Macropredators as shapers of invaded fouling communities in a cold temperate port

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ABSTRACT

Ports are vulnerable to biological invasions because of the high shipping exchange and the abundance and diversity of artificial structures. These artificial environments provide new habitats for fouling communities, commonly hosting a large number of exotic species. The colonization of artificial structures is influenced by large and small scale processes, such as differences in recruitment time (that may vary with season and availability of new substrates) or predation. In cold temperate regions, with a marked seasonality, not only the starting time of colonization may influence fouling community structure but also the community of macropredators associated. This study addressed the following question: What is the effect of macropredators on invaded fouling communities started at different time in a cold temperate port? To asses this, the following experimental treatments were assigned to three plates attached to a fiberglass structure: exclusion, open cage and open plate. At the beginning of each season, seven of these structures were tied to port pilings, each one containing the three experimental treatments. We found that fouling communities are shaped by macropredators, such as sea urchins, gastropods and crabs, and that their effect on community structure depends on the time or season in which the colonization started. Exotic ascidians were absent in open plates and open cages when macropredators were present, and species diversity was highest when these predators were excluded. Our results suggest that predation at high latitudes in cold temperate regions might be more important than what is predicted in recent works. Although our study is conclusive on specific points, it also exposes a need for further research disentangling the processes regulating the colonization of artificial fixed versus floating structures at different latitudes.

1. Introduction

The amount of human population living on coastal areas worldwide is constantly growing. Nearly a 20% of the human population lives within a range of 200 km away from the coast. As a consequence, the coastal geomorphology has been largely modified by artificial structures such as jetties, wharfs and a variety of floating structures (Airoldi and Bulleri, 2011). These artificial structures supply novel habitats where fouling organisms thrive, showing not only different diversity and abundance compared to natural nearby rocky bottom communities (Holloway and Connell, 2002) but also hosting a larger number of exotic species (Dafforn et al., 2012; Glasby et al., 2007; Tyrrell and

Byers, 2007). Indeed, ports, harbours, marinas and surrounding areas are known to concentrate a variety of artificial habitats that tend to favour the survival and spread of exotic species (Bortolus et al., 2015; Carlton, 1996; Glasby and Connell, 1999; Lambert and Lambert, 1998; Marraffini et al., 2017).

The differences in the time of reproduction and settlement of each species may strongly influence the species composition, richness and abundance of fouling communities. Therefore, it is expected that in cold temperate regions where seasonal fluctuations in temperature are marked, the succession will differ depending on the time or season when the colonization starts. Recent evidences show that the abundance of early colonizers is affected by their recruitment peaks

(Cifuentes et al., 2010) and that the diversity of the resulting community is significantly correlated with sea water temperature (Rico et al., 2009), affecting the time of reproduction, interspecific competition and altering the availability of space (Lord, 2016; Rico et al., 2009).

Local biological factors, such as predation, may also have an important effect on fouling communities, with different outcomes according to the stage of colonization at which they act (Oricchio et al., 2016; Osman and Whitlatch, 2004; Vieira et al., 2012). In the initial stages of colonization, small predators consume recruits of some specific species, with different consequences on the final community. In some cases, this consumption increases the availability of bare spaces for more competitive species to establish (Nydam and Stachowicz, 2007), but in other communities it may facilitate the development of less competitive species in localized areas (Osman and Whitlach, 1995; Osman and Whitlatch, 2004). In later stages, when the availability of bare space decreases, only larger predators may have a strong effect on these communities (Oricchio et al., 2016). Thus, the community structure during succession seems to be differentially affected by the time in which predators act and the kind of predators acting (Rico et al., 2015; Vieira et al., 2012).

