

Research Article

The role of *Didemnum perlucidum* F. Monniot, 1983 (Tunicata, Ascidiacea) in a marine fouling community

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Editor's note:

This paper is a contribution to the proceedings of the 3rd International Invasive Sea Squirt Conference held in Woods Hole, Massachusetts, USA, on 26–28 April 2010. The conference provided a venue for the exchange of information on the biogeography, ecology, genetics, impacts, risk assessment and management of invasive tunicates worldwide.

Abstract

Didemnum perlucidum is a colonial ascidian that is cryptogenic in southern Brazil but introduced in many regions around the world. It is common in ports and marinas where it may form large colonies although its role in fouling communities is poorly understood. The goal of this study was to evaluate the role of *D. perlucidum* in a marine fouling community comprised mainly of non-indigenous species. Treatment pairs (*D. perlucidum* removal and unmanipulated controls) of experimental plates were exposed during 14 months at a mussel farm in southern Brazil. Taxonomic richness and percent cover of the species were compared between treatments (with and without *D. perlucidum*). *D. perlucidum* did not influence taxonomic richness or inhibit colonization by any species. Effects of this species on the abundance of others were sporadic, and suggest that it may be a weak competitor. The small effect of *D. perlucidum* in this community is explained by its low abundance and its occupation of secondary substrate without having detrimental effects on the species it grew over. Given that *D. perlucidum* is more abundant, and problematic, in other regions of southeastern and southern Brazil, continuous monitoring is desirable to better understand its fouling dynamics.

Key words: tunicate, ascidian, competition, colonization plates, didemnids, invasiveness, succession

Introduction

The transportation and introduction of species are among the most pervasive threats to coastal ecosystems and, once introduced, an invasive species may affect local communities on ecological and evolutionary scales (Grosholz 2002). Furthermore, invasive species often have characteristics typical of opportunistic species, such as pioneer habitat use, rapid growth and high fecundity (McKinney and Lockwood 1999; Sakai et al. 2001) and frequently they are competitively dominant (Castilla et al. 2004a; Turon et al. 2007). Together, these factors suggest the possibility of important detrimental effects and some authors suggest that

homogenization of the global biota is occurring (McKinney and Lockwood 1999; Olden et al. 2004). However, non-native species may also have facilitative interactions in a new environment (Castilla 2004b; Rodriguez 2006), including facilitation of other exotic species (Grosholz 2006) as well as a complex interaction of negative and positive effects on the native community (Thieltges et al. 2006). Also, once introduced, these species may have impacts that vary over time, depending on local biotic and abiotic factors (Thieltges et al. 2004; Grosholz 2006). All of these interactions will determine whether the non-native species will remain in low abundance or become a dominant species in the invaded community.

With so many possible outcomes, no clear patterns connect species characteristics or phylogenetic background to the capacity of the species for interference within a new community. Accumulating evidence from a larger group of transported species in different environmental situations will increase our predictive ability. Here we report the results of interactions between *Didemnum perlucidum* F. Monniot, 1983 and a fouling community. This species commonly fouls shellfish farms in Brazil (Rocha et al. 2009) where its prolific reproduction allows it to quickly colonize bare substrates as well as established communities (Kremer et al. 2010). In southern Brazil, it is classified as cryptogenic because of the uncertainty of origin due to the lack of historical records as well as its disjunct distribution (for a more detailed discussion about *D. perlucidum* distribution and classification, see Kremer et al. 2010). *D. perlucidum* is a widespread didemnid colonial ascidian that is introduced elsewhere around the world, where colonies may cover large areas (Monniot and Monniot 1997; Lambert 2002; Golbuu et al. 2005). While its effect on local communities has never been studied, evidence from reproductive output, colonization ability (Kremer et al. 2010) and colony size suggest that *D. perlucidum* can be a dominant competitor and consequently, when introduced, it should strongly influence the community.

