrestrial habitats (Scheer, 1945). Thus, Sutherland (1974) has proposed a theory of several possible stable or climax communities, which seems plausible for many epifaunal hard-bottom communities. Numerous factors influence the establishment of propagules and the formation of fouling communities. They include abiotic factors, such as substrate type (Brown, 2005), orientation (Glasby and Connell, 2001; Ushiama et al., 2016) and substrate heterogeneity (Grégoire et al., 1996; Lapointe and Bourget, 1999; Pech et al., 2002), sedimentation rates (Maughan, 2001; Fava et al., 2016) and water turbidity (Gabriele et al., 1999). On the other hand, biotic factors include the reproductive capacity of the species, associated with availability of larvae (Sutherland, 1981), post-settlement mortality often associated with predation (Breitburg,

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https://doi.org/10.1016/j.rsma.2021.101818

1985; Hunt and Scheibling, 1997; Nydam and Stachowicz, 2007), the life strategy of individual species (Khalaman, 2010) and their competitive abilities (Cifuentes et al., 2010). The plethora of these interrelated influences on the fouling community is reflected in the patchiness of such communities (Terlizzi et al., 2007).

The successional patterns of fouling communities usually follow Conell–Slatyer's Inhibition model (Harms and Anger, 1983; Greene et al., 1983; Vrišer, 1986), which postulates that the first species colonizing empty space inhibit the growth of other settlers (Connell and Slatyer, 1977). Seasonality is another source of temporal variation in community composition in temperate seas, as the seasons reflect differences in many of the factors mentioned above (e.g. Underwood and Anderson, 1994; Qiu et al., 2003; Dziubińska and Janas, 2007). Based on these two observations regarding the temporal changes in the fouling community, the placement season could have a significant influence on the development of fouling communities. It has already been shown to be important in subtidal tropical (Rajagopal et al., 1997; Satheesh and Wesley, 2011), intertidal tropical (Underwood and Anderson, 1994) and temperate coastal seas (Brown, 2005; Qvarfordt et al., 2006; Lezzi et al., 2017). Different times of placement can lead to significant differences in the colonization of invertebrate larvae and consequently the development of fouling communities, both in terms of biomass and community composition (Qiu et al., 2003; Satheesh and Wesley, 2011).

The northern Adriatic Sea is mainly characterized by muddy and sandy bottom, occasionally interrupted by high-biodiversity biogenic formations (Lipej et al., 2016). However, other hard-bottom features are also present in these "sedimental plains", which are often overlooked. These are human-made hard substrates, such as pipelines or other concrete structures. Our study focused on the temporal changes in the fouling communities associated with such substrates, which are submersed bare, but are quickly covered by a colourful invertebrate community. In the northern Adriatic, studies on temporal changes of sessile invertebrate communities have focused mostly on changes in communities found on natural substrates over time (Ponti et al., 2011) or on communities formed after a single placement event on artificial substrates (e.g. Vrišer, 1986; Fava et al., 2016; Nerlović et al., 2018). As far as we know, the effect of the time of placement in the Adriatic Sea has not been evaluated to date. Considering that this is area is characterized by one of the highest rates of introduction of alien species and that the local fauna is changing rapidly (Occhipinti-Ambrogi, 2002), further studies on the temporal changes of this potentially affected community are required.

The objectives of our study were (1) to identify the dominant and alien species established on artificial substrates and their temporal occurrence, both in terms of season and duration of submersion and (2) to assess the impact of the placement period on developing communities. We focused mainly on three groups that dominate the fouling communities: bryozoans, serpulid polychaetes and bivalves.

2. Materials and methods

2.1. Study area and experimental site

The Slovenian coastal sea is a part of the Gulf of Trieste, a shallow gulf at the top of the northern Adriatic Sea, which is characterized by large tidal differences (Boicourt et al., 1999) and low winter temperatures averaging around 10 °C (Grilli et al., 2020). Rivers have a major impact on this inlet, as they act as sources of strong freshwater inflow with pronounced seasonal variability (Boicourt et al., 1999), suspended sediment (Ogorelec et al., 1991), and pollution (Turk and Potočnik, 2001). Piran Bay, where the experimental site of this study is located, is a submerged valley of Dragonja River, with high sedimentation rates. The superficial sediment composition in the shallow coastal layer, which reaches down to a depth of about 5 m, consists of silt and sandy silt (maximum 15% clay and 40% sand), while the sediments covering most of the deeper areas are clayey silt (maximum 50% clay and 5% sand) (Ogorelec et al., 1991).

The microlocation of the study site (GPS position: 45.51871 °N, 13.56761 °E) lies at a depth of between 8.5 m and 10 m, where the bottom is silty, and anthropogenic elements providing hard artificial substrates are present (pipeline system for meteoric water, remains of fishing nets and tires).

2.2. Fieldwork and laboratory analysis

Environmental data were collected monthly from March 2018 to February 2020 during the national monitoring program using a CTD probe in the middle of Piran Bay-point 00MA (GPS: 45.50015 ° N, 13.5721 °E) at the depth of experimental structures. Temperature, salinity and dissolved oxygen were recorded.

Starting in March 2018, a metal construction carrying 30 vertically oriented terracotta plates with sand inclusions (25 × 12 × 3 cm) was placed on the experimental site every month. Thus, after one year, in March 2019, 12 constructions carrying 360 plates were placed at the site. The distance between the constructions was approx. 1.5 m–14 m. In the months following placement (1, 2, 3, 4, 5, 6, 7, 8, 9, 10 and 12), a new plate was removed from each construction (see Fig. 2 for the experimental set-up). Two types of analysis were performed on each sampled plate: (1) sessile invertebrates on the plates were determined with a stereomicroscope and (2) a photo analysis estimating coverage was performed on the front part of the plate. The total number of analysed plates was 132.

Each sampled plate was fully examined under a stereomicroscope, inspecting a surface area of approximately 822 cm^2. Voucher specimens were anaesthetized with magnesium chloride (Williams and Van Syoc, 2007) and preserved in a formalin substitute, the fixative FineFIX (Milestone Medical). Sessile invertebrates were identified to the lowest possible taxonomic level using taxonomic keys and relevant literature. The main literature used for each taxa was: Bryozoa – Zabala and Maluquer, 1988; Hayward and McKinney, 2002; Polychaeta – Fauvel, 1927; Bianchi, 1981; ten Hove and Kupriyanova, 2009; Mollusca – Tebble, 1966; Cossignani and Ardovini, 2011; Scaperrotta et al., 2009-2013; Hydrozoa – Peña Cantero and Garcia-Carracosca, 2002; Bouillon et al., 2004; Cirripedia – Igić, 2007; Ascidiacea – Mastrototaro and Brunetti, 2017. Due to the nature of this work, a high proportion of juvenile specimens were found in the samples, which is why certain taxa were grouped into broader categories (Spirorbinae spp. and Anomiidae spp.) or were treated separately (Serpulidae indet. juv and *Hydroides* sp. juv). The entire surface of the plates was analysed at the laboratory, i.e. species found on the edges of the plate, as well as the more sciaphilic microhabitats (behind the bars holding the plates, etc.).