In the Southwestern Atlantic (SWA), several interactions between native and exotic species have been studied in natural coastal habitats, such as rocky shores and salt marshes (Mendez et al., 2014; Raffo et al., 2014; Schwindt et al., 2009; Sueiro et al., 2013), and in port areas focusing in succession, recruitment and predation (Rico et al., 2009, 2012, 2015; Schwindt and Bortolus, 2017). The port of Puerto Madryn in Patagonia is one of the most important ports within the region, in terms of shipping activity and the diversity of exotic species present (Schwindt et al., 2014). There, several ascidian species -none of which are natives- are among the most abundant exotic species in fouling communities (Schwindt et al., 2014). Ascidians are considered good models to the study of marine bioinvasions because of their short-lived lecitothrophic larvae with restricted natural dispersion distances (Lambert, 1968; Zhan et al., 2015). Indeed, without human transportation, the dispersal range of ascidians is extremely limited (Lambert and Lambert, 1998). In this way, the goal of this study was to evaluate the effect of macropredators on invaded fouling communities started at different time in a cold temperate port. More specifically, we evaluated the effect of excluding macropredators on the structure (i.e. cover of different sessile organisms), total cover and diversity of all sessile organisms, and the abundance of exotic ascidian species on the advanced succession stage in the fouling community. In addition, we evaluated how the season in which the colonization starts influences these variables. We hypothesize that (1) the presence of macropredators decrease the cover and diversity of the advanced succession communities as well as the abundance of exotic ascidians, and that (2) the structure of the fouling community varies according to the season when the colonization starts.

2. Materials and methods

2.1. Study area

This study was conducted over one year (October 2011 and September 2012) in the A. Storni port at Puerto Madryn city (PM), Nuevo Gulf (Argentina, SWA, 42°49′ S; 65°04′ W, Fig. 1a). Annual mean sea temperature during the experimental period was 13.3 °C, ranging from 9 °C in winter and 19.8 °C in summer. The salinity was relatively constant over time, with a mean value of 34.3 (a minimum salinity of 33 from January to April and a maximum salinity of 35 from April to January). Chlorophyll *a* reached a maximum of 2.69 mg/m^3 during April (fall) and a minimum of 0.32 mg/m^3 during August (winter). The port is situated in a wave protected area, with mean tidal amplitude of 5 m, and a semidiurnal tidal regime (Servicio de Hidrografía Naval, 2019). The depth during high tide reaches 9 m.

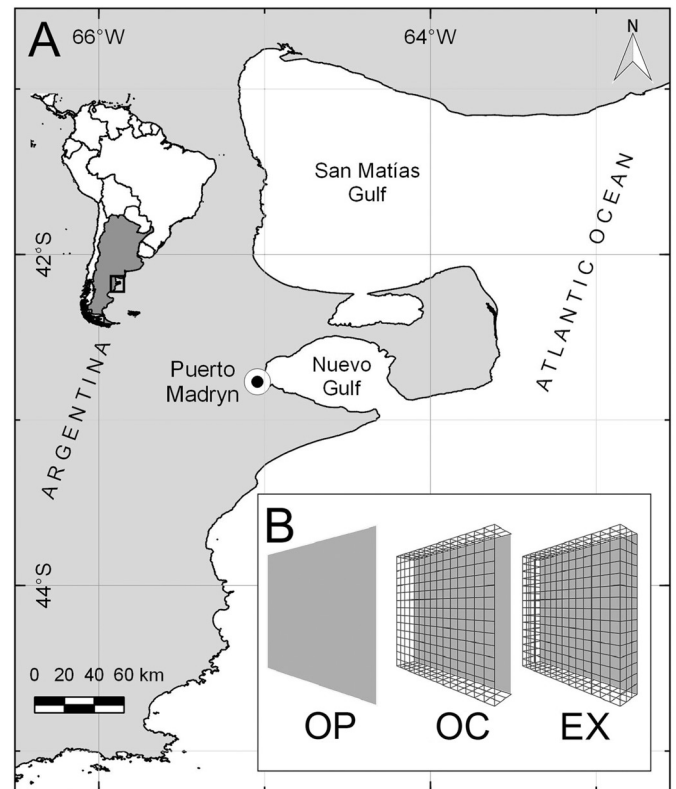The fouling communities of Puerto Madryn port are characterized

Fig. 1. (A) Map showing the study area and (B) the design of the experimental recruitment plates (OP: open plate, OC: open cage, EX: exclusion).

