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Does primary colonization or community structure determine the succession of fouling communities? ☆

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ABSTRACT

Predicting the relevance of initial colonization and subsequent species interactions for succession in marine sessile communities is difficult because the effects of both factors depend on highly variable environmental processes (e.g. currents, topography, upwelling and others). Depending on the successional stage at which a new species arrives, it can either rapidly colonize in large numbers or its colonization success might be suppressed by resident species. In order to assess the roles of (i) initial colonization and (ii) subsequent species interactions on community development, we examined the succession of fouling assemblages that established on artificial substrata during two different seasonal periods, i.e. austral winter/spring and spring/summer. At 16 weeks of age communities that were initiated in different seasons varied significantly in composition and diversity. During each period (winter/spring and spring/summer), multispecies fouling consortia of different ages (hereafter termed “old” and “young”) were reciprocally transplanted between two neighbouring study sites and their succession was documented. After 8 weeks of transplantation communities of different ages maintained their differences in diversity even in the face of environmental change. However, during winter/spring the spreading of the dominant species *P. chilensis* caused more rapid convergence between all communities at both sites. During the spring/summer period, the high initial abundances of the weak competitor *Bugula neritina* led to the maintenance of differences between resident and transplanted assemblages within each site. Later colonizers, including the dominant competitor *P. chilensis*, however, could recruit onto *B. neritina* and started to spread in the communities. These results suggest that the early and intermediate succession of fouling communities in highly productive marine environments such as the Humboldt Current System is driven by the temporal and spatial variability of propagule supply, while the long-term stability of these communities depends on the identity of colonizers and their competitiveness.

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1. Introduction

Terrestrial and aquatic communities are frequently exposed to newly arriving species that attempt to settle in them (Connell and Slatyer, 1977; Sutherland and Karlson, 1977; Gaines and Roughgarden, 1985; Snelgrove et al., 2001; Lu and Wu, 2007; Picaud and Petit, 2007). Their long-term establishment, following successful reproduction or growth, can change the course of community succession through either positive or negative interactions with resident species (Connell

and Slatyer, 1977). Large temporal variations in disturbance as well as in the intensity and composition of propagule supply can make succession and therefore the diversity and structure of mature communities unpredictable (i.e. contingent succession; Berlow, 1997; Petraitis and Dudgeon, 1999). While these historical effects can lead to a rather stochastic initial succession, strong species interactions could drive communities towards a unique and predictable mature state that is dominated by few species (i.e. canalized succession; Berlow, 1997). As a consequence, reliable predictions about the course of succession require a good knowledge of the arrival sequence of colonizers, their competitive abilities as well as of the interactions between residents and new settlers (Benedetti-Cecchi, 2000a,b). In order to understand how community succession proceeds in marine benthic habitats, it is important to (i) uncover the spatial and temporal patterns of initial colonization, and (ii) examine how initial settlers determine the colonization success of later arrivals.

☆ This paper is dedicated to the memory of Drs. Louis H. DiSalvo and Carlos Antonio Viviani who initiated studies on the fouling communities from Bahía La Herradura.

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The simple fact of arriving first on open space confers advantages to primary colonizers, especially for opportunistic pioneer species, which are often weak competitors that commonly exploit open substrata only for short time periods. Hence, arrival sequence can produce priority effects (Paine, 1977), which occur when primary colonizers with high growth rates quickly monopolize resources (e.g. space), thereby suppressing later colonizers. The persistence of priority effects depends on the life histories and relative competitiveness of primary and secondary colonizers (Berlow, 1997). In the marine benthic environment, the sequence of colonizer arrival can therefore have a strong influence on the diversity and structure of mature communities (Sutherland and Karlson, 1977; Benedetti-Cecchi, 2000b; Lu and Wu, 2007).

Recruitment in communities at early successional stages, composed of short-lived species of small body size, fast reproduction and putatively low competitiveness, is suggested to be relatively independent from biotic interactions compared with communities at advanced successional stages (see e.g. Odum, 1969; Connell and Slatyer, 1977). During the course of succession, some species may spread by asexual reproduction or lateral growth, leading to competitive exclusion of neighbors or new colonizers. Growth of large species during community succession reduces the amount of free space, making the potential arrival of new colonizers difficult. Disturbances can break this barrier and can therefore change the course of succession in communities of sessile invertebrates by creating free space suitable for colonization (Osman, 1977; Connell and Slatyer, 1977; Sousa, 1979).

A theoretical model by Platt and Connell (2003) emphasizes that catastrophic disturbances producing colonizable space completely free of competitors will always lead to directional species replacement (i.e. primary colonizers being replaced by secondary colonizers). However, under natural conditions catastrophic disturbances are not common and most disturbance events leave some survivors, especially secondary species that could recolonize the adjacent disturbed sites. Secondary colonizers are often larger and stronger competitors than primary colonizers, and they can better resist physical and biological disturbances that might be catastrophic for primary colonizers (see e.g. Pianka, 1970; Gadgil and Solbrig, 1972; Wilbur, 1974; Sousa, 1979; Weis et al., 2007). Here the rapid recolonization of small disturbed patches via vegetative ingrowths from the remaining species, as shown e.g. by Sousa (1984), will suppress recruitment of colonizers from the water column, thereby breaking the directional replacement during the successional process (Platt and Connell, 2003).

While the general factors affecting the succession of communities are known, the exact mechanisms driving community succession under variable scenarios of species arrival and availability of open space are not yet well understood. The temporal (mis)match between the provision of colonizable substratum (Cifuentes et al., 2007) and propagule supply (Gaines and Roughgarden, 1985; Snelgrove et al., 2001; Lagos et al., 2005) could produce variable sequences of colonization in a similar way as proposed by Platt and Connell (2003).

In this study, we used communities of sessile macroinvertebrates and macroalgae to study (i) how the starting time of colonization affects the initial succession of fouling consortia, and (ii) how a change in environmental conditions influences the course and speed of advanced succession. To test this, we conducted a transplant experiment with fouling communities, which was repeated during two different seasons (austral winter/spring and spring/summer). This approach allowed us to generate assemblages with different starting times of colonization and simultaneously explore the importance of community structure in driving their succession.

In the study system, the tunicate *Pyura chilensis*, the colonial ascidian *Diplosoma* sp. and the arborescent bryozoan *Bugula neritina* are the most abundant taxa, and *P. chilensis* is considered the dominant competitor (Ambler and Cañete, 1991; Valdivia et al.,

2005; Cifuentes et al., 2007). Previous studies conducted in the same geographic region indicated that these taxa have different seasonal peaks of reproduction (Valdivia et al., 2005; Cifuentes et al., 2007). To identify these seasonal peaks, we monitored the arrival of their recruits at each study site throughout the entire experimental period.

