

**Edson Aparecido Vieira Filho**

**“Efeitos da predação, recrutamento e eventos de perturbação na  
estruturação de comunidades incrustantes marinhas do  
sublitoral subtropical.”**

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sublitoral subtropical”**

Este exemplar corresponde à redação final da tese defendida pelo(a) candidato (a) <u>EDSON APARECIDO VIEIRA FILHO</u> <u>A. V. F.</u> e aprovada pela Comissão Julgadora.
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Orientador: Prof. Dr. Augusto Alberto Valero Flores  
Co-Orientadora: Profa. Dra. Fosca Pedini Pereira Leite

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Augusto Alberto Valero Flores [Orientador]

Alexander Turra

Fabiane Gallucci

Antônia Cecília Zacagnini Amaral

Gustavo Fernandes Camargo Fonseca

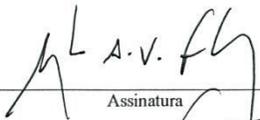
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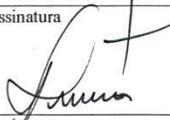
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**BANCA EXAMINADORA**

Prof. Dr. Augusto Alberto Valero Flores (Orientador)

  
Assinatura

Prof. Dr. Alexander Turra

  
Assinatura

Profa. Dra. Fabiane Gallucci

  
Assinatura

Profa. Dra. Antônia Cecília Zacagnini Amaral

\_\_\_\_\_  
Assinatura

Prof. Dr. Gustavo Fernandes Camargo Fonseca

\_\_\_\_\_  
Assinatura

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*'I read somewhere how important it is in life  
not necessarily to be strong, but to feel strong'*

*Christopher McCandless*

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## RESUMO

Os processos que afetam o desenvolvimento e estruturação de comunidades incrustantes é um tema central em Ecologia. Entender como distúrbios naturais e antrópicos interagem com esses processos, e identificar os mecanismos responsáveis por sua recuperação, ou pela transferência da comunidade para outro estado de equilíbrio, são questões muito importantes, principalmente devido às diversas modificações recentes promovidas pela ação humana. Numa primeira fase, investiguei experimentalmente como as comunidades incrustantes do sublitoral são afetadas por diferentes pressões de predação, exclusão de predadores e diferentes taxas de recrutamento. Observei um fraco efeito da predação como um todo, não havendo relação entre o padrão de riqueza e a estrutura das comunidades com o padrão de pressão de predação. Além disso, a exclusão de consumidores teve efeitos pontuais, tanto para riqueza quanto para a estrutura da comunidade. O padrão de recrutamento mostrou grande associação com o padrão de riqueza, entretanto esse fator também não foi importante para explicar a variação na estrutura da comunidade. A grande variação em pequena escala da estrutura das comunidades indica que esses são processos locais, que podem não ser perceptíveis em uma escala maior, onde outros processos atuam. Interessado no efeito de distúrbios na estruturação de comunidades, simulei uma alteração no regime de predação e recrutamento, transplantando comunidades em desenvolvimento entre locais com valores extremos desses fatores. No geral, as comunidades transplantadas ficaram mais similares aos destinos do que à origem, independente da direção do transplante e no momento em que ele foi feito. Esse resultado evidencia a importância de condições pós-distúrbio na trajetória da comunidade em direção a um novo estado de equilíbrio. Entretanto, apesar de mais similares, elas não ficaram idênticas ao destino, evidenciando a existência de um legado dos momentos iniciais de desenvolvimento.

## **ABSTRACT**

Processes affecting the development and the structure of incrusting communities are of central importance in Ecology. Understanding how natural or anthropogenic disturbance interact with such processes, and identifying the mechanisms by which communities recover, or otherwise develop to new stable states, is a very important question, particularly at present, after increased habitat modifications promoted by humans. I had first investigated, experimentally, how incrusting communities are affected by different predation pressure, exclusion of consumers and different recruitment rates. I observed a weak overall effect of predation and no relation between richness and levels of predation pressure. Besides that, the exclusion of predators showed only local effects, either on species richness or community structure. Recruitment rate was correlated to richness, but also it was not important to explain variations in community structure. The large variation at a very small scale, within localities, indicates that predation and recruitment act locally, and their effects may not be noticed in a large scale, where other processes are important. I was also interested in the effect of disturbance in the structure of communities, so I simulated an alteration of predation and recruitment regimes by transplanting developing communities between localities with extreme values of these factors. Overall, transplanted communities became more similar to destination, regardless of direction and moment of transplant. This result shows an important role of post-disturbance conditions guiding community development towards a new equilibrium state. However, although similar, transplanted communities did not become equal to destination, evidencing the existence of some legacy from early moments of development.

## INTRODUÇÃO GERAL

Como ocorre a estruturação de comunidades e como elas resistem ou se recuperam frente a distúrbios são questões de grande interesse em ecologia (Dayton, 1971; Menge e Sutherland, 1976, 1987; Osman et al., 2010a,b). Entender como as comunidades se organizam é importante frente às grandes alterações provocadas por ações humanas. Quanto mais informações pudermos acumular sobre os processos que guiam a trajetória de comunidades, melhor poderemos prever as consequências da ação antrópica e melhores serão as ações que visam conservar ou recuperar áreas degradadas (Osman et al., 2010a,b). Dentre as comunidades mais impactadas por ações antrópicas atuais estão as comunidades marinhas costeiras, cujos processos regulatórios são diversos, complexos e ainda pouco conhecidos (Dayton, 1971; Menge e Sutherland, 1987). Nesse ambiente, comunidades de organismos incrustantes são reguladas tanto por fatores internos como interações competitivas, como por fatores externos como pressão de predadores, taxa de recrutamento e distúrbios (Dayton 1971; Connell, 1972; Baynes, 1999). O balanço entre esses fatores pode influenciar a estrutura das comunidades durante o seu desenvolvimento, bem como sua resistência e resiliência a perturbações externas (Menge, 1978; Menge e Sutherland, 1976, 1987).

Dentre as interações bióticas, o impacto de predadores sobre a organização das comunidades é uma das questões mais investigadas no ambiente marinho. A predação pode afetar direta e indiretamente o desenvolvimento e estrutura da comunidade (Paine, 1966; Menge e Sutherland, 1976, 1987; Menge et al., 1986; Osman e Whitlatch, 2004). Como efeitos diretos, os predadores podem diminuir a abundância tanto de adultos como recrutas (Stoner, 1990; Osman e Witlatch, 1995; Osman e Witlatch, 2004; Nydam e Stachowicz, 2007), e, conseqüentemente, resultar na redução da riqueza e diversidade (Day, 1977). Esse impacto é evidenciado no meso e infralitoral de áreas tropicais, onde a intensidade de predação é maior do que em regiões de clima temperado, principalmente devido à diversidade de predadores, com alta mobilidade e localização

visual das presas (Bertness et al., 1981; Menge e Lubchenco, 1981; Freestone et al., 2011). Indiretamente, predadores podem contribuir para um aumento da diversidade, principalmente se forem seletivos e sua ação for direcionada a presas que monopolizam o espaço (Paine, 1966; Day, 1977). A retirada dos melhores competidores resulta na liberação de espaço, o qual pode ser colonizado por espécies com menor habilidade competitiva, levando a um aumento da diversidade (Paine, 1966; Connell, 1972, 1978; Day, 1977; Russ, 1980; Osman e Whitlatch, 2004). Os trabalhos de Russ (1980), Osman e Whitlatch (2004) e Vieira et al. (2012) mostraram que na presença de predadores, alguns grupos de organismos incrustantes como ascídias, animais de corpo mole e briosos monopolizadores de espaço, tem sua abundância e riqueza diminuídas, o que promove liberação de espaço e possibilita a ocorrência de outras espécies como briozoários, ou pelo menos uma modificação da identidade dos organismos que compõem a comunidade. Resultados como estes deram origem a importantes teorias como a de espécie-chave (Paine 1966, 1969) e nível intermediário de perturbação (Connell, 1978).

Apesar do forte efeito de predadores em suas comunidades, conforme amplamente constatado em diversos habitats e regiões, vários trabalhos recentes demonstram que esses efeitos podem estar ausentes (Sams e Keough, 2007), restritos a algumas espécies (Connell, 2001; Brazão et al., 2009) ou ainda ser muito fracos e não generalizados (Vieira et al., 2012). Várias características podem contribuir para a não detecção de efeitos de predação. A alta diversidade de presas e predadores aumenta a redundância funcional de espécies (Rosenfeld 2002), e, portanto, também o número de interações possíveis, o que enfraquece a importância relativa de cada interação (Duffy, 2002; Hillebrand e Cardinale, 2004; Duffy et al., 2007; Edwards et al., 2010). Assim, a retirada de alguns consumidores ou presas não necessariamente resulta em uma reestruturação da comunidade, podendo haver um tamponamento da biodiversidade (Hillebrand e Cardinale, 2004; Byrnes et al., 2006; Ives e Cardinale, 2004). Além disso, o efeito de consumidores

pode apresentar intensidade variável (Navarrete e Berlow, 2006), ou gerar padrões a escalas espaciais e temporais distintas (Menge e Lubchenco 1981). Por exemplo, efeitos substanciais à pequena escala podem não ser percebidos à grande escala (Shurin e Allen, 2001).

Outro processo que pode moldar o perfil da comunidade é o recrutamento, uma vez que este tem grande influência nas espécies que ocorrerão na comunidade e na abundância dos adultos (Underwood e Fairweather, 1989; Minchinton e Scheibling, 1991; Sih e Wooster, 1994; Palmer et al., 1996; Connolly e Roughgarden, 1999; Chesson, 2000; Arellano e Young, 2011). Áreas onde o recrutamento é intenso, geralmente apresentarão um grande número de adultos e conseqüentemente menos espaço livre (Menge e Sutherland, 1987; Menge, 1991; Connolly e Roughgarden, 1998; Connolly et al., 2001). Assim como a predação, o recrutamento também pode ter um efeito variável, variando de intensidade tanto no espaço como no tempo (Stobutzki, 2001; Sams e Keough, 2012). Espacialmente, essa variação está atrelada ao fato de muitos organismos incrustantes produzirem larvas de curto período planctônico, o que causa uma retenção de novos recrutas da mesma espécie nas proximidades dos adultos (Olson, 1985; Sammarco e Andrews, 1988; Connolly e Roughgarden, 1999). Temporalmente, picos de recrutamento massivo de algumas espécies podem levar a grandes alterações da estrutura da comunidade, e inclusive afetar ou anular efeitos de outros processos como a predação (Menge e Sutherland, 1987). Em locais em que a taxa de recrutamento é muito alta, os efeitos de consumidores podem ser mascarados, uma vez que todo espaço liberado é rapidamente ocupado por novos recrutas (Sams e Keough, 2007). Assim, o suprimento larval pode alterar a importância da predação na estruturação de comunidades (Cooper et al., 1990; Palmer et al., 1996). Em situações com grande disponibilidade de propágulos, o recrutamento só não regulará a comunidade quando a ação de predadores for totalmente ou majoritariamente voltada para os jovens recrutas, o que é comum para pequenos predadores como juvenis de gastrópodes e caranguejos (Osman et al., 1992; Nydam e Stachowicz, 2007).

A interferência provocada por distúrbios naturais ou antrópicos sobre o recrutamento e a predação pode alterar significativamente as propriedades de uma comunidade. Distúrbios são naturalmente comuns no ambiente marinho devido à ação das ondas e desalojamento de organismos, o que libera espaço e provoca uma grande alteração na dinâmica de sucessão (Menge e Sutherland, 1976, 1987; Dayton, 1971). Atualmente, a ação antrópica vem direta ou indiretamente gerando perturbações expressivas nas comunidades. Negativamente contribui para o aumento da temperatura média dos oceanos e para a diminuição do estoque de peixes, que são os predadores mais comuns de comunidades incrustantes em ambientes costeiros. Por outro lado, a criação de estruturas artificiais como pilares de píers e estruturas flutuantes promove a geração de novos habitats potencialmente colonizáveis por organismos incrustantes (Osman et al., 2010a,b). Frente a essas alterações, as comunidades podem resistir, sofrer alterações e retornar rapidamente ao estado original, ou se alterar profundamente e seguir uma nova trajetória que resultará em um novo estado alternativo de equilíbrio (Holling, 1973; Connell e Sousa, 1983; Sutherland, 1990; Gunderson, 2000; Beisner et al., 2003). Comunidades que retornam rapidamente a estados anteriores são caracterizadas como resilientes, mas é comum, principalmente quando o distúrbio é muito severo, que essas comunidades não consigam retornar ao seu estado original e alcancem outros estados de equilíbrio (Sutherland, 1990; Beisner et al., 2003). O que regula a volta ou não é uma série de características tanto ambientais como biológicas (Franklin and MacMahon, 2000; Nyström and Folk, 2001; Golinsky et al., 2008) que funcionam como uma forma de memória ecológica, garantindo o retorno ao estado pré-distúrbio (Bengtsson et al., 2003).

Interessado nessas questões, busquei investigar nesse trabalho como alguns processos ecológicos afetam a estruturação de comunidades incrustantes marinhas e como estas se reorganizam após distúrbios. No Capítulo 1 avaliei como a ação de predadores e a disponibilidade de recrutas afetam a estruturação de comunidades incrustantes, em duas escalas espaciais, de

poucos metros a dezenas de quilômetros. Além disso, abordei no Capítulo 2 como essas comunidades incrustantes se comportam após sofrerem um distúrbio, que simulou a diminuição ou aumento da pressão de predação e da taxa de recrutamento.

## OBJETIVOS

Esta dissertação teve como objetivo geral investigar o efeito de importantes processos no desenvolvimento e estruturação de comunidades marinhas incrustantes do sublitoral, e como essas comunidades se comportam e se desenvolvem após distúrbios. Especificamente, o trabalho teve como objetivos:

- Capítulo 1. Investigar como comunidades incrustantes se desenvolvem e se estruturam frente a diferentes pressões de predação por grandes predadores (peixes e caranguejos) e taxas de recrutamento, tanto à pequena (dentro de cada local, separação por metros) como à grande escala (entre locais separados por quilômetros).
- Capítulo 2. Investigar como comunidades incrustantes se desenvolvem e se estruturam após transplantes entre locais com características extremas, simulando um distúrbio relacionado à queda ou aumento na pressão de predação e taxa de recrutamento.

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## **CAPÍTULO 1**

# **EFEITO DEPENDENTE DE ESCALA DA PREDACÃO POR PEIXES E RECRUTAMENTO EM COMUNIDADES INCRUSTANTES MARINHAS AO LONGO DE UMA COSTA SUBTROPICAL**

**SCALE-DEPENDENT EFFECTS OF FISH PREDATION AND RECRUITMENT IN  
MARINE INCRUSTING COMMUNITIES ALONG A SUBTROPICAL  
COASTLINE**

**ABSTRACT**

Predation effects on marine communities have been largely studied since the 1960'. Although broadly observed as a key process in community development and structure, recent studies have shown null, weak or either confusing effects of predation. In tropical areas, the absence of effects can be due to weak interactions, resulting from the action of a diverse assemblage of prey and consumers, or even due to the dampening effect of high recruitment rates. The effects of variable predation pressure and recruitment rate in the structure of marine incrusting communities were investigated in subtropical localities at both a large (unit km) and a small scale (unit to tens of m). We observed no effect of predation pressure, and the exclusion of predators affected species richness and community structure only in a few situations. Recruitment rate was correlated to richness, but it did not exert an apparent effect on community structure. There was, however, very high variability of richness and community structure inside each locality (small-scale). The low effect of predation, when observed, was associated to this small-scale variation. This localized effect, probably coupled with localized variations in recruitment due to a large larval retention from patchy adult populations, cannot be perceived at the large-scale. Yet, diffused effects can be very important to maintain diversity and can contribute to system resilience against disturbance.

## INTRODUCTION

Predation has been largely studied in ecological communities and was proved to be an important interaction that shapes the structure of marine assemblages (Menge and Sutherland, 1976, 1987; Menge et al., 1986; Osman and Witlatch, 2004). By gathering observational and experimental data, researchers have shown that consumers may limit the abundance of adults and recruits of specific prey (Stoner, 1990; Osman and Witlatch, 1995; Osman and Witlatch, 2004; Nydam and Stachowicz, 2007), generate and maintain diversity (Paine, 1966; Russ, 1980; Osman and Witlatch, 2004) and influence ecosystem functioning (Pace et al., 1999; Duffy, 2002; Worm and Duffy, 2003; Wojdak, 2005). With these informations, classical theories, such as keystone species (Paine, 1966) and intermediate disturbance level (Connell, 1978), were formulated and validated with several empirical data.