by the presence of native species as large mussels (*Aulacomya atra* (Molina, 1782), *Mytilus* spp.) and sea anemones (e.g. *Actinothoe lobata* (Carlgren, 1899)). Mussels thrive on the pilings, with a mean density of nearly 807 ind/m^2 (authors unpublished data), covering most of the subtidal surface along the pilings and hosting small invertebrates, such as polychaetes, crabs and isopods. There, the most common exotic species are solitary ascidians including *Ascidiella aspersa* (Müller, 1776) and *Ciona* spp. and the cryptogenic *Asterocarpa humilis* (Heller, 1878) (Schwindt et al., 2014; Tatián et al., 2010). *Ascidiella aspersa* and *Ciona* spp. are well known invasive species able to thrive on artificial structures in port areas (Lambert and Lambert, 2003). The community of macropredators is represented by sea urchins (*Arbacia dufresnii* (Blainville, 1825)), sea stars (*Allostichaster capensis* (Perrier, 1875), *Anasterias antarctica* (Lütken, 1857) and *Cycethra verrucosa* (Philippi, 1857)), and crabs (*Leucippa pentagona* H. Milne Edwards, 1834; *Carcinus maenas* (Linnaeus, 1758)). The most common species of fish associated to the fouling community is *Helcogrammoides cunninghami* (Smitt, 1898), a small native species (6 cm of maximum length) with a diet based on amphipods (Muñoz and Ojeda, 1997). Largest fish such as *Acanthistius patachonicus* (Jenyns, 1840), *Pseudopercis semifasciata* (Cuvier, 1829) and *Pinguipes brasilianus* Cuvier, 1829 can also be found at the surrounding areas, however, these fish are benthic species associated to nearby rocky reefs (Galván et al., 2009).

2.2. Experimental setup

Three acrylic plates (15 × 15 × 0.3 cm) were placed 12 cm away from each other within a fiberglass structure (50 × 50 × 0.2 cm). The external surface of the plates was covered with a cloth with granulated silicon carbide glued to one face (FEPA standard #50) to increase its roughness. The fiberglass structures containing the experimental plates were tied vertically to the port pilings with nylon ropes (diameter 6 mm) and 2 m below mean low tide level. Since the dock and pilings

can cause different shade and turbulence under and around them, the structures were deployed facing the same cardinal direction (south west) to avoid potential artefact effects due to differences in water characteristics like current speed, turbulence or shading (Glasby, 1999).

To evaluate the effect of macropredators on the fouling community, the following treatments were assigned to the experimental plates: (A) exclusion *EX*: a cage made of inert plastic to exclude macropredators was attached to the plate with cable ties (1.5×1.5 cm mesh, cage height 7 cm); (B) open cage *OC*: the same mesh used in EX leaving two open sides to allow free movement of macropredators, this was the control treatment to evaluate any potential cage effect; and (C) open plates *OP*: a plate without any kind of cage (Fig. 1b). In the exclusion treatment, only micropredators, such as small gastropods (*Tegula patagonica* (d'Orbigny, 1835) as the most abundant species) and small shrimps can access to the exclusion plates. The open cage allowed the free movement of benthic macropredators and small species of fish associated to the fouling community. Treatments were randomly assigned to the plates of the first structure and rotated clockwise in subsequent structures. To evaluate the effect of macropredators on invaded fouling communities started at different time, seven of the fiberglass structures and their corresponding experimental plates were attached to seven random pilings at the beginning of each season (i.e. $n = 7$ structures $\times 4$ seasons (spring: SP; summer: SM; fall: FA; and winter: WT) = 28 fiberglass structures with three experimental plates each). Every two weeks, cages were cleaned underwater by SCUBA diving and photographs of each plate were taken. At the end of each season (i.e. when the settled communities were 4 months old), structures were removed from water and plates were carefully detached, bagged separately with sea water and transported to the aquarium with air supply until all species were identified. Every time the divers removed the structures from the water, special attention was directed to prevent small mobile and loose sessile organisms from falling apart or escaping. To avoid edge effects, abundance of solitary ascidians and species cover of all sessile organisms were measured in a 10×10 cm central area of each plate. Cover of sessile organisms was measured as the proportion of the plate cover by the vertical projection of the organisms. Plates were deployed from October 2011 to January 2012 in spring, February to May in summer, April to July in fall, and July to September in winter. Dangerous weather conditions made impossible for the team to scuba dive during the fourth month of winter, then the photographs of communities of 3 months old were used for measure cover of organisms as the advanced succession community of winter.