Due to the high proportion of colonial species and the importance of evaluating the space used in successional competition, the coverage estimate was used to measure total community composition (Bohnsack, 1979). The sampled plates were photographed at the laboratory prior to subsampling. Coverage of the sessile community was assessed using the annotation software CPCe (Kohler and Gill, 2006). The front part of the plate (surface 200 cm^2) was used for analysis, with 100 stratified random points superimposed on the photo of the plate and all underlying sessile organisms assigned to morphologically identifiable categories (MIC). This proved to be an efficient method for estimating the coverage of sessile organisms (Drummond and Connell, 2005). It

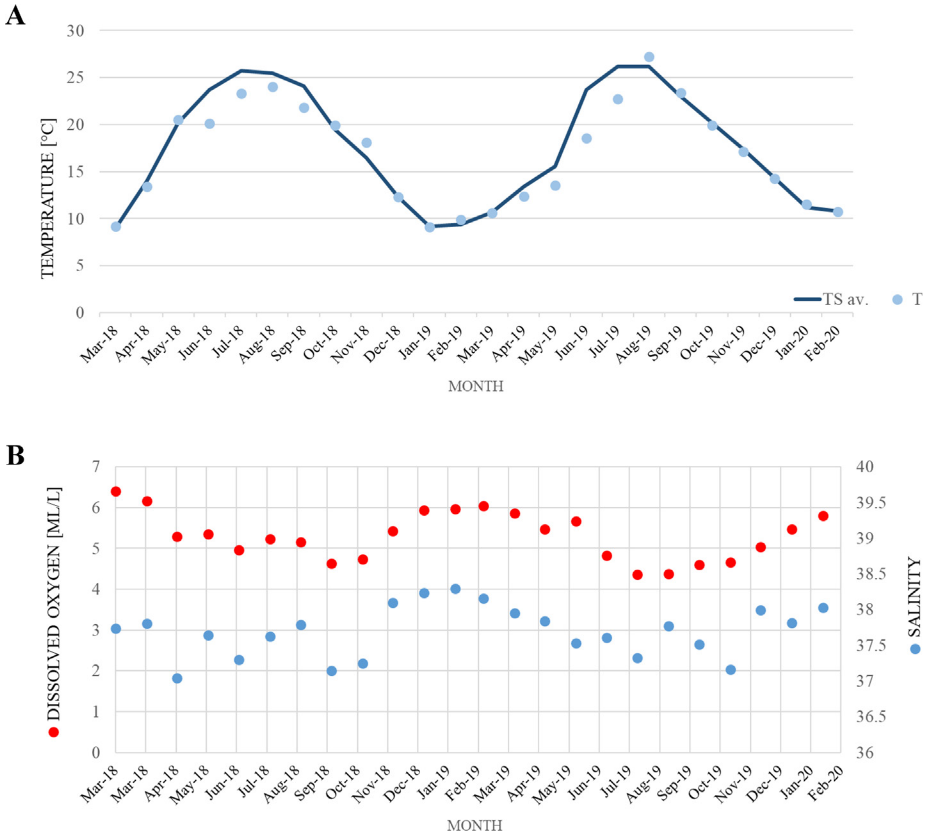

Fig. 1. Average values of monthly measurements taken with a CTD probe between 8.5 and 10 m depth. (A) Temperature, (B) Dissolved oxygen and Salinity. T - temperature, TS av. – average surface temperature. * Average monthly surface temperature data was obtained from the automatic hydrological station in Koper (provided by Slovenian Environment Agency (ARSO), 2020).

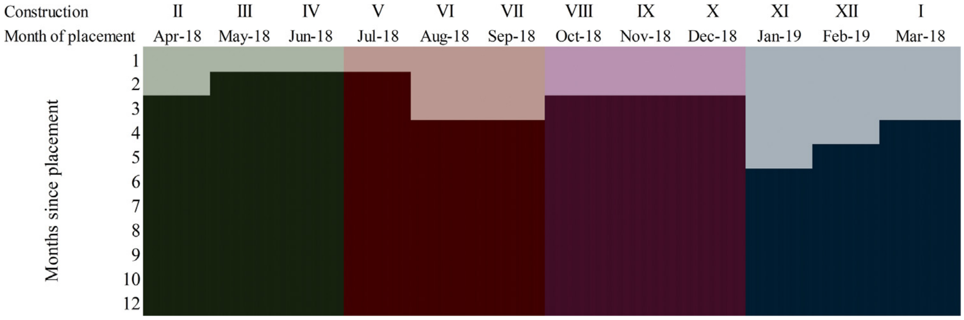

Fig. 2. Experimental design drawings: constructions (marked with Roman numerals), deployed monthly (from March 2018 to February 2019) are shown in columns and samples collected monthly are shown in rows. Lighter cells represent samples with less than 20% fouling coverage and darker ones represent those with more than 20% fouling coverage. Green-spring, red-summer, pink-autumn, blue-winter. Note that the first construction placed under water (I) is part of the winter placements. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

did not include rare and inconspicuous species (Bohnsack, 1979), but these were considered in the laboratory analysis. MICs were formed on the basis of taxonomic classification (invertebrates) and morphological classification (algae) (the list of MICs is given in Table 1). Points with no visible macro-organisms, such as bare substrate or sediment accumulation (excrement or corophiid amphipod tubes) were left blank. In cases of overgrowth, it was possible to assign more than one category to each point, and thus total coverage exceeded 100%.

2.3. Data analysis

Presence/absence data obtained from laboratory analyses were used to study the temporal patterns of dominant taxa. In order to identify pioneers and late colonizers, the absolute occurrence of species on plates with the same duration of submersion (1–12 months) was calculated. Moreover, in order to test whether their presence is influenced by seasonality, the occurrence of species on plates sampled in the same season was calculated, as well. Since the taxa on the experimental plates were less than one year old, their occurrence on the plates tells us little about their reproductive and colonization period. Therefore, the seasonal occurrence of species present on the plates for up to three months within the same season was investigated. Months were grouped into seasons: Spring (April–June), summer (July–September), autumn (October–December) and winter (January–March) (according to Grilli et al., 2020). Presence/absence data for taxa that occurred on five or more plates is shown in Figs. 3 and 4. The frequency distribution between seasons was tested for taxa that occurred on 20 plates or more using the chi square

Table 1
Categories used for photo analysis of the fouling community along with their total percentage on all analysed plates and representative examples for wider categories. MIC category: morphologically identifiable category.

Taxonomic group	MIC category	Total coverage [%]	Representative examples
Serpulidae	*Spirobranchus triqueter*	16.15	
	Salmacina sp.	2.77	
	Spirorbinae	1.37	
	Serpulidae other	13.04	*Hydroides elegans*, *Serpula vermicularis*
Bryozoa	*Schizoporella errata*	16.98	
	Schizobrachiella sanguinea	11.05	
	Calpensia nobilis	18.31	
	Schizoporella dunkeri	2.58	
	Umbonula ovicellata	2.28	
	Bryozoa other	9.76	*Terwasipora complanata*, *Cryptosula pallasiana*
Bivalvia	*Ostrea edulis*	13.47	
	Anomiidae	0.62	
Algae	algal turf[a]	11.88	
	erect macroalgae	2.82	*Cutleria multifida*, *Polysiphonia* sp., *Bryopsis* sp.
	sciaphilic encrusting macroalgae	1.25	order Corallinales, *Zanardinia typus*
Porifera	Porifera	0.61	
Ascidiacea	Didemnidae	0.44	
	Styela plicata	0.08	
	Botryllus schlosseri	0.15	
	Ascidiidae	0.03	
Hydrozoa	Hydrozoa	6.30	
Cirripedia	*Balanus trigonus*	0.01	

[a] Definition of algal turf: mat-forming algal community, lower than 1 cm, composed of species of diatoms, cyanobacteria, Chlorophyta, Rhodophyta and Phaeophyta (Connell et al., 2014).

test, and assuming even distribution. Graphical representations were made using the following software programs: PRIMER v7, Microsoft Excel 2016 and GIMP 2.8.22 (GNU Image Manipulation Program).