Effects of predators in marine systems were broadly observed, from the intertidal zone, as the classic studies of Connell (1961) and Paine (1966, 1969), to more recent studies from deep vent communities (Micheli et al., 2002). Even omnivorous consumers can regulate marine communities, as observed by Christofolletti et al. (2010) in experiments selectively excluding a small omnivorous crab. Also, a latitudinal pattern has been proposed, with predation increasing in intensity (Bertness et al., 1981; Menge and Lubchenco, 1981; Sandford et al., 2003) and effectiveness toward the tropics (Schemske et al., 2009; Freestone et al., 2011). Menge and Lubchenco (1981) observed a continuous and intense regulation of the incrusting community by consumers at Panamá (tropics), contrasting to New England (temperate area). They attribute this pattern to the effect of a diverse fauna of fast-moving tropical consumers, mostly fish, which visually find their prey and are active all year around. Opposite traits are observed for temperate consumers, such as sea stars and gastropods, which are slow predators, not visually oriented, and whose effects are strongly seasonal.

However, during the last decades, with the rising of new research groups around the world, many other studies had reported variable (Witman and Sebens, 1992) or no effects of predation, either on a set of prey species (Connell, 2001; Brazão et al., 2009), or in the whole community (Sams and Keough, 2007; Vieira et al., 2012), including other aquatic environments, like streams (Dahl and Greenberg, 1996 and references there in). The latitudinal pattern has also been challenged, with some studies showing no effects of predation in tropical areas, even among assemblages where several species of fish and invertebrate consumers interact (Vieira et al., 2012). Therefore, it is necessary to test processes that, coupled with predation, may affect community structure (Connell, 2001; Nydam and Stachowicz, 2007).

One important tropical characteristic that can blur eventual latitudinal patterns is the great diversity of both consumers and prey (Duffy, 2002; Hillebrand and Cardinale, 2004). Several studies show that the strength of trophic interactions and the effects of predators become weaker as diversity increases (Duffy et al., 2007; Edwards et al., 2010). In more diverse assemblages of consumers, intra-guild predation is common (Fink and Denno, 2004, 2005), competition is intense (Dahl and Greenberg, 1996) and several species become generalists (Duffy et al., 2007), thus weakening trophic interactions and diluting the effects of predators. Besides that, in more diverse prey assemblages, consumers exhibit low preference (Ostfeld and LoGiudice, 2003; Kessing et al., 2006), predation pressure on each species is low (Steiner, 2001; Duffy et al., 2007), and prey are frequently well defended against predators (Duffy, 2002; Duffy et al., 2007; Edwards et al., 2010). Diversity may thus act like a buffer, further weakening trophic interactions (Steiner, 2001; Hillebrand and Cardinale, 2004), and promoting functional redundancy of both consumers and prey (Clarke and Warwick 1998; Nyström et al., 2000; Rosenfeld, 2002). Therefore, exclusion of predators or prey in diverse systems may not result in structural and functional changes of the whole community (Byrnes et al., 2006; Ives and Cardinale, 2004).

Despite of being generally neglected, recruitment may strongly affect prey-predator interactions (Connell, 2001) and also shape important attributes of marine communities (Underwood and Fairweather, 1989; Menge, 1991; Minchinton and Scheibling, 1991; Sih and Wooster, 1994; Palmer et al., 1996; Connelly and Roughgarden, 1999; Chesson, 2000; Arellano and Young, 2011). Recruitment rate may modulate the abundance of prey and dampen predation effects. Extremely high recruitment rate would totally rule out prey removal because new individuals are constantly occupying free space (Sams and Keough, 2007). Even when moderate, recruitment can be more important than predation in regulating community structure (Cooper et al., 1990; Palmer et al., 1996).

As observed by Navarrete and Berlow (2006), variation in the strength of predator-prey interactions can lead a community to stability by enhancing resilience. Because their distribution is usually patchy within sites, mobile and generalist fishes can have a variable effect on prey in a scale of meters but may not be noticed in the large scale of kilometers (Shurin and Allen 2001). As predation (Berlow, 1999), recruitment can also vary at relatively small spatial scales (Sams and Keough, 2012). Most encrusting marine species present mechanisms for larval retention and produce short-living propagules (minutes to hours) with very little dispersal potential, which leads to increased local recruitment (Olson, 1985; Sammarco and Andrews, 1988; Connelly and Roughgarden, 1999). These variable effects of predation and recruitment can lead to no overall large-scale effects, but to strong small-scale patterns within a given locality.

A previous study on the dynamics of shallow subtidal assemblages developing on artificial substrates in southeastern Brazil showed that the impact of predators was not important to shape community structure after a few months, and that the exclusion of consumers did not affect species richness, although community composition differed between exposed and protected panels (Vieira et al., 2012). These results motivated us to investigate how variable consumers pressure can affect

predation effects on the structure of incrusting communities from large (among sites separated by km) to very small scales, within each site. Because we also have a substantial variation in recruitment rate among different localities, we also examined how recruitment can mediate prey-predation effects in the structure of these marine assemblages.

## MATERIAL AND METHODS

### Study area

We conducted this experiment at the São Sebastião Channel, SP, southeastern Brazil, from December 2010 to April 2011. Tidal and wind currents may be very intense in the middle of the channel but hydrodynamism close to shore, along both margins, is much reduced. Most of the channel is also relatively sheltered from wave action. Thus, the advective potential in the area is likely low and fouling assemblages developing in hard substrates are expected to be a result of reproductive activities of invertebrates and macroalgae nearby. Along the channel we selected four localities: Curral Beach (23°51'37.80''S / 45°25'49.63''W), Feiticeira Beach (23°50'45.19''S / 45°24'36.29''W), Figueira Beach (23°44'55.43''S / 45°24'36.11''W) and Yacht Club Ilhabela (23°46'26.95''S / 45°21'21.26''W) (Fig. 1). These sites were piers or marinas that were at least 3 m deep, allowing us to attach plate sets at a 1.5 m depth and at least 1.5 m above the bottom, since most of the encrusting organisms have filter-feeding habits and proximity to sand could be a problem.

In previous surveys we observed that all localities presented taxonomically diverse communities, composed by sessile organisms that were observed growing at the pier and marina structures and at the natural substrata nearby. The proportion of ascidians, sponges, bryozoans, polychaetes, hydrozoans, bivalves and barnacles covering the natural and artificial substrata visually varied from site to site. These observations were posteriorly confirmed by our results. We

could also observe different kinds of predators, mainly benthic-feeding fishes like *Abudefduf saxatilis* (Linnaeus, 1758), *Stephanolepis hispidus* (Linnaeus, 1766), *Diplodus argenteus* (Valenciennes, 1830) and *Malacoctenus delalandii* (Valenciennes, 1836). Invertebrate predators were also common varying from highly mobile small (*Microphrys bicornutus*) and large spider crabs (*Mithrax hispidus*), to more sedentary consumers such as juvenile and adult gastropods of the species *Cymatium parthenopeum* (Von Salis, 1793).

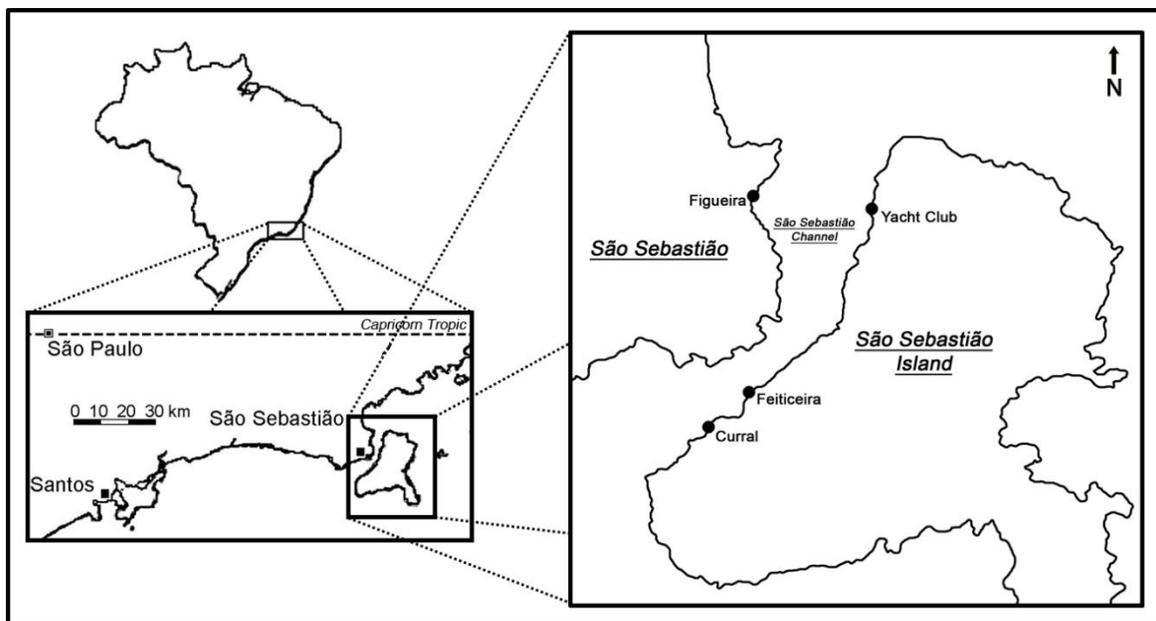


Figure 1. Experimental localities at São Sebastião Channel, SP, Southeastern Brazil

### Estimation of predation pressure

To have an overall estimate of predation pressure at each locality, we measured the consumption rate of baits instead of undertaking visual censuses of fishes, because counting the number of these consumers during a period of time do not necessarily provide a good estimate of predation on encrusting organisms. We evaluated predation pressure using carrageenan baits fixed to PVC plates as to mimic consumption of encrusting organisms by an array of possible predators. This method is commonly used in chemical bioassays to assess the deterrent effect of chemicals by

comparing treated and control baits (Fenical & Pawlik 1991). Baits were prepared using a mixture of 0.312 g carrageenan (Sigma C-1013 type I), 2.5 mL of canned mashed tuna muscle in aqueous solution (fish attractive) and 7.5 mL of distilled water. The mixture was brought to boiling into a microwave oven and then stirred vigorously with a glass rod. Then we poured the mixture into a container (3 x 3 x 0.5 cm) over a PVC plate (10 x 10 x 0.2 cm) (Fig. 2A). In order to ensure bait attachment, we glued a screen fabric piece in the plate to increment adhesion (Fig. 2B). After hardening, we kept the baited plates in a refrigerator, for no longer than 10 hours, until the beginning of the experiments.

In each locality we used 7 baited plates attached to pier pilings, which were deployed at a depth of 1.5 m, and 1.5 – 2 m above the bottom, keeping a minimum distance of 1 m from each other. This set up was the same to that used to assess the effects of predation on communities, as an attempt to provide adequate site-specific estimates of predation pressure at the experimental sites.

After 2 hours ( $\pm 0.1$ ), we removed all plates and visually evaluated the loss of mass, estimating the percentage consumed by fishes as in Gama et al. (2002) (Fig. 2B). The percentage of bait consumed, standardized by the time it remained in the field, was used to estimate consumption rate.

The experiment was replicated four times in a year (June and August 2010, and April and May 2011), as to test temporal consistency of eventual spatial patterns. The first two surveys were conducted before and the later two were conducted during the experiment, and these dates were randomly chosen due to logistic convenience. Data were analyzed using a mixed two-way ANOVA model. Consumption rates were thus compared among localities (fixed factor; four levels) and over time (random factor; four levels). The arcsine transformation (Zar, 1999) did not solve variance heterogeneity among groups. However, because the experiment was balanced and replication high,

analyses were robust allowing safe interpretations of results. *Post-hoc* pairwise comparisons were undertaken using the Tukey test.

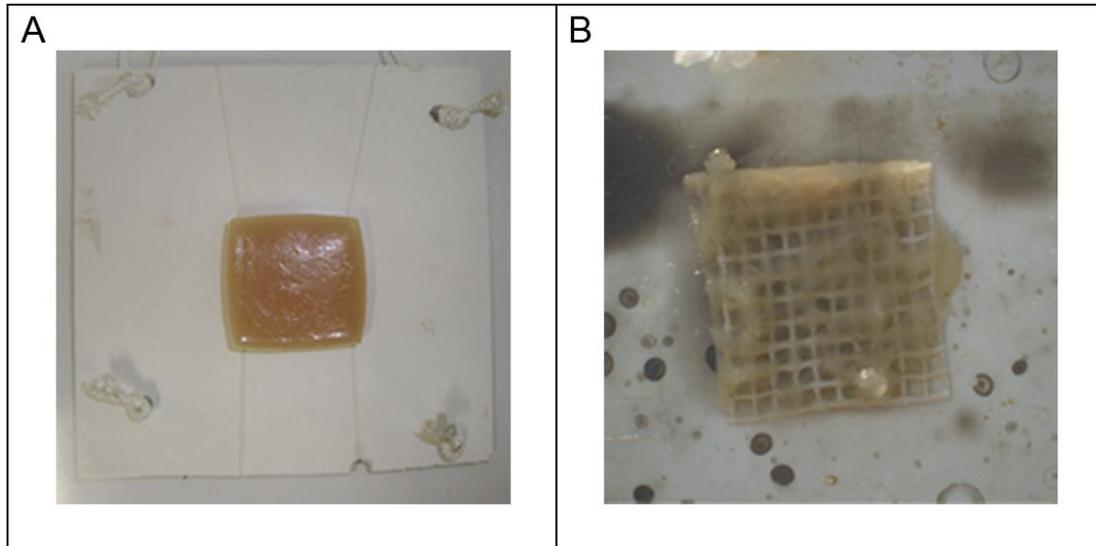


Figure 2. A) Carrageenan bait, attached to a PVC plate, used to estimate predation pressure. B) Detail of a bait partially consumed showing the meshed screen fabric used to enhance bait adhesion.

#### Estimation of recruitment rate

Because recruitment can swamp effects of predation (Cooper et al., 1990; Palmer et al., 1996; Chesson, 2000; Sams and Keough, 2007) and regulate community structure, we designed an experiment to compare recruitment rates among localities. Here we use recruitment as the new recent individuals settled in a period of days. In each locality six PVC plates (10 x 10 x 0.2 cm), covered with roughened acetate sheets were disposed in the field, following the procedure above. After three days, we removed all plates and scanned them under a dissecting microscope to quantify the number of recruits per taxonomic group (ascidians, sponges, bryozoans, soft tube polychaetes, hydrozoans, barnacles, serpulids and bivalves).

We repeated the procedure two times (April and May of 2011), and the dates were randomly chosen by logistic convenience. Then we compared the number of recruits, using the same ANOVA model as for estimating predation pressure, but using only two levels for the factor

‘time’. Data were  $\log(x+1)$  transformed but, again, homoscedasticity could not be achieved. This should however not affect results of the analysis for the reasoning above. *Post-hoc* pairwise comparisons were conducted using the Tukey test. We also used relative abundance data for recruits of main taxonomic groups to describe the settling community at the different sites. We performed the test from a matrix (local replicates  $\times$  relative abundance of main taxa) using Bray-Curtis distances among replicates in the software Primer (Clarke and Gorley, 2006). These data were arcsine transformed and used to construct an nMDS plot (Clarke, 1993), which provided a general overview of similarities and was used for clarifying relationships among localities. The differences among localities, and over time, established a priori in nMDS, were analyzed using a PERMANOVA test with 999 permutations (formerly NP-MANOVA; Anderson, 2001). This analysis is an appropriate and intuitive form of multivariate ANOVA that enables direct additive partitioning of variance and the use of any semi metric distance measure (Anderson, 2001; McArdle and Anderson 2001). The model used in PERMANOVA was the same of the ANOVA model described above. Significant sources of variation were subjected to pairwise comparisons with 999 permutations.