Colonial organisms are often superior spatial competitors (Jackson 1977; Buss 1986) and colonial ascidians are sometimes competitively dominant (Nandakumar et al. 1993). Considering their dominance and the antifouling nature of their tunic (Osman and Whitlatch 1995 a, b; Bryan et al. 2003), once introduced to a new environment, ascidians may inhibit the settlement of other species by preemption of space or by direct competition, covering and excluding adults of those other species. In addition, some ascidians are opportunistic and quickly occupy new gaps in communities (Berman et al. 1992; Nydam and Stachowicz 2007). Many introduced ascidians have these characteristics and have become established successfully in new environments, changing the structure of the community. Among colonial species, many examples are in the family Didemnidae; *Didemnum vexillum* Kott, 2002 has had a detrimental impact in several regions where it was introduced (Minchin and Sides 2006; Bullard et al. 2007; Osman and Whitlatch 2007; Valentine et al. 2007), and *Diplosoma*

listerianum (Milne-Edwards, 1841) became dominant and changed the community structure in the North Sea (Vance et al. 2008). Native didemnid species may also be invasive by overgrowing vulnerable species in the community under favorable conditions. *Diplosoma simile* (Sluiter, 1909) and *Trididemnum solidum* (Van Name, 1902) have overgrown and killed coral reef benthos in the Pacific Ocean and the Caribbean Sea, respectively (Vargas-Ángel et al. 2008; Sommer et al. 2010).

Here, we evaluate the competitive ability of *D. perlucidum* in the fouling community of a shellfish farm. We experimentally tested the hypothesis that *D. perlucidum* is a dominant competitor for space either by preventing settlement or by covering and smothering neighbors, and that consequently it reduces species richness at the community level.

Methods

Study area

This study was conducted in a brown mussel (*Perna perna*) farm at Armação do Itapocoroy Bay, Penha, Santa Catarina, Brazil (26°46'30"S, 48°36'34"W). Armação do Itapocoroy Bay is protected from strong waves and is influenced by the plume of the river Itajaí-açu that opens to the sea 20 km south. Salinity is usually less than 34 and surface temperature ranges from 19°C to 28°C (Schettini et al. 1999). Depth ranges between 9 and 12 m (Marenzi et al. 2006). The mussel culture is not a vector for the introduction of non-native species as the spat is collected locally. However, Penha is close to two important marine ports: Itajaí and São Francisco. Therefore, this environment constitutes a likely entry region for the colonization and establishment of non-native species via shipping vectors.

The community that colonizes and encrusts mussels and associated structures is poorly known. Of the sixteen ascidian species known from the region, only one is considered native (Rocha et al. 2009). The fouling community also includes sponges, hydrozoans (18 species, E. Bornancin, pers. comm. 2006), barnacles (six species on the plates, none of which are native in Brazil, LPK, RMR personal observation) and bryozoans.

Experimental design

To test how *Didemnum perlucidum* may influence the fouling community, we conducted an experiment using paired black polyethylene plates (15×15 cm)

with each plate of the pair assigned to a different treatment. In one treatment, all visible colonies of *D. perlucidum* were carefully removed with a small spatula, monthly (removal treatment). The other plate was the control treatment, in which plates were allowed to accumulate the natural encrusting community over time. At each sampling, plates were withdrawn from the water, photographed and placed again in their original positions. Prior to the first placement, all plates were roughened with sandpaper, and attached to a rack which was hung from the main longline of the culture at 0.5, 1.5, 3.0 and 5.0 m below the water surface. Plates were fixed in a horizontal position, parallel to the sea floor, and the underside was analyzed. Each treatment had four replicates at each depth. The experiment was carried out from March 2006 to May 2007 and sampled at monthly intervals. For sampling, all plates were taken from the water, put into a container with seawater and photographed using a high resolution digital camera (Canon - 5 Mp). Following photography, *Didemnum perlucidum* were scraped from the removal treatment plates after which all plates were quickly replaced in their original positions. Treatments (and comparisons) were initiated after an exposure of two months, in May 2006, when the plates were almost totally occupied by encrusting organisms.