The presence/absence data were used to compile a list of alien and cryptogenic species found in this study. The relative frequency of occurrence for each species was calculated as the proportion of the plates on which the species was present out of the total number of plates examined (132). Data on the status (alien or cryptogenic), the presence in the Adriatic Sea (common, casual or first observation), the year of the first record in the Mediterranean Sea and invasiveness in the Adriatic Sea were obtained from the relevant literature (Zenetos et al., 2005; Streftaris and Zenetos, 2006; Zenetos et al., 2010; Marić et al., 2016; Ulman et al., 2017; Zenetos et al., 2017; Ferrario et al., 2018; Galil et al., 2018).

In order to assess the influence of the placement season on the composition of the community, multivariate statistical analyses were performed using MIC coverage data. We excluded communities with low total coverage (<20%), thus eliminating the samples with high relative standard error of coverage estimation (Bohnsack, 1979). Because of this elimination, the number of plates per season varied. The total number of plate communities compared for similarities was 104, of which 21 were placed in winter, 29 in spring, 27 in summer, and 27 in autumn. Pretreatment included standardization of all data due to uneven coverage of the plates (Clarke and Gorley, 2015) and square root transformation. A cluster analysis using the group average linkage method based on the Bray–Curtis Similarities was performed to visualize the relationships between the communities. To test whether the composition of the communities significantly differed in response to the placement season, permutational multivariate analysis of variance (PERMANOVA; (Anderson et al., 2008), with pairwise comparison, was carried out on the same matrix, using a single factor design with 4 levels (corresponding to placement season) and the "unrestricted permutation of row data", as recommended in Anderson et al. (2008). To determine which taxonomic groups contributed most to the similarities within the communities on plates placed in the same season, a SIMPER analysis was performed. The data were analysed using PRIMER v7 software.

3. Results

3.1. Environmental conditions

Data on abiotic conditions are presented in Fig. 1. A clear seasonal pattern was recorded for temperature, but not for salinity and dissolved oxygen. Temperature in winter ranged from 9.13 to 11.52 °C (average surface $T = 9.92$ °C), 12.39 to 20.51 °C (average surface $\mathrm{T} = 18.43$ °C) in spring, 21.81 to 27.26 °C (average surface $\mathrm{T} = 25.12$ °C) in summer, and 12.33 to 19.94 °C (average surface $\mathrm{T} = 16.70$ °C) in autumn. Salinity ranged from 37.04 to 38.30 with a slight peak in winter, which was also true for dissolved oxygen, which ranged from 4.36 to 6.41 ml/l.

3.2. Temporal occurrence of dominant taxonomic groups

In this study, we identified 87 taxa of sessile invertebrates (see Appendix for the complete list of taxa). Bryozoans, serpulids and bivalves were the most common animal taxa on the experimental plates in terms of coverage and, therefore, better characterized

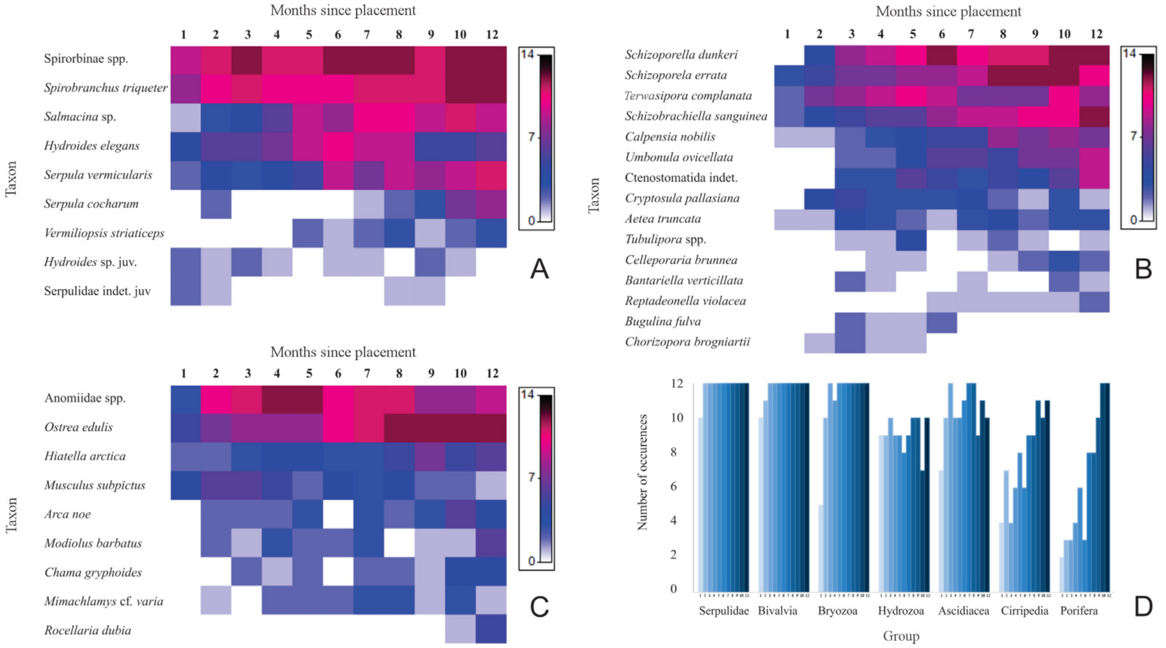

Fig. 3. Shade plot of taxa belonging to (A) Bryozoa, (B) Serpulidae and (C) Bivalvia, which occurred on plates submersed for 1–12 months. Colour-coded numbers (depicted in the key) represent absolute number of occurrences for each taxa. (D) Number of occurrences for representatives of all taxa with different length of submersion (1–12 months). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

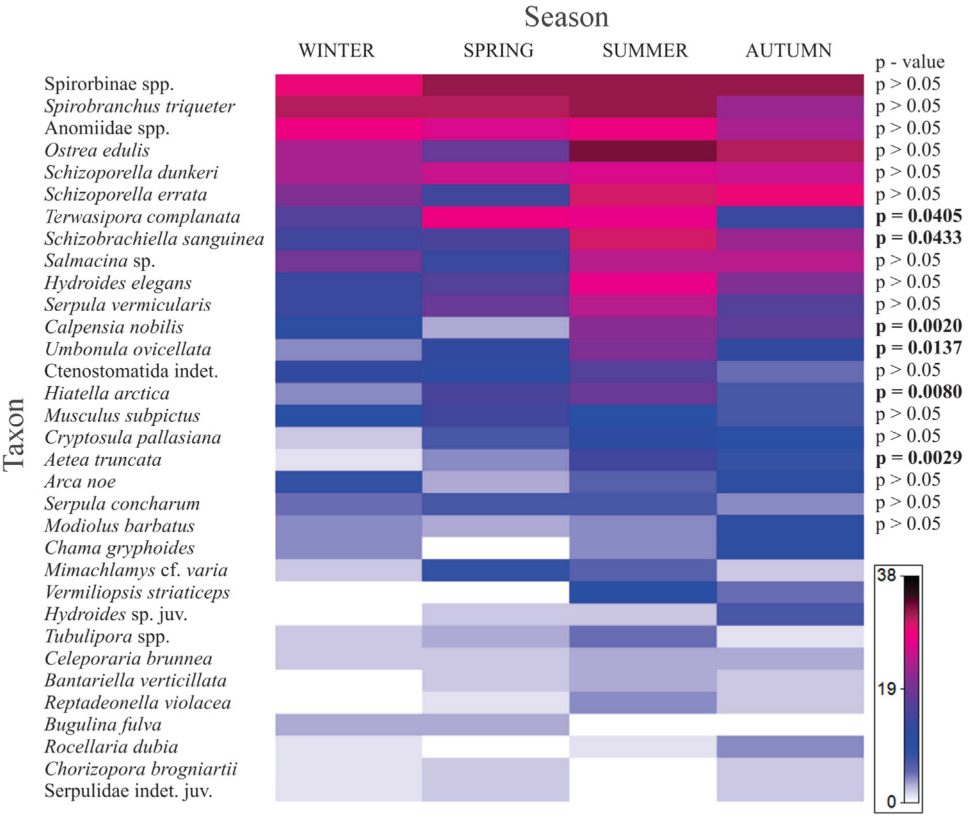

Fig. 4. Seasonal occurrence of taxa belonging to three dominant taxonomical groups, along with p-values of chi square test. Colour-coded numbers (depicted in the key) represent absolute number of occurrences for each taxa. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

taxonomically. Other important groups included hydrozoans, ascidians, sponges and barnacles. Taxa with lower species richness included sabellid polychaetes, vermetid gastropods, scyphozoan polyps and sea anemones.

