

Research Article

Predation and competition interact to determine space monopolization by non-indigenous species in a sessile community from the southwestern Atlantic Ocean

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Abstract

Non-indigenous fouling species (NIS) often dominate coastal facilities, such as harbors and marinas. Along the subtropical Coast of Brazil, sessile communities from artificial habitats are mostly dominated by the NIS ascidian *Didemnum perlucidum* and the bryozoan *Schizoporella errata*, which show contrasting life-history traits. To understand the dynamics between these species and better predict the identity of the dominant NIS in the sessile community, we conducted an experiment where colonies of *S. errata*, *D. perlucidum* and the cryptogenic ascidian *Botrylloides niger* were submitted to the following three interaction scenarios: colonies growing without competition, under intraspecific competition and under interspecific competition. All competition treatments were crossed with the following two predation treatments: exposed or protected to predators. The experiment was repeated in two different seasons (Winter and Summer). When released from predation and competition, the three species grew at least 10 times faster in the Summer than in the Winter, and *S. errata* always grew slower than the ascidian species. Predation reduced *D. perlucidum* survival in the Winter but not during the Summer, when the fast colony growth seemed to buffer partial colony removal by predation. Colonial growth of *B. niger* was affected by competition only in treatments without predators, growing almost 50% more without competition than when competing, regardless of the competitors' identity. When exposed to predation, *D. perlucidum* was more limited by interspecific than intraspecific competition. *S. errata* growth was not affected by biotic interactions and was linked to intrinsic seasonal variation. Mineralized clonal organisms, such as bryozoans, were less predated than most of the ascidians species but they grew slower. Ascidians were more often predated but were also strong competitors that were able to overgrow several taxa. The contrasting growth strategies resulted in different successes of NIS and cryptogenic species at the studied locality. Ascidians were favored under low predation pressure while bryozoans were survivors when predation was intense.

Key words: indirect interactions, trade-off, *Botrylloides niger*, *Didemnum perlucidum*, *Schizoporella errata*, life history trait, growth strategies

Introduction

Most of the human population lives on the coast or close to it, exerting a strong pressure on marine shallow habitats. The human use of shores is often associated with a reduction in the heterogeneity of natural habitats

due to habitat destruction, leading to highly modified and homogenized coastal landscapes that standardize the selective pressures worldwide, favoring opportunistic synanthropic species (Airoldi et al. 2005; Hall et al. 2018). One of the consequences of coastal urbanization is the construction of marinas and piers, which increase the substrate available for sessile organisms. Communities developing on artificial substrata, however, hardly resemble those from natural rocky shores nearby, often being dominated by non-indigenous species (NIS) that can tolerate environmental stressors associated with ocean sprawl (Tyrrell and Byers 2007; Dafforn et al. 2015; Bishop et al. 2017).

Benthic fouling communities from the shallow subtidal are composed of species with different life histories (Jackson 1977; Jackson and Hughes 1985). Although solitary species, such as mussels, barnacles and ascidians can monopolize substrata, colonial organisms tend to be the dominant organisms in the tropics (Jackson 1977; Jackson and Hughes 1985). Most colonial ascidians grow fast but lack structural defenses against predators, relying on chemical defenses or partial colony predation and subsequent rebuilding (Jackson 1977; Buss 1986; Hiebert et al. 2019). Calcified colonial animals, such as bryozoans, can grow slower (Jackson 1977) but are more susceptible to overgrowth and less vulnerable to predation (Lidgard 2008; Smith 2014). Thus, the conditions of the impacted environments may determine the structure of the communities and the traits of the dominant NIS. For example, ascidians are usually consumed by predators (Osman and Whitlatch 2004; Freestone et al. 2011), but when overfishing or pollution (Briggs 2012) restricts the occurrence of fish, one of the main predators of sessile communities (Oricchio et al. 2016b), non-indigenous ascidians can overgrow species with lower growth rates and monopolize space (Lambert 2002; Kremer and Rocha 2011). On the other hand, when predation is intense, calcified bryozoans could be positively selected for. Thus, predation pressure in artificial habitats can predict the functional traits and identities of dominant NIS (Vieira et al. 2012; Oricchio et al. 2016b).