Analysis

Digital photographs were adjusted to 169 cm², comprising the central area of the plate, to avoid edge and handling effects. To evaluate the effects of *Didemnum perlucidum* on the community, the coverage area of each species that colonized the plates and the number of species on plates with and without *D. perlucidum* were compared by paired Student's *t* tests. Percent cover of taxa was estimated visually, aided by a grid of 25 small squares, inside of which space occupied by each species was ranked as 0, 1, 2, 3 and 4 corresponding to 0, 25, 50, 75 and 100% cover, respectively, in each of the small quadrats. The 0.5 value indicated that a species was present, yet notably less than 25%. The sum of ranks of the 25 squares was used to estimate total plate coverage (Terlizzi et al. 2002). Frequently this percentage exceeded 100% as a result of overgrowth by one species on another. The covered species was only counted if not completely overgrown, that is if the species was alive, but no distinction was made in relation to substrate occupation (secondary – epibiosis, or primary – the plate

itself). As the goal of the study was to evaluate the influence of *D. perlucidum* on the other species, pairs of plates in which any species was absent, or occupied less than 5% of the area of one of the paired plates during any month, were not analyzed for that species in that month. Significance for all comparisons was $\alpha = 0.05$. The effect of depth on community pattern was previously tested by ANOVA with no significant results ($p > 0.5$). Thus plates were pooled across depths as replicates and depth was no longer included in analyzes. The July 2006 plates were not evaluated due to the low resolution of the photographs. Only the conspicuous species of February 2007 were analyzed due to the same problem.

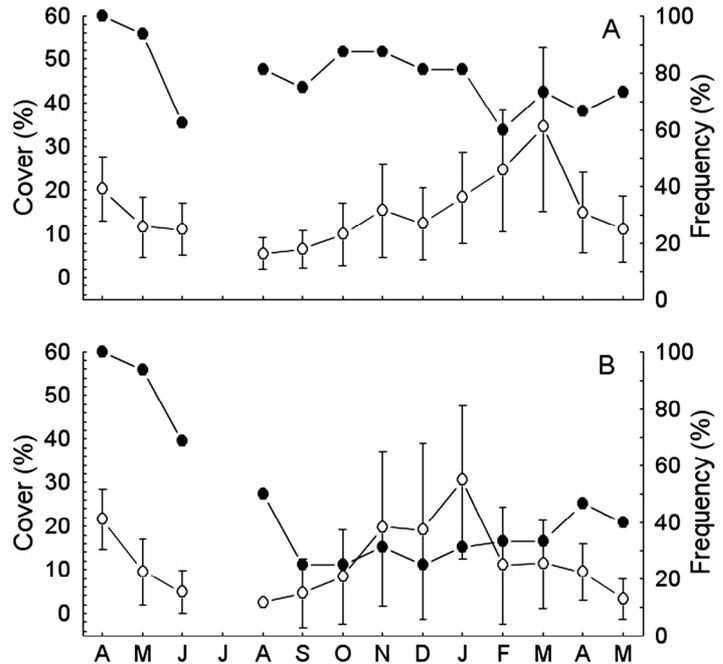
Results

At least 33 taxa, most of which were identified to the species level, colonized the plates (Table 1). All taxa colonized plates in both treatments, except for *Carijoa riisei* (Duchassaing & Michelotti, 1860) and *Amphibalanus reticulatus* (Utinomi, 1967) which were found sporadically and only on the removal treatment. *Didemnum perlucidum* occurred on 79% of the control plates and new colonization of the species occurred in 47% of the removal treatment plates. *D. perlucidum* occupied 13.4±2.8 % (mean cover ± 95% CI) of control plates and 4.6±1.5% cover of removal plates. Even though *D. perlucidum* reoccupied plates in the removal treatment in all months, the number of re-colonized plates was low and cover on those plates was rather variable, only a few with greater coverage than the control plates (Figures 1A, B). *Didemnum perlucidum* frequently used other species like barnacles and solitary ascidians as substrate (LPK and RMR personal observation).