The occurrence of taxa on plates with the same duration of submersion (1–12 months) is shown in Fig. 3A–C. The most common pioneers on the plates were spirorbins, while the most common species was *Spirobranchus triqueter* (Linnaeus, 1758), with 75% frequency of occurrence after one month of submersion (out of 12 plates sampled) and 88% on all plates examined (out of 132 plates sampled). Bivalves were the other early colonizers of the plates [*Ostrea edulis* Linnaeus, 1758 and *Musculus subpictus* (Cantraine, 1835). The majority of taxa were present on the plates throughout the submersion period. Some common species were evenly distributed throughout the submersion period [Spirorbinae spp., Anomiidae spp. and *Terwasipora complanata* (Norman, 1864)], while others were more common towards the end of the submersion period [*S. triqueter*, *Schizobrachiella sanguinea* (Norman, 1868), *Serpula vermicularis* Linnaeus, 1767, *Schizoporella errata* (Waters, 1878), *Ostrea edulis, Schizoporella dunkeri* (Reuss, 1848), *Salmacina* sp., *Calpensia nobilis* (Esper, 1796) and *Hiatella arctica* (Linnaeus, 1767)]. Few taxa were more frequent in the first months after placement [*M. subpictus, Cryptosula pallasiana* (Moll, 1803)]. Two taxa were observed only in the first months [*Bugulina fulva* (Ryland, 1960) and *Chorizopora brongniartii* (Audouin, 1826)]. *C. brongniartii* was present on plates until the fifth month after placement. Conversely, *Reptadeonella violacea* (Johnston, 1847) did not occupy any plates until the sixth month after placement. Late arrivals also included *Vermiliopsis striticeps* (Grube, 1862) and *Rocellaria dubia* (Pennant, 1777).

After one month of submersion, all major taxonomic groups (Bryozoa, Serpulidae, Hydrozoa, Ascidiacea, Porifera and Cirripedia) were present on the plates. Serpulids, bivalves and bryozoans colonized almost all the plates that had been submerged for two months or longer (Fig. 3D). Sponges and barnacles settled on the plates more slowly, and their frequency of occurrence on the plates increased with the duration of submersion (Fig. 3D). Hydrozoans showed a steady presence on the plates, with no discernible trends regarding the duration of submersion. In addition, their coverage on the plates was very seasonal. Higher hydrozoan coverage (above 20%) was observed only in winter (February and March). No obvious trends were observed for ascidians.

The majority of taxa were observed throughout the year and their frequency did not differ significantly among seasons (Fig. 4). The species with the most striking seasonal distribution were *C. nobilis, H. arctica* and *Aetea truncata* (Landsborough, 1852); the former occurred mainly in summer and autumn, the second one in spring and summer and the latter in autumn. Other taxa with significant seasonal occurrence were *Umbonula ovicellata* Hastings, 1944 (summer), *T. complanata* (spring and summer) and *S. sanguinea* (summer and autumn). Settlement was observed in spring for *C. nobilis* and *C. pallasiana*, in summer for *A. truncata* and in autumn for *C. brongniartii*.

3.3. Occurrence of alien and cryptogenic species

We found seven alien and four cryptogenic species, which together account for almost 13% of all taxa found during this study. Data on the relative frequency of occurrence, status, presence in the Adriatic Sea and year of the first record in the Mediterranean Sea are given in Table 2. The most common alien species and the only one from the family Serpulidae, was *Hydroides elegans* (Haswell, 1883). It occurred from the first month after placement of the experimental plates until the 12th month and was most frequent in the intermediate months (Fig. 3A). Cirriped *Balanus trigonus* Darwin, 1854 and ascidians *Botryllus schlosseri* (Pallas, 1766) and *Styela plicata* (Lesueur, 1823) were also frequent; they were present on about one third of the plates. The first two species occurred on the plates regardless of season and duration of the submersion, while *S. plicata* occurred more frequently in the first seven months after placement and was observed in all seasons, but was less frequent in the spring. Cryptogenic *Amphibalanus improvisus* (Darwin, 1854) appeared only once in the summer. Bryozoans were represented by three alien (*Celleporaria brunnea* (Hincks, 1884), *Arbopercula tenella* (Hincks, 1880) and *Watersipora arcuata* (Banta, 1969) and two cryptogenic species [*B. fulva* and *Bugula neritina* (Linnaeus, 1758)]. *C. brunnea* occurred on plates in all seasons and was more frequent in the last months of the submersion period (Figs. 3 and 4A), while *B. fulva* occurred in winter and spring and only until the sixth month after placement (Figs. 3 and 4A). *A. tenella* occurred twice, in winter and spring, while *W. arcuata* and *B. neritina* appeared only once in winter. *Anadara transversa* (Say, 1822) was the only alien bivalve and occurred on three plates, in autumn and winter.

3.4. Influence of the placement season on developing communities

Regarding coverage of the experimental plates, the communities were dominated by calcified organisms, namely Bryozoa (46% of total coverage), followed by Serpulidae (Polychaeta) (25%) and Bivalvia (11%). Algae represented 12% of the total coverage and Hydrozoa 5%. The groups that represented less than 1% of the total coverage were Ascidiacea, Porifera and Cirripedia. Total coverage increased unevenly between series of simultaneously placed plates. The slowest colonization was observed on plates placed in winter (Fig. 2), with 20% coverage reached only four to six months after placement, whereas the faster colonization was observed on plates placed in spring, with 20% coverage reached primarily in the second month (Fig. 2). No significant trends in coverage growth between series of communities were observed. On plates placed in winter and spring, the coverage of bryozoans was higher than that of serpulids. A different pattern was observed on plates placed in summer and autumn, when serpulids were more important (Fig. 5). However, on the plates that were submerged the longest, there is an evident upward trend as regards coverage by bryozoans, especially on plates placed in autumn (Fig. 5).

Two distinct groups of structurally different communities were observed based on cluster analysis (Fig. 6). The first one (on the right) includes all communities placed in summer and some of those placed in autumn and spring, while the second one (on the left) includes all communities placed in winter and some placed in spring and autumn. The first group showed higher similarity between samples (43.76%) than the second group (36.69%).

A sequence of communities placed in May 2018 (construction III) showed high similarity due to the dominance of *Ostrea edulis* (59.33% similarity, Fig. 6). The second sequence of communities, homogeneously different from the others (construction IV) was placed in June 2018 and was dominated by the bryozoan *Schizoporella errata* (56.82% similarity, Fig. 6).

The results of PERMANOVA routine show significant differences between communities with the same placement season (pseudo-F $= 15.04$, $p = 0.001$), which was also confirmed by paired tests between groups ($p = 0.001$ for all groups).