To avoid taxonomic misidentifications, fish, crabs and algae were examined with the assistance of expert taxonomists (see Acknowledgements). Molluscs, cnidarians, echinoderms and solitary ascidians were identified with the appropriate reference material deposited at the Invertebrate Collection of IBIOMAR-CONICET (CNP-INV). Identification at the species level, especially for algae, was difficult with subaquatic photographs, and the taxonomical resolution varied across taxa. Therefore, experts advised the identification unified at major taxonomic groups (see Table 1) for the analyses, giving the highest priority to taxonomic reliability.

2.3. Statistical analysis

To evaluate the effect of the exclusion of macropredators at different times on the structure of sessile organisms community (including bare space), a PERMANOVA test with a Bray-Curtis similarity matrix was performed between "season" and "treatment", as fixed factors. Pilings were added to the analysis as blocks nested in season factor, to test the variability among pilings in the same season. In this way, the statistical design used was "season" (fixed with four levels: summer, fall, winter and spring), crossed with "treatment" (fixed with three levels: exclusion, open cage and open plates), and "piling" (random with seven levels: 1 to 7) nested in "season". We did not evaluate the interaction between "piling" and "treatment" because we only had one replicate of

Table 1
Taxa found during the colonization period, grouped in major taxonomic groups used in statistical analysis (in bold).

Taxa	Status
Algae	
Ascidians	
Ascidiella aspersa	Exotic
Ciona spp.	Exotic
Asterocarpa humilis	Cryptogenic
Diplosoma listerianum	Exotic
Bryozoans	
Bugulina flabellata	Exotic
Cnidarians	
Actinothoe lobata	Native
Anthothoe chilensis	Native
Hydroids indet.	
Crustaceans	
Rochinia gracilipes	Native
Leucippa pentagona	Native
Echinoderms	
Arbacia dufresnii	Native
Fish	
Helcogrammoides cunninghami	Native
Molluscs	
Trophon geversianus	Native
Tegula patagonica	Native
Fissurella sp.	Native
Pleurobranchaea maculata	Exotic
Polychaetes	
Subfamily Spirorbinae	Native

each treatment level in each piling. Prior to the analyses, cover data of major taxonomic groups of sessile organisms (algae, ascidians, bryozoans, cnidarians and polychaetes, see Table 1) were fourth-root transformed to decrease the influence of the dominant species (Clarke and Warwick, 2001). A posteriori pairwise tests were performed (Anderson et al., 2008) when significant differences ($P < 0.05$) were observed, and a SIMPER test was used to analyse which taxa most contributed to dissimilarity within significant different pairs. To test whether differences were caused by the treatments and not by the dispersion of the data, a PERMDISP test was performed among groups to address the question of interest of this work, following Anderson et al. (2008). All multivariate analyses were performed using PRIMER 6 (Clarke and Warwick, 2001).

To evaluate the effect of the exclusion of macropredators at different times on diversity (Shannon Index), total cover of sessile organisms and abundance of exotic ascidians, ANOVA tests were performed for each variable using the design explained above. Differences in ascidians abundance were compared among spring, summer and fall, because there were no ascidians recorded during winter. For diversity, only sessile organisms were considered using both primary and secondary (as epibionts) form of growth. Homocedasticity was evaluated with Levene tests and normality through modified Shapiro-Wilks tests. Cover values were arcsin transformed before the analysis and ascidians abundance and Shannon Index diversity were transformed when assumptions of normality or homoscedasticity were not met ($\log(X + 1)$ and square-root transformation respectively). Differences among levels of each factor were analysed with a posteriori Tukey tests. The analyses were performed with the software InfoStat (Di Rienzo et al., 2016), except for diversity index which were obtained using DIVERSE package of PRIMER 6 (Clarke and Warwick, 2001).

3. Results

3.1. Effect of exclusion of macropredators at different times on the structure of fouling communities

Regarding the exotic/cryptogenic/native status of the animal taxa

Table 2
Results of PERMANOVA test for sessile organisms cover (including bare space) among seasons (winter, fall, spring and summer) and treatments (open plate, open cage and exclusion). Significant *p*-values are in bold ($P < 0.05$).