Taxonomic richness during the experiment varied between 2 and 13 taxa, with an average of nine taxa per plate. It was similar in both treatments throughout the experiment (Figure 2A).

Few species were adversely affected by the presence of *D. perlucidum*. The sponge *Lissodendoryx isodictyalis* (Carter, 1882) covered a greater area on plates in the removal treatment than in the controls on 70% of the pairs of plates analyzed, but the difference was statistically significant only in October 2006 (Table 1, Figure 2B). Cover of the bryozoan *Jellyella tuberculata* (Bosc, 1802) was higher in the removal treatment on 61% of the pairs analyzed; the difference was greatest in April 2007 when approximately 90% of

Figure 1. Frequency on plates (solid circle) and percent cover (empty circle) of *Didemnum perlucidum* on control (A) and *D. perlucidum* removal treatment plates (B), before the removal of colonies each month. Only plates with *D. perlucidum* were considered in percent cover calculation. The vertical bars indicate the confidence interval 95%. N=16 from April 2006 until January 2007 and N=15 in the other months.



the pairs analyzed presented higher cover on the removal treatment ($17.2 \pm 11.1\%$) than on control plates ($2.0 \pm 3.7\%$) ($P < 0.05$). The solitary nonindigenous ascidian *Styela plicata* (Lesueur, 1823) was present on 117 pairs of plates and the coverage of this species was higher on removal treatment on 83 pairs (Table 1, Figure 2C) but the differences were not statistically significant. *Diplosoma listerianum* presented a higher cover on removal treatment on 60% of the pairs analyzed. In the final month of study, nine of ten pairs had a greater abundance of *D. listerianum* on the removal treatment ($8.1 \pm 5.0\%$) than on control plates ($1.0 \pm 1.4\%$) ($P < 0.05$).

Pinauay crocea (L. Agassiz, 1862) was the only species to show a result consistent with a favourable effect of *D. perlucidum*, although this was observed in only one month. Occupancy of *P. crocea* was lower in the removal treatment ($14.0 \pm 5.7\%$) than the control ($26.7 \pm 9.1\%$) in August 2006.

Discussion

The results demonstrate that the presence of *Didemnum perlucidum* did not inhibit recruitment of any species nor did it influence taxonomic richness on experimental plates. Open space is often the main

limiting resource in marine fouling communities as well as the most important factor that influences invasibility of communities (Stachowicz et al. 1999; Stachowicz et al. 2002a; Stachowicz and Byrnes 2006). The little available open space in this community, even at the beginning of the experiment, suggests that any change in availability of space should result in subsequent changes in community composition or structure. Because *Didemnum perlucidum* is a colonial ascidian that often covers large areas (Lambert 2002) and is generally not used as a substrate itself (in accordance with many other colonial ascidians, Osman and Whitlatch 1995a; Valentine et al. 2007), we predicted that the effect of its removal would be an increase in free space for other species to settle or to grow laterally and a subsequent increase in coverage by those other species. Also, if *D. perlucidum* could compete directly by covering and smothering competitively inferior species, its removal would release those species from direct competition. Thus, at the community level, we predicted that the removal treatment would result in an increase in species richness, as in other experiments (Blum et al. 2007).

However, only two species were found exclusively in the removal treatment and their occurrence could not be clearly attributed to removal of *D. perlucidum*. All other species

Table 1. List of species with the mean covered area (%) \pm 95% CI per plate (144 cm²) and percentage of pairs analyzed on which the coverage of the species was higher on removal treatment than on the control plates (number of pairs analyzed in parenthesis). The total number of pairs analyzed was 172.