Communities on plates placed in winter showed higher average similarity (63.96%) compared to the ones placed in other seasons (from 46.25% to 51.70% similarity) (SIMPER analysis; Table 3). *Calpensia nobilis* was a characteristic species of communities on plates placed in winter, contributing 29.28% to the overall similarity, followed by *Schizobrachiella sanguinea* (SIMPER analysis, Table 3). The bryozoan *Schizoporella errata* and the bivalve *Ostrea edulis* dominated the plates placed in spring (SIMPER analysis, Table 3). Communities on plates placed in summer and autumn were mainly represented by the serpulid *Spirobranchus triqueter* and the ‘‘Serpulidae other’’ category (SIMPER analysis, Table 3), which consisted largely of *Hydroides elegans* and *Serpula vermicularis*.

Table 2
Alien and cryptogenic species found in this study along with their relative frequency of occurrence (FO), status, data on their presence in the Adriatic Sea and year of first record in the Mediterranean Sea (according to Zenetos et al., 2005, 2010; Marić et al., 2016; Ulman et al., 2017; Zenetos et al., 2017; Ferrario et al., 2018; Galil et al., 2018). Missing data is marked with the symbol /.

Taxonomical group	Species	FO [%]	Status	Presence in Adriatic Sea	1st record for Med. Sea
Serpulidae	[a]*Hydroides elegans*	65	Alien	Common	1870
Cirripedia	*Balanus trigonus*	37	Alien	Common	1927
Ascidiacea	*Styela plicata*	33	Alien	Casual	1883
Ascidiacea	*Botryllus schlosseri*	27	Cryptogenic	Common	/
Bryozoa	*Celleporaria brunnea*	8	Alien	Casual	2004
Bryozoa	*Bugulina fulva*	5	Cryptogenic	Casual	/
Bivalvia	[a]*Anadara transversa*	3	Alien	Common	1972
Bryozoa	*Arbopercula tenella*	2	Alien	First observation	1990
Cirripedia	*Amphibalanus improvisus*	<1	Cryptogenic	Common	1940s
Bryozoa	*Bugula neritina*	<1	Cryptogenic	Common	18th century
Bryozoa	*Watersipora arcuata*	<1	Alien	Casual	2013

[a] Denotes species, regarded as invasive in the Adriatic Sea (according to Streftaris and Zenetos, 2006).

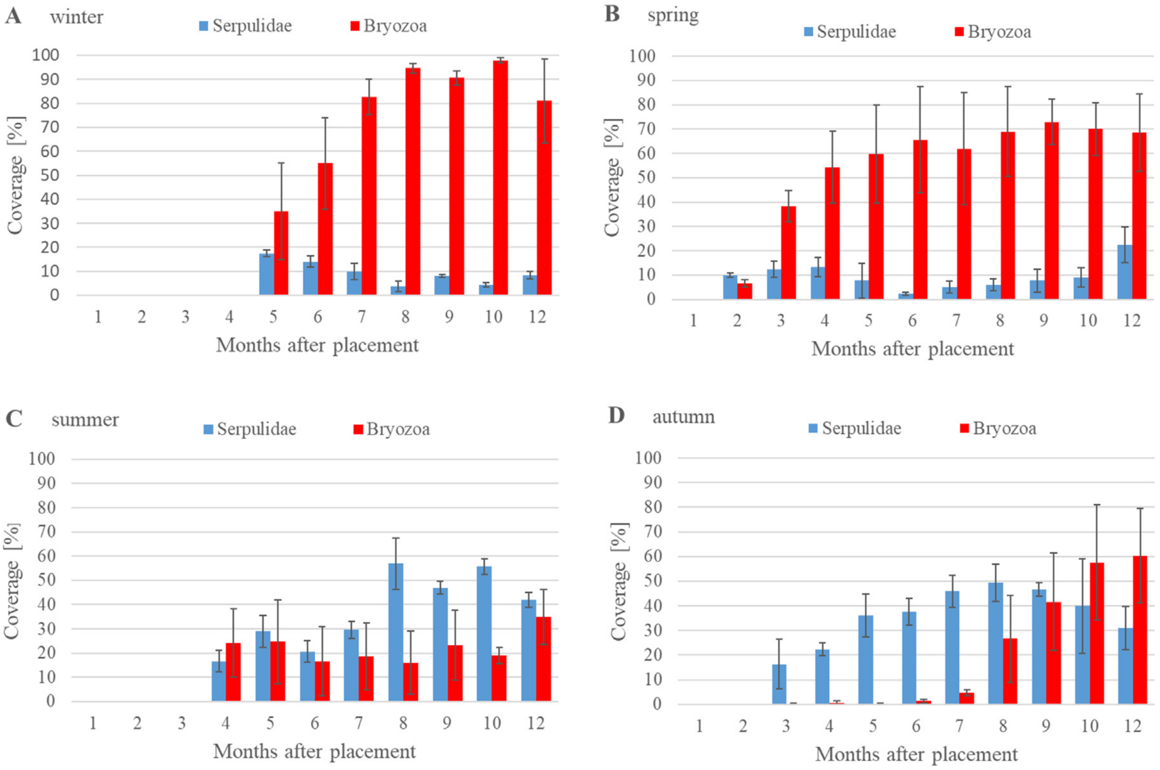

Fig. 5. Average coverage (± SE) of bryozoans and serpulids on plates with different lengths of submersion on (A) plates placed in winter, (B) plates placed in spring, (C) plates placed in summer and (D) plates placed in autumn. Data of plates with less than 20% total coverage are not shown.

4. Discussion

The study consisted in monitoring annual succession on experimental plates placed monthly over a period of two calendar years. In this way, some interannual abiotic variation was incorporated in the sampling design. The experimental design included time-independent sampling units (as in Underwood and Anderson, 1994) and followed seasonal and successive changes over one year after placement.

4.1. Temporal occurrence of dominant taxonomic groups

Succession patterns and seasonal occurrence for some fouling taxa, such as the native bryozoans, are poorly known, given that Mediterranean studies have focused primarily on low-abundance habitats (e.g. Kocak et al., 1999; Fava et al., 2016; Nerlović et al., 2018), or this topic was of no interest. Most taxa in this study colonized the plates quickly after placement and dominated them throughout the entire experiment, which is similar to the observations of Antoniadou et al. (2010). Moreover, only a few taxa displayed a clear tendency to occur in a particular successional phase (Fig. 3). The first settlers, such as spirorbins and *Spirobranchus triqueter*, are known Mediterranean pioneer species (Gravina et al., 1989; Fava et al., 2016). *S. triqueter* is a fast-growing species with high productivity and year-round reproduction (Bianchi, 1981; Cotter et al., 2003) as well as long-range dispersal potential (Segrove, 1941). However, the occurrence of this species has not decreased over time, as is common for pioneer species. Even after the death of specimens, new recolonization possibilities arose over time, when a new hard substrate was created in the form of oyster shells or dead bryozoans. All these features could explain why this species is so successful in many hard-bottom habitats (e.g. Gravina et al., 1989; Gabriele et al., 1999; Pitacco et al., 2014).