Given different seasonal peaks in propagule supply, these fouling communities are ideally suited to explore the theoretical model proposed by Platt and Connell (2003), i.e. the importance of arrival sequence during initial colonization versus taxon interactions in driving community succession. Following the Platt and Connell model, we propose that the provision of colonizable space at different times should offer establishment opportunities for different taxa of primary colonizers, such as e.g. *Diplosoma* sp. and *B. neritina*. After initial colonizers have established, the between-taxon interactions then become the main mechanism of community regulation. During aging of communities, these between-taxon interactions, rather than colonization processes, should gain in importance due to the occupation of resources such as space. This will then suppress further colonization. Therefore, transplantation of established communities to a site with different regimes of colonizer arrivals should not affect the canalization of those communities towards a unique and dominated successional stage. In highly productive systems, such as the Humboldt Current System, high growth rates of all sessile colonizers should enhance the importance of competition for substratum, favoring the spread of dominant taxa. The solitary tunicate *P. chilensis*, a species well adapted to these productive conditions, is expected to dominate and produce a canalized succession in these fouling communities.

2. Materials and methods

2.1. Study sites

2.1.1. Site description

The study was conducted in Bahía La Herradura (3.3 km²) situated on the northern-central coast of Chile (29°59'S, 71°22'W). Surface water temperatures range from ~13 °C in winter to ~20 °C in summer (Moraga and Olivares, 1993). The bay has a west-facing opening of 0.7 km, an average depth of 30 m and negligible freshwater inflow. Coastal waters in the study area are under the influence of an upwelling centre about 40 km southwest of Bahía La Herradura (Acuña et al., 1989), and the complete volume of the bay is exchanged on average every three days (Moraga and Olivares, 1993). The growth rates of fouling communities are therefore high in this productive system and artificial substrata are usually rapidly and intensively colonized by bryozoans, hydrozoans, solitary and colonial ascidians, barnacles and macroalgae (Viviani and DiSalvo, 1980).

The two sites used in this study were located within the bay over a sandy bottom at 6–7 m depth; one site was close to the opening of the bay, and the other near a loading pier in the interior part of the bay (Fig. 1). Along the northern and central Chilean coast strong equatorward winds are common during spring and summer (Pizarro et al., 1994; Shaffer et al., 1999; Rutllant et al., 2004). These wind conditions are well known to produce upwelling events, but also induce currents that move surface waters in wind direction (Gill and Clarke, 1974). During strong wind events, the site close to the bay opening is more exposed to wave surge than the site behind the loading pier, and we therefore refer to them in the following as 'exposed' and 'protected', respectively. This difference should lead to a reduced frequency and intensity of larval transport at the latter site compared to the exposed site.

2.1.2. Recruitment monitoring

At each of the two study sites, we monitored the natural sequence of colonizer arrival with recruitment panels. We placed one PVC ring (25 cm high, 60 cm diameter) with 9 panel positions at each study site. PVC panels (15 cm × 15 cm and 3 mm thick) were used as

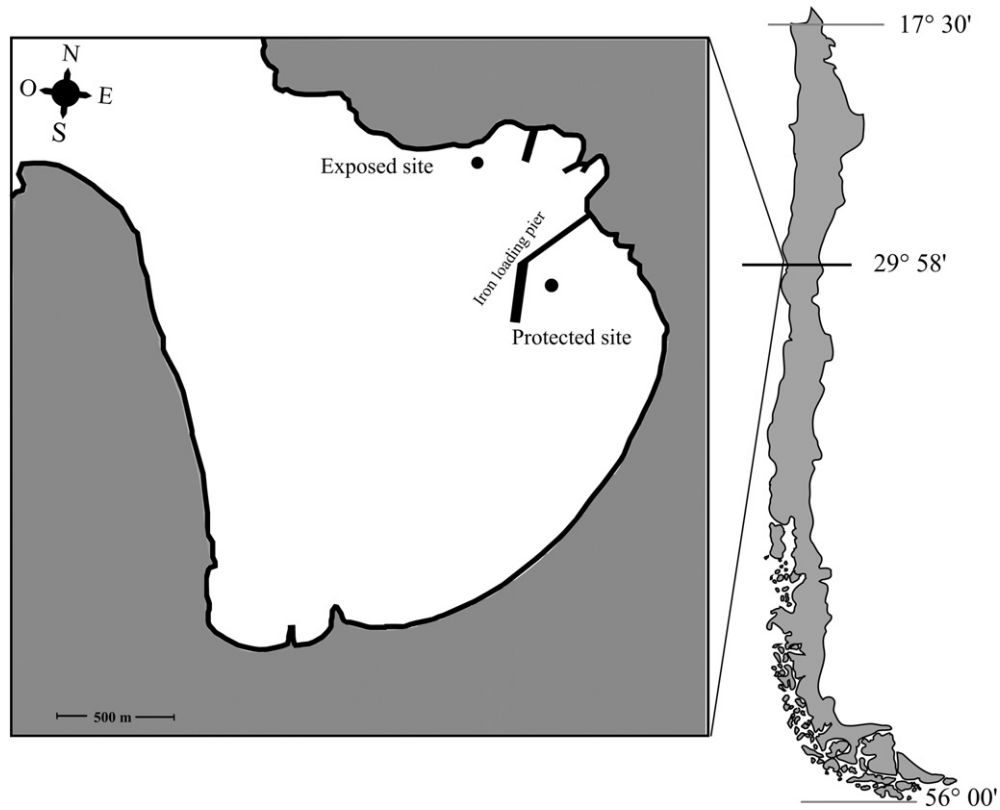


Fig. 1. Map of Bahía La Herradura, Chile and the two study sites (●). The exposed site is the same site that had been used in previous studies (Valdivia et al., 2005; Cifuentes et al., 2007, where this was the northern site).

artificial recruitment substrata. One side of the panels was roughened with sandpaper (grain 60) to facilitate larval settlement. Panels were attached in vertical position to the inside of rings with cable ties, with at least 10 cm between adjacent panels. The rings were suspended 0.5 m below the surface on a mooring buoy. The recruitment monitoring started with 3 settlement panels randomly placed onto the ring, and every 2 weeks 3 new panels were added until all panel positions were filled (after 4 weeks). After that, the first 3 panels, which had been exposed for 6 weeks, were removed and replaced by 3 new panels. Recruitment was monitored from 27th October 2005 (first sampling) to 14th April 2006 (last sampling). Recruit densities on each panel corresponded to the temporal integration of 6 weeks of recruitment. At the end of each 6-week recruitment phase, the 3 panels from each site were transported to the laboratory and the percent cover of *B. neritina* and *Diplosoma* sp. and the number of recruits of *P. chilensis* were estimated under the dissecting microscope. Although we monitored the recruitment of all species we only present those three, because they have been observed to be among the most important species inhabiting fouling communities in the study system (see Table S1; Valdivia et al., 2005; Cifuentes et al., 2007).

2.2. General design and experimental set-up

We conducted two identical experiments, one in austral winter/spring and one in spring/summer (Fig. 2a and b). We used these two experiments to analyze (i) how different starting times of colonization affected the initial structure of fouling communities, i.e. cover of each taxon inhabiting a community (Fig. 2a), and (ii) how the structure of fouling communities proceeded after a change in the environmental conditions (Fig. 2b). We ran two identical seasonal experiments, because intensity of settlement and the composition of

the colonizer pool differ substantially between seasons in this geographical region (Lagos et al., 2005, 2007). For the first experiment (austral winter/spring), colonization panels were placed on 16th August and on 11th October 2005, and for the second experiment (austral spring/summer) on 8th November 2005 and on 3rd January 2006 (Fig. 2). A subset of the data from both experiments was used to examine the effects of different starting times on the structure of fouling communities (Fig. 2a). We then analyzed the full data sets to explore how a change in environmental conditions (after transplantation of panels) influenced community succession. For this, the two seasonal experiments were analyzed separately (Fig. 2b).