In the transition zone between the tropical and subtropical western Atlantic Ocean, the dominant organisms in sessile communities from artificial habitats are almost exclusively cryptogenic or non-indigenous species (Marques et al. 2013; Oricchio et al. 2019). Artificial hard substrata from marinas are either dominated by the exotic bryozoan *Schizoporella errata* (Waters, 1878) or by the exotic ascidian *Didemnum perlucidum* (Monniot, 1983) (Oricchio et al. 2019). Predation seems to be the main cause of the dominance shift, as removal of *D. perlucidum* results in the prompt monopolization of space by *S. errata* (Oricchio et al. 2016a, b). As a consequence, for this region, predation hardly results in an increase of diversity but only a change in the identity and functional traits of the dominant exotic species (Vieira et al. 2012; Oricchio et al. 2016a, b). This scenario highlights the importance of understanding how the interaction

between competition ability and predator resistance can affect the success of NIS to dominate invaded communities, since their traits might play a fundamental part in this process. In this context, we developed an experiment to evaluate the effect of predation on the competition success of three of the most frequent and abundant species in local Brazilian marine communities. To do so, we compared the survival and growth rates of each species when competing with each other, under intraspecific competition or when free of competitors crossed with predation treatments in which communities were either exposed to or protected from predators. Because recruitment and survival of the three species may change seasonally, we also explored the consistency of the results through time, repeating the experiment during the Austral Summer and Winter. We expected that predation would negatively affect ascidians more than bryozoans, mainly in the winter, when we expected a lower colonial growth. However, we also hypothesized that bryozoans would be susceptible to competition with ascidians and show reduced growth in the presence of other species, irrespective of predator presence.

Materials and methods

Study location

We conducted this experiment at the Yacht Club Ilhabela (YCI) (23°46'S; 45°21'W), located at São Sebastião channel, at the north end, at the São Sebastião Island, Ilhabela city, Brazil. The YCI consisted of floating concrete-made platforms, with walls covered by benthic fouling invertebrates. Fish were the most common predators at the shores nearby and at the marina itself (Oricchio et al. 2016b). The marina was enclosed by a breakwater, which reduced water turbulence within the study site, which was located at the area where the boats berth. We deployed PVC experimental panels at the inner portions of the marina (for map, see Oricchio et al. 2016b).

Experimental design

To test how the survival and growth rates of three abundant species were affected by predation and competition, we developed an experiment where colonies were exposed to or protected from predation in different competition scenarios. We selected the species based on previous studies conducted in the same region and their abundance and ability to dominate the substrate (Vieira et al. 2012, 2016; Oricchio et al. 2016a, b, 2019). The exotic colonial ascidian *Didemnum perlucidum*, the cryptogenic colonial ascidian *Botrylloides niger* (Herdman, 1886) and the exotic encrusting bryozoan *Schizoporella errata* were among the most abundant and dominant species in sessile communities in the region (Oricchio et al. 2019). The three species varied in abundance under different predation