The bivalve *Rocellaria dubia* was one of the rare examples of a late occurring species. Its ability to burrow holes in the substrate makes it one of the important bioeroders in the fouling

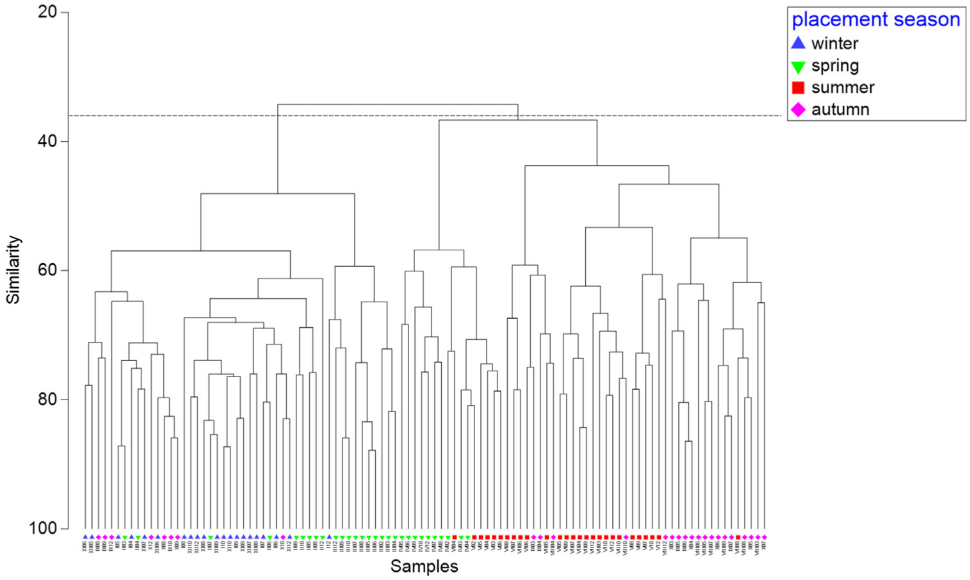

Fig. 6. Relationships between communities with the same placement season shown with clustering of samples based on Bray–Curtis similarity of group averages (standardized, square root transformed data).

Table 3
Similarity among communities with same season of placement and taxa contributing to similarity (SIMPER analysis). Av. Coverage = average coverage.

Taxon	Av. coverage	Contribution (%)	Cumulative (%)
Placement season: spring (av. similarity 50.12)			
Schizoporella errata	4.13	21.37	21.37
Ostrea edulis	3.94	18.67	40.04
Schizobrachiella sanguinea	2.46	12.20	52.25
Serpulidae other	2.19	12.00	64.25
Bryozoa other	2.11	9.87	74.11
Placement season: summer (av. similarity 51.70)			
Serpulidae other	3.88	24.69	24.59
Spirobranchus triqueter	3.66	17.45	42.04
Ostrea edulis	2.65	14.00	56.03
Schizoporella errata	3.27	13.58	69.61
Algal turf	2.42	10.15	79.76
Placement season: autumn (av. similarity 46.25)			
Spirobranchus triqueter	5.31	36.62	36.62
Serpulidae other	3.09	19.30	55.92
algal turf	2.59	13.28	69.20
Bryozoa other	1.55	6.28	75.48
Placement season: winter (av. similarity 63.96)			
Calpensia nobilis	5.70	29.28	29.28
Schizobrachiella sanguinea	3.98	19.25	48.53
Bryozoa other	2.87	12.54	61.07
Serpulidae other	2.15	9.88	70.95

community. This bivalve is a well-known borer of limestone and sandstone substrate as well as biogenic carbonates (Morton et al., 2011). The bivalve appeared only after a thick layer of biogenic carbonate had formed on the plates due to *Ostrea edulis* shells and bryozoan skeletons, suggesting that it was unable to drill into the terracotta plates.

Based on our observations of the surrounding macrozoobenthos community, it is unlikely that the community on the experimental plates reached a late stage of succession after one year. The former differed from the investigated community mainly by the presence of larger sponges. The occurrence and coverage of the sponges began to increase on the plates with longer submersion, but never rose above 11%. Nevertheless, visual observations of the experimental plates after two to three years of submersion did not reveal large increases in sponge coverage overall (data not shown here), which could be explained by the most important recruitment process observed in sponges, lateral encroachment (Fava et al., 2016). In fact, the development of fouling communities in the northern Adriatic could take more than three years, as suggested by Fava et al. (2016) and the abundance of these late succession species might increase in the future.

Reproduction times and seasonal occurrence of fouling species can vary considerably between different locations within the Mediterranean Sea (Vrišer, 1986). Data on the seasonal occurrence of species in the Adriatic Sea are sparse or very old and may not reflect the current situation if one considers global warming and the arrival of new species. Most taxa in our study did not show significant differences in occurrence during the year, regardless of the placement time. However, a higher number of taxa were recorded in summer time. The bryozoan *Calpensia nobilis* is an example of a species whose seasonality is poorly known. This bryozoan is considered to be an important habitat-forming organism in the Mediterranean Sea (Lombardi et al., 2013), as well as an epizoan on the seagrass *Posidonia oceanica* (Linnaeus) Delile, 1813, with significant impact on its growth (Colmenero and Sánchez Lizaso, 1999). In our study, we found that this species was characterized by high coverage and frequency of occurrence on the experimental plates. Its settlement was observed in spring and its highest occurrence in summer and autumn.

Predation is a factor that can have a major influence on the development of the fouling community. Predation of selected species or taxa influences the composition of epibenthic communities, which consequently are dominated by species that are not exposed to the pressure of local predators (Mook, 1981). Although predation was not specifically addressed in this study, the presence of multiple predators was observed on and near the experimental plates. The gastropod *Hexaplex trunculus* (Linnaeus, 1758), pagurid and porcelanid crustaceans as well as *Dromia personata* (Linnaeus, 1758), *Maja* sp. and *Eriphia verrucosa* (Forskaal, 1775) were frequently observed. Thirteen species of sea slugs, which are known to feed on hydrozoans, bryozoans, ascidians and sponges (Chadwick and Thorpe, 1981; Lipej et al., 2018) were directly detected on experimental plates (data not shown here). Ascidians were likely the group most preyed upon, as the tunic of colonial species was often torn and solitary ascidians rarely reached adult sizes. Holes drilled into the shells and marginal chipping of oysters were also observed frequently. Both are indications of the predation behaviour that muricid gastropods adopt depending on the size of their prey (Peharda and Morton, 2005).

Only limited older studies on the temporal changes of the fouling communities carried out in the study area have been carried out (Vrišer, 1978, 1986), but it is important to compare our results with earlier works. This is especially true with regard to major events [e.g. the population explosion of the grazer *Paracentrotus lividus* (Lamarck, 1816) (Vukovič, 1982)] and other factors influencing changes in epifaunal hard-bottom community composition. The results of studies conducted in the 1980s on experimental plates of similar size and orientation in Piran Bay show differences in the general composition of the community and in the early succession pattern (Vrišer, 1978, 1986) compared to the results of our study. With regard to the composition of the communities in the fouling study conducted during that period, the most significant difference is related to the coverage of bryozoan species on the plates. While in our study the community on the experimental plates placed in winter was dominated by bryozoans (the most abundant being *C. nobilis* and serpulid polychaetes (the most abundant being *S. triqueter*), in the 1980s study *Ostrea edulis* and *Balanus trigonus* predominated from the early stages of community development (Vrišer, 1986). The reason for the gradual increase in the occurrence of this species and the low total coverage in our study is unknown; it might be related to the choice of substrate, as pointed out by Vrišer (1978), similarly to the occurrence of *R. dubia* discussed above. *Hiatella arctica* is an example of an animal that, in our study, was frequently (33%) present on the plates from the beginning of placement, while Vrišer (1986) reported the occurrence of this species only after 2.5 years of submersion. The historical changes in community composition could, to a certain extent, be explained by the different substrate (limestone compared to terracotta) and different microlocation (inner part of the bay, closer to the river mouth); other possibilities are discussed below.