For each seasonal experiment, 64 panels were used as artificial settlement substrata. Panels were equally distributed over 8 PVC rings, 4 rings at each study site with 8 panels on each ring. To obtain communities of different ages, for each seasonal experiment 2 rings (yielding "old" communities) were deployed at each site 8 weeks before the second set of rings (yielding "young" communities); during transplantation panels were randomly distributed among the rings (see subchapter 2.5.). At each of the two study sites, the rings were positioned randomly at a minimum distance of 4 m (to exclude the risk of touching) but within an area of approximately 200 m² to minimize spatial heterogeneity.

2.3. Sampling of fouling communities

Communities on panels were first surveyed on the day of transplantation and then every two weeks during the 8 weeks after transplantation. Panels were carefully transported to the nearby laboratory and were constantly submerged in seawater to minimize disturbances. Percent cover of all sessile taxa >2 mm (in height, diameter or width) was estimated without magnification, while the cover of smaller taxa was quantified using a dissecting microscope. A

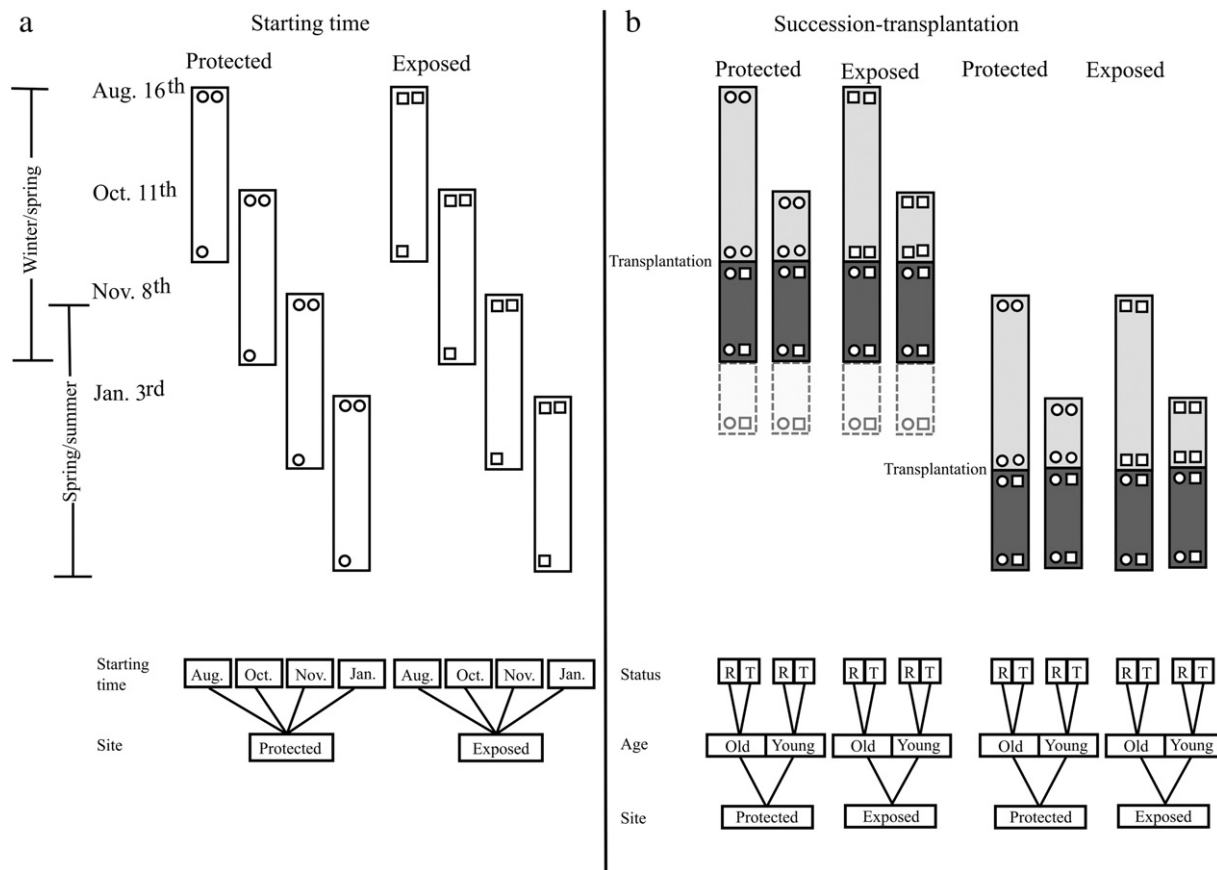


Fig. 2. Data from the same experimental setup were used to evaluate (a) the effect of starting time on the structure of fouling communities of identical age (4 months) during different time periods, and (b) the impact of a change in environmental conditions on the structure of young and old fouling communities; i.e. reciprocal transplantation of communities between protected (squares) and exposed (circles) sites, where R = resident communities and T = transplanted communities. The experiment was repeated in winter/spring and in spring/summer periods but while in (a) we only used resident communities from both experiments to analyze the effects of 4 different times in the structure of fouling communities, in (b) each experiment was analyzed separately. In winter/spring the experiment was monitored until 12 weeks after transplantation (stippled area), but for reasons of inter-experimental comparison only the data until week 8 were used for the statistical evaluation.

1-cm wide margin along the border of panels was excluded to avoid sampling of potential edge effects. Multi-strata cover, considered in our sampling, could result in a total cover >100%. Mobile taxa were excluded from the analysis, because most of them were able to escape when the communities were sampled. Sea urchin recruits were manually removed to avoid potentially confounding grazing effects, which (due to the patchy distribution of sea urchins) would have interfered with the experimental design. To remove the dense overgrowth developing on rings, which could interfere with community succession on the panels, we scrubbed the PVC rings with a hand-brush and rinsed them with freshwater, first at the transplantation event and then during each subsequent sampling event.

2.4. Effect of starting time on initial colonization of open substratum

In order to determine the effects of starting time on the structure of fouling communities, we compared communities at their site of origin (resident communities; Fig. 2a) when they reached an age of 16 weeks. Combining data from both seasonal experiments allowed us to examine the effects of different starting times of colonization during the reproductive periods of the most common fouling taxa in the study region. In total there were 4 different starting times, 2 per seasonal period, and we had 8 replicate resident communities per starting time and site. Starting times of colonization combined with temporal and spatial variability in larval supply were hypothesized to produce communities of similar age but with different structure.

