Effects of temporal variability of disturbance on the succession in marine fouling communities in northern-central Chile

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Abstract

We investigated the effects of temporal variability in a disturbance regime on fouling communities at two study sites in a northern-central Chilean bay. Fouling assemblages grown on artificial settlement substrata were disturbed by mechanical removal of biomass at different time intervals. Using one single disturbance frequency (10 disturbance events over 5 months) we applied 7 different temporal disturbance treatments: a constant disturbance regime (identical intervals between disturbance events), and 6 variable treatments where both variableness and sequences of intervals between disturbance events were manipulated. Two levels of temporal variableness (low and high, i.e. disturbance events were either dispersed or highly clumped in time) in the disturbance regime were applied by modifying the time intervals between subsequent disturbance events. To investigate the temporal coupling between disturbance events and other ecological processes (e.g. larval supply and recruitment intensity), three different sequences of disturbance intervals were nested in each of the two levels of temporal variableness. Species richness, evenness, total abundance, and structure of communities that experienced the various disturbance regimes were compared at the end of the experiment (15 days after the last disturbance event). Disturbance strongly influenced the community structure and led to a decrease in evenness and total abundance but not species richness. In undisturbed reference communities, the dominant competitor *Pyura chilensis* (Tunicata) occupied most available space while this species was suppressed in all disturbed treatments. Surprisingly, neither temporal variableness in the disturbance regime nor the sequence of intervals between disturbance events had an effect on community structure. Temporal variability in high disturbance regimes may be of minor importance for fouling communities, because they are dominated by opportunistic species that are adapted to rapidly exploit available space.
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1. Introduction

Many natural systems are characterized by a high degree of variability on various scales (temporal, spatial, and functional). In general, in community ecology the term variability is used to characterize (i) variations in processes that are known to cause and maintain community patterns

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(i.e. predicting variables) and (ii) spatial and temporal variations in community patterns (i.e. response variables). Heterogeneous responses have often been observed in nature, mainly measured in function of the mean effect of independent variables, e.g. disturbance frequency and intensity (Dayton et al., 1992; Collins et al., 2001; Speidel et al., 2001), food supply (Saiz et al., 1999; Crawford et al., 2006) or recruit supply (Roughgarden et al., 1988; Broitman et al., 2001). However, relatively little attention has been paid to the importance of variance around the mean effect of these (and other) predicting variables in ecological processes (but see: Benedetti-Cecchi, 2000; Cardinale et al., 2002; Hutchings et al., 2003; Miner and Vonesh, 2004; Benedetti-Cecchi et al., 2005).

In benthic communities, disturbance is one of the most important driving forces that generate changes in community diversity (Connell and Slatyer, 1977; Davis and Wilce, 1987; McCabe and Gotelli, 2000) and community state (Petraitis and Methratta, 2006). A disturbance represents any discrete event in time that disrupts ecosystem, community or population structure and changes resource availability (White and Pickett, 1985). In this study, we defined disturbance as an external force, which results in a loss of biomass (Grime, 1977). In benthic communities, disturbance mainly provides primary space, which can be colonized during the successional process following a disturbance event (Platt and Connell, 2003). Consequently, community structure depends on numerous factors, many of which are highly variable (e.g. disturbance, larval supply, and recruitment). However, while ecological studies have for a long time focused on the mean influence of these factors in terrestrial (for recent examples see e.g. Collins, 2000; McCabe and Gotelli, 2000; Collins et al., 2001) and aquatic systems (e.g. Gaines et al., 1985; Lenz et al., 2004; Valdivia et al., 2005; and many others), the effect of variability around the mean has only been addressed recently (Benedetti-Cecchi, 2000; Cardinale et al., 2002; Hutchings et al., 2003; Miner and Vonesh, 2004; Benedetti-Cecchi et al., 2005, 2006).

Spatial and temporal variability of recruitment processes have been reported for several systems (e.g. Chapman and Underwood, 1998; Balch and Scheibling, 2000; Bellgrove et al., 2004). Variability in reproduction, pre-settlement predation, and oceanographic transport processes are the main factors affecting recruitment success and intensity (e.g. upwelling and relaxation events; Ebert and Russell, 1988; Connolly and Roughgarden, 1998). Further, previous studies suggest that disturbance (generating space) and propagule supply (providing recruits) could be spatially and temporally out of phase (e.g. Sousa, 1979b; Navarrete, 1996; Menge, 2000; Moore et al., 2004;

Bram et al., 2005; Fig. 1). Therefore, depending on the temporal coupling between disturbance and recruitment events, species succession, structure, and composition of benthic communities may vary.