4.2. Occurrence of alien and cryptogenic species

Settlement plates, placed in marinas and other hotspots have been shown to be a good proxy for fouling communities in these habitats (Marraffini et al., 2017). In fact, recently, several studies on alien species have been conducted on experimental plates (e.g. Canning-Clode et al., 2013; Lezzi et al., 2017; Tait et al., 2018; Oricchio et al., 2019). In our study, the experimental structures were placed in the natural environment, but near hotspots for alien invertebrates, such as mussel farms (distance: 3 km) and the local harbour (distance: 1 km). As such, they can serve as observation points for early detection of the occurrence and spread of alien fouling species in the area. 13% of all taxa found on the plates were either alien or cryptogenic. This is a high percentage compared to a study with a similar sampling design conducted at a site considered a hotspot for alien species in the Taranto Sea, where the proportion of these species was almost 23% (Lezzi et al., 2017).

Several alien species found in our study were important findings for the area. *Celleporaria brunnea*, a recent discovery in Slovenia (Fortič et al., 2019), was present on the plates regardless of the season (Fig. 4), suggesting that the species settles all year round. The occurrence of *Watersipora arcuata* on the experimental plates was the second record for the Slovenian coast (Fortič et al., 2019), while the occurrence of *Arbopercula tenella* was the first one for the Adriatic Sea (Fortič and Rosso, 2021). The findings of these alien species indicate that artificial structures, which are not located in typical hotspot sites, are nevertheless important and potentially a stepping-stone for the dispersal of alien species.

The alien species most frequently found in this study, *Hydroides elegans*, is an old acquaintance of Mediterranean fouling researchers. It was introduced into the Mediterranean Sea in the 19th century and is considered invasive due to its impact on local biodiversity and infrastructure in ports and marinas (Streftaris and Zenetos, 2006). Based on its occurrence on the plates, it settles all year round, with a peak in summer at this site. *Styela plicata*, which was found on one third of the plates, is frequently found in Slovenia (Katsanevakis et al., 2020) and therefore may prove to be more common in the northern Adriatic in the future than previously reported (Marić et al., 2016). Some species were detected sporadically, such as *Celleporaria brunnea, Anadara transversa, Arbopercula tenella, Amphibalanus improvisus, Bugula neritina* and *Watersipora arcuata*. For these species, the environment of the experimental plates may not represent the ideal habitat, but their presence has nevertheless been noted, as bare substrates without well-established communities are more likely to be colonized by alien species (Clark and Johnston, 2009). In fact, *B. neritina* and *W. arcuata* were found only once, in low-covered plates during the winter season.

4.3. Influence of the placement season on developing communities

The taxonomic composition was very similar on plates with different placement times. However, there were some significant differences between the coverage of taxa on plates placed in the same season. The most important differences between the plates were observed on plates placed in summer and winter, the former being characterized by serpulids and the latter by encrusting bryozoans. Qiu et al. (2003) observed similar results with respect to plates placed in summer in Yan Chau Tong embayment, Hong Kong. *Hydroides elegans* was abundant in both studies, thus confirming the global competitive advantage of this serpulid in early successional stages (Dos Santos Schwan et al., 2015). The ability to colonize the substrate rapidly after placement (Unabia and Hadfield, 1999) most likely provided a competitive advantage for *H. elegans* and other serpulids in the warmer season. On the other hand, the common bryozoans dominated the plates placed in the colder period, probably because at the time of settlement (spring for *Calpensia nobilis*) the plates were less colonized by other taxa and, at the time, bryozoans were able to outcompete them by overgrowth (Sutherland and Karlson, 1977; Rubin, 1985; Nandakumar et al., 1993). Overgrowth by asexual reproduction gives bryozoans a competitive advantage over solitary animals, and allows them to dominate in some environments (Greene et al., 1983; Rubin, 1985). Nevertheless, after the death of the bryozoans, the serpulids were able to resettle on their skeletons and thus maintain their share in the community. In sequences of communities initially dominated by serpulids, namely the ones on plates placed in summer and autumn, bryozoan coverage began to increase in older communities (Fig. 5. This could indicate that older communities began converging towards the same state (as in Brown, 2005; Cifuentes et al., 2010).

Regarding the two sequences of communities (III — placement in May and IV — placement in June) dominated by one species (*Ostrea edulis* in III and *Schizoporella errata* in IV), there are several possible explanations. The sea warmed up very quickly in 2018, and average sea surface temperature in May 2018 was 3.7 °C above the long-term average (1981–2010) (ARSO, 2020) and jumped from 14.0 °C in April to 20.2 °C in May (Fig. 1). This may have caused an early and sudden start of spawning of *Ostrea edulis* in 2018, as it spawns at temperatures above 14.0 °C (Cano et al., 1997). This could explain the dominance of the oyster in the temporal sequence of plates placed in May 2018. The dominance of the bryozoan *Schizoporella errata* on the plates placed in June 2018 could also be explained by the high number of larvae in the area at the time and the favourable environment for the rapid growth of this species. The fast-growing

S. errata (Sokolover et al., 2018) quickly occupied the available space on the plates. It prevented subsequent recruitment of other organisms and most likely inhibited the growth of neighbouring species, as demonstrated by previous studies (Sutherland and Karlson, 1977). Succession on constructions III and IV are a striking example of the "Inhibition model" of succession (*sensu* (Connell and Slatyer, 1977) and a reminder that settlement and succession patterns are not easy to predict.

The fouling community is subject to many of the above-mentioned biotic and abiotic factors and often "multiple stable points" are possible (*sensu* (Sutherland, 1974). Nevertheless, we demonstrated that the seasonal influence of placement has a noticeable impact on the early development (up to one year) of the communities studied, which might be observed as a small-scale patchiness of sessile communities in the natural environment (Terlizzi et al., 2007). The effect of the placement season is the result of many factors, but there are two main ones. The first is the seasonality of species, i.e. their reproductive period and the time of their settlement, and the second is the interaction between other organisms, which results in the occurrence of species in the specific phase of fouling development. We hypothesized that over time the composition of the community would become more stable and that its changes over time would be more related to the actual season and less to the time of placement.

The important question that now arises is: Who will be the winner in this "race for space", as the development of the fouling community could be called. In the case of this study, the species that appeared in the early stages maintained their role in the community until the end. These were mainly the bryozoans *Calpensia nobilis, Schizobrachiella sanguinea, Schizoporella errata, Terwasipora complanata* and *Cryptosula pallasiana*, the oyster *Ostrea edulis* and the serpulids *Spirobranchus triqueter, Hydroides elegans* and *Serpula vermicularis*. The aforementioned species are efficient filter feeders (Hughes et al., 2005) and fast-growing organisms under optimal conditions (Grant et al., 1990; Smith, 2014; Sokolover et al., 2018), with efficient reproductive capacity (Bianchi, 1981; Cano et al., 1997; Sokolover et al., 2018). For some of them, high fluctuations were observed in their coverage, while others were more steadily present on the plates. An example of such behaviour is found within Schizoporellidae; *S. sanguinea*, with a steady occurrence in our study, is an example of a well-adapted species in these parts of the world, as shown by specialized predators such as *Knoutsodonta neapolitana* (Delle Chiaje, 1841), (Mcdonald and Nybakken, 1999) and an obligate commensal *Halocoryne epizoica* Hadzi, 1917 (Hayward and McKinney, 2002). *S. errata*, on the other hand, is a fast-growing (Sokolover et al., 2018) fouling species with a rapid colonizing potential (Hayward and McKinney, 2002), which has not been reported in previous studies of the fouling community in this area (Vrišer, 1986; Frumen et al., 2003). With the increase in temperature, a shift of the dominant species could be observed in the future. Eurythermal species and species with year-round reproduction, such as the cosmopolitan *S. errata* (Sokolover et al., 2018) and the alien *H. elegans* (Dos Santos Schwan et al., 2015) could prevail over more sensitive species. The introduction of new species can also drastically change communities and have profound effects on ecosystem functioning (Hobbs et al., 2009).