#### *Predation exclusion experiment*

*Experimental design* – We conducted a predator exclusion experiment in order to assess how predation can affect the development of the encrusting community at localities with contrasting predation pressure and recruitment rate. We used 72 roughened PVC plates (10 x 10 x 0.2 cm) for community establishment at each locality. Half of them were covered by plastic screen cages (10 x 10 x 6 cm, 1 cm mesh), avoiding the presence of large predators (Fig. 3A), and the remaining plates were covered by open cages, allowing consumption by predators of any size and controlling possible cage artifacts (Fig. 3B). We didn’t use open plates without any cage since previous tests

already showed us that this kind of treatment were similar in community structure and abundance of most groups to partially caged plates (Vieira et al., 2012). To avoid cage recovering by incrusting organisms, which leads to a decreased water flow inside the cage, we periodically cleaned all cage sides with a stainless brush.

Plates were distributed in six PVC back panels (50 x 50 x 0.5 cm), each one containing six protected and six exposed plates in random positions, at least 3 cm apart from each other (Fig. 3C). In each area, panels were suspended horizontally about 1.5 m below the MLW and 2 m above sea bottom, spaced at least 1.5 m from each other and fixed by cables to the artificial pier or marina structures. Experimental plots were set at the downward facing surface of each plate to avoid problems of sedimentation and algal growth.

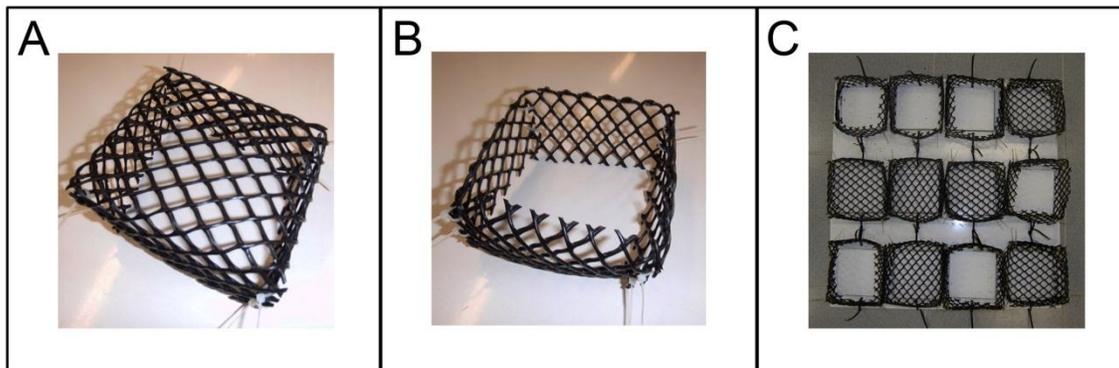


Figure 3. A) Closed and B) open screened plastic cages used in the predator exclusion experiment, and C) example of a random arrangement of plates in a panel.

Thirty days after the beginning of the experiment (survey one; January 2011), we removed two protected and two exposed plates of each panel, at each area, and took them to the laboratory. We scanned each plate under a dissecting microscope and identified all the encrusting organisms to the lowest possible taxonomic level. We then photographed plates for later quantification of the area covered by each taxonomic group using the CPCe image analysis software and a grid of 100 intersections (Kohler & Gill 2006). Because colonial organisms, such as ascidians, bryozoans and sponges, could monopolize settlement plates through clonal reproduction, we used the area covered

by each taxonomic group instead of the number of individuals, to estimate the relative abundance of each taxon (Vieira et al., 2012).

This procedure was repeated 100 days after the beginning of the experiment (survey two; April 2011). At this second survey we removed all remaining plates (three protected and three exposed, from each panel) from all six panels, except from Curral, where storms torn support cables and we had to exclude this locality from 100-days analyses.

*Data analyses* – We used the data obtained for panels retrieved after 30 days to assess changes in community structure due to contrasting conditions of predation pressure and recruitment rate, and at different spatial scales, among localities separated by unit km and among experimental panels just a few meters apart. In a first analysis, species richness was compared using an ANOVA model with ‘predation pressure’ (PP), as a fixed factor with two levels (high and low); ‘locality’ (LO), random and nested in PP, with two levels at each PP condition; ‘panel’ (PA), random and nested in LO and used as a block, with six levels; and ‘consumer exclusion’ (CE), as a fixed factor with two levels (closed and open cage). *Post-hoc* pairwise comparisons were done using the Tukey test. We also examined the effects of predation on the area covered (abundance estimate) by main taxonomic groups using an nMDS plot performed from a matrix (treatment replicates × percent cover of each taxon) of Bray-Curtis distances among replicates with arcsine transformation of data. We only used taxa that occurred at least in two different replicates. A PERMANOVA procedure, using the same model described above for richness comparisons, was run to verify statistical significance of sources of variation, and all significant differences were compared with a *post-hoc* pairwise comparisons test. The species that most contributed to group sample units (SIMPER<sub>SIM</sub>) and to differences observed among groups (SIMPER<sub>DISSIM</sub>) were obtained by SIMPER analyses. In a

second analysis we used the same model, but rearranging localities by their ‘recruitment rate (RR)’ instead of ‘predation pressure’.

We could not incorporate a test for effects of predation pressure, or recruitment rate, after 100 days in the same overall analysis because proper replication of localities was no longer possible due to the loss of plots at Curral. However, we compared community attributes among the remaining localities to verify whether patterns observed after 30 days were consistent across time, at least for these sites. Species richness was compared using an ANOVA test with ‘locality (LO)’, random with three levels (Feiticeira, Figueira and Yacht Club); ‘panels (PA)’, random nested in LO (PA(LO)) and used as a block, with six levels; and ‘consumer exclusion’, fixed with two levels (closed and open cage). *Post-hoc* pairwise comparisons were done using the Tukey test. Cover area data were first explored in an nMDS plot and the PERMANOVA procedure, using the same model above, was run to test for differences in assemblage structure. All significant differences were compared with a *post-hoc* pairwise comparisons test, and the SIMPER analysis was performed to identify the species that most contributed to observed groups and differences among groups.

## RESULTS

### Characterization of experimental localities

Consumption rate of baits showed a site-specific variation across sampling dates (Table 1). Curral and Figueira always showed a very low consumption rate, never above 3%.hour<sup>-1</sup>. Instead, baits at Feiticeira and Yacht Club were at times largely consumed, but there was large variability through time. Consumption rate was highest in April 2011 at Feiticeira, and in June and August 2010 at Yacht Club (Tukey,  $p < 0.05$  in both cases). These results suggest that Feiticeira and Yacht Club are localities that may sometimes experience substantial predation pressure, which is apparently not the case for Curral and Figueira (Fig. 4).

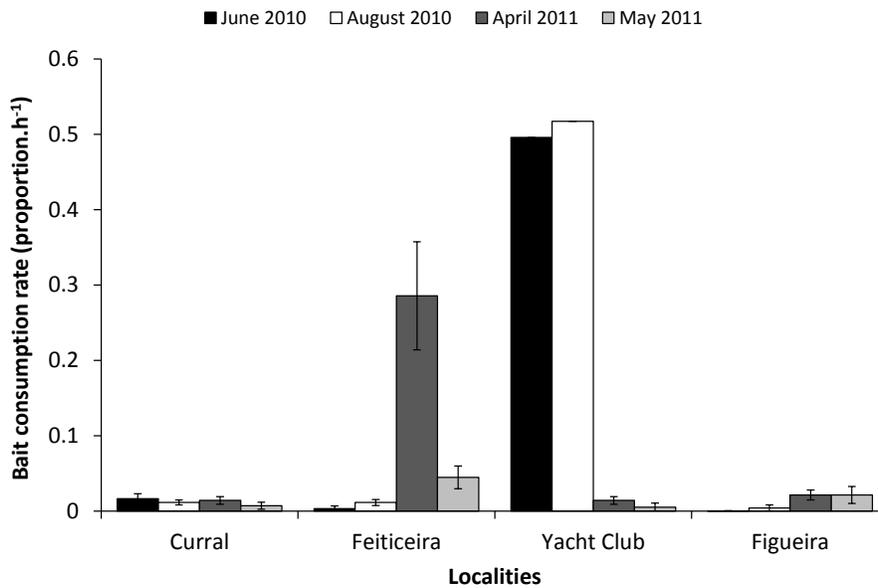


Figura 4. Consumption rate of baits (mean  $\pm$  SE) at Curral, Feiticeira, Yacht Club and Figueira during experimental surveys.

Differences in recruitment rate among localities varied through time (Table 1) and the general pattern was different from predation. In April, recruitment was higher at Curral and Feiticeira and lower at Yacht Club and Figueira (Tukey,  $p < 0.05$ ). In May, the pattern was similar but values for Yacht Club were intermediate (Tukey,  $p < 0.05$ ). Thus, we considered for latter analyses that Yacht Club and Figueira, and Curral and Feiticeira are localities prone to high and low recruitment rate, respectively.

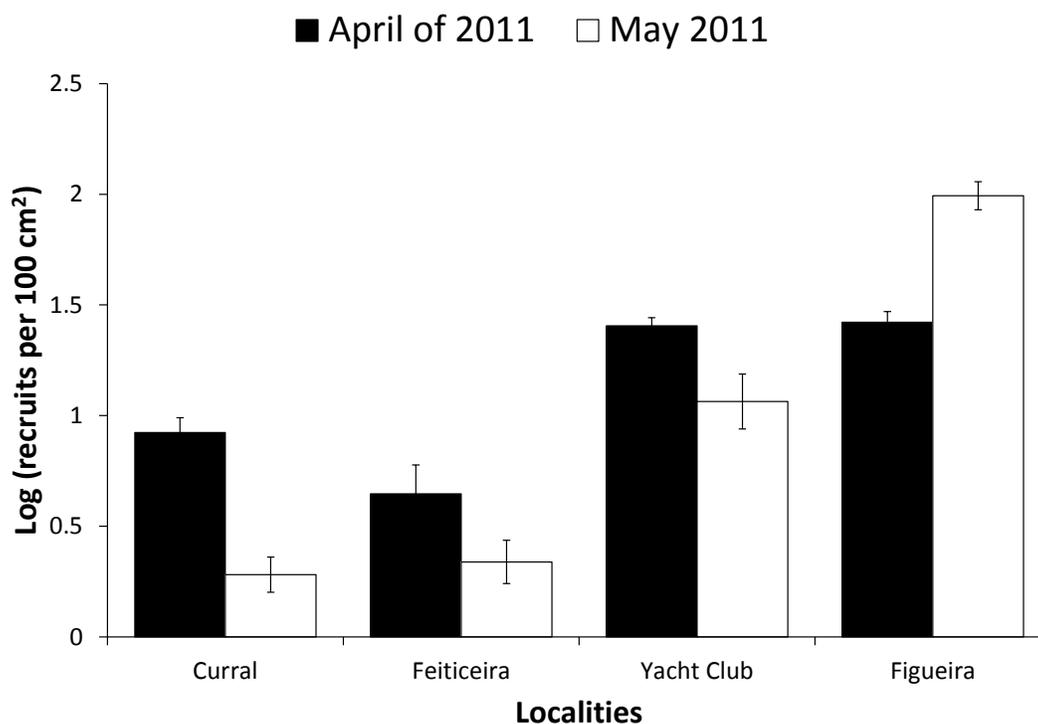


Figure 5. Overall recruitment rate (mean  $\pm$  SE) at Curral, Feiticeira, Yacht Club and Figueira during experimental surveys.

Table 1. Two-way ANOVA summary results of bait consumption rate (predation pressure) and overall recruitment rate according to locality (Curral, Feiticeira, Figueira and Yacht Club) and sampling date (June and August 2010 and April and May of 2011 for bait consumption; April and May 2011 for recruitment rate). *C* = Cochran's *C* test.

Source of Variation	Consumption Rate <i>C</i> = 0.355 ( <i>p</i> < 0.001)				Recruitment Rate <i>C</i> = 0.420 ( <i>p</i> = 0.038)			
	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Locality	3	0.14	0.3	0.826	3	2.98	6.0	0.088
Time	3	0.68	47.9	< <b>0.001</b>	1	0.07	2.0	0.162
Locality x Time	9	0.46	32.5	< <b>0.001</b>	3	0.05	14.7	< <b>0.001</b>
Error	96	0.01			40	0.03		

Experimental localities also differed in the composition of recruits across time (Table 3). Curral and Feiticeira were similar both on April and May (Pairwise test,  $p > 0.05$ ) and formed a single group in the nMDS plot. Although similar on April and May, the interaction with time was probably due to these locations being more similar on May ( $p = 0.992$ ) than on April ( $p = 0.616$ ) (Fig. 6). Their recruits were mostly ascidians (Curral – SIMPER<sub>SIM</sub>: 95.3%, Feiticeira – SIMPER<sub>SIM</sub>: 89.5%), with barnacles, sponges, bivalves, soft tube polychaetes and serpulids being rarely observed. Figueira and Yacht Club formed distinct groups in the nMDS plot (Pairwise test,  $p < 0.05$ ). Recruits at Figueira were basically encrusting bryozoans (SIMPER<sub>SIM</sub>: 62.6%), with low occurrence of ascidians, while Yacht Club was dominated by serpulids (SIMPER<sub>SIM</sub>: 44.9%) and ascidians (SIMPER<sub>SIM</sub>: 44.7%), with small occurrence of bryozoans.

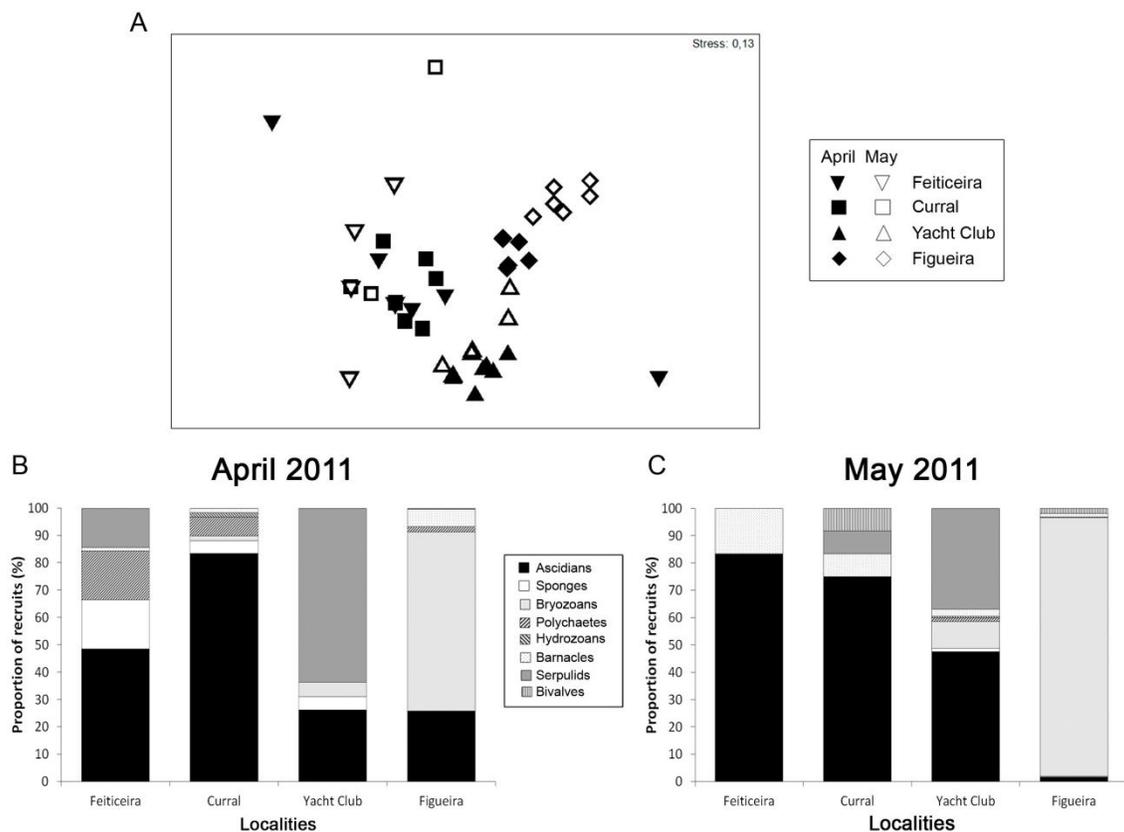


Figure 6. A) nMDS plot of relative abundance of recruits of main taxonomic groups at Feiticeira, Curral, Yacht Club, and Figueira for April and May 2011, and their mean share across sites for B) April and C) May 2011.

Table 3. PERMANOVA comparing composition of early recruiting assemblages across sites and sampling dates (April and May 2011).