The structure and composition of the communities with the 4 different starting times was compared with a permutational method of

variance analysis, i.e. PERMANOVA (Anderson, 2001; McArdle and Anderson, 2001). For this, Bray-Curtis dissimilarity, calculated from percent cover data, was used as a distance measure, performing 4999 unrestricted permutations of raw data (Anderson, 2005). To ensure statistical independence among panels of one ring, a Mantel test (Mantel, 1967) was performed by correlating the distance matrices for community structure with the spatial dissimilarity of compared communities. Variance assumptions were tested with PERMDISP (Anderson, 2004) and when significant effects were detected by PERMANOVA ($p < 0.05$), differences between levels within treatments were identified comparing all possible pair combinations (i.e. post-hoc pairwise comparisons). The contribution of individual taxa to Bray-Curtis similarities and dissimilarities within and between experimental treatment levels, respectively, was examined with SIMPER analyses (PRIMER software; Clarke and Warwick, 2001). While we based our analyses on the matrix cover of all sessile macroinvertebrates and macroalgae present in the communities, to better understand the outcome of the colonization experiments, we also present the phenology of three main taxa in the developing fouling communities: *P. chilensis*, *Diplosoma* sp. and *B. neritina*.

In the PERMANOVA design, the fixed factors were starting time with 4 levels (August, October, November and January) and site (exposed and protected). We further included ring as a random block factor, which was nested in the interaction of starting time and site, to evaluate small-scale spatial heterogeneity. Discriminant plotting methods (nMDS plots; Clarke and Warwick, 2001) were used to help in the interpretation of multivariate data by visualizing the differences between treatment levels.

2.5. Community structure and its importance for the persistence of fouling assemblages

We compared resident and transplanted communities of different ages (early and advanced stages of succession) to examine the relative importance of environmental variability and within-community interactions on the succession of fouling communities during each season (see design Fig. 2b). We reciprocally transplanted young and old fouling communities between the two study sites. To obtain young and old fouling communities, 16 settlement panels were deployed at each site 16 weeks (on 16th August and 8th November for the winter/spring and spring/summer experiments, respectively) and 8 weeks (on 11th October and 3rd January) before the start of the experiment (i.e. day of transplantation). Thus, each seasonal experiment started with 16 old (16 weeks) and 16 young (8 weeks) communities at each site. Once the colonization phase was completed (i.e. 100% cover), all panels were surveyed and half (eight per successional stage) were randomly transplanted to the other site (Fig. 2b). Each transplanted community was then randomly paired with a resident assemblage of the same age. This pair arrangement between resident and transplanted communities of the same age served to minimize possible negative effects on the arrival of new larval colonizers. Organisms inhabiting older fouling communities might eliminate new colonizers arriving from the water column by filter-feeding or repellent activity (see, Young and Gotelli, 1988; Osman and Whitlatch, 1995; Navarrete and Wieters, 2000), or overgrow successful settlers by lateral spreading toward neighboring communities (Sousa, 1984). Furthermore, we were primarily interested in how fast communities of the same age would structurally converge, rather than how communities at different successional stages affect each other. Finally, since there was a distance of 10 cm between panels, which prevented any direct interaction such as overgrowth, we considered that neighboring communities were independent of each other.

Each of the 4 rings (blocks) at each site held 2 replicate panels for each treatment combination: (1) old resident OR, (2) old transplanted OT, (3) young resident YR, and (4) young transplanted YT. The position of each pair of panels on each ring was determined using a random number assignment. We expected an interactive effect between community age and site at the day of transplantation, indicating that the structures of resident and transplanted communities were different at the start of the experiment.

The rationale for this comparison between ages and sites is that communities with a particular initial structure can suppress later colonizers and impede or delay the convergence of transplanted communities to resident ones. Furthermore, the speed of convergence may depend on the age of communities since older assemblages have fewer open niches and thus might converge at slower rates than younger ones.

The effects of age and site on resident and transplanted communities were evaluated with data collected on the day of transplantation and eight weeks thereafter. A duration of 8 weeks after the transplantation day (i.e. about 6 months after initiation) of the panels was selected because at the study site succession of fouling communities was observed to proceed relatively fast once the initial settlers had established (Valdivia et al., 2005; Cifuentes et al., 2007). Furthermore, those previous studies had shown that diversity started to decrease in undisturbed fouling communities of about 6 months of age; this was due to the spread of *P. chilensis*, which competitively excluded other taxa (Valdivia et al., 2005). To confirm this tendency of increasing competitive exclusion, herein we also show the percent cover of the three principal taxa (*P. chilensis*, *Diplosoma* sp. and *B. neritina*) for the winter/spring experiment during weeks 10 and 12 after transplantation. For reasons of comparability with the spring/summer experiment the statistical comparisons were only done for week 8 after transplantation.

Both seasonal experiments (winter/spring and spring/summer) were analyzed separately but with identical statistical design. A fully

crossed factorial PERMANOVA (using Bray-Curtis, 4999 unrestricted permutations of the raw data set) was used with the fixed factors community age (young and old), site (protected and exposed) and community status (resident and transplanted). The random factor block nested in site allowed us to examine the small-scale spatial heterogeneity within a site. Assumptions of homogeneity of variances were tested with PERMDISP (Anderson, 2004) and post-hoc pairwise comparisons were used to explore significant factor effects. SIMPER analysis allowed quantifying the contribution of individual taxa to Bray-Curtis similarities and dissimilarities within and between experimental treatment levels, respectively (Clarke and Warwick, 2001). Discriminant plotting methods were used to help in the interpretation of PERMANOVA results (nMDS plots; Clarke and Warwick, 2001).

3. Results

3.1. Recruitment

Recruitment rates of the three dominant taxa fluctuated in time (Fig. 3). *B. neritina* showed a pronounced seasonal peak during austral summer (January). It started to recruit earlier at the protected site than at the exposed site (Fig. 3). The abundance of *P. chilensis* recruits was relatively constant over time, but a distinct recruitment peak was observed at the exposed site in March (Fig. 3). *Diplosoma* sp. showed variable colonization patterns at both study sites with moderate recruitment throughout the experiment and a singular peak in December/January (Fig. 3). These results suggest that *Diplosoma* sp. and *P. chilensis* could recruit into fouling communities during most of the year, while *B. neritina* may monopolize colonizable space during austral summer.

3.2. Effect of starting time on initial colonization of open substratum

The structure of 16-week old communities was strongly affected by both location and start of settlement, while the effect of the latter was not consistent across sites (significant interaction, Table 1, Fig. 4). At the exposed site, different seasonal starting times led to communities with different structures, while at the protected site structures were not influenced by the moment of substratum provision (November–January; pairwise comparisons $P > 0.05$; Fig. 4). Although between-site differences in community structure were found in August, November and January (pairwise comparisons $P < 0.05$; small insert in Fig. 4), no differences were detected between communities initiated in October (pairwise comparisons $P > 0.05$; small insert in Fig. 4).

Furthermore, >60% dissimilarities were detected between communities that started to develop in August compared with those that started in November and January (Table 2). *Diplosoma* sp. and *P. chilensis* were mostly responsible for within-group similarities in communities that were initiated on 16th August (Table 2), while a strong influence of *B. neritina* on the structure was found in communities started on 11th October, 8th November and 3rd January, probably caused by the high recruitment rate of this species during early summer (December and January; Fig. 3).