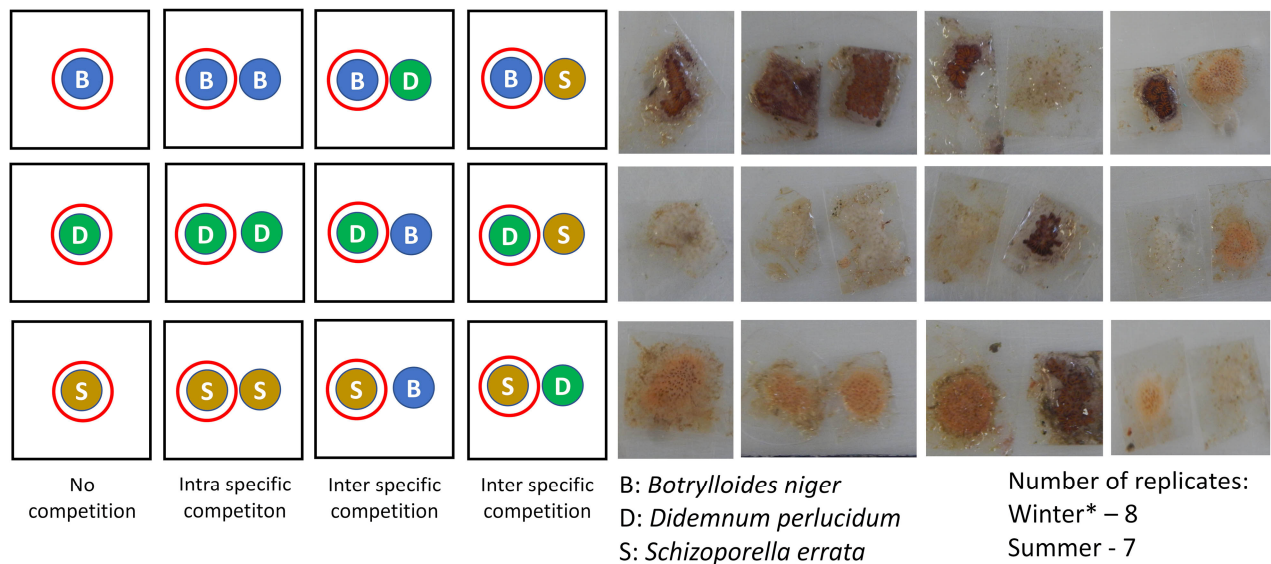


Figure 1. Experimental design. Left: schematic representation of the experiment. The red circles represent the focal colony, which was the only colony under analyses. Right: Representative photos of the colonies corresponding to each treatment. All of these competition treatments were fully crossed with predation treatments (protected or exposed). * during the Winter, *D. perlucidum* had 5 replicates per treatment; the other two species had 8 replicates per treatment.

pressures scenarios. When predation was intense, *S. errata* dominated up to 80% of the available substrate in experimental plates. However, when experimental plates were protected from predators, the abundance of *S. errata* was consistently low, and *D. perlucidum* often covered most of the available area (Vieira et al. 2012; Oricchio et al 2016b). On the other hand, *B. niger* was a very frequent and abundant species in both predation scenarios, occupying most of space not monopolized by the exotic species mainly at the early stages of community development (Oricchio et al. 2016a, b).

We used colony recruits to develop an experiment that consisted of colonies of each species free of competitors, competing both intra- and inter-specifically, in scenarios with and without predation. Because different growth strategies may be favored at different seasons of the year, the experiment was conducted from June to July 2017 (Austral Winter) and repeated in November to December 2018 (Austral Summer). To obtain the colonies, we deployed 200 (30 × 30 × 0.4 cm) recruitment plates horizontally, with acetate sheets attached to the downward face of the panels. After 30 days, we removed and transported the acetate sheets containing the recruits in insulated coolers to the Center of Marine Biology at the University of São Paulo (CEBIMar-USP), a 10 minute boat trip from the sampled location. In the laboratory, we kept the colonies under flowing sea water and cut the acetates into individual colonies based on species.

Once the colonies were individualized by species, we glued individual colonies of *D. perlucidum* (n = 40; 5 replicates for each level of predation × competition treatments) and the other two species (n = 64 each; 8 replicates each) onto 25 × 25 cm PVC plates for the winter. During the summer, 56 colonies (7 replicates for each level of predation × competition treatments) of each species were adhered to individual (25 × 25 cm) PVC plates (Figure 1).