Source of Variation	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Locality	3	20145	4.2	<b>0.026</b>
Time	1	11588	10.5	<b>0.001</b>
Locality x Time	3	4846	4.4	<b>0.001</b>
Error	40	1106		

The sampled sites can be thus separated in groups of contrasting predation intensity and recruitment rate. Also, the composition of early assemblages differed among areas (Table 4).

Table 4. Summary of general characteristics of experimental localities.

Locality	Predation intensity	Recruitment	Main recruits
Curral	Low	Low	Ascidians
Feiticeira	Moderate-High	Low	Ascidians
Yacht Club	High	Moderate-High	Ascidians/Serpulids
Figueira	Low	High	Bryozoans

### Predation exclusion

Overall, after 30 days, species richness varied at both the large (among localities, LO effect) and small-scale (inside localities, PA effect), with no effect of predation pressure (Table 5). Between localities with low predation pressure, species richness was lower at Curral and higher at Figueira, and between sites of high predation pressure, species richness was lower at Feiticeira and higher at Yacht Club. Among-panel variation was only found at Feiticeira and Yacht Club (Tukey,

$p < 0.05$ ; Fig. 7). Consumer exclusion had an effect only at Curral, where plates protected from predators attained a higher richness (Fig. 8).

Different results were obtained when locations were distributed in recruitment categories. Within each level of recruitment rate, localities did not differ in richness, but localities of high recruitment category (Figueira and Yacht Club) were correspondent to higher richness values, while localities of low recruitment category (Curral and Feiticeira) were correspondent to low richness values (Table 5, Fig. 7). Also, when distributing localities according to their overall recruitment rate, smaller-scale richness variation is only significant at sites where recruitment is lower (Fig. 7).

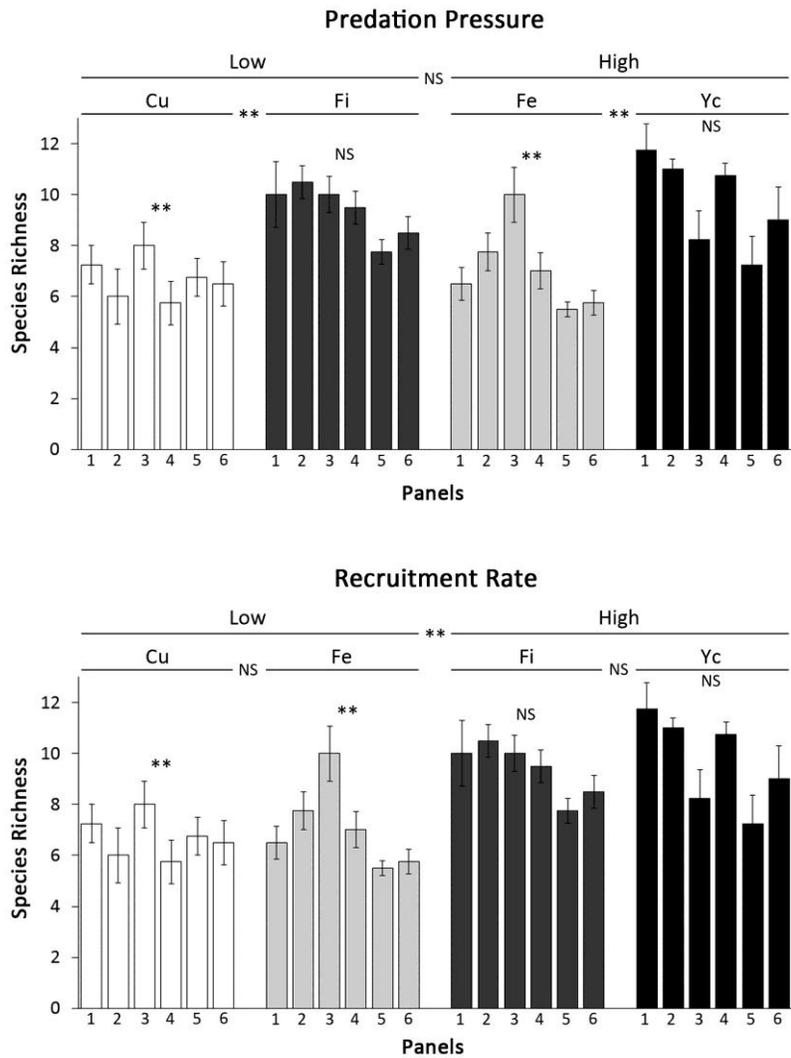


Figure 7. Species richness (mean ± SE) after 30 days on panels at Curral (Cu), Feiticeira (Fe), Figueira (Fi) and Yacht Club (Yc) considering different levels of predation pressure (above) and recruitment rate (below). ns: not significant; \*\*  $p < 0.01$ .

Table 5. Summary ANOVA results for comparisons of species richness after 30 days between levels of predation pressure (PP) and recruitment rate (RR), separately, and between levels of consumers' exclusion (CE), at both the among-localities (LO) and among-panels (PA) spatial scales. Panels within sites test for small-scale spatial variation (unit to tens of meters). *C* = Cochran's *C* test; ns = not significant.

Source of Variation	<i>Df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
<b>30 days – Predation Pressure</b> ( <i>C</i> = 0.098, ns)				
PP	1	2.7	0.0	0.874
LO (PP)	2	82.7	10.9	<b>&lt; 0.001</b>
PA (LO (PP))	20	7.6	2.9	<b>0.001</b>
CE	1	8.2	0.7	0.483
PP x CE	1	4.2	0.4	0.604
CE x LO (PP)	2	11.2	5.6	<b>0.011</b>
CE x PA (LO (PP))	20	2.0	0.8	0.754
Error	48	2.7		
<b>30 days – Recruitment Rate</b> ( <i>C</i> = 0.098, ns)				
RR	1	165.4	122.1	<b>0.008</b>
LO (RR)	2	1.4	0.2	0.838
PA (LO (RR))	20	7.6	2.9	<b>0.001</b>
CE	1	8.2	3.6	0.198
RR x CE	1	22.4	9.7	0.089
CE x LO (RR)	2	2.3	1.1	0.339
CE x PA (LO (RR))	20	2.0	0.8	0.754
Error	48	2.6		

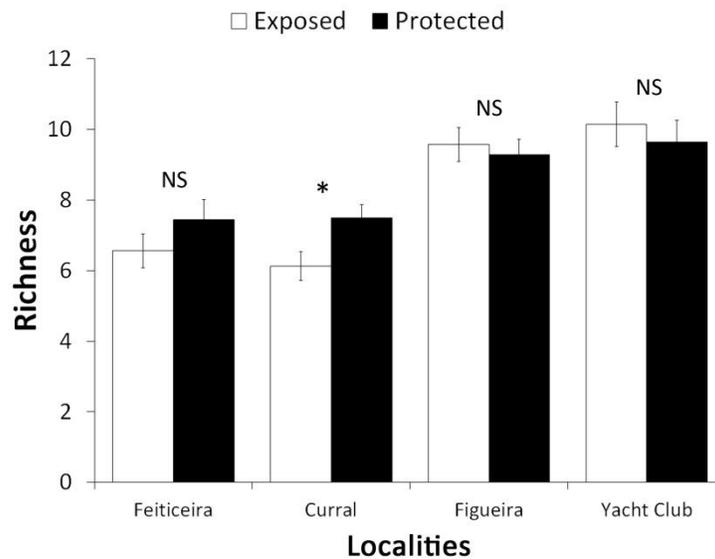


Figura 8. Species richness (mean  $\pm$  SE) after 30 days on panels exposed and protected from predators at Curral, Feiticeira, Figueira and Yacht Club. ns: not significant; \*  $p < 0.05$ .

After 100 days differences of richness among localities were similar to what was verified for 30-day plates, with Feiticeira and Figueira showing low richness values compared to Yacht Club (Tukey,  $p < 0.05$ ). We also observed small-scale, among-panels variation, but only at Feiticeira, with variable values of richness among panels (Table 6, Fig. 9). Comparing to 30 days richness pattern, we observe an increase of mean number of species at Feiticeira and Yacht Club but a stagnation for Figueira, changing this locality from high richness category at 30 days to low richness at 100 days.

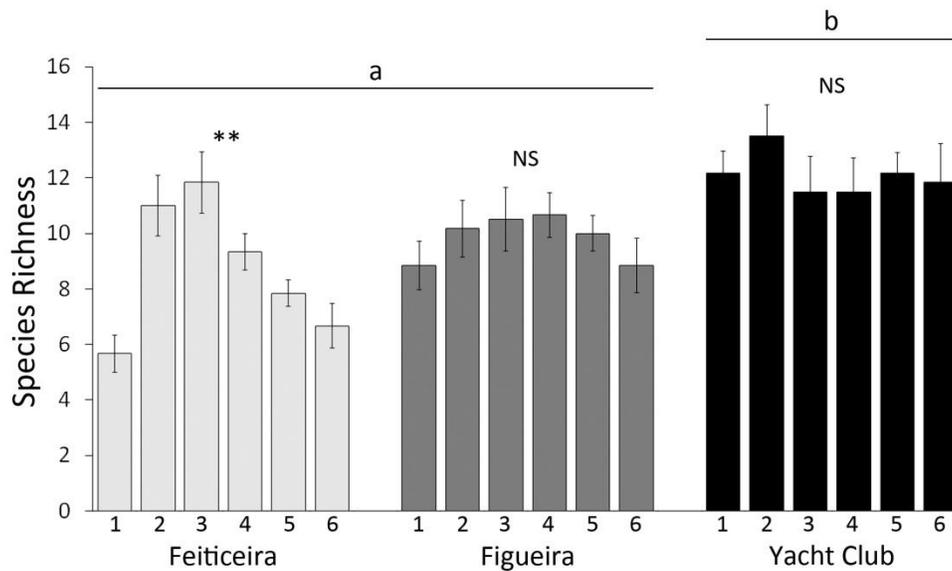


Figura 9. Species richness (mean  $\pm$  SE) after 100 days on panels at Feiticeira, Figueira and Yacht Club. Equal letters indicate no difference between localities; ns: not significant; \*\*  $p < 0.01$ .

Table 6. Summary ANOVA results for comparisons of species richness after 100 days between consumers' exclusion treatments (CE) and across localities (LO, large-scale). Panels (PA) within sites test for small-scale spatial variation (unit to tens of meters). *C* = Cochran's *C* test; ns = not significant.

Source of Variation	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P</i>
LO	2	99.44	7.16	<b>0.007</b>
PA (LO)	15	13.47	2.75	<b>0.002</b>
CE	1	0.04	0.00	0.948
LO x CE	2	12.70	1.52	0.250
CE x PA (LO)	15	8.35	1.70	0.070
Error ( <i>C</i> = 0.098, ns)	72	4.91		

After 30 days, community structure did not change between levels of predation pressure or recruitment rate, but there were differences between localities, within levels of those higher-order factors. Hence, predation pressure or recruitment rate do not explain variation among localities. There was also small-scale variation, among panels within all localities. Effects of consumer exclusion were not consistent across localities, being observed only at Yacht Club (Pairwise test,  $p < 0.05$ ) (Table 7).

The species that most contributed to differences among localities were the ascidian *Diplosoma listerianum* (SIMPER<sub>DISSIM</sub>: 19.8%), hydrozoans (SIMPER<sub>DISSIM</sub>: 11.6%) and the bryozoan *Bugula neritina* (SIMPER<sub>DISSIM</sub>: 8.7%). At Curral and Feiticeira the occupation of space was slower, with no more than 50% of the available area covered after 30 days. Both localities were composed mainly by hydrozoans (SIMPER<sub>SIM</sub>: 52.9 % at Feiticeira and 57.8 % at Curral) and by ascidians (SIMPER<sub>SIM</sub>: *Symplegma* sp1. – 10.7 % at Feiticeira; *Didemnum psammatodes* – 20.5 % at Curral), but bryozoans also occurred at Feiticeira (SIMPER<sub>SIM</sub>: *Catenicella uberrima* – 22.7 %). Figueira was the locality with the largest area covered (almost 90 %) after 30 days, where ascidians dominated the substrata (more than 50 % of total area; SIMPER<sub>SIM</sub>: *Diplosoma listerianum* – 44.5

% and *Symplegma brakenhelmi* – 11.3 %), while bryozoans (SIMPER: *Bugula neritina* – 18.8%) and hydrozoans were less abundant. A similar pattern was observed at Yacht Club, but space occupation was lower than at Figueira. The dominant groups were ascidians (SIMPER<sub>SIM</sub>: *Diplosoma listerianum* – 30.9 %), bryozoans (SIMPER<sub>SIM</sub>: *Schizoporella* sp. – 20.0 % and *Bugula neritina* – 10.7 %) and hydrozoans (SIMPER<sub>SIM</sub>: 21.2 %). Furthermore, Yacht Club was more heavily colonized by ascidians in plates exposed to predators than in protected units, which, coupled with the prevalence of hydrozoans at exposed plates at Feiticeira, explains the observed interaction between predation and locality (Pairwise test,  $p < 0.05$ ) (Fig. 10).

After 100 days we still observe a variation of relative abundance of species among and inside localities. We also see an effect of consumers exclusion but not consistent, being evident only for some panels inside each locality (Table 7). Overall differences were due to the colonial ascidian *Didemnum perlucidum* (SIMPER<sub>DISSIM</sub>: 10.3%), the bryozoan *Schizoporella* sp. (SIMPER<sub>DISSIM</sub>: 9.0%) and the solitary ascidian *Phallusia nigra* (SIMPER<sub>DISSIM</sub>: 7.1%) Plates at Feiticeira were almost 90% covered, with occurrence of bryozoans but dominated by the ascidians *Didemnum perlucidum* (SIMPER<sub>SIM</sub>: 47.23%), *Phallusia nigra* (SIMPER<sub>SIM</sub>: 24.54%) and *Diplosoma listerianum* (SIMPER<sub>SIM</sub>: 7.21%). Plates at Figueira also had a large cover area (about 80%) but the opposite pattern of Feiticeira, with small occurrence of ascidians and dominance of the bryozoans *Schizoporella* sp. (SIMPER<sub>SIM</sub>: 39.87%) and *Bugula neritina* (SIMPER<sub>SIM</sub>: 15.57%). Yacht Club showed the smaller cover area, about 70%, with occurrence of bryozoans (SIMPER<sub>SIM</sub>: *Amathia* sp. – 26.13%) and also dominated by ascidians (SIMPER<sub>SIM</sub>: *Didemnum perlucidum* – 23.26% and *Herdmania pallida* – 10.00%) (Fig. 10).

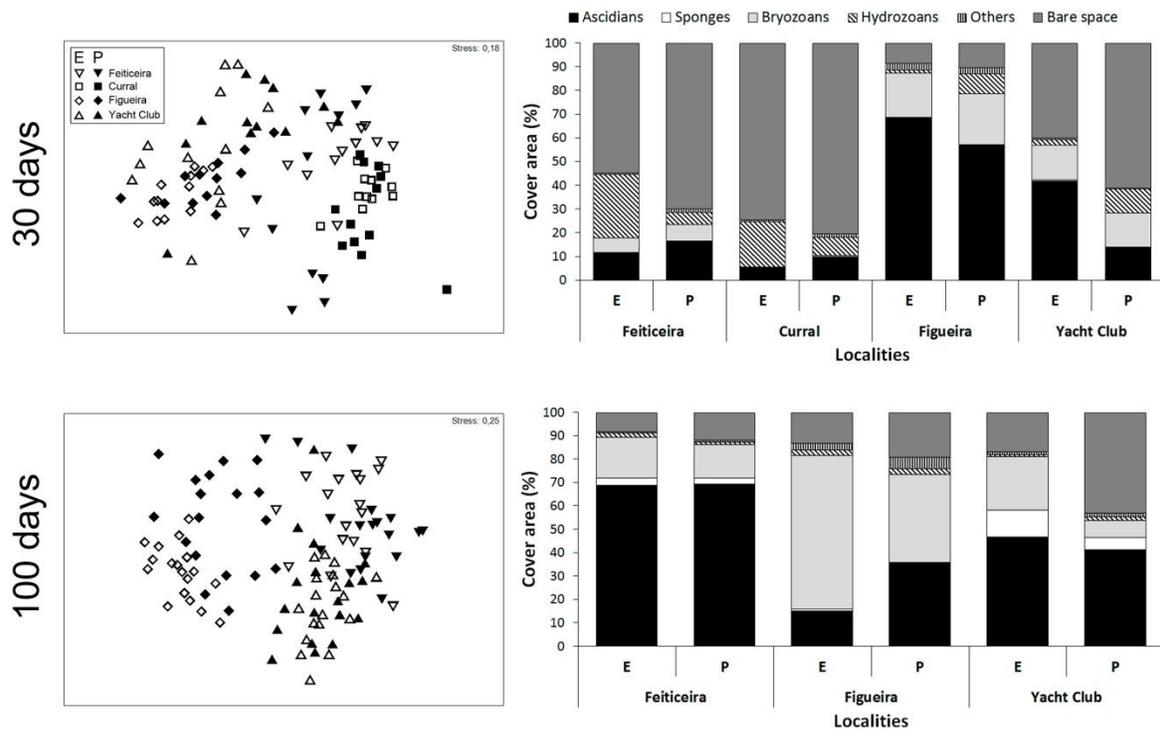


Figure 10. Left: nMDS plots of cover area of main taxonomic groups after 30 and 100 days at Feiticeira (inverted triangles), Curral (squares), Yacht Club (triangles), and Figueira (diamonds) for plates exposed (white symbols) and protected (black symbols) from predators. Right: Mean proportion of cover area of different groups (ascidians, sponges, bryozoans, hydrozoans and others, in which polychaetes, barnacles and bivalves were grouped), after 30 and 100 days, in both exposed (E) and protected (P) plates at sampling sites. Data from Curral were not included in 100 d plots due to loss of replicates.