	Df	SS	MS	Pseudo F	P (perm)
Season (S)	3	7524.7	2508.2	2.712	< 0.05
Treatment (T)	2	6479	3239.5	9.405	**0.001**
Piling(Season)	24	22,200	925	2.685	**0.001**
S × T	7	4896.7	816.1	2.369	< 0.05
Error	48	16,533	344.4		

identified, from a total of 16 taxa, five of them (31%) were exotics (the ascidians *Ascidiella aspersa*, *Ciona* spp. and *Diplosoma listerianum* (Milne Edwards, 1841), the sea slug *Pleurobranchaea maculata* (Quoy & Gaimard, 1832) and an arborescent bryozoan, *Bugulina flabellata* (Thompson in Gray, 1848)), one (6%) cryptogenic (*Asterocarpa humilis*) and 10 (63%) natives (Table 1).

The PERMANOVA test (Table 2) showed that the effect of the exclusion of macropredators on the structure of the sessile organisms community depends on what season the colonization started. As the interaction between factors (Treatment and Season) was significant ($P = 0.001$), pairwise tests were performed between pairs of levels of Treatment factor for each level of Season factor. Communities starting in fall and spring were affected differently by predation. In both season communities developed in the presence of predators differed from those developed in their absence (Fall: OP vs EX, $P < 0.01$; OC vs EX, $P < 0.01$. Spring: OP vs EX, $P < 0.05$). However, also differences between controls (OP and OC) were observed in spring ($P < 0.01$). SIMPER analysis showed that this difference was due to the high cover of algae in the presence of predators during this season (Table 3, Fig. 2 and Supplementary material). In the case of fall communities, SIMPER analysis showed a higher abundance of ascidians in the absence of predators (Table 3, Fig. 2 and Supplementary material). Dispersion effect for the interaction (Treatment x Season) was non-significant (PERMDISP, $P > 0.05$), thus differences observed among communities were caused by the assignment of the treatments and not by the dispersion of the data. Dispersion was not tested for the main effects because interaction among factors was significant (Anderson et al., 2008).

Table 3
SIMPER analysis of cover data comparing pairs of levels of Treatment factor for each level of Season factor with significant differences in PERMANOVA pairwise tests.

| Taxa	Average abundance	Average abundance	Contribution (%)	Cumulative contribution (%)
FALL				
	OP	*EX*		
Ascidians	0.16	1.5	31.2	31.2
Algae	1.04	0.25	22.3	53.5
Polychaetes	0	0.9	20.4	73.9
	OC	*EX*		
Ascidians	0.24	1.5	32.4	32.4
Polychaetes	0	0.9	21.5	53.9
Algae	0.83	0.25	19.3	73.2
SPRING				
	OP	*EX*		
Algae	2.18	1.37	32.7	32.7
Ascidians	0.2	1.08	23.1	55.8
Bare space	2.39	2.94	15.9	71.7
	OC	*OP*		
Algae	0.88	2.18	40.6	40.6
Bare space	3.01	2.39	16.8	57.4
Ascidians	0.71	0.2	16.7	74.1
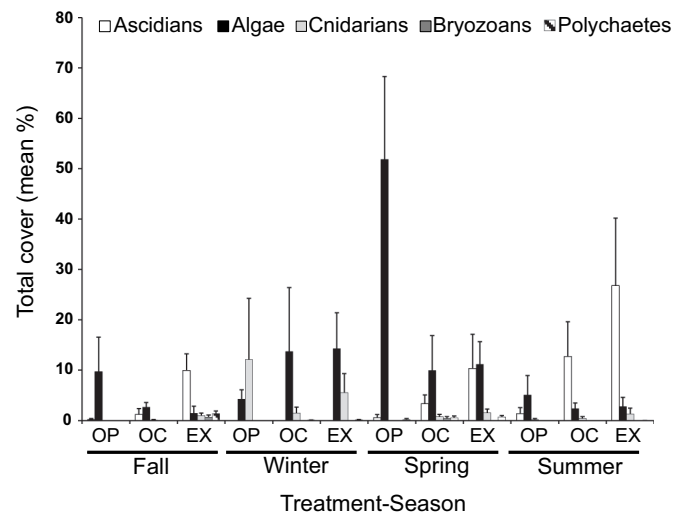
Fig. 2. Total cover of each taxon (mean % ± SE) in the advanced succession communities for each treatment (OP, open plate; OC, open cage; EX, exclusion) and season.
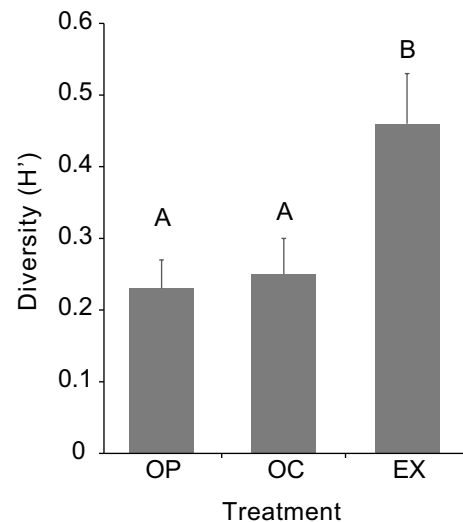