We have shown that the placement season is important for the development of the fouling community. However, the adopted experimental design did not allow us to assess the influence of the interaction between placement season and duration of submersion, which plays an important role in the development of this community (Brown and Swearingen, 1998; Lezzi et al., 2017). Another factor not addressed in our study relates to the proximity of structures bearing experimental plates in the microlocation. The propagule pressure of the already established species could therefore be higher compared to other species, due to the small dispersal radius of the invertebrate larvae. In view of the aforementioned limitations, this study can serve as a baseline for future investigations of the temporal changes of the fouling communities in the study area.

The community that has developed on the experimental plates is representative of initial to intermediate successive stages of fouling communities on vertically oriented artificial substrates in coastal sublittoral zones, such as concrete infrastructure elements (e.g. pipelines, breakwaters). A similar community can also be observed on shells of the endangered *Pinna nobilis* Linnaeus, 1758 or vertical sides of large natural rocks. All these substrates are also important breeding grounds for cephalopods, fish, snails, etc. (e.g. Cabanellas-Reboredo et al., 2014), also observed in this study).

5. Conclusions

The results of this study show the importance of anthropogenic structures for local communities in terms of larval supply of important fouling species, including aliens. It contributes to filling the knowledge gaps as regards species diversity of less studied taxa of suspension-feeding communities in this part of the Adriatic Sea, such as bryozoans, and their temporal occurrence. Finally, but importantly, it sheds light on the importance of the placement period for the development of the fouling community. Although the effect of placement timing may not be large or even long-term, it is important in increasingly frequent short-term panel experiments, such as Autonomous Reef Monitoring Structure (ARMS) studies and alien species monitoring, and should be considered in experimental design. Sessile invertebrates are limited in space and movement; they are often unable to spread over long distances and may therefore be damaged by catastrophic events and rapid changes in the abiotic environment. Common sessile Mediterranean foulers, such as the three most common taxa considered in this study, have a calcified exoskeleton and may be exposed to the acidification process of the ocean (Orr et al., 2005; Kroeker et al., 2010; Lombardi et al., 2013). If the marine environment changes as rapidly as it is currently changing in the north Adriatic Sea (Grilli et al., 2020), short and long-term changes in biotic communities are inevitable. Thus, more knowledge about temporal changes in hard bottom communities is needed to assess these impacts.

CRediT authorship contribution statement

Ana Fortič: Methodology, Formal analysis, Investigation, Writing - original draft. **Borut Mavrič:** Conceptualization, Investigation, Supervision, Writing - review & editing. **Valentina Pitacco:** Formal analysis, Writing - review & editing. **Lovrenc Lipej:** Conceptualization, Supervision, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We are very grateful to Milijan Šiško and Matej Marinac for their contribution during fieldwork and especially Tihomir Makovec for his contribution in the form of photography, SCUBA diving and technical support. We wish to thank Martina Orlando-Bonaca for the identification of macroalgal species and helpful advice during preparation of the manuscript. Finally, we are grateful to three reviewers for providing helpful comments and suggestions on the manuscript.

Table A.1
List of all sessile invertebrate taxa found in this study. Taxonomical groups used in the analysis of occurrence distribution are indicated in bold.

Group	Taxon
Bryozoa	*Aetea truncata* (Landsborough, 1852)
	Arbopercula tenella (Hincks, 1880)
	Bantariella verticillata (Heller, 1867)
	Bugula neritina (Linnaeus, 1758)
	Bugulina fulva (Ryland, 1960)
	Bugulina simplex (Hincks, 1886)
	Calpensia nobilis (Esper, 1796)
	Celleporaria brunnea (Hincks, 1884)
	Chorizopora brongniartii (Audouin, 1826)
	Cryptosula pallasiana (Moll, 1803)
	Hagiosynodos sp.
	Microporella spp.
	Reptadeonella violacea (Johnston, 1847)
	Rhynchozoon sp.
	Schizobrachiella sanguinea (Norman, 1868)
	Schizomavella cf. *adriatica* Reverter-Gil, Souto, Novosel & Tilbrook, 2015
	Schizoporella dunkeri (Reuss, 1848)
	Schizoporella errata (Waters, 1878)
	Tubulipora spp.
	Umbonula ovicellata Hastings, 1944
	Watersipora arcuata Banta, 1969
	Terwasipora complanata (Norman, 1864)
	Ctenostomatida indet.
Bivalvia	*Anadara transversa* (Say, 1822)
	Anomia ephippium Linnaeus, 1758
	Anomiidae indet.
	Arca noae Linnaeus, 1758
	Arcidae indet. juv
	Chama gryphoides Linnaeus, 1758
	Heteranomia squamula (Linnaeus, 1758)
	Hiatella arctica (Linnaeus, 1767)
	Mimachlamys varia (Linnaeus, 1758)
	Pectinidae indet. juv
	Modiolus barbatus (Linnaeus, 1758
	Musculus subpictus (Cantraine, 1835
	Mytilidae indet. juv
	Ostrea edulis Linnaeus, 1758
	Ostreidae indet. juv
	Pododesmus patelliformis (Linnaeus, 1761)
	Rocellaria dubia (Pennant, 1777)
	Spondylus cf. *gaederopus* Linnaeus, 1758 juv
Gastropoda	*Thylacodes arenarius* (Linnaeus, 1758)
	Vermetus sp.
Serpulidae	*Hydroides elegans* (Haswell, 1883)
	Hydroides sp. juv
	Hydroides cf *norvegica* Gunnerus, 1768
	Josephella marenzelleri Caullery & Mesnil, 1896
	Neodexiospira cf. *pseudocorrugata* (Bush, 1905)
	Pileolaria militaris Claparède, 1870
	Protula sp.
	Salmacina sp.
	Serpula concharum Langerhans, 1880
	Serpula vermicularis Linnaeus, 1767
	Serpulidae indet. juv
	Simplaria cf. *pseudomilitaris* (Thiriot-Quievreux, 1965)
	Spirobranchus triqueter (Linnaeus, 1758)
	Spirorbinae indet.
	Vermiliopsis striaticeps (Grube, 1862)
Sabellidae	*Sabella* sp.
Hydrozoa	*Anthoathecata* indet.
	Bougainvillia cf. *muscus* (Allman, 1863)
	Bougainvillidae indet.
	Campanulariidae indet.
	Clytia hemisphaerica (Linnaeus, 1767)
	Clytia sp.
	Obelia cf. *dichotoma* (Linnaeus, 1758*)*
	Corydendrium cf. *parasiticum* (Linnaeus, 1767)

(*continued on next page*)

Table A.1 (*continued*).

Group	Taxon
	Ectopleura sp. juv *Halecium* sp. *Halocoryne epizoica* Hadzi, 1917 *Pennaria disticha* Goldfuss, 1820
Anthozoa	*Actiniaria indet.*
Scyphozoa	Scyphopolyps
Cirripedia	*Amphibalanus improvisus* (Darwin, 1854) *Balanidae* indet. juv *Balanus trigonus* Darwin, 1854 *Perforatus perforatus* (Bruguiere, 1789) *Verruca spengleri* Darwin, 1854
Ascidiacea	Ascidiacea indet. juv Ascidiidae indet. *Botryllus schlosseri* (Pallas, 1766) Didemnidae indet. Polyclinidae indet. Pyuridae indet. *Styela plicata* (Lesueur, 1823) Styelidae indet. juv
Porifera	Porifera indet.

Funding

This study was funded by the ARRS (Young Researcher) postgraduate grant. The authors also gratefully acknowledge the financial support obtained from the Slovenian Research Agency in the form of Research Core Funding No. P1-0237. Data on abiotic parameters originate from national monitoring programs funded by the Slovenian Environment Agency, Ministry of Environment and Spatial Planning.

Appendix

See Table A.1.

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