Table 7. Summary PERMANOVA results for comparisons of assemblage structure after 30 and 100 days between levels of predation pressure (PP) and recruitment rate (RR), separately and only for 30 d data, and between treatments of consumer exclusion (CE) and across localities (LO) (large-scale). Panels (PA) within sites test for small-scale spatial variation (units to tens of meters).

Source of Variation	<i>Df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
<b><i>30 days – Predation Pressure</i></b>				
PP	1	16428	0.3	1.000
LO (PP)	2	47806	16.6	<b>0.001</b>
PA (LO (PP))	20	2882	3.3	<b>0.001</b>
CE	1	2289	0.4	0.616
PP x CE	1	631	0.1	0.733
CE x LO (PP)	2	5242	4.7	<b>0.001</b>
CE x PA (LO (PP))	20	1106	1.3	0.055
Error	48	879		
<b><i>30 days – Recruitment Rate</i></b>				
RR	1	75300	4.1	0.340
LO (RR)	2	18370	6.4	<b>0.001</b>
PA (LO (RR))	20	2882	3.3	<b>0.001</b>
CE	1	2289	3.5	0.119
RR x CE	1	9810	15.0	0.060
CE x LO (RR)	2	652	0.6	0.817
CE x PA (LO (RR))	20	1106	1.3	0.060
Error	48	879		
<b><i>100 days</i></b>				
LO	2	46977	12.9	<b>0.001</b>
PA (LO)	15	3649	2.4	<b>0.001</b>
CE	1	9522	3.4	<b>0.005</b>
CE x LO	2	4957	1.8	0.054
CE x PA (LO)	15	2775	1.8	<b>0.001</b>
Error	72	1511		

## DISCUSSION

Our results showed a marked variation in the community structure at both the large and micro scales, and suggest that these differences are not caused in general by predation or recruitment, at least not by their isolated effects. We did not observe effects of predation pressure, and the exclusion of consumers was important just in specific situations or localities. The exclusion

of predators has some effect after 30 days, promoting coexistence of more species at Curral and the occurrence of a large proportion of bryozoans at Yacht Club, and affecting only some panels inside each locality after 100 days. These restricted effects are probably related to the micro-scale variation inside each locality, which will be discussed later on.

The experimental localities are situated in a subtropical area, at a latitude close to the one at Florida, where Freestone et al. (2011) sampled. As in this study, they did not find important predation effects, indicating that at 23-27° processes ruling subtidal shallow assemblages are more similar to those operating in temperate communities than in tropical ones. On the other hand, our system is very diverse and space occupation occurs very fast (Vieira et al., 2012), the opposite to what is reported for temperate localities. Thus, our study area seems to have characteristics of both tropical and temperate regions, and the results are apparently a balance of process taking place in these two regions.

The considerable diversity of fishes found in Brazil, and the generalist habit of most of them (Ferreira et al., 2004), may be a cause of the weak predator-prey interactions found in this study, similarly to what was suggested by others (Duffy, 2002; Hillebrand and Cardinale, 2004; Duffy et al., 2007; Edwards et al., 2010). In addition, the prey community at São Sebastião is also diverse (about 60 species, Appendix), which possibly decreased further the strength of interactions (Duffy et al., 2007; Edwards et al., 2010). Several studies show that in diverse prey communities there is a low chance of each prey to be eaten due to the abundance of food that predators can find (Steiner, 2001). Furthermore, the more diverse a community, the greater the occurrence of chemical defenses that might deter consumers (Duffy, 2002; Duffy et al., 2007; Edwards et al., 2010). In the study area there is a high diversity of ascidians and sponges, which are organisms frequently bearing well-known chemical compounds for defense (Lindquist et al., 1992; Ruzicka and Gleason, 2009), and many flat bryozoans (personal observation), which the mineralized body can make

difficult the action of consumers, even if predation pressure is high. All of these factors can contribute to the lack of effects we found. We tend to expect that diverse predator assemblages exert intense effects, but, in this case, diversity seems to act like a buffer, either to consumers or preys, so that the exclusion of one or the other does not result in any detectable impact, because the high number of possible interactions confers stability to the system (Byrnes et al., 2006; Ives and Cardinale, 2004).

Besides the effects of large predators, some studies indicate the important role of micropredators (Osman et al. 1992; Nydam and Stachowicz, 2007). These small consumers feed on the new recruits that just settled and can control richness and abundance of species on late community stages. At our study localities, we can frequently see juvenile and small adults of gastropods, crabs and fishes feeding in both protected and exposed plates since the mesh cannot exclude organisms smaller than 1 cm. Although we did not measure this impact, they can have an enormous effect in the community structure and, since they could assess all the plates, mask large predators' effects in the exclusion experiment.

Another factor that can dampen predation effects is recruitment rate (Cooper et al., 1990; Palmer et al., 1996). Our results showed that localities with high values of richness is also localities with high recruitment rate. This pattern of recruitment is closely connected to the species richness values and the feedback between these two factors can contribute to maintain communities patterns, and is very important to communities resilience (Peterson, 2002). Diverse communities can quickly recover after disturbance, once the supply of recruits is often high, contributing to restore pre-disturbance patterns (Nyström and Folk, 2001; Bengtsson et al., 2003). However, like predation, recruitment did not appear to regulate the relative abundance of organisms, probably because it dampen the effects of consumers, with new recruits reaching the community constantly, and occupying the space made available by predation (Sams and Keough, 2007). In localities with low

recruitment rate and high predation pressure, we expected to detect differences between exposed and protected panels, but this was not the case. However we did not conduct a factorial experiment allowing us to test the synergistic effect of predation and recruitment.

Although there might be an interactive effect of predation and recruitment on community structure across localities, our results show a consistent variation of richness and assemblage structure within each locality. Richness variation among panels was evident only at Curral and Feiticeira, which are localities with low recruitment rates. When recruitment is low, we can expect that a small variation in the number of settlers may result in a variable number of coexisting species later on. At Yacht Club and Figueira, the rate of recruitment is so high that panels will always receive recruits for a large number of species, preventing the occurrence of among-panel variation.

In contrast, assemblage structure varied among panels within all tested localities, possibly due to the low capacity of dispersion of larvae released by encrusting organisms (Olson, 1985; Sammarco and Andrews, 1988; Connelly and Roughgarden, 1999; Samas and Keough, 2012). Since these larvae cannot swim for a long time and over long distances, and also because settlers tend to be attracted by co-specifics (Durante, 1991; Pacheco et al. 2010), assemblage structure at experimental panels would be similar to natural surrounding communities. This variation of composition can explain the variable effect of consumers exclusion, as some groups can be more easily affected. Panels with a major occurrence of non-defended ascidians will be more affected than panels occupied by more resistant organisms like mineralized bryozoans (Russ, 1980; Osman and Whitlatch, 2004). Also, the behavior of consumers can also contribute to the large variation inside each locality. The majority of fishes we find at our study area are mobile and generalist (Ferreira et al., 2004). Since these predators do not have to swim long distances to search for specific prey, they can easily specialize to a specific feeding area, having a great impact in some panels but not in others. The localized habitat of predators can result in a wide spatial and temporal

variation of predator-prey interaction strength (Berlow, 1999). Navarrete and Berlow (2006) showed that this variation is far important to maintain the stability of the regional community, but also local-specific patterns (Berlow, 1999) as observed in our study area. It is suggested that response variation at the scales we tested may ultimately maintain diversity in these communities, and largely contribute to stability and high resilience against disturbance (Connell and Sousa, 1983; Osman et al., 2010).

Our results showed that processes usually regarded as key drivers of community structure may not always exert considerable effects. In complex systems like tropical or subtropical habitats, many factors can interact and their isolated effects can be dampened by others. Also, we highlight the necessity to include several scales in studies of this kind, since some processes can have different impacts and effects from regional to local spatial scales.

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## **CAPÍTULO 2**

# **IMPORTÂNCIA RELATIVA DO LEGADO DA COLONIZAÇÃO INICIAL E DE CONDIÇÕES PÓS-DISTÚRBIO DIRECIONANDO A TRAJETÓRIA DE COMUNIDADES TARDIAS**

## **RELATIVE IMPORTANCE OF EARLY COLONIZATION LEGACY AND POST-DISTURBANCE CONDITIONS DRIVING LATE COMMUNITY TRAJECTORY**

### **ABSTRACT**

Disturbance is a common process which drives community organization and mediates ecosystem processes. How communities face disturbance is an important issue in ecological studies. The time needed to a community restore the pre-disturbance state, or the amount of disturbance necessary to take a community to an alternative stable state is called resilience. The group of characteristics, both environmental conditions and important species that promote feedback mechanisms of state maintenance (biological legacy), which ensures resilience, set the ecological memory. If this memory is small, community easily reaches another stable equilibrium after a disturbance. Interested in how encrusting communities face decrease or increase exposure of predation and recruitment rates, we simulated disturbance by transplanting developing communities between two localities with extreme values of these two characteristics. Transplanted communities became more similar to the destination equilibrium state, independently of direction and moment of transplant. However, they remain unequal to destination communities, indicating the existence of some legacy from early colonization at origin. These results showed us that severe disturbance can lead communities to alternative trajectories, towards new stable states, mainly if there is a loss of biological legacy, and post-disturbance conditions were substantially different from pre-disturbance ones.

## INTRODUCTION

Disturbance is a common process, occurring across all kinds of habitats, even in the most stable ones. It can vary in kind, frequency, duration and intensity (Sutherland, 1990; Turner and Dale, 1998) and can affect individual traits, community organization and ecosystem processes (Dayton, 1971; Turner and Dale, 1998; Hughes et al., 2007). How communities tolerate disturbance and how they recover to original states or reach alternative stable states is the aim of recent ecological studies (Osman et al., 2010a,b).

Communities with high level of tolerance are classified as resistant (Holling, 1973; Sutherland, 1990). In the other hand, great part of the communities affected by disturbance may reach stability again in the same previous state or in another stable state, after a variable amount of time (Holling, 1973; Connel and Sousa, 1983; Sutherland, 1990; Beisner et al., 2003). In this context, the idea of resilience was created (Holling, 1973; Gunderson, 2000; Osman et al., 2010b), to which two distinct concepts were ascribed (Peterson et al., 1998; Gunderson, 2000). First, the 'engineering resilience' considers a single stable state (global equilibrium) and resilience in this way is defined as the time the community takes to return to this unique state after a disturbance. Second, the idea of 'ecological resilience', which assumes several possible stable states (multiple equilibrium). In this case, resilience is defined as the amount of disturbance necessary to bring a community from one stable state to another. Since alternative stable states are often observed (Sutherland, 1990; Gunderson, 2000), ecological resilience has proved to be a more useful and appropriate concept.

Holling (1986, 1992) defined phases during the successional process and ways in which the system can be affected by disturbance at each of such phases (Gunderson, 2000). Initially the community is in a so-called 'exploitative phase', in which several opportunistic species grow fast and reproduce intensively, allowing a fast use of resources. During this phase resilience is very high

due to the simplicity of the system. The next moment is the “conservative phase”, during which the community accumulates energy and early colonizers are replaced by slow-growing species and competitive interactions become common. During this phase the system reaches stability, but in a very narrow range, so that disturbance events can lead to great changes in the community. This final moment of the conservative phase is called ‘creative destruction’ and corresponds to a poorly resilient stage. After some disturbance, the community enters in the ‘reorganization phase’. During this moment the system is still very fragile and every random factor can drive the community to an alternative state (Nyström and Folk, 2001).

Several characteristics can maintain the system state and ensure that the community will return to the previous stable state after a disturbance (Nyström and Folk, 2001; Golinsky et al., 2008). The group of these factors can be referred to as ecological memory. Bengtsson et al. (2003) defined ecological memory as the “network of species, their dynamic interactions between each other and the environment, and the combination of structures that make reorganization after disturbance possible”. The species that contribute the most to an ecological pattern constitute the biological legacy (Franklin and MacMahon, 2000). When ecological memory exists and is strong, processes and patterns of the system are straightly connected in a looping feedback (Peterson, 2002) ensuring stability. Due to this feedback mechanism, it is expected that ecological memory arises in communities where biotic interactions are strong and profoundly affect community dynamics (Peterson, 2002; Nyström and Folk, 2001). Because tropical communities are usually diverse, making possible several different biological interactions, foodwebs tend to be complex but strength of single interactions tend to be weak (Hillebrand and Cardinale, 2004). In this scenario, ecological memory may be low and alternative states expected to arise after disturbance.

Human activity have redesigned urban coastlines, with the introduction of several new structures like piers and marinas, which have redistributed standing stocks of fishes and created new

encrusting habitat for invertebrates and algae in different areas (Folke, 2003). In tropical diverse assemblages, free space in the sublittoral zone may be occupied in many different ways. Because many colonial organisms may show similar competition abilities to occupy available space, one could anticipate that a lottery competitive system, largely dictated by first arriving larvae, would be a major determinant of community structure (Sale, 1977, 1982; Shinen and Navarrete, 2010). On a previous study (Vieira et al., in preparation) we sampled two sites with contrasting environmental conditions, one with high recruitment rate and predation pressure, thus holding a more 'open' community, and the other one with low intensity of both recruitment and predation, and therefore more 'closed' to nearshore biotic influence. We took advantage of this large difference to simulate a shift on environmental conditions, by transplanting developing communities from one place to the other, and examine ways in which communities drifted from the original situation. This allowed us to test whether assemblages are robust to environmental change, taking place from sites just a few km apart, or if they depart at some extent from an initial configuration at some specific succession stage in which communities are more susceptible to changes in habitat conditions. We expected that changes from a 'closed' to an 'open' setting would lead transplanted communities to drift to a state close to the destination structure. In the other hand, a change in the opposite direction would lead to slighter changes, and retention of community attributes found at the origin. Also, we expected that panels transplanted at an early development stage may become more similar to destination than those that remained more time at original localities, and acquired a larger legacy from earlier colonizers.

## MATERIAL AND METHODS

### Study area

We conducted this experiment at the São Sebastião Channel, SP, southeastern Brazil, from September to December 2011. Sites along the channel are relatively sheltered from wave action and show a diverse fouling community developing at rocks and man-made structures. From a set of sites used for previous predation exclusion experiments (Vieira *et al.* in preparation), separated by a few km and consisted of man-made large physical structures such as jetties and piers, we selected the two sites with more contrasting characteristics. These were a jetty at Curral Beach (23°51'37.80''S; 45°25'49.63''W) and the pier of the Yacht Club of Ilhabela (23°46'26.95''S/45°21'21.26''W). Curral is a location with extremely low recruitment rates and low consumption by fish predators. In the opposite way, the Yacht Club is subjected to a more intense recruitment rate and consumption potential by fishes is high (Vieira *et al.* in preparation).