Fig. 3. Diversity (Shannon Index, mean ± SE) of the advanced succession communities for each treatment (OP: open plate, OC: open cage, EX: exclusion), including all the seasons. Different letters denote significant differences ($P < 0.05$).

3.2. Effect of exclusion of macropredators at different times on diversity, total cover of sessile organisms and abundance of exotic ascidians

Both diversity of fouling communities and abundance of exotic ascidians were higher in the exclusion treatment (Diversity, Fig. 3; exotic ascidians, Fig. 4), with no differences among seasons (Table 4). For the rest of exotic species, the sea slug *Pleurobranchaea maculata,* was found only once during summer, while bryozoans were observed only during fall and showed lower cover than ascidians (Fig. 2). The total cover of sessile organisms was not affected by the exclusion of macropredators or season (Table 4).

4. Discussion

Our results show that benthic macropredators, such as sea urchins, gastropods and crabs, strongly affected the structure and diversity of fouling communities invaded by exotic ascidians in a cold temperate port. This effect was particularly strong on the abundance of ascidians.
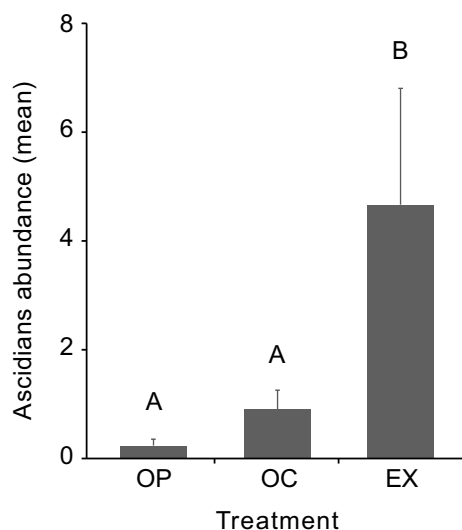
Fig. 4. Abundance of ascidians (mean ± SE) for the advanced succession communities for each treatment (OP: open plate, OC: open cage, EX: exclusion) including spring, summer and fall communities. Different letters denote significant difference (P < 0.05).

Table 4
Results of ANOVA test for the effect of macropredators on diversity, total cover of sessile organisms and ascidians abundance of the advanced succession communities, among seasons (S), treatments (T), interaction between those factors (S × T) and pilings nested in season (Piling(Season)). Significant differences are shown in bold (P < 0.05).

	Diversity		Total cover of sessile organisms		Ascidians abundance	
	F	P	F	P	F	P
Season (S)	1.09	0.37	1.68	0.2	0.59	0.56
Treatment (T)	6	**< 0.01**	1.79	0.18	11.41	**< 0.001**
S × T	1.25	0.3	1.55	0.18	0.48	0.75
Piling(Season)	2.72	**< 0.01**	1.45	0.13	2.36	**< 0.05**

Despite the marked seasonality that characterizes the SWA, abundance of exotic ascidians and diversity of fouling communities were negatively affected by predation, independently of the season in which the colonization started. In this way, our work supports the hypothesis that benthic macropredators can shape fouling communities of temperate ports, in opposition to the *biotic interaction* and *biotic resistance* hypotheses, which establish a decrease in predation and biotic resistance in high latitudes (Freestone and Osman, 2011; Freestone et al., 2013; Kremer and da Rocha, 2016).