Hard-bottom communities, especially in the intertidal zone, are one of the best-studied marine systems with respect to the effects of natural disturbance on species diversity and community structure (Sousa, 1979a,b; Wethey, 1985; Davis and Wilce, 1987; McGuinness, 1987a,b; Airoldi and Cinelli, 1997). Common physical disturbances on rocky shores are colliding tree trunks, stones, ice scour and strong waves (Dayton, 1971; Paine and Levin, 1981; Suchanek, 1981; Petraitis and Methratta, 2006), while predation and grazing are biological disturbance factors (Navarrete, 1996; Sommer, 2000). Models of climate change predict a higher frequency of storms with an increasing stochasticity (Smith and Buddemeier, 1992; Michener et al., 1997). Therefore, disturbance regimes could become more variable and unpredictable in space and time (e.g. waves and currents). Considering these predictions, it is important to understand how the variance in ecological processes affects the structure of populations and assemblages (Benedetti-Cecchi, 2000; Cardinale et al., 2002; Benedetti-Cecchi, 2003; Hutchings et al., 2003; Miner and Vonesh, 2004; Benedetti-Cecchi et al., 2005; Benedetti-Cecchi et al., 2006), and experimental studies on the effects of temporal variability in predation, disturbance, and larval supply are necessary.

In this study, we examined the effect of different time intervals of disturbance events on the structure and diversity of marine fouling communities in northern-central Chile. A previous study on the importance of disturbance frequencies has been conducted in this study system showing that species richness was highest at intermediate disturbance frequencies (Valdivia et al., 2005). Herein we used only one single disturbance frequency, which was applied at different scales of temporal variability. To test for effects of disturbance variability, we used a similar experimental approach as recommended by Benedetti-Cecchi (2003) and Benedetti-Cecchi et al. (2006). Specifically, we examined whether (1) temporal variability of disturbance (herein termed "variableness"), and (2) the time when a disturbance event occurs (herein termed "sequence"), influence the diversity and structure of fouling communities.

2. Material and methods

2.1. Study sites

The study was conducted in Bahía La Herradura in northern-central Chile (29° 59′S, 71° 22′ W), a semi-
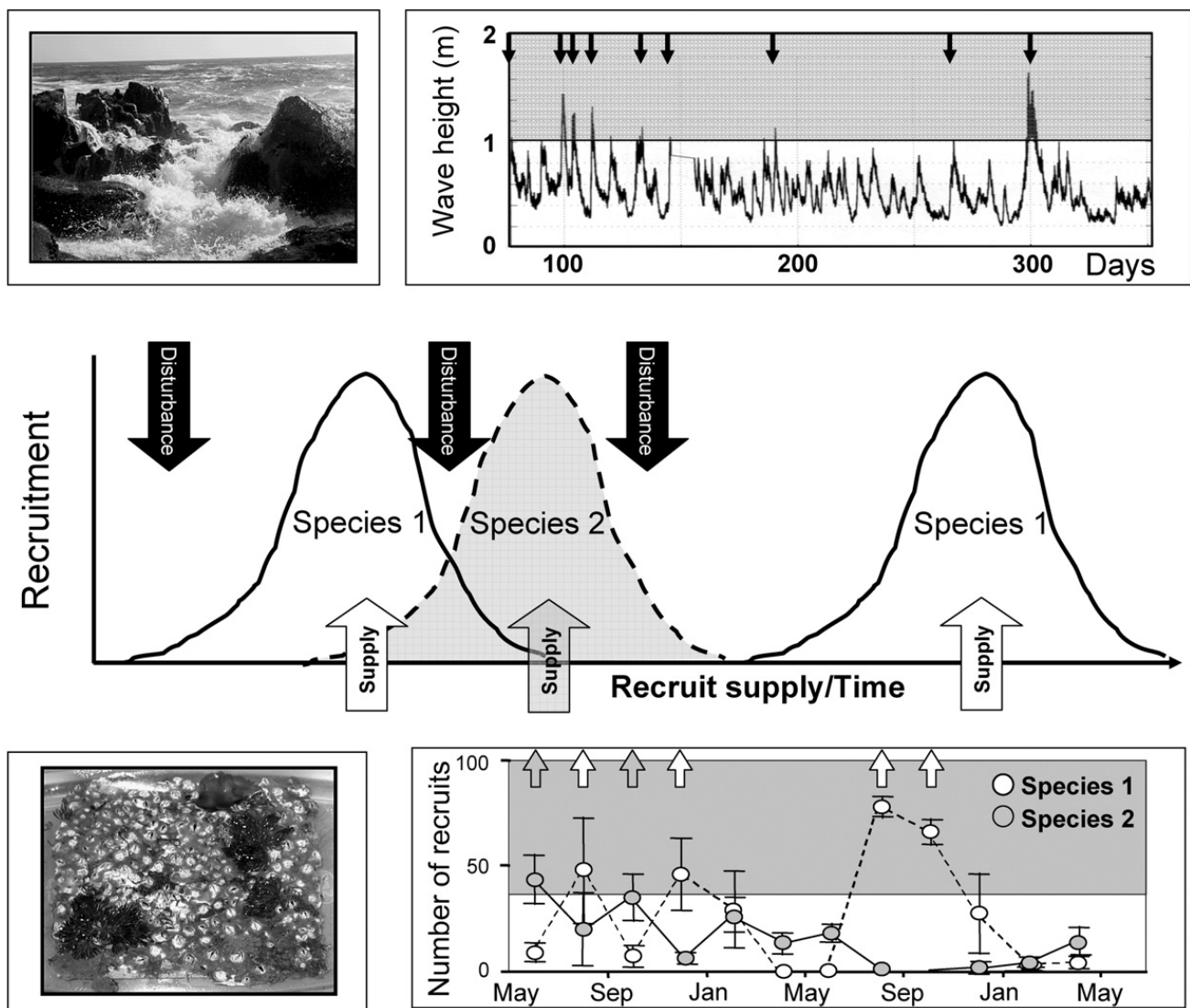
Fig. 1. Schematic example for match/mis-match between disturbance events and recruitment pulses. Inserts on top show examples for disturbance events and temporal variability of these (modified after Vassie et al., 2004), inserts on bottom show examples of monospecific communities resulting from settlement pulses coinciding with availability of primary substratum (modified after Bram et al., 2005).