The variation in the number of colonies among species during the Winter reflected the limited recruitment of *D. perlucidum*. The colonies were then equally divided amongst the four competition treatments: 1) no competition (the focal colony was glued alone on the plate) 2) intraspecific competition (the focal colony was glued beside another colony of the same species), 3 and 4) under interspecific competition (the focal colony was glued beside a colony of one of the other two species). The initial size of the focal colonies varied from 0.05 to 2.00 cm². For treatments 2, 3 and 4, competing colonies were the same size as focal colonies, assuring equal initial conditions of competition.

We equally divided the plates from each competition treatment into the following two predation scenarios: 1) protected by a cage of 2.4 cm mesh, which is effective in preventing predator access (Oricchio et al. 2016a) and 2) exposed, without a cage, allowing predator access. Previous studies in the same region have shown no artifacts of caging in these types of experiments, even using mesh sizes smaller than those used here (Vieira et al. 2012; Oricchio et al. 2016a), so we did not include a cage control in our experiment. We then returned the plates to the study site and let the colonies grow for four weeks. After this period, the panels were retrieved and photographed to estimate survivorship and growth rate of the colonies, which was calculated by subtracting the initial area of the colony from the final area and dividing by the number of days of exposure. All treatments associated with the identity of the competitor were independent and for each one of the plates, growth data was obtained only for the focal species, assuring the experimental independency of the data.

Statistical analyses

To compare the intrinsic differences in growth rates among the three species when released from biotic interactions, we used an analysis of variance (ANOVA) considering only the plates where species were free of competitors and predators (no competition, caged treatment). Season (Summer or Winter) and species identity were treated as fixed factors. Dead focal colonies were not used to estimate colony growth. To reach homoscedasticity the data were log transformed.

To compare the susceptibility of each species to predation within each season, we compared the proportion of colonies that survived in predation exposed and protected treatments, regardless of competition treatment, using chi-square analyses. For this analysis all colonies used during the experiment were included, regardless if it was used as a focal or a competing colony. A total of 174 colonies of *B. niger*, 103 of *D. perlucidum* and 183 colonies of *S. errata* were used in the analyses, where chi-square assumptions were met.

Growth rates of the species under combined predation and competition scenarios were tested using an ANOVA, where predation (exposed or protected), focal species identity and competitor identity were treated as

Table 1. Analysis of variance for the growth rate of the three species when released from predation and competition in the two seasons (Winter and Summer).

Source	df	MS	F	p
Season	1	2.866	121.58	< 0.001
Species identity	2	0.606	25.721	< 0.001
Season x Species identity	2	0.333	14.127	< 0.001
Error	25	0.024		