3.3. Community structure and its importance for the persistence of fouling assemblages

3.3.1. Structure of resident and transplanted communities on the transplantation day

In both experiments (winter/spring and spring/summer), a significant interaction between age, site and transplantation status confirmed a difference in community structure when we started the experiment, i.e. transplanted half of the communities (Table 3; Fig. 5). However, communities that developed during spring/summer, for example YR and YT communities at the protected site, did not differ at the day of transplantation (Fig. 5). This similarity in community

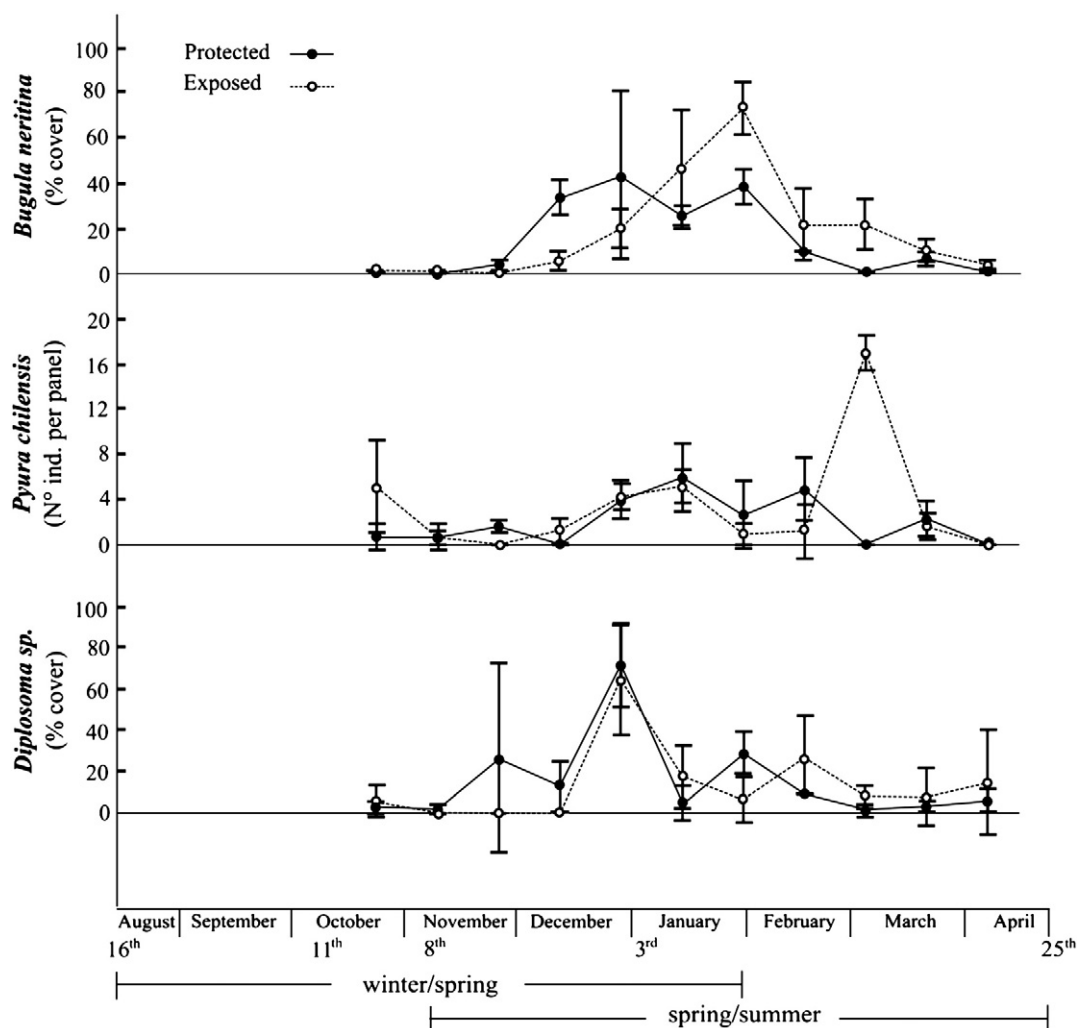


Fig. 3. Recruitment patterns during the experimental period. Average percent cover of recruits of *Bugula neritina* and *Diplosoma* sp. and number of recruits of *Pyura chilensis* throughout the experimental period (winter/spring and spring/summer) at each study site (protected and exposed). Each point represents the mean ± 1 standard deviation of recruits found on panels of 196 cm² exposed to the natural pool of colonizers for 6 weeks.

structure was confirmed by between-site comparisons showing that YT communities at the protected and exposed site also did not differ from each other (central inserts in Fig. 5).

During the winter/spring experiment, only opportunistic taxa such as *Diplosoma* sp. (average of both sites ~7%) and *B. neritina* (average of both sites ~1%) were present in the young communities (8 weeks old) before transplantation, while all three dominant organisms were found in the old communities (16 weeks old) (Fig. 6 and Fig. S1). In the spring/summer experiment, *B. neritina* and *Diplosoma* sp. were highly dominant in young as well as old communities at the day of

transplantation, but recruits of *P. chilensis* were already present, albeit in low abundance (~1% at each site).

3.3.2. Structure of resident and transplanted communities after transplantation

In both seasonal experiments differences in structure between fouling communities of different ages persisted for eight weeks after transplantation (Table 3; Fig. 5). In the winter/spring experiment the persisting interaction between site and status (Table 3) indicates that transplanted communities remained similar in structure to their sister communities at their site of origin. Nevertheless, a convergence in community structure of resident and transplanted same-age communities was observed at each site, with exception of old transplanted and resident communities at the exposed site; these old communities caused the significant interaction between age, site and transplantation status of the communities (Table 3; Fig. 5). In the winter/spring experiment, the three main taxa (*Diplosoma* sp., *B. neritina* and *P. chilensis*) increased in cover after transplantation (Fig. 6). In the young communities, the dominant competitor *P. chilensis* started to increase (from 1% to 15% cover) towards week 8 after transplantation, while in old communities it was already among the most abundant species and continued to increase from 24% to 80% cover (Fig. 6 and Fig. S1). At the two extra samplings of the winter/spring experiment (weeks 10 and 12 after transplantation; Fig. 6), percent cover of

Table 1
PERMANOVA results of comparisons in the structure of communities of same age (16 weeks) that had different starting times of colonization (starting time – ST) at two experimental sites (site – SI). Significant values are highlighted in bold.

Source	Community structure			
	df	MS	F	P(perm)
SI	1	2518.07	4.90	0.012
ST	3	16,536.43	32.20	0.000
RI(SI×ST)	24	513.62	1.15	0.260
SI×ST	3	1893.60	3.69	0.008
Residual	32	447.89		

SI = site; SP = starting time; RI = ring.