enclosed circular bay with a small (0.7 km) opening to the Pacific. Growth rates of fouling organisms in Bahía La Herradura are very high (Viviani and DiSalvo, 1980), presumably facilitated by nutrient-rich water originating from an important upwelling area, located 40 km to the south–west (Acuña et al., 1989). Surface water temperatures in Bahía La Herradura vary from 13 °C in winter to 20 °C in summer (Moraga and Olivares, 1993). Two experimental sites, located 1.6 km from each other on sandy substratum at 6 to 7 m in depth, were selected for their proximity to the northern and southern shores of the bay. Hard-bottom communities are common at short distances (<100 m) from the experimental sites, on natural rock or on artificial concrete substrata dominated by crustose algae. Typical fouling organisms on suspended structures (e.g. buoys,

ropes) in Bahía La Herradura are bryozoans, hydrozoans, colonial and solitary ascidians, such as *Pyura chilensis* and *Ciona intestinalis*, and the barnacle *Austromegabalanus psittacus* (Valdivia et al., 2005).

2.2. Experimental set-up and design

To provide a settlement substratum for the macrobenthic fouling organisms, we used 15×15 cm PVC panels (thickness=3 mm) with the surface roughened with sand-paper. Ten panels (experimental units) were fixed on the inside of a PVC ring (height 25 cm, diameter 60 cm), representing an experimental block. A total of 12 rings were suspended from a buoy at ∼0.5 m depth. To assure fast removal and re-attachment, the panels were fixed with cable ties. The usefulness of this

experimental set-up for disturbance manipulations had been proven by Valdivia et al. (2005), who manipulated the disturbance frequency at seven levels (i.e., 2 to 12 disturbance events over a time period of 5 months). All settlement panels were previously exposed to natural colonization for three months (August–October 2004) at the Northern site before starting the experiment. The colonization process was initiated at only one site in order to obtain similar communities. At the beginning of the experiment (November 2004), six randomly selected rings (blocks) were transplanted to the Southern site while the other six rings remained at the northern site. The rationale of transplantation was to distinguish between the effects of variable disturbance treatments (applied in identical manner at both sites) from those that were due to environmental conditions at each site (e.g. exposure to wave action, food or propagule supply). To avoid any contact between the rings (i.e., collisions), which could have influenced the communities developing on them, they were placed at a minimum distance of 4 m (i.e. requirement for randomized block design; Hurlbert, 1984).

Maintaining the disturbance frequency constant (10 disturbance events over 5 months), we manipulated the temporal variableness of disturbance at two levels (i.e. low and high, Fig. 2) to examine the effects on the diversity and composition of fouling communities. At disturbance frequencies similar to those used herein, Valdivia et al. (2005) found a negative effect on species richness, but that previous study did not examine whether

and how temporal variability in disturbance affects the structure and species richness of fouling communities. The low and high levels of temporal variance used herein were selected to simulate scenarios where disturbance events occur in a relatively unpredictable way (e.g. ENSO — El Niño Southern Oscillation related storms and colliding stones). Along the Chilean coast one important source of disturbance are the strong winds that force coastal upwelling (Rutllant et al., 2004). Those winds produce high onshore waves and thus cause physical disturbance to intertidal and shallow subtidal hard-bottom communities. Wind-induced upwelling events (with high wave action) occur on an irregular weekly–biweekly basis (Garreaud et al., 1992). Furthermore, along the coasts of northern and central Chile, there exists high inter-annual variability in upwelling and wave action due to ENSO events (Thiel et al., 2007). Since differences in community diversity due to temporal variability of disturbance events may partly depend on the synchrony between events that open space and that provide recruits, we used three different arrangements of variability of disturbance ("sequence" — see Fig. 2) that were nested within each level of the main factor ("variableness" — see Fig. 2). This ensures the opening of a free area at different time periods, potentially allowing recruitment of different species into the already established communities throughout the study period. We also included a constant disturbance treatment as control with fixed interval of 15 days between disturbance events (Fig. 2), resembling a system (e.g. biweekly spring tides) where the removal of