### Experimental design

In this study, we experimentally exposed developing communities of encrusting organisms, with different ages, to an abrupt change in the surrounding environment, imposing a natural decrease (when transplanting from Yacht Club to Curral) or increase (from Curral to Yacht Club) of predation intensity and settlement rate. We assessed the relative role of early processes in ecological succession and later environmental effects as determinants of the structure of shallow benthic assemblages. Because we used a reciprocal transplant design including different transfer dates, we also compared outcomes resulting from environmental change in opposed directions, and assess whether there is a stage in succession after which further changes are markedly restrained.

At each location we deployed 32 roughened PVC plates (10 x 10 x 0.2 cm) for community establishment. All plates were attached in a plastic screen frame distant at least 3 cm from each

other, and fixed horizontally by cables to artificial pilings. We undertook three field surveys after the initial experimental setup, at weeks 2, 5 and 8. During each survey, four plates from each site were recovered and brought to laboratory for detailed description of the communities in different successional stages, while five other plates were reciprocally transplanted, from Curral to Yacht Club and vice-versa. Five extra plates were left at each site, and used to describe stable community states at the end of the experiment. Except for sampling units used to describe the communities in the laboratory, plates remained underwater for a total of 15 weeks to allow stability (Russ, 1980; Connell, 2001), before further analyses. By doing so, we could compare each set of transplanted plates with sets that were not moved and remained at Curral and Yacht Club during the whole experiment. To control a possible effect of transplants, we always took all plates into the boat, even the ones that would not be transplanted. Doing this, all plates stayed out of water during at least 30 minutes while we detach the transplant plates, and organisms of both treatments (transplant and not transplant plates) suffered the same level of stress.

Initially we intended to conduct the transplant experiment considering three areas; Curral, Yacht Club and additionally Figueira ( $23^{\circ}44'55.43''S$  /  $45^{\circ}24'36.11''W$ ). Figueira is exposed to low pressure of predators but an extremely high recruitment rate (Vieira *et al.* in preparation), being a locality with intermediate characteristics of those found at Curral and Yacht Club. Unfortunately, between the third transplantation survey (8 weeks) and the end of the experiment (15 weeks), we lost several plates at Figueira because supporting cables were torn by storms and strong waves. Because this would prevent an adequate balanced analysis, we decided to exclude Figueira from the original experimental design. However, plates that were transplanted from Figueira to both Curral and Yacht Club remained intact in these destination sites, and hence were used to evaluate early colonization effects, as described below. General procedures are illustrated in Figure 1.

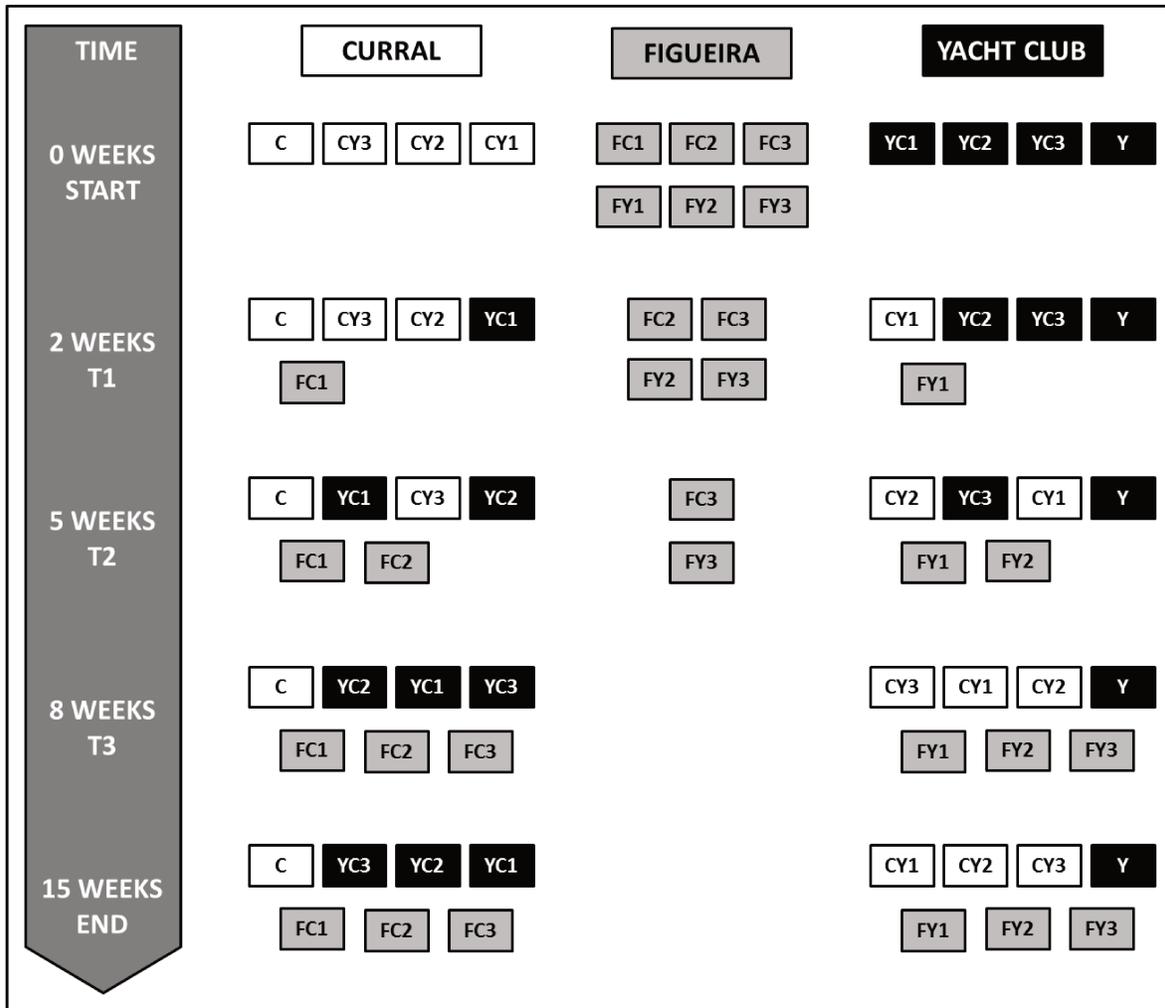


Figure 1. Diagram of the reciprocal transplant design used at experimental sites Curreal(C)and Yacht Club (Y). White and black rectangles represent replicate sets of plates originally deployed at Curreal and Yacht Club, respectively. T1, T2 and T3, stand for reciprocal transplants at times 1 (2 wk), 2 (5 wk) and 3 (8 wk). C and Y represent sets of plates left at original sites, while CY and YC indicate plates transplanted from Curreal to Yacht Club, and vice-versa. Plate groups from a third location, Figueira, transplanted to Yacht Club (FY) or Curreal (FC) are shown in grey. Numerals after transplant groups indicate transplant dates.

### Laboratory analyses

We scanned the downward facing surface of each plate under a dissecting microscope and identified all the encrusting organisms found to the lowest possible taxonomic level. We then photographed the plates for later quantification of the area covered by each taxonomic group using

the CPCe image analysis software and a grid of 100 intersections (Kohler and Gill, 2006). Because colonial organisms, such as ascidians, bryozoans and sponges, could monopolize settlement plates through clonal reproduction, we used the area covered by each taxonomic group, instead of the number of individuals, to estimate the relative abundance of each taxon. The most dominant groups were those with the highest covered area (Vieira et al., 2012).

### Data analyses

*Successional stages* – We assessed assemblage development using the general standard descriptors: species richness and substrate cover. Richness data were analyzed by a two-way ANOVA, with local and time as fixed factors and four replicates. *Post-hoc* comparisons were carried out using the Tukey test. Cover data were analyzed in two different ways. First we compared bare space using exactly the same model, and then we compared species assemblages using their relative cover as a proxy of relative abundance. In this latter case, we first performed an nMDS plot using the Bray-Curtis distance (Clarke, 1993), and then tested spatial and temporal orthogonal effects with a two-way PERMANOVA, using 999 permutations (formerly NP-MANOVA; Anderson, 2001). Because two plates were still bare at Curral after 2 weeks, and since unbalanced designs cannot be run using the PERMANOVA routine, we removed these two uncovered plates from analyses, and also the two other plates with minimum cover from each of the remaining sites. The contributions of species responsible for grouping sample units ( $SIMPER_{SIM}$ ) and for differences between groups ( $SIMPER_{DISSIM}$ ) were obtained by SIMPER analysis. All the analyses were done using the software PRIMER (Clarke and Gorley, 2006), and pairwise comparisons were done for significant differences, also using 999 permutations.

*Reciprocal transplants*—Statistical procedures were designed to verify (i) whether assemblages in a given group of transplanted plates remained similar to the origin community or, alternatively, if they drifted to a state closer to the destination community, and (ii) if the successional stage at which transplants were undertaken affects final outcomes. To answer these questions we estimated the extent of drift (DR) due to environmental change, by calculating the ratio between the distance of the transplanted group to the group which remained at the origin site throughout the experiment (*do*), and the distance to the group left at the destination site (*dd*).  $DR > 1$  would indicate more similarity to the stable community state at the destination (Fig. 2A), while  $0 < DR < 1$  more similarity to the community which developed at the origin (Fig. 2B).

To assess these distances and estimate ratios, we initially calculated a similarity matrix using the Bray-Curtis distance between all replicates of transplanted groups and replicate plates which were not transplanted, and characterized stable states at Curral and Yacht Club. Distance estimates were obtained by subtracting similarity values to 1. Any given transplanted plate provided a single replicate measure of drift by first computing the means of its distances to the plates maintained at the origin and to those that remained at the destination ( $n = 5$ ), and then calculated the ratio of such average values (Fig. 2C).

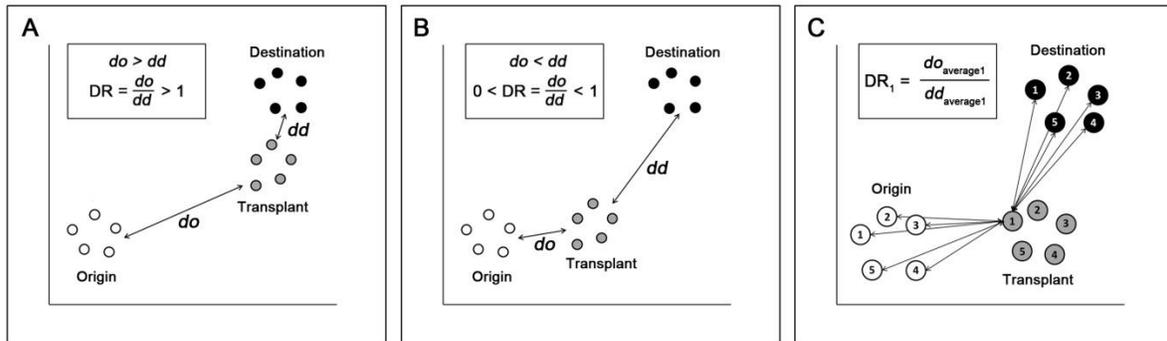


Figure 2. Examples of spatial organization for destination (black circles), origin (white circles) and transplanted (grey circles) plate groups when (A) drift from the stable state at origin is substantial, and assemblages in transplanted units resemble those held at destination ( $DR > 1$ ), (B) drift is reduced and assemblages in transplanted plates retain similarity to the state developed at origin ( $0 < DR < 1$ ). Plate C shows how drift estimates (distance ratios) were derived from average distances to plots where stable states were achieved at both the origin and destination. Note that these distances are only an illustration, not the actual metrics used for analyses. DR: Drift, *do*: distance to origin, *dd*: distance to destination.

Drift was then analyzed using a two-way ANOVA, in which transplant direction (Currel-Yacht Club and Yacht Club-Currel) and time at transplant (2, 5 and 8 weeks) were both fixed factors, and number of replicates were 5. *Post-hoc* comparisons were performed using the Tukey test. In order to characterize drift patterns and identify key groups responsible for state shifts, we used a parallel multivariate approach. We first plotted an nMDS plot using cover data of all taxa, from panels residents all the time at destination and panels transplanted in both directions and at all the 3 transplant times, using Bray-Curtis distances. The differences were tested using a two-way PERMANOVA with destination (Currel and Yacht Club) and history (transplanted at 2, 5 or 8 wk and never transplanted) as fixed factors. The contributions of species responsible for grouping and for possible differences between groups were obtained by SIMPER analysis.

*Effects of early colonization* – Eventual differences between transplanted groups and the stable state at destination can be attributed to two competing hypotheses. The first one is that the presence of pioneering colonizers somehow restrained possible ways of later succession. The second one is that

transplanted plates were simply not allowed enough time for processes at the destination site, responsible for final community attributes, to be fully completed.

In order to clarify this issue, we separately compared transplanted plates from Figueira and Curral at Yacht Club, and from Figueira and Yacht Club at Curral. If early colonization at the origin is responsible for differences with destination communities, then groups of transplanted plates, from different allochthonous sites, should harbor divergent communities. Alternatively, if these communities converge to a similar state, then the more plausible explanation is that, given the appropriate time, they would eventually match the destination community state.

We used cover data of all taxa to construct nMDS plots to show spatial organization of transplanted communities at Curral (from Figueira and Yacht Club) and Yacht Club (from Figueira and Curral), using Bray-Curtis distances. Additionally, we performed a PERMANOVA test to evaluate the differences between all transplanted groups at each locality separately. We decided to use plates of all transplant dates because the effects of early colonization can depend on the stage they were transferred. In this analysis we used origin (Curral and Figueira at Yacht Club analysis and Yacht Club and Figueira at Curral analysis) and transplant date (2, 5 or 8 wk) as fixed factors. The contributions of species responsible for grouping sample units and for possible differences between groups were obtained by SIMPER analysis. All significant differences were analyzed with *post-hoc* pairwise comparisons.

## RESULTS

### Succession at Curral and Yacht Club

Succession patterns at experimental sites were greatly different. At Curral we recorded a total of 21 species while at Yacht Club this number was larger, reaching 31 species (Appendix). From this total richness, 17 species occurred at both sites, which means that only four species were

exclusive to Curral while 14 species were exclusive to Yacht Club. There was marked spatial divergence between areas and clear temporal trends of both species richness and space occupation, with no significant interaction of main factors (Table1). Yacht Club attained higher species richness during all the experiment. At both sites, the number of species increased across the weeks 2, 5 and 8 (Tukey,  $p < 0.05$ ), reaching maximum values at week 8, which was maintained until week 15 (Tukey,  $p > 0.05$ ) (Fig. 5A).

Available space decreases at each week for both Curral and Yacht Club (weeks 2, 5, 8 and 15; Tukey,  $p < 0.05$ ). Curral showed a larger bare space during all the time and the spatial occupation is slower, resulting in almost 30% of bare space at the end of the experiment, while at Yacht Club plates were almost totally covered by encrusting organisms at the end of the experiment (Fig. 5B).

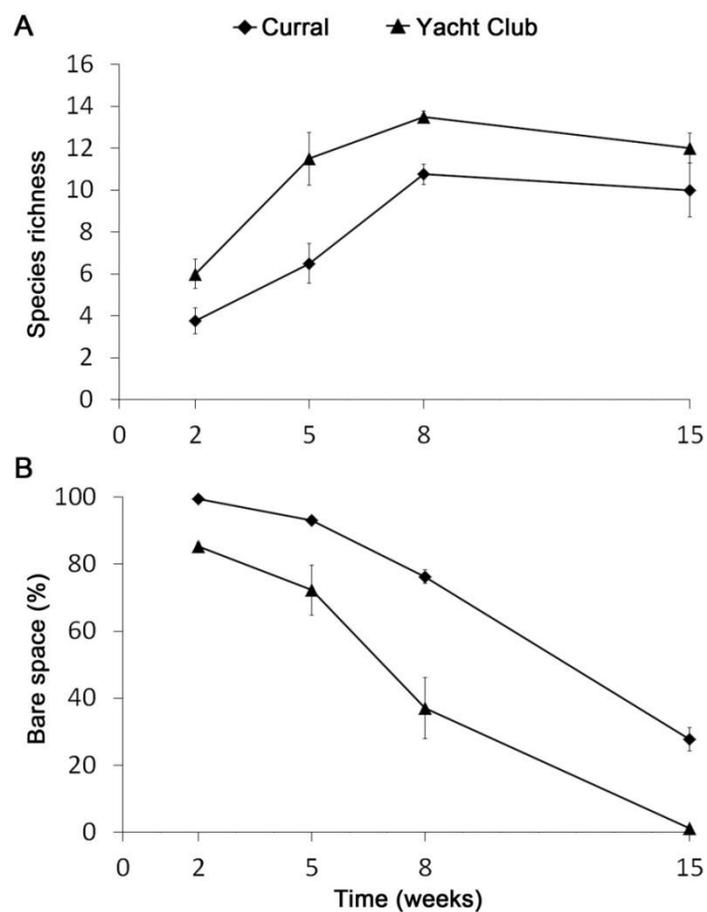


Figure 5. A) Species richness (mean  $\pm$ SE) and B) percentage of bare space (mean  $\pm$ SE) at Curral and Yacht Club during the transplantation experiment.