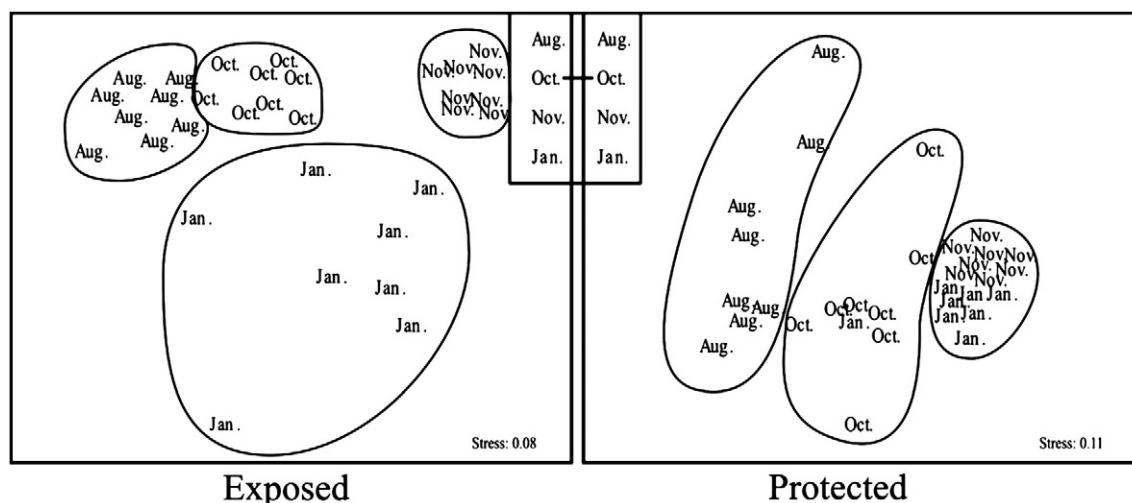


Fig. 4. nMDS ordination of structure of communities of similar ages but different starting time of initial colonization (i.e. August, October, November, and January). Between-site differences in the structure of communities are shown in the small central inserts of the figure: a line connecting the two sites indicates no difference. Lines surrounding points in the main plots separate the communities within a site that differ significantly in structure. Between-site line connectors and within-site circles are the graphical representation of post-hoc pairwise comparisons performed after PERMANOVA analysis.

Table 2
Comparative matrix showing similarities and dissimilarities between communities with the same and different starting time of colonization, respectively. For each pair, the average community similarity (S) or dissimilarity (D) and the species that contributed more than 10% to those values are shown (SIMPER).

	16 August	11 October	8 November	3 January
16 August	S = 66.23 <i>Diplosoma</i> sp. = 57.24 <i>Pyura chilensis</i> = 18.16 <i>Bugula neritina</i> = 11.03			
11 October	D = 46.06 <i>Bugula neritina</i> = 33.68 <i>Diplosoma</i> sp. = 21.99 <i>Pyura chilensis</i> = 12.64 <i>Obelia</i> sp. = 11.60	S = 70.56 <i>Diplosoma</i> sp. = 43.53 <i>Bugula neritina</i> = 41.65 <i>Obelia</i> sp. = 6.30		
8 November	D = 77.35 <i>Bugula neritina</i> = 38.62 <i>Diplosoma</i> sp. = 30.61 <i>Pyura chilensis</i> = 11.35	D = 48.52 <i>Diplosoma</i> sp. = 43.08 <i>Bugula neritina</i> = 21.25 <i>Obelia</i> sp. = 11.84	S = 83.27 <i>Bugula neritina</i> = 85.83	
3 January	D = 64.85 <i>Bugula neritina</i> = 30.27 <i>Diplosoma</i> sp. = 25.34	D = 45.64 <i>Diplosoma</i> sp. = 31.40 <i>Bugula neritina</i> = 21.33 <i>Obelia</i> sp. = 11.74	D = 39.40 <i>Bugula neritina</i> = 29.49 <i>Diplosoma</i> sp. = 22.93 <i>Ciona intestinalis</i> = 16.86	S = 68.06 <i>Bugula neritina</i> = 53.07 <i>Diplosoma</i> sp. = 18.18 <i>Ciona intestinalis</i> = 12.09

Table 3
Winter/spring and spring/summer experiments. Differences in community structure on the initial day and 8 weeks after transplantation. Site (exposed and protected), age (young and old) and transplantation status (resident and transplanted) were included in the PERMANOVA model. Degrees of freedom (df), mean squares (MS), F-ratios (F) and permuted probability values (P) are shown. Significant values are in bold.

Source	df	Winter/spring						Spring/summer					
		Transplant day			Eight weeks after transplantation			Transplant day			Eight weeks after transplantation		
		MS	F	P(perm)	MS	F	P(perm)	MS	F	P(perm)	MS	F	P(perm)
AG	1	62,255.32	64.30	0.000	17,759.380	23.64	0.000	7,774.97	20.67	0.000	16,448.14	40.20	0.000
SI	1	569.32	0.70	0.746	260.248	0.19	0.946	691.46	1.58	0.211	2845.59	4.15	0.054
ST	1	837.09	1.00	0.425	799.578	0.88	0.460	459.68	1.69	0.182	520.19	1.06	0.395
RI(SI)	6	809.35	0.77	0.737	1359.018	2.72	0.000	436.88	1.32	0.177	685.19	1.21	0.249
AG × SI	1	1165.74	1.20	0.286	323.179	0.43	0.744	208.33	0.55	0.608	293.39	0.72	0.487
AG × ST	1	410.72	0.49	0.684	−255.400	−1.10	1.000	696.83	2.77	0.063	759.79	1.19	0.319
AG × RI(SI)	6	968.19	0.93	0.540	751.151	1.50	0.093	376.08	1.14	0.308	409.13	0.72	0.803
SI × ST	1	8318.45	9.96	0.000	5342.985	5.91	0.002	3962.76	14.55	0.000	5356.34	10.87	0.000
ST × RI(SI)	6	835.52	0.80	0.706	903.678	1.81	0.028	272.43	0.83	0.676	492.70	0.87	0.615
AG × SI × ST	1	16073.61	19.12	0.000	1152.026	4.96	0.010	1290.53	5.13	0.011	1443.55	2.27	0.102
AG × ST × RI(SI)	6	840.60	0.80	0.700	232.175	0.46	0.975	251.47	0.76	0.756	634.62	1.12	0.321
Residual	32	1045.22			499.104			330.27			566.22		

AG = age; SI = site; ST = transplantation status; RI = ring.