Species	Treatment		R > C % (n)
	Removal(R)	Control(C)	
Porifera			
<i>Lissodendoryx isodictyalis</i> (Carter, 1882)	11.2 \pm 2.6	6.4 \pm 2.4	69 (85)
<i>Mycale microsigmatosa</i> Arndt, 1927	8.4 \pm 8.9	19.8 \pm 11.2	45 (22)
Hydrozoa			
<i>Obelia dichotoma</i> (Linnaeus, 1758)	x*	x	---
<i>Pennaria disticha</i> Goldfuss, 1820	5.4 \pm 1.6	5.9 \pm 1.7	47 (121)
<i>Pinauy crocea</i> (Agassiz, 1862)	11.2 \pm 3.3	12.2 \pm 3.9	47 (98)
<i>Turritopsis nutricula</i> McCrady, 1857	x	x	---
Anthozoa			
unidentified anemone	x	x	---
<i>Carijoa riisei</i> (Duchassaing and Michelotti, 1860)	x	x	---
Polychaeta			
<i>Hydroides</i> sp.	x	x	---
<i>Pomatoceros minutus</i> Rioja, 1941	x	x	---
Bivalvia			
<i>Perna perna</i> (Linnaeus, 1758)	x	x	---
unidentified oyster	x	x	---
Amphipoda¹			
<i>Laticorophium</i> sp.	x	x	---
<i>Monocorophium</i> sp.	x	x	---
<i>Jassa</i> sp.	x	x	---
Cirripedia			
<i>Amphibalanus amphitrite</i> (Darwin, 1854)	x	x	---
<i>Amphibalanus eburneus</i> (Gold, 1841)	3.4 \pm 1.5	2.4 \pm 0.9	53 (51)
<i>Amphibalanus reticulatus</i> (Utinomi, 1967)	x	--	---
<i>Balanus trigonus</i> Darwin, 1854	x	x	---
<i>Megabalanus coccopoma</i> (Darwin, 1854)	10.8 \pm 2.7	9.7 \pm 2.7	55 (147)
<i>Megabalanus tintinnabulum</i> (Linnaeus, 1758)	x	x	---
Bryozoa			
<i>Bugula neritina</i> (Linnaeus)	3.5 \pm 1.8	2.5 \pm 1.4	45 (79)
<i>Jellyella tuberculata</i> (Bosc, 1801)	12.2 \pm 4.1	10.7 \pm 4.7	61 (76)
<i>Schizoporella</i> sp.	x	x	---
Ascidacea			
<i>Aplidium accareense</i> (Millar, 1953)	20.4 \pm 4.1	21.3 \pm 4	56 (71)
<i>Diplosoma listerianum</i> (Milne-Edwards, 1841)	19.9 \pm 4.2	17.3 \pm 4.3	60 (130)
<i>Trididemnum orbiculatum</i> (Van Name, 1902)	9.1 \pm 2.7	6.7 \pm 3.2	62 (79)
<i>Styela canopus</i> (Savigny, 1816)	4.2 \pm 1.2	3.5 \pm 1.0	48 (93)
<i>Styela plicata</i> (Lesueur, 1823)	12.7 \pm 2.9	5.3 \pm 2.3	83 (117)
<i>Symplegma brakenhielmi</i> (Michaelsen, 1904)	x	x	---
<i>Botrylloides nigrum</i> Herdman, 1886	x	x	---
<i>Botrylloides giganteum</i> (Pérès, 1949)	x	x	---
<i>Microcosmus exasperatus</i> Heller, 1878	x	x	---

* X = species present on plates, but with less than 5% coverage in all months ¹ Genera not identified to species level because the photographic method did not permit accurate identification

occurred on plates in both treatments and therefore *D. perlucidum* did not inhibit the recruitment of any species in this experiment. Many ascidians produce secondary metabolites that may inhibit the settlement of species (Lambert 2005). However, this phenomenon has mainly been demonstrated in the laboratory