Table 1. Summary results of two-way ANOVA testing the effects of locality (Curral and Yacht Club) and time (2, 5, 8 and 15 weeks) on species richness and bare space percentage in experimental plots. *C* = Cochran's *C* test; ns = not significant.

Source of Variation	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
<b><i>Species richness</i></b> ( <i>C</i> = 0.284, ns)				
Locality	1	72.0	24.5	< 0.001
Time	3	81.4	27.7	< 0.001
Locality x Time	3	3.8	1.3	0.305
Error	24	2.9		
<b><i>Bare space</i></b> ( <i>C</i> = 0.476, <i>p</i> = 0.046)				
Locality	1	1.2	97.0	< 0.001
Time	3	1.6	136.8	< 0.001
Locality x Time	3	0.0	1.2	0.338
Error	24	0.0		

Differences of composition between localities changed across time (Table 2). These areas were different at nMDS plot resulting in two distinct groups, but plates from initial moments (2 and 5 weeks) are quite similar between the two localities (Pairwise test,  $p > 0.05$ ) while plates from later moments (8 and 15 weeks) are more different (Pairwise test,  $p < 0.05$ ) (Fig. 6A).

The general differences between Curral and Yacht Club are due to the dominance of the bryozoan *Membranipora* sp. at Yacht Club (SIMPER<sub>DISSIM</sub>: 11.29%) and hydrozoans at Curral (SIMPER<sub>DISSIM</sub>: 34.28%). Yacht Club was dominated by hydrozoans at early stages (2 weeks). As community developed, there was a decrease of area covered by hydrozoans and an increase of the area occupied by ascidians and bryozoans (5 and 8 weeks), ending after 15 weeks with, basically, a full cover of bryozoans. Plates from Curral were initially almost devoid of fouling organisms (2 weeks). After the first weeks plates were progressively occupied by hydrozoans (5 weeks) and barnacles (8 weeks). At the end (15 weeks), plates were dominated by hydrozoans with some occurrence of barnacles and ascidians (Fig. 6B).

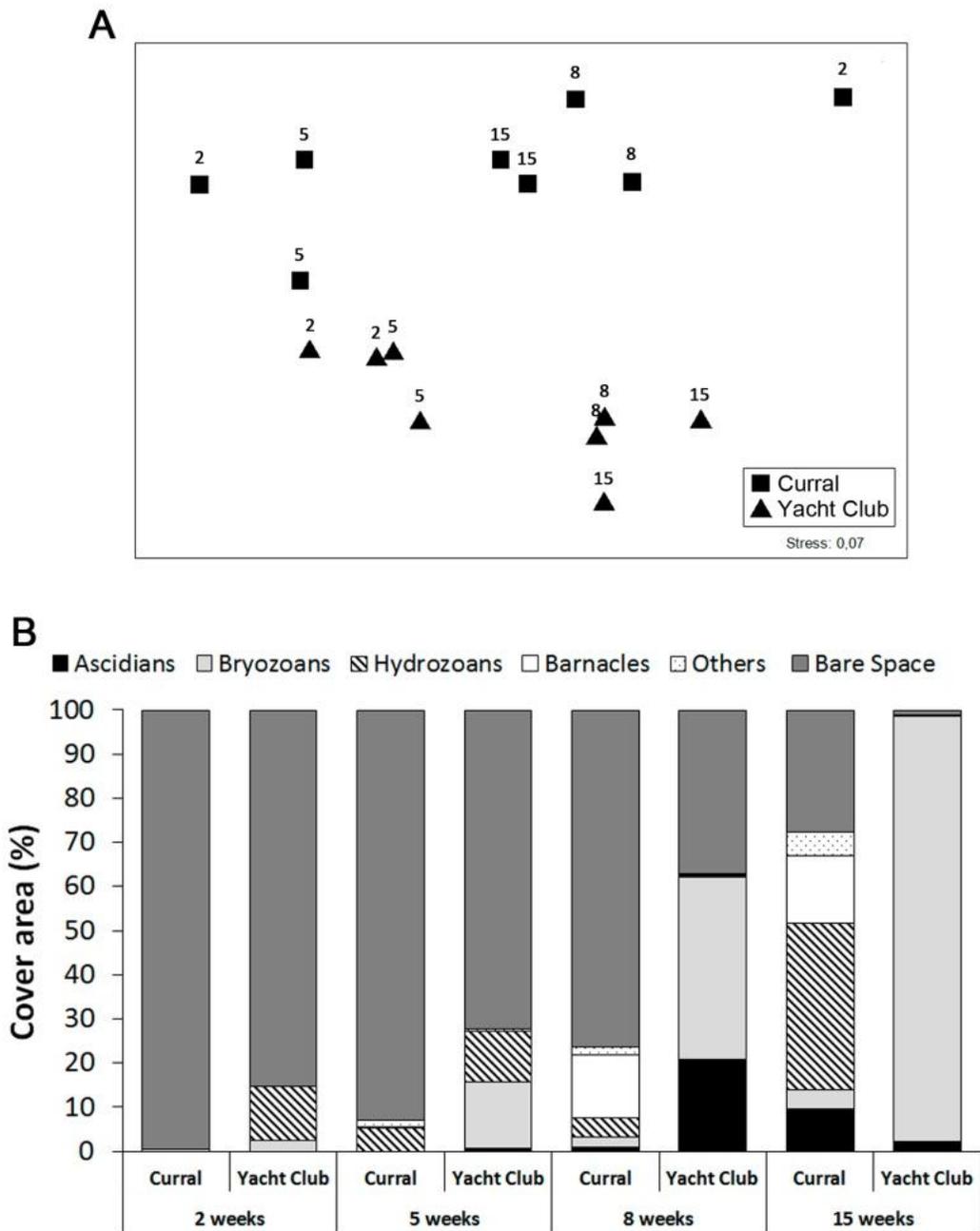


Figure 6. A) nMDS plot of cover area of different groups after 2, 5, 8 and 15 weeks of community development at Curral (squares) and Yacht Club (triangles); B) Mean cover of different main groups (ascidians, bryozoans, hydrozoans, barnacles) and other, less abundant taxa (sponges, bivalves and polychaetes) after 2, 5, 8 and 15 weeks at Curral and Yacht Club.

Table 2. Summary results of two-way PERMANOVA testing the effects of locality (Currel x Yacht Club) and time (2 x 5 x 8 x 15 weeks) on the structure of fouling communities.

Source of Variation	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Locality	1	6017	4.1	<b>0.009</b>
Time	3	4759	3.2	<b>0.005</b>
Locality x Time	3	4347	3.0	<b>0.001</b>
Error	8	1468		

Reciprocal transplants

All mean drifts (DR) were larger than one, showing that at the end of the experiment all transplanted groups were more similar to stable states at destination, independently of the direction and moment of transplantations (Table 3; Fig. 7).

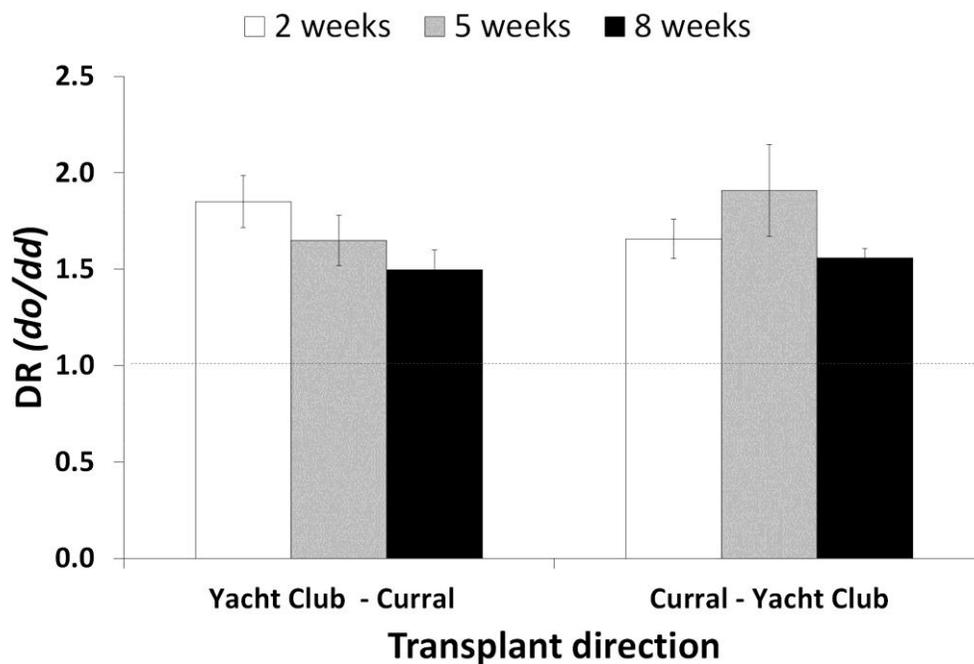


Figure 7. Community drifts (DR) from stable state at origin (mean ± SE) for plates transplanted at weeks 2, 5 and 8 in both directions (from Yacht-Club to Currel and from Currel to Yacht Club). *do*: distance to origin; *dd*: distance to destination.

Table 3. Summary results of two-way ANOVA testing the effects of direction (Yacht - CurralandCurra l- Yacht Club) and transplant date (2, 5, 8 and 15 weeks) on community drift. *C* = Cochran's C-test; ns = not significant.

Source of Variation	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Direction	1	0.013	0.14	0.712
Transplant date	2	0.192	1.99	0.159
Direction x Transplant date	2	0.129	1.34	0.281
Error	24	0.096		
<i>(C</i> = 0.490 , ns)				

The resulting nMDS plot shows the trend very clearly. There is spatial segregation along the first (horizontal) axis, with plates of transplanted groups clustering close to plates of destination (Fig. 8) (Table 4). The separation between destinations is mostly due to the bryozoan *Crisia* sp1. (SIMPER<sub>DISSIM</sub>: 20.27%), common at Yacht Club, and hydrozoans (SIMPER<sub>DISSIM</sub>: 15.15%), common at Curral.

Although transplanted plates become similar to stable states at destination, they retained some differences (Table 4). At Yacht Club all transplanted plates are similar among each other (Pairwise test, *p* > 0.05) and different from destination ones (Pairwise test, *p* < 0.05). At Curral all transplanted groups are also different from destination ones (Pairwise test, *p* < 0.05), but 2 wk transplanted group are segregated (Pairwise test, *p* < 0.05) from 5 and 8 wk, which clustered in the same group (Pairwise test, *p* > 0.05).

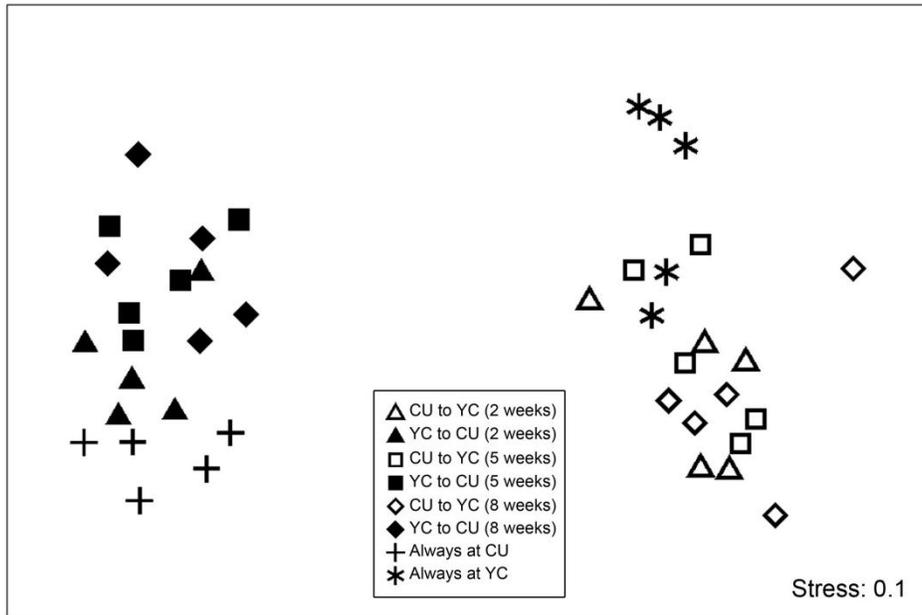


Figure 8. nMDS plot representing similarities among transplant groups and stable states at study sites, using percentage cover data for main groups (see Figure 6). Crosses represent plates that were held at Curral and stars plates that were left at Yacht Club throughout the experiment. Black symbols are plates transplanted from Curral to Yacht Club and white symbols are plates transplanted from Yacht Club to Curral. Triangles, squares, and diamonds correspond to plates transplanted after 2, 5 and 8 weeks, respectively, after initial deployment.

Table 4. Summary results of two-way PERMANOVA testing the effects of destination (Curral x Yacht Club) and history (transplanted 2, 5 and 8 wk and never transplanted) on the structure of fouling communities.

Source of Variation	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
Destination	1	59310	65.47	<b>0.001</b>
History	3	2352	25.97	<b>0.001</b>
Destination x History	3	3619	3.99	<b>0.001</b>
Error	32	906		

Effects of early colonization

The results observed above can indicate either an effect of early colonization at origin sites, which prevented transplanted plates to become equal to those held at destination over the course of

the study, or that plates were not left at destination long enough to allow local processes to be complete.

Results provide support for the first hypothesis, because transplanted plates from different sites developed distinct communities in a common destination locality, both at Curral and Yacht Club (Fig. 9, Table 5). At Yacht Club the differences between transplanted plates from Curral and Figueira are consistent for all transplant dates and the species that most contributed were the bryozoans *Membranipora* sp. (SIMPER<sub>DISSIM</sub>: 18.74%) and *Amathia* sp. (SIMPER<sub>DISSIM</sub>: 14.76%), common at Figueira plates and *Crisia* sp1. (SIMPER<sub>DISSIM</sub>: 14.50%) e *Crisia* sp.2 (SIMPER<sub>DISSIM</sub>: 13.75%), common at Curral plates. At Curral differences were due to the presence of the Bryozoan *Schizoporella* sp. (SIMPER<sub>DISSIM</sub>: 16.95%), common at Figueira plates, and the Ascidian *Didemnum perlucidum* (SIMPER<sub>DISSIM</sub>: 12.13%), common at Yacht Club plates, however, there are differences among plots transplanted at different dates since earlier transplant plates (2 wk) are different from the others (Pairwise test  $p < 0.05$ ) (Table 5).