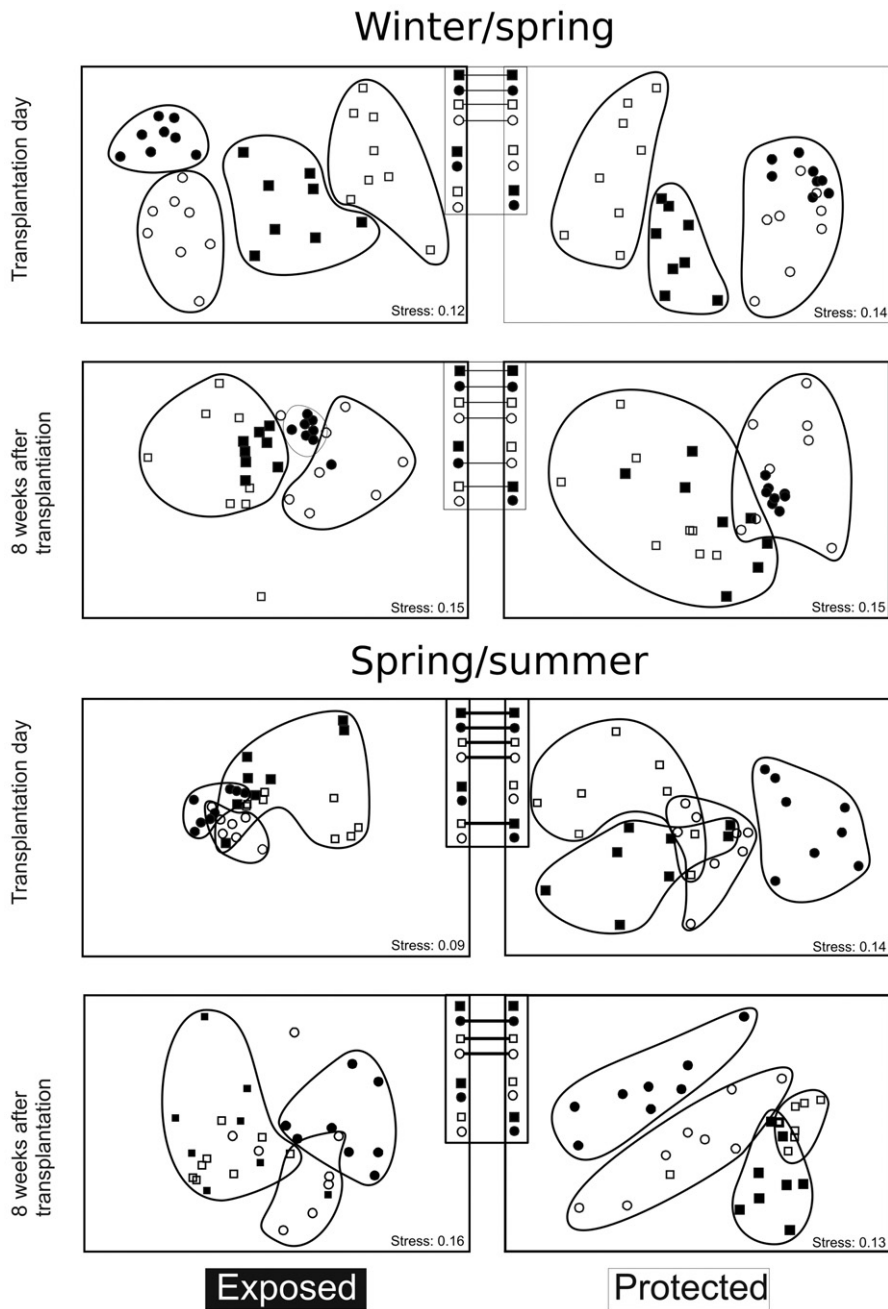


Fig. 5. Winter/spring and spring/summer experiments. nMDS ordination of within-site community structure the transplantation day and eight weeks after transplantation. Half of the young (squares) and old (circles) communities were exchanged between sites. Communities originally (before transplantation) grown on the exposed site are shown in black and those initially grown on the protected site are shown in white. See Fig. 4 for statistical details.

P. chilensis increased to 30% in young communities, while in old communities it reached abundances close to 100% (Fig. 6).

In the spring/summer experiment, most communities within each site maintained the differences in structure they showed at the transplantation date; only YR and YT communities at the exposed site converged during the 8 weeks of the experiment (Fig. 5). Furthermore, during spring/summer the resident communities from the protected and exposed site remained different after 8 weeks; similarly, the transplanted communities placed on the protected and exposed site differed in structure between the two sites at 8 weeks after transplantation (central insert in Fig. 5). In this experiment, *B. neritina*, which dominated at transplantation, decreased in coverage in both young and old communities after transplantation, while *P. chilensis* increased in abundance (Fig. 6)

and started to spread in the communities towards the end of the experiment.

4. Discussion

Our results suggest that the structure of mature fouling communities of Bahía La Herradura is mainly controlled by between-taxa interactions rather than by the timing of colonizer arrival. However, variable sequences of early colonizers (over a 4–6 month study period) produced initial priority effects that were evident until intermediate successional stages. During the winter/spring experiment all assemblages tended to converge towards a canalized community dominated by the tunicate *P. chilensis*. The opportunistic life histories, which are characteristic of the taxa inhabiting these fouling communities, make it

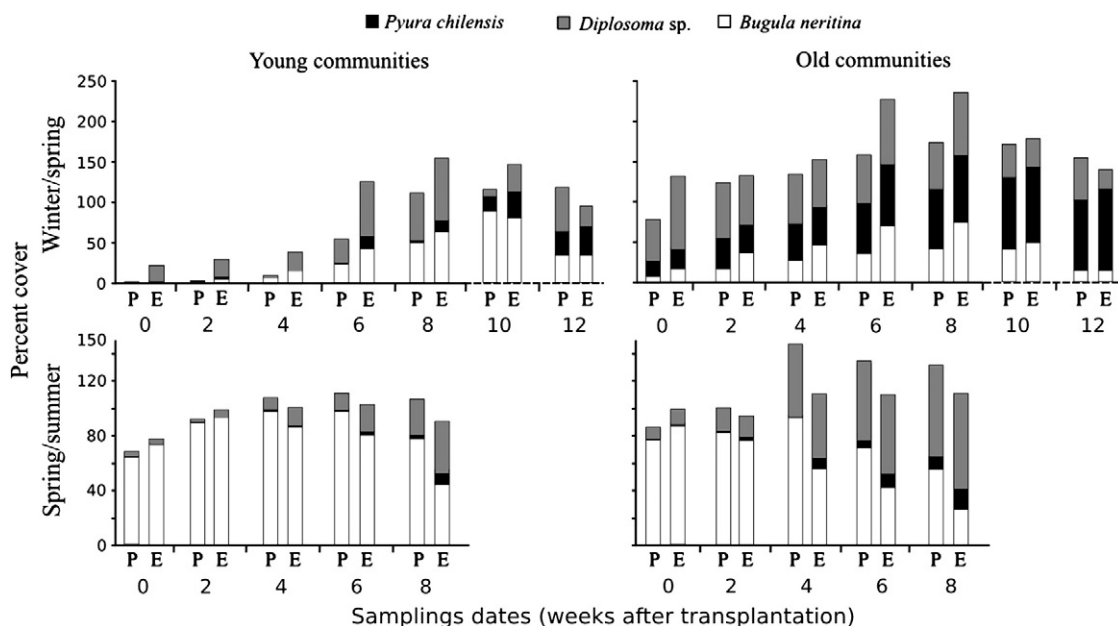


Fig. 6. Change in abundance of the three main species (bars) over time in resident communities at the protected (P) and exposed (E) site. For the winter/spring experiment we also show the data for two extra samplings (weeks 10 and 12); for reasons of comparability between the winter/spring and spring/summer experiments these data were not included in the statistical analyses.

difficult to predict any particular temporal structure in the succession of communities as predicted by Platt and Connell (2003).

At early stages, the succession of fouling communities from Bahía La Herradura appears to follow at least partly the tolerance model proposed by Connell and Slatyer (1977). Pioneer taxa determined initial succession, but dominant taxa later canalized further community development towards a common successional endpoint as suggested by Berlow (1997). Our results thereby permit to refine the predictions by Platt and Connell (2003), indicating that the pool of early colonizers may include various opportunistic and competitive taxa that vary in abundance in accordance with their seasonal reproductive peaks. This consortium of initial colonizers cannot fully inhibit the arrival of others, and later in the successional process the dominant taxa take over and determine the direction of community succession.