(Krug 2006) and field studies have failed to show similar inhibition (Bullard et al. 2004; Dias 2008; Dijkstra and Harris 2009). At any rate, there was no evidence of this type of competitive interaction in this study. Nor did we find evidence of the exclusion of species by direct competition with *D. perlucidum*. Despite

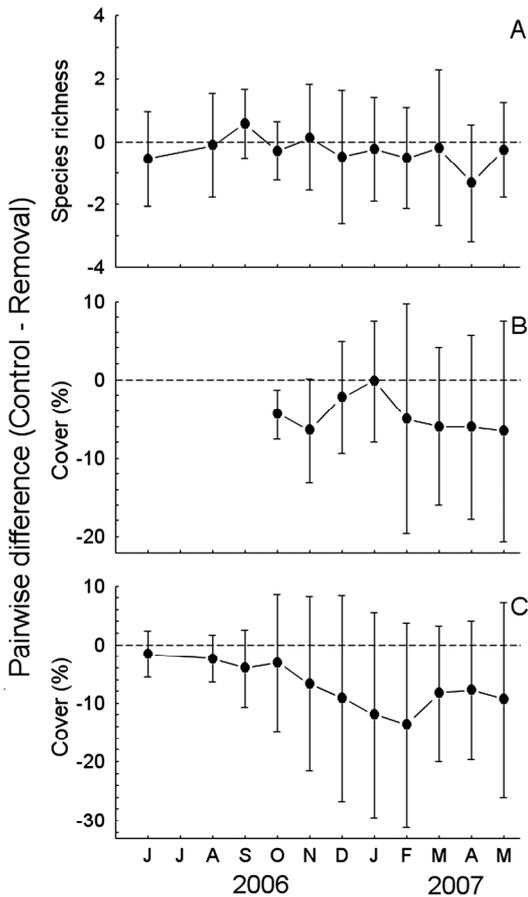


Figure 2. Paired comparison of the taxonomic richness (A), percent cover of *Lissodendoryx isodictyalis* (B) and *Styela plicata* (C) between the control and *D. perlucidum* removal plates. Mean difference between the treatments and the 95% confidence interval are indicated. Positive values indicate that richness and percent cover are greater on control than on *D. perlucidum* removal plate. For (B) and (C), only pairs of plates that were both colonized by the species were included.

occupation of secondary substrate (LPK, RMR personal observation), *D. perlucidum* did not smother species that it covered but rather coexisted with them, similar to results found for another widely distributed didemnid, *Diplosoma listerianum* (Lambert and Lambert 1998). Our study, Lambert and Lambert (1998) and a recent review by Bruno et al. (2005) suggest that exclusion of native species through competition is rare, even at small scales. Nonetheless, the congeneric *Didemnum vexillum* has grown over and excluded many species in most areas to

which it has been introduced (Minchin and Sides 2006; Bullard et al. 2007; Osman and Whitlatch 2007; Valentine et al. 2007).

The lack of an effect of *D. perlucidum* at population and community levels may be explained by population dynamics. Fluctuation in abundance of species appears to be an important mechanism for species coexistence, through the periodical liberation of space after the death of colonies (Dijkstra and Harris 2009). On control plates, we found peaks of *D. perlucidum* abundance (when its cover was > 50%) followed by abrupt declines in cover, without any apparent seasonal pattern. Also, coverage on control plates was low (< 35% in any month) while recruitment was high in the removal treatment. These trends suggest that either colonies have short lifetimes or they may be controlled by predation or some other density dependent process. Many ascidians have life cycles with degenerative phases and abrupt population declines (Turon and Becerro 1992). While decline in *Didemnum vexillum* was associated with a rapid drop in water temperature (< 15°C) (Valentine et al. 2007), *D. rodriguezii* colony size decreased during the summer with an increase in water temperature (Ritzman et al. 2009) in an area near the present study.