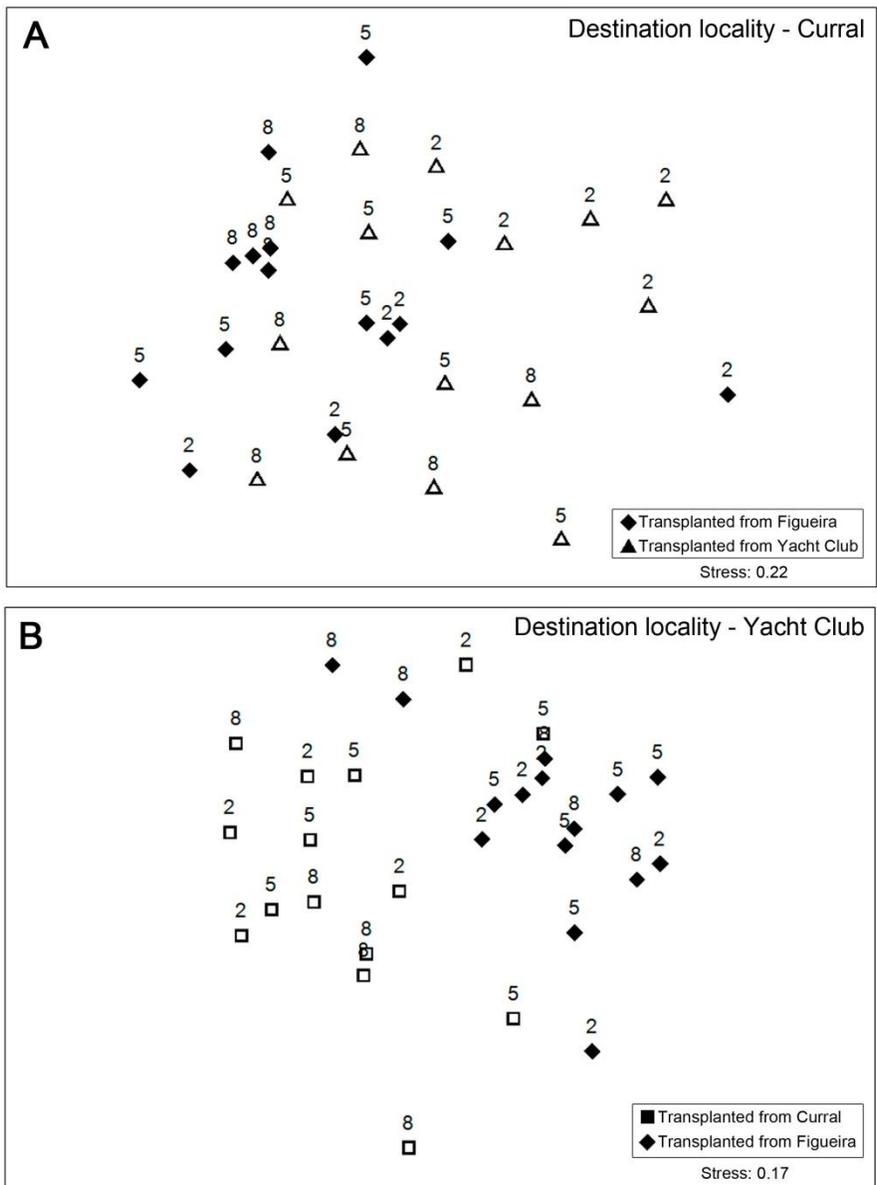


Figure 9. nMDS plots comparing transplanted plates from Figueira and Yacht Club at Curral (A) and from Curral and Figueira at Yacht Club (B). Numbers indicate the transplant date in weeks.

Table 5. PERMANOVA comparing composition of assemblages from Figueira (FI) and Yacht Club (YC) at Curral (CU) and from Figueira and Curral at Yacht Club, in panel groups transplanted at different dates (2, 5 and 8 wk).

Source of Variation	<i>df</i>	<i>MS</i>	<i>F</i>	<i>p</i>
<b><i>FI vs. YC at CU</i></b>				
Origin	1	2909	3.50	<b>0.005</b>
Transplant Date	2	2261	2.72	<b>0.004</b>
Origin x Transplant Date	2	1039	1.25	0.275
Error	24	830		
<b><i>FI vs CU at YC</i></b>				
Origin	1	8513	9.54	<b>0.001</b>
Transplant Date	2	827	0.93	0.556
Origin x Transplant Date	2	1333	1.49	0.138
Error	24	892		

## DISCUSSION

Our results demonstrate that communities deeply drifted from the original situation and become more similar to destination ones, regardless the direction and the moment of transplant. Even communities shifted from an open (Yacht Club) to a closed locality (Curral) became more similar to destination. These results show us that the communities considered exhibit very low resilience (Holling, 1973; Connel and Sousa, 1983; Sutherland, 1990; Gunderson 2000;), at least when faced a shift on pelagic conditions, including the quantity and taxonomic structure of both potential settlers and consumers. Changes in predation and recruitment rates may actually severely affect communities, and lead them to a different stable state (Connell and Sousa, 1983; Sutherland, 1990; Beisner et al., 2003), showing a great importance of current conditions as determinants of communities structure. In this study, however, some unidentified legacy from early colonization avoided communities to become equal to destination.

In a new, more dynamic condition, Curral communities that shifted to Yacht Club received a bunch of new recruits and were always facing consumer pressure, which, allied to a large

unoccupied area (at the last transplant, Curral still had about 30% of free space), resulted in a developing path bringing transplanted communities to a state similar to destination. Besides two local-specific species, the whole invertebrate assemblage found at Curral was also found at Yacht Club, so we can see Curral species as a subset of Yacht Club species, whose populations had just developed at Yacht Club, but with the addition of new species. The opposite transplant direction, from Yacht Club to Curral, also resulted in a shift to a condition similar to destination. Almost all species from Curral were present at Yacht Club, but 10 species were exclusive to Yacht Club. These exclusive species probably could not be maintained at Curral either because they were susceptible to the new abiotic conditions or by the absence of new recruits (Mullineaux et al., 2009). The bryozoan *Amathia* sp. and a red sponge are common at Yacht Club, but were no longer found at Curral after transplant. The death of these species released space and made communities similar to those at Curral.

This situation exemplifies one crucial point of resilience theory. After a disturbance, a community can only return to a pre-disturbance state if environmental conditions (biotic or abiotic) allow restoration of all past attributes (Nyström and Folk, 2001). Because pelagic larvae of the encrusting invertebrates colonizing plates are short-lived, critical conditions affecting shifts include the structure of natural assemblages and predator guilds nearby. When we transplanted these communities to another area, all the set of surrounding conditions were altered and drivers species (Walker, 1992) were removed, avoiding the return to a pre-disturbance pattern (Nyström and Folk, 2001; Mullineaux et al., 2009). The moment right after the disturbance is the most critical, because it is when the community is most susceptible to change, and when developing paths can lead to the widest array of possible stable states (Nyström and Folk, 2001; Holling, 1986, 1992). When the set of conditions was altered, the disturbed (transplanted) communities easily followed a new

trajectory, suggesting that a return route was no longer possible (Connel and Sousa, 1983; Sutherland, 1990; Beisner et al., 2003).

The modifications in the surrounding conditions can explain why plates transplanted in different periods were very similar at the end of the experiment. Even the later transplants (8 wk), which developed during a longer time at the origin, became similar to destination. . The dynamic conditions at Yacht Club and the mortality of non-exclusive species at Curral could quickly shift transplanted communities to destination states, even if they remained several weeks at the origin. The only difference we observed was the segregation of 2 wk transplants at Curral, coming from Yacht Club. This indicates that 5 and 8 wk, although similar to destination panels were slightly different from 2 wk panels. This suggests that a more consolidated community from Yacht Club could maintain some memory, and be more resistant to disturbance when compared to early transplanted communities.

The fact that transplanted communities had become similar, but not equal, to destination showed that early colonization at original sites still play a role (Peterson, 2002; Mullineaux et al., 2009). Comparisons with Figueira transplanted panels indicate that the pioneering assemblage may somehow restrict developing pathways. Ecological memory ensures that community can return to an original state after a disturbance (Peterson, 2002; Bengtsson et al., 2003, Golinsky et al., 2008). In our case this turn back did not happen, probably because of the lack of surrounding conditions at destination. Yet, intrinsic characteristics of transplanted communities avoided a total shift to a destination pattern. Those species that occurred exclusively at each site could maintain this legacy after the transplantation and contribute to the retention of some characteristics from the original site (Franklin and MacMahon, 2000). For instance, the bryozoan *Crisia* sp1., only occurred at Yacht Club in panels transplanted from Curral. Also, early colonizers at Curral, barnacles and hydrozoans remained abundant even after transplanted to Yacht Club. Other bryozoans like *Watersipora*

*subtorquata* and *Catenicella uberima*, exclusive to Yacht Club, survived in low abundances at Curral, after transplantation, and probably contributed to Yacht Club legacy after disturbance. Interestingly, most of these species are bryozoans and can indicate a trend of resistance either to environmental conditions or to predators activity, as suggested by other studies (Russ, 1980; Osman and Whitlatch, 2004).

The kind of disturbance we simulated was intense and led transplanted communities to follow trajectories distinct from those at original sites, taking them to an alternative state, similar to that of the destination community. Apparently, the lack of surrounding conditions similar to the original site avoided transplanted communities to return to pre-disturbance states. This can indicate that the simple reposition of species in disturbed areas probably won't lead to a restoration of the system, unless environmental conditions have been also restored. However, our study show that intrinsic characteristics, like survivor of exclusive species, maintained an ecological memory and contributed to the retention of some original traits, avoiding the total similarity among transplanted and destination communities. After severe disturbance, communities may still be capable to track original pathways, provided that 'ecological memory' is strong enough. This study shows that original legacy can be insufficient, even when developing assemblages are close to climax, and that post-disturbance drivers can be strong enough to cause a shift in direction to a determined state.

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## CONSIDERAÇÕES FINAIS

Este trabalho mostrou como alguns processos classicamente tidos como importantes afetam a estrutura de comunidades incrustantes e como essas comunidades seguem a sucessão após um distúrbio severo. Especificamente este estudo mostra que:

1. Os efeitos da predação sobre atributos e na estruturação da comunidade podem ser fracos em larga escala, mas são observados de forma mais localizada. Já os efeitos da exclusão de predadores, apresentaram uma grande variação em micro escala, sendo evidenciados em alguns painéis dentro de um mesmo local.
2. O padrão de recrutamento foi coincidente com o padrão de riqueza, com locais mais ricos apresentando maior taxa de recrutamento. Isso evidencia um possível feedback entre esses dois fatores, o qual pode ser importante para a manutenção da diversidade da comunidade e sua resiliência frente a distúrbios.
3. O efeito localizado da predação, associado à possível variação à micro escala do recrutamento, pode contribuir para a grande variação em riqueza e estrutura que vimos dentro de cada localidade. Essa grande variação também pode ser importante para a manutenção da diversidade regional, contribuindo também para uma maior resistência a distúrbios.
4. Após um distúrbio severo, as comunidades manipuladas não voltaram aos seus padrões originais, ficando semelhantes às comunidades do destino. Como esse resultado foi geral, considerando ambas as direções e os vários momentos de transplante, conclui-se que as condições do destino, foram mais fortes, determinando novas trajetórias para as comunidades transplantadas e levando-as a novos estados de equilíbrio.
5. Apesar da importância das novas condições, efeitos do legado da colonização e desenvolvimento inicial foram constatados, embora fracos e ineficientes para garantir a recuperação da comunidade para padrões originais.

## **APÊNDICE**

(listagem das espécies encontradas)

## CAPÍTULO 1

Table 1. List of ascidians, barnacles, bivalves, bryozoans, hydrozoans, polychaetes and sponges species and morph-species found at study localities after 30 and 100 days during the predation pressure and recruitment rate experiment. Data from Cural is not shown for 100 days due to loss of sample units.

	30 days				100 days		
	Feiticeira	Cural	Figueira	Yacht Club	Feiticeira	Figueira	Yacht Club
<b>Ascidians</b>							
<i>Ascidia curvata</i>	X	X	X	X	X	X	X
<i>Ascidia interrupta</i>			X		X	X	X
<i>Botrylloides nigrum</i>	X	X	X	X	X	X	X
<i>Botryllus tabori</i>						X	
<i>Ciona intestinalis</i>						X	X
<i>Clavelina oblonga</i>	X			X	X	X	X
<i>Didemnum perlucidum</i>	X	X	X	X	X	X	X
<i>Didemnum psammotodes</i>	X	X	X	X	X	X	X
<i>Didemnum</i> sp1.				X	X		X
<i>Didemnum</i> sp2.		X			X	X	X
<i>Didemnum</i> sp3.							X
<i>Diplosoma listerianum</i>	X	X	X	X	X	X	X
<i>Diplosoma</i> sp.							X
<i>Distaplia bermudensis</i>							X
<i>Herdmania pallida</i>	X	X		X	X	X	X
<i>Lissoclinum</i> sp.	X		X	X	X		X
<i>Microcosmus exasperatus</i>					X	X	X
<i>Phallusia nigra</i>	X	X	X	X	X	X	X
<i>Policlinum</i> sp.			X	X		X	
<i>Polyandrocarpa zorritenses</i>			X			X	X
<i>Styela plicata</i>						X	X
<i>Symplegma brakenhelmi</i>			X		X	X	X
<i>Symplegma rubra</i>			X		X	X	X
<i>Symplegma</i> sp1	X	X	X	X	X	X	X
<i>Symplegma</i> sp2		X	X		X	X	X
<i>Trididemnum orbiculatum</i>		X		X	X	X	X
<b>Barnacles</b>							
<i>Balanus trigonus</i>	X	X	X	X		X	X
<i>Megabalanus coccopoma</i>		X	X		X	X	
<b>Bivalves</b>							
Ostreidae sp1.	X	X	X	X	X	X	X
Ostreidae sp2.						X	
Unidentified bivalve 1							X
Unidentified bivalve 2					X		X
<b>Bryozoans</b>							
<i>Amathia</i> sp1.				X	X	X	X
<i>Bugula neritina</i>	X	X	X	X		X	
<i>Catenicella uberrima</i>	X	X	X	X	X	X	X
<i>Crisia</i> sp1.				X	X	X	X
<i>Crisia</i> sp2.					X		
<i>Membranipora</i> sp.	X	X		X		X	X
<i>Savignyella lafontii</i>	X	X	X	X		X	X
<i>Schizoporella</i> sp.	X	X	X	X	X	X	X
<i>Scrupocellaria</i> sp.	X		X	X	X	X	X

	Unidentified bryozoan 1		X	X				
	<i>Watersipora subtorquata</i>			X	X			X
	<i>Zoobotrium</i> sp.	X		X	X	X	X	
<b>Hydrozoans</b>								
	<i>Acharadria crocea</i>							X
	<i>Aglaophenia latecarinata</i>	X	X		X	X		
	<i>Eudendrium caraiuru</i>	X	X	X	X	X	X	X
	<i>Obelia dichotoma</i>	X	X	X	X	X	X	X
	<i>Plumularia strictocarpa</i>	X	X			X	X	
<b>Polychaetes</b>								
	Non-calcareous polychaetes			X	X	X	X	X
	Serpulidae	X	X	X	X	X	X	X
<b>Sponges</b>								
	<i>Desmanthus meandroides</i>	X	X	X	X	X	X	X
	<i>Leucandra serrata</i>		X		X	X	X	X
	<i>Mycale americana</i>	X	X	X	X	X	X	X
	<i>Mycale magnirhaphidifera</i>	X	X		X	X		X
	<i>Mycale microsigmatosa</i>					X	X	

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## CAPÍTULO 2

Table 1. List of ascidians, barnacles, bivalves, bryozoans, hydrozoans, polychaetes and sponges species and morph-species found at study localities during the transplant experiment.

	Curral	Yacht Club
<b>Ascidians</b>		
<i>Botrylloides nigrum</i>	X	X
<i>Botryllus tuberatus</i>	X	X
<i>Clavelina oblonga</i>	X	X
<i>Didemnum perlucidum</i>	X	X
<i>Didemnum psammotodes</i>	X	
<i>Didemnum</i> sp4.		X
<i>Diplosoma listerianum</i>	X	X
<i>Herdmania pallida</i>		X
<i>Microcosmus exasperatus</i>		X
<i>Perophora</i> sp.		X
<i>Symplegma brakenhelmi</i>	X	
<i>Symplegma rubra</i>	X	X
<i>Symplegma</i> sp1.	X	
<i>Trididemnum orbiculatum</i>	X	X
<b>Barnacles</b>		
<i>Balanus trigonus</i>	X	X
<i>Megabalanus coccopoma</i>	X	X
<b>Bivalves</b>		
Ostreidae sp1.	X	X
Unidentified bivalve 3		X
<b>Bryozoans</b>		
<i>Amathia</i> sp.		X
<i>Bugula neritina</i>		X
<i>Catenicella uberrima</i>		X
<i>Crisia</i> sp1.	X	X
<i>Crisia</i> sp2.	X	
<i>Membranipora</i> sp.	X	X
<i>Schizoporella</i> sp.	X	X
<i>Scrupocellaria</i> sp.		X
<i>Watersipora subtorquata</i>		X
<i>Zoobotrium</i> sp.		X
<b>Hydrozoans</b>		
<i>Acharadria crocea</i>	X	X
<i>Eudendrium caraiuru</i>		X
<i>Obelia dichotoma</i>	X	X
<b>Polychaetes</b>		
Serpulidae	X	X
<b>Sponges</b>		
<i>Desmanthus meandroides</i>	X	X
<i>Mycale americana</i>		X
<i>Mycale microsigmatosa</i>		X