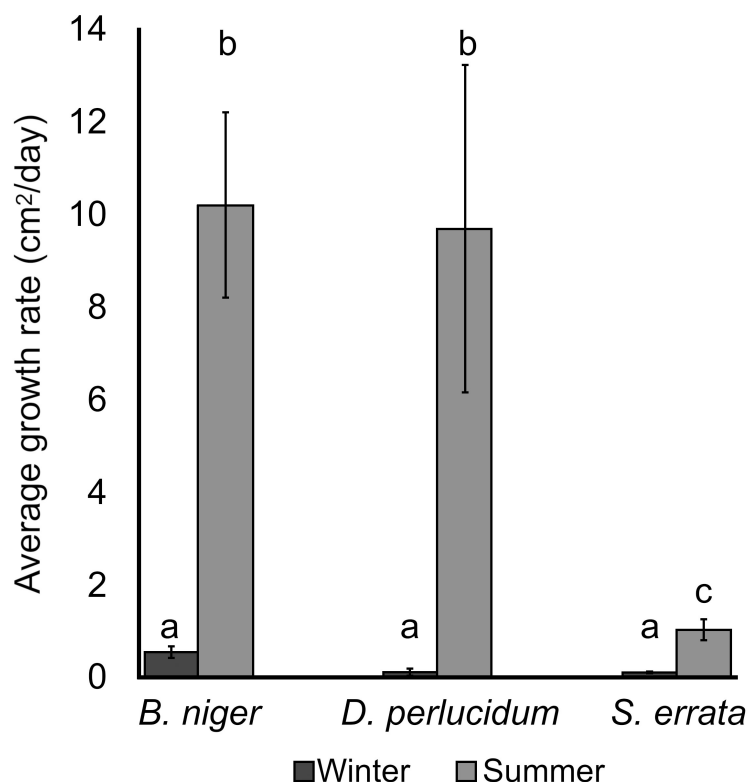


Figure 2. Growth rate per day for the three species when released from predation and competition. Error bars represent standard error. Different letters over the bars represent significant different mean values (Tukey $p < 0.05$).

fixed orthogonal factors. The high mortality of *D. perlucidum* in Winter prevented us from assessing the temporal variation of these results; therefore only Summer data were used in this analysis. The data were log transformed to reach homoscedasticity.

For both ANOVA analyses, we ran Tukey pairwise analyses when significant factors were identified (Quinn and Keough 2002). All tests were conducted using SYSTAT 12, and all model assumptions (normality and homoscedasticity) were assessed by examining residual plots.

Results

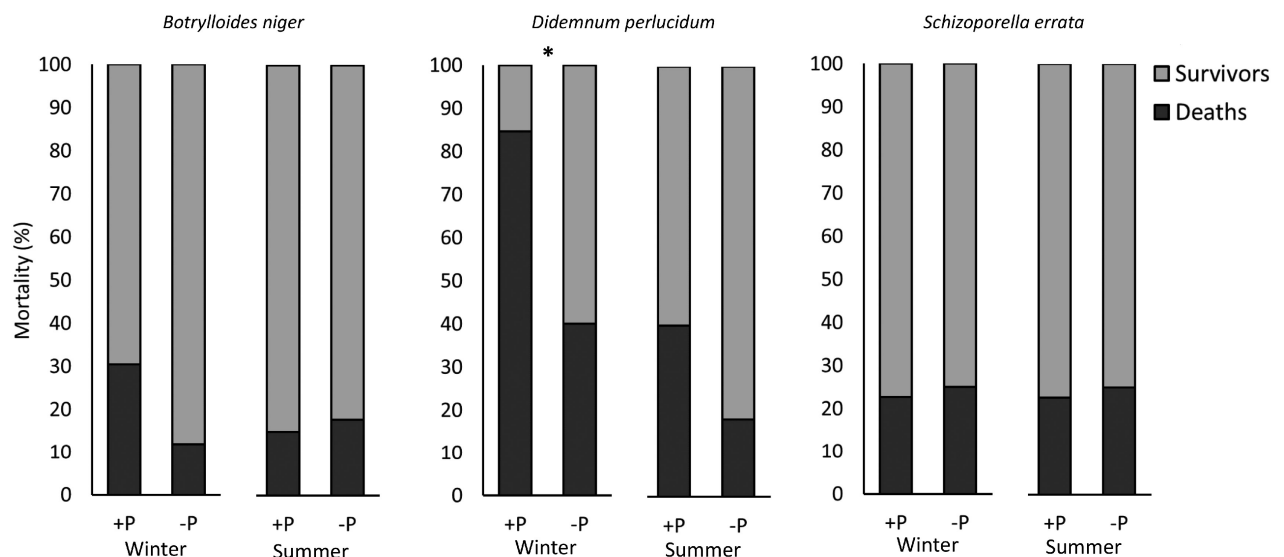
When released from competition and predation, species grew at different rates only during the Summer, when both ascidian species grew almost 10 times faster than *S. errata*. During the Winter, species grew at similar rates. The three species showed more intense growth during the Summer, but the magnitude of the difference was higher for ascidian species than for *S. errata* (Table 1, Figure 2). Predation reduced the survivorship of the exotic ascidian

Table 2. Chi-square values for the three species in the two experimental seasons (Winter and Summer) considering the number of dead and survivor colonies.