4.1. Starting time of initial colonization and intermediate succession of fouling communities

Temporal and spatial changes in richness and abundances of initial colonizers have been observed to influence the succession in marine communities (Sutherland and Karlson, 1977; Lubchenco and Menge, 1978; Sousa, 1979; Benedetti-Cecchi, 2000a; Zajac and Whitlatch, 2003; Lu and Wu, 2007). Along the Chilean coast, invertebrate propagule supply varies over large temporal and spatial scales (Lagos et al., 2005, 2007, 2008), which concurs with our observation of seasonally varying settlement rates in Bahía La Herradura. Additionally, in our experiments, the loading pier possibly caused spatial variation in frequency, intensity and sequence of propagule supply by affecting the current regimes.

Fouling communities that started to develop in different seasons clearly differed in taxonomic diversity and in the general course of succession, although we observed some temporal overlap in their development. This contrasts with a previous study in the same system (Cifuentes et al., 2007), in which the succession of fouling assemblages was not affected by the moment in time when space became available for colonization. This discrepancy probably is due to the differences between the experimental approaches used in the two studies. In the present study we exposed uncolonized panels to recruitment at different starting dates, whereas Cifuentes et al. (2007) generated

open space in already established communities by small-scale disturbances that occurred at irregular time intervals over the course of months. While in our experiment the recruitment panels (196 cm² surface area) were exclusively colonized by planktonic propagules, the small cleared patches (16 cm²) in the study by Cifuentes et al. (2007) were mainly re-occupied by lateral in-growth from the patch margin as also observed by Sousa (1984). The high productivity in the coastal waters of northern-central Chile (Thiel et al., 2007) facilitates for instance the rapid lateral growth of colonial and large solitary ascidians. Therefore, the succession of small patches in this system is controlled by neighboring resident taxa, which excludes recruitment as a driving force for community development (Cifuentes et al., 2007). In a natural scenario, temporally and spatially variable disturbances, such as the impact of drifting logs, might favor different opportunistic taxa, thereby producing communities that vary in species composition as proposed by Platt and Connell (2003). Furthermore, these variable disturbances lead to the coexistences of assemblages at different successional stages. However, in the absence of disturbances superior competitors will exclude opportunistic species.

4.2. Community structure and its importance for the persistence of fouling assemblages

Our naturally assembled communities were heterogeneous with respect to taxonomic and functional composition, and showed contrasting effects in the survival and spread of late colonizers. For example, in the winter/spring experiment, at the time when *P. chilensis* reached its maximum abundance, *B. neritina* decreased and no new recruits settled on the experimental panels, even though large numbers of *B. neritina* colonized substrata that were free of competitors (see Fig. 3). On the other hand, in the spring/summer experiment, communities were dominated by *B. neritina* but recruits of *P. chilensis* were still able to establish between the branches of the bryozoans. Another example of temporal monopolization of substratum comes from a previous colonization study in the same system, in which individuals of the giant barnacle *Austromegabalanus psittacus* were able to recruit extensively at the beginning of the experiment (Cifuentes et al., 2007). However, during succession the dominant competitor *P. chilensis* overgrew the barnacles. These observations strongly suggest

that the life history traits of the taxa inhabiting these communities control the colonization success of settlers from the water column.

Fouling and benthic communities along the Chilean coast are dominated by few taxa (Navarrete and Castilla, 2003; Valdivia et al., 2005; Wieters, 2005; Cifuentes et al., 2007), and the ascidian genus *Pyura* can monopolize (natural and artificial) hard bottom substrata. *P. chilensis* is the superior competitor along the entire Chilean coast (Ambler and Cañete, 1991; Valdivia et al., 2005; Cifuentes et al., 2007), while *P. praeputialis* prevails in northern Chile (Paine and Suchanek, 1983). In our study, two different patterns of intermediate community succession were observed during two seasons. At least in the winter/spring experiment priority effects were of minor importance for the long-term succession of fouling communities from Bahía La Herradura. The high abundance of *P. chilensis* during the winter/spring experiment may have accelerated community convergence towards a *Pyura*-dominated state via conspecific attraction (e.g. Manríquez and Castilla, 2007), thereby leading to rapid displacement of subordinate species. In contrast, during the spring/summer experiment, the high abundance of *B. neritina* might have initially suppressed the recruitment of other colonizer species (pers. obs.). Only some taxa such as the tunicates *P. chilensis* and *Ciona intestinalis* were able to settle among the branches of *B. neritina*, where they were shaded against direct UV radiation, what probably favored their development (see e.g. Bates, 2005). Protection against predation could have been another advantage mediated by *B. neritina*, especially by the juvenile stages of this bryozoan, which produce large amounts of bryostatins with strong anti-predatory effect (see Lopanik et al., 2006).

While *P. chilensis* has lower recruitment rates than other invertebrates in the study system (Ambler and Cañete, 1991), this species nevertheless tends to dominate fouling communities over time. Given the favorable conditions for suspension-feeders on suspended structures, it can be generalized that fouling communities should usually be dominated by tunicates such as *P. chilensis* (present study), bivalves (Greene and Grizzle, 2007) and bryozoans (Lopez, 1989; Barnes and Clark, 1998; Bram et al., 2005). Although our study did not cover late community succession during the spring/summer, our results and those of other studies (Ambler and Cañete, 1991; Valdivia et al., 2005; Cifuentes et al., 2007) allow us to formulate predictions about further succession. Herein the temporary dominance of *B. neritina* underlined the importance of the initial colonization in setting intermediate successional stages, but mature communities are usually dominated by the superior competitor *P. chilensis*.

4.3. Conclusions and outlook

Although there are remarkable differences in the composition of fouling communities throughout the world, some common characteristics should make it possible to extend our conclusions to assemblages in similar environments. Fouling consortia, by definition, are generally placed far above the sea bottom, out of the reach of large predators, which influence the populations of benthic organisms and in consequence the structure of hard bottom communities (Connell, 1961; Fairweather and Underwood, 1991; Alvarado and Castilla, 1996; Menge, 2000; Navarrete and Castilla, 2003; Osman and Whitlatch, 2004). Therefore, competitive interactions among colonists are more important in determining the succession of fouling communities than external agents (Bram et al., 2005; Greene and Grizzle, 2007). In many benthic communities, tunicates are superior competitors (Svane, 1983; Monteiro et al., 2002; Lambert and Lambert, 2003), and competitive dominance is either achieved by asexual expansion or by species-specific attraction of conspecifics (e.g. Yakovis et al., 2008).

This study is one of the first attempts to test the successional model proposed by Platt and Connell (2003). Our results suggest that in highly productive systems, variability in recruitment peaks of colonizers might result in initial and intermediate differences in the structure of fouling communities (priority effects), but competitive

exclusion due to the presence of dominant competitors (e.g. *P. chilensis*) will rapidly homogenize the community resulting in a single stable state (canalized community succession). We propose that initial and intermediate successional stages in such systems can be highly variable (i.e. succession determined by varying initial sequences of colonizers), while late successional stages are highly deterministic if a dominant species is present that efficiently uses the available energy. This leads to convergence into one climax state that is dominated by this/these superior competitor(s) (i.e. succession determined by species interactions).

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Appendix A. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.jembe.2010.08.019.

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