Rapid occupation of free substrates, as described for other ascidians (Berman et al. 1992; Bram et al. 2005; Nydam and Stachowicz 2007), is also an important characteristic of invasive potential (Sakai et al. 2001). The invasive *Botrylloides violaceus* Oka, 1927 quickly colonizes primary space in early successional communities and secondary space in established communities along the Atlantic coast of North America (Berman et al. 1992 - *B. violaceus* cited as *B. diegensis*). In the present study, available substrate (either primary or secondary) was often colonized by *D. perlucidum*, which suggests, along with its large reproductive output (Kremer et al. 2010), that *D. perlucidum* may easily become invasive. Yet, neither reproductive effort nor colonization ability were reflected in its coverage of experimental plates which is consistent with low competitive ability, as reported by Dias (2008). This result was surprising, given that colonial ascidians may often be dominant competitors in fouling communities (Nandakumar et al. 1993) and other introduced colonial species, such as *Didemnum vexillum*, often dominate and may occupy 90% of the space in fouling communities (Bullard et al. 2007).

Some evidence suggests that predation may have controlled *D. perlucidum* in this experiment, causing low cover even on control plates. In another experiment with plates forming sandwiches, in which the inside was available for colonization but not accessible to predators, *D. perlucidum* was often found in and dominating the protected side, while nearly absent on the exposed side (Bornancin, unpublished data). In an oyster culture, *D. perlucidum* dominated the internal (protected) shelves of the lantern nets used in the culture, but was nearly non-existent on the exposed side of the bottom shelf (Rocha et al., unpublished data). Predation may be an important control of the invasive potential of some species (Osman and Whitlatch 1998; Sax et al. 2007) and therefore further experimental study must be carried out to understand how it may limit *D. perlucidum* and other potentially invasive species.

Timing of substrate exposure and identity of initial colonizers may also be important in understanding invasive potential (Osman and Whitlatch 1995a, b; Nandakumar 1996; Stachowicz et al. 2002a; Kang et al. 2005). We began our experiment in March, which was subsequently discovered to be the end of the greatest recruitment of *D. perlucidum* (Kremer et al. 2010). If the experiment had been initiated earlier in the beginning of summer, in December, the results may have been different. However, the experimental method should still have detected a difference between treatments even if not at the peak of recruitment, so we feel that timing is not a complete explanation of the surprising lack of trends in this study.

In conclusion, we find that *D. perlucidum* did not pose a threat for communities in this study. This is in agreement with the observation that nearly half of the studies on exotic species found no detectable effect on any parameter studied (Bruno et al. 2005). Yet, in contrast, a few other didemnids, either introduced or native, are exceptions to this trend and are known to have great potential for exponential growth and space dominance (Bak et al. 1996; Oren and Benayahu 1998; Minchin and Sides 2006; Bullard et al. 2007). Thus, these species may also benefit from changes in both natural and artificial environment (Witman and Smith 2003). Some species may switch from being innocuous to becoming a threat due to small modifications in biotic and abiotic conditions (Stachowicz et al. 2002b; Grosholz 2006; Gittenberger 2007). *Didemnum perlucidum* has already demonstrated

this capacity (rapid growth in artificial substrates) in other places in Brazil (Lotufo 1997; Rocha et al., unpublished data).

Clearly, invasive ability is complex and for the reasons described here, more study is needed to understand when and why *D. perlucidum* may become dominant - and when not, how it is controlled. Also, this species has not yet been found on natural substrates in southern Brazil and it is interesting that when found on artificial substrates, the community comprises mainly nonindigenous species, such as *Styela plicata*, many barnacle species and *Bugula neritina* and this community is in constant flux. The dominant species of the nonindigenous community is often that which has the greatest reproductive effort at the moment (Kremer, unpub. data). Thus, constant monitoring of *Didemnum perlucidum*, and other potentially invasive species, is recommended on both natural and artificial substrates in southern Brazil. Only then can we understand invasion dynamics, and use that information to avoid disastrous consequences to natural marine communities.

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