	<i>Botrylloides niger</i>		<i>Didemnum perlucidum</i>		<i>Schizoporella errata</i>	
	χ^2	P	χ^2	P	χ^2	P
Winter	2.468	0.146	5.812	0.027	0.057	0.486
Summer	0.069	0.483	2.153	0.17	0.035	0.491

Table 3. Analysis of variance for the growth rate per day for the three species only the second moment (summer) considering predation, focal species identity and competitor identity.

Source	df	MS	F	P
Focal Species (Foc)	2	3.345	102.66	< 0.001
Predation (Pred)	1	1.054	32.351	< 0.001
Competitor identity (Comp)	3	0.274	8.409	< 0.001
Foc x Pred	2	0.375	11.504	< 0.001
Foc x Compet	6	0.072	2.215	0.049
Pred x Compet	3	0.108	3.324	0.024
Foc x Pred x Compet	6	0.155	4.756	< 0.001
Error	84	0.033		


Figure 3. Mortality proportion of the three species under different predation scenarios (+P: exposed to predators and -P: protected from predators) in the two different experimental seasons (Winter and Summer). * represents $p < 0.05$.

D. perlucidum only during the Winter. For the other species, predation did not affect survivorship in either season (Table 2, Figure 3).

Considering the combined effects of predation and competition during the Summer, competition did not affect the growth of *B. niger* when exposed to predation. However, when protected against predators, competition restricted growth of *B. niger* by 46% regardless of the competitors' identity (Table 3, Figure 4). When exposed to predators, *D. perlucidum* growth was reduced by interspecific competition regardless of the competitor identity, growing almost 8 times faster in the absence of competition. When protected from predation, *D. perlucidum* grew more when competing with *S. errata* than under intraspecific competition; *D. perlucidum*'s growth rate under competition with *S. errata* increased when the community was protected