Predation was reported having a strong negative effect on the abundance of ascidians in subtropical (Vieira et al., 2012) and other temperate ports of the Northwestern Atlantic (Osman and Whitlatch, 2004). Recruits recently settled on the substrate are the most exposed to predators, but this vulnerability decreases while ascidian body size increases, enabling ascidians to escape predation as they grow (Osman and Whitlatch, 2004; Vieira et al., 2012). Therefore, the ascidians living on the pilings in our study area are likely to be those recruits that found refuge in between mussels and other sessile organisms until reaching adult size. When this happens, competition for space could be also an important process affecting community structure after ascidians have escaped from predation, however more experiments are needed to evaluate this.

The absence of macropredators favoured the diversity of species, suggesting that small organisms are directly benefited from the exclusion of predators, or that indirectly, ascidians might favour these organisms by creating new refuge. Among the solitary ascidians, *Ascidiella*

aspersa was the most abundant species on the plates. This species is an excellent competitor for space (Zhan et al., 2015), however, we found the largest values in diversity where the cover of ascidians was also the highest, suggesting they might create new habitats for benthic and epibionts species (Claar et al., 2011). Despite the fact that some ascidians have chemical defences that avoid epibiosis (McClintock et al., 2004; Stoecker, 1978, 1980; Wahl et al., 1994), there are several works showing that ascidians species can increase the diversity of macro-invertebrate communities (Castilla et al., 2004; Monteiro et al., 2002; Rimondino et al., 2015). Alternatively, ascidians can also obstruct the movement of benthic predators, such as sea urchins and gastropods, indirectly decreasing predation (Nydam and Stachowicz, 2007). They also can modify the water flow by creating microhabitats with low flow velocities that facilitate the settlement of larvae of sessile organisms (Koehl, 1982, 1984). Further work is necessary to test which processes are responsible for the high diversity we found, or if there is a threshold in the abundance of ascidians above which diversity starts dropping.

The negative effect of predation on fouling communities in temperate ports is unexpected according to the *biotic interaction hypothesis* (Freestone and Osman, 2011) and the *biotic resistance hypothesis* (Freestone et al., 2013; Kremer and da Rocha, 2016) discussed in marine communities. These hypotheses establish that tropical communities present stronger biotic interactions (i.e. predation) and biotic resistance (because of the higher control of exotic species by predators) than temperate and cold communities at high latitudes (Freestone et al., 2013; Freestone and Osman, 2011). In tropical regions, where these hypotheses were tested, fish are active predators of the fouling communities in artificial structures (Freestone et al., 2013; Kremer and da Rocha, 2016). However, predation pressure was found also important at high latitudes (Cheng et al., 2018; Dumont et al., 2011; Forrest et al., 2013; Rico et al., 2015; Simkanin et al., 2013) and the main difference reported between regions is the pool of potential predators. While fish play a key role in tropical regions, benthic predators are more important in cold areas. In our fouling communities studied, only small fish species, such as *Helcogrammoides cunninghami*, were reported (Irigoyen et al., 2018) or observed (authors pers. obs.) and they mainly feed upon small amphipods (Muñoz and Ojeda, 1997), suggesting that predation pressure by these organisms is not as important as in other regions. In sum, the diversity of predators, the season in which predation peaks occur (Byrnes and Stachowicz, 2009; Cheng et al., 2018) and the type of structure colonized by fouling organisms (Dumont et al., 2011) are among the most significant factors affecting fouling communities, suggesting that small scale processes are more important than those occurring at large scale (Simpson et al., 2017).

This work provides new evidences to better understand the processes regulating port fouling communities at different latitudes. Nevertheless, it is possible that floating devices, such as buoys and even ships, are relatively less available to predators than fixed structures like pilings and boulders. Indeed, while fixed substrates are available to all kind of predators, floating structures are available only to swimming organisms (like fish or swimming molluscs and crabs), since walking (crabs, molluscs or sea urchins) and crawling (sea cucumbers, sea slugs and polychaetes) predators will be naturally excluded. Although our study is conclusive on specific points, it also exposes a need for further research disentangling the processes regulating the colonization of artificial fixed versus floating structures at different latitudes.

Declaration of Competing Interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2019.151177.

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