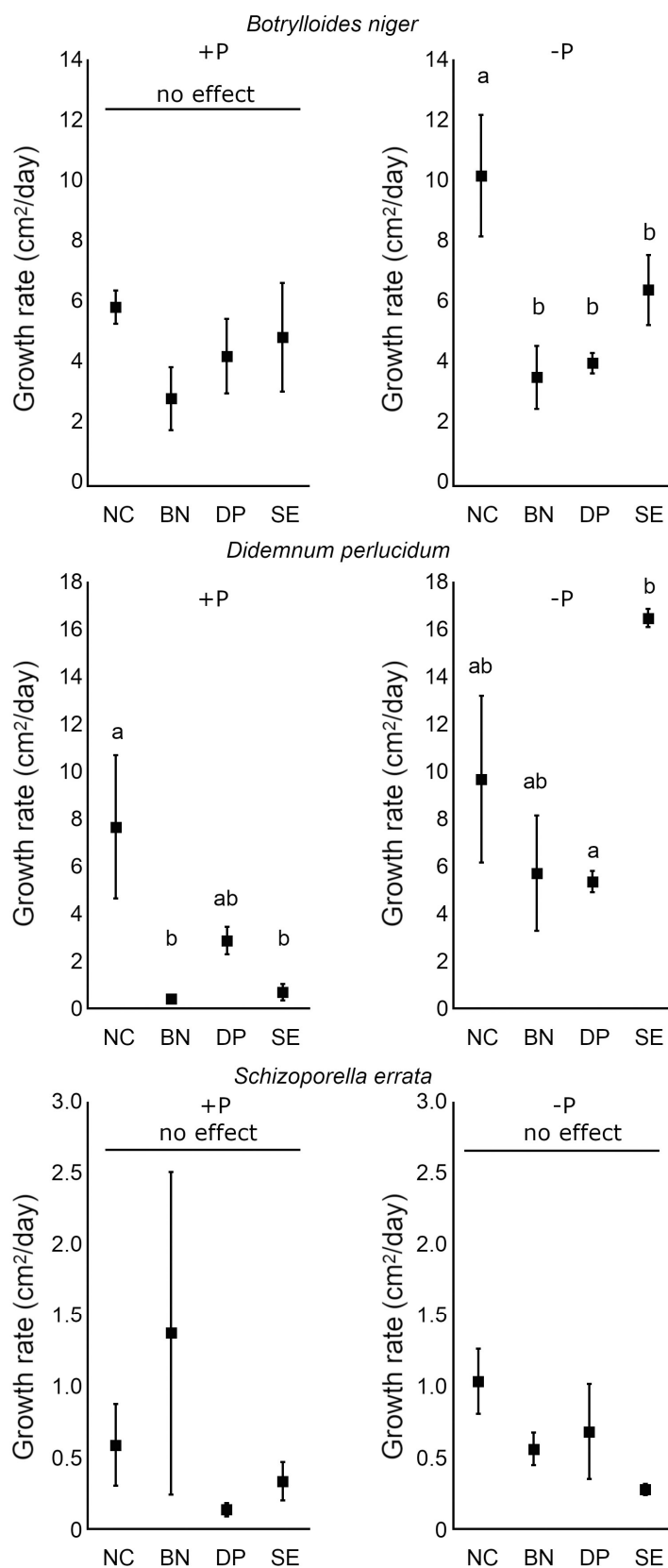


Figure 4. Mean growth rate per day for the three species during Summer when exposed to predators (+P) and protected from predators (-P) under different competition scenarios (NC: no competitor, BN: focal species competing with *Botrylloides niger*, DP: focal species competing with *Didemnum perlucidum* and SE: focal species competing with *Schizoporella errata*). Error bars represent standard error. Different letters over the bars represent significant different mean values (Tukey p < 0.05).

from predation. We found no effect of competition or predation in determining the growth rate of *S. errata* (Table 3, Figure 4).

Discussion

The results presented here corroborated the hypothesis that the combination of contrasting life history traits and distinct local selective pressures determine the success of organisms when competing for resources (McPeck 2004; Epelbaum et al. 2009). Considering that the species studied here are frequent non-indigenous species (NIS) or cryptogenic species in coastal communities of southeastern Brazil, the variation of competitive ability, resistance to predation and colony growth strategies among species should regulate the success of invaders at early stages of community development (Tyrrell and Byers 2007), which can also be reflected in resource monopolization at latter stages of the invasion (Vieira et al. 2018). Tunicates are good competitors (Jackson 1977; Russ 1980) and often dominate sessile communities even when recruitment rates are relatively low (Edwards and Stachowicz 2010). However, most ascidians lack efficient structural defenses against predators (Lambert 2005), except for some didemnids and pyurids; thus predation may control ascidian abundance. Encrusting bryozoans, on the other hand, are less susceptible to direct top down control due to their low energetic content (Jackson 1977). In our study, the exotic ascidian *Didemnum perlucidum* was the most negatively affected species in terms of both predation and competition. *Didemnum perlucidum* also showed seasonally restricted growth; when released from trophic interactions, growth rates for this species was almost 100 times greater in the Summer than during the Winter. When *D. perlucidum* grew less (Winter), the presence of predators reduced its survival and limited its growth, suggesting that *D. perlucidum* relied on colony growth from remaining colony tissues after predation (Hiebert et al. 2019). However, *S. errata* seemed to adopt a less variable growth strategy by continually increasing in area slowly; our results showed that this species was not affected by predation or competition, regardless of the competitors' identity.

The three species possess different life histories and, when released from trophic interactions, grew differently. Bryozoans are mineralized clonal organisms, and their growth is a relatively slow process of calcareous deposition (Jackson 1977). In comparison, colonial tunicates, also clonal organisms, are known as fast growing organisms that are able to overgrow many different taxa in fouling communities (Todd and Turner 1988; Kremer and Rocha 2011). Fouling ascidians represent a significant economic cost for human activities that occur along the coastline, such as aquaculture, as they can overgrow commercially exploited species and structures (Carman et al. 2010; Cordell et al. 2013). The success of different life histories will depend on the local environmental conditions (Epelbaum et al. 2009). *Didemnum perlucidum* occurs from tropical to temperate

zones (Dias et al. 2016), but evidence of harmful effects are usually reported in artificial habitats (Sheehy and Vik 2010; Rocha et al. 2009) or degraded natural habitats (Simpson et al. 2016; Roth et al. 2018) where overfishing is expected to remove the main ascidian predators (Oricchio et al. 2016b). In addition, human induced changes in the temperature regime can strongly affect species growth, as suggested by the 10-fold difference in growth of ascidians between Summer and Winter and consequently increase the risk of bioinvasions (Huang et al. 2011).

When competing for space the species also performed differently. While *S. errata* growth was not affected by predation or competition, *B. niger* and *D. perlucidum* growth was impacted by the interaction between the two ecological processes. While predation on *S. errata* has been rarely reported (Oricchio et al. 2016b), the lack of competition effect was in contrast with our initial hypothesis. The effects of competition could take longer to manifest or depend on a scenario where resources are more limited, as in advanced stages of community succession. *B. niger*'s ability to monopolize space was only evident when free of competitors and predators. This result was confirmed by Pisut and Pawlik (2002), who showed that *B. niger* was the only species among 17 ascidians from different families collected in Northwest Atlantic Oceans that had no evidence of chemical defenses. Besides, in the studied site, *B. niger* is considered an early colonizer with a short life span of only a few months (Rocha 1991), which can explain its occurrence mainly during the early successional stages (Oricchio et al. 2016a). When protected from predation, *D. perlucidum* seemed to not be limited by competition with *S. errata*, highlighting the superior competing ability of some ascidians over bryozoans (Osman and Whitlatch 1995) but also the importance of predation on the result of the interaction. The fact that *D. perlucidum* grew more when competing with *S. errata* than under intraspecific competition might be seen as facilitation. However, if that were true, *D. perlucidum* growth would be higher when competing with *S. errata* than when growing without competitors. When exposed to predators, *D. perlucidum* growth was negatively affected by competition; this effect was more pronounced under interspecific competition than intraspecific competition. The reduction of *D. perlucidum*'s competitive ability when colonies were exposed to predation may explain why this species is not dominant in artificial hard substrata along Brazil's coastline. This, however, is in contrast with populations in Australia, where *D. perlucidum* represents a nuisance species in harbor areas (Kremer and Rocha 2011; Smale and Childs 2012).

The ultimate outcome of the interactions among these NIS and cryptogenic species in artificial hard substrata is shaped by local environmental conditions. The bryozoan *S. errata* grew slower than the ascidians used in this study, but the growth rate and survival of *S. errata* was not impacted by predation or competition. Competition negatively

affected the growth rate of *B. niger*, but only when protected from predators. Finally, *D. perlucidum* survival was reduced by predators only in the Winter, and its growth was mediated by the presence of predators and competitors' identity. Some marinas in this local area are characterized by a strong dominance of *S. errata*, while others have high abundances of *D. perlucidum* (Oricchio et al. 2019). Our experiment suggested that predation was probably the main process behind this pattern. Regions with large predatory fish populations will result in fouling species with growth strategies that may reduce the negative effects of predation, such as bryozoans. However, if predation pressure is reduced, the space at these sites will likely be monopolized by fast growing organisms without effective chemical or structural defenses against predators, such as some ascidians. Understanding the differences in growth strategies and the success of specific functional traits among abundant NIS is important to establish more effective management actions. Protecting fish populations and eradication efforts during the winter, when *D. perlucidum* is less likely to recover from remaining pieces of colonies, may represent an effective mechanism to prevent the establishment of fast-growing, undefended ascidians. In addition, predators may be important in reducing the gateway role that artificial hard substrata poses to biological invasion in natural rocky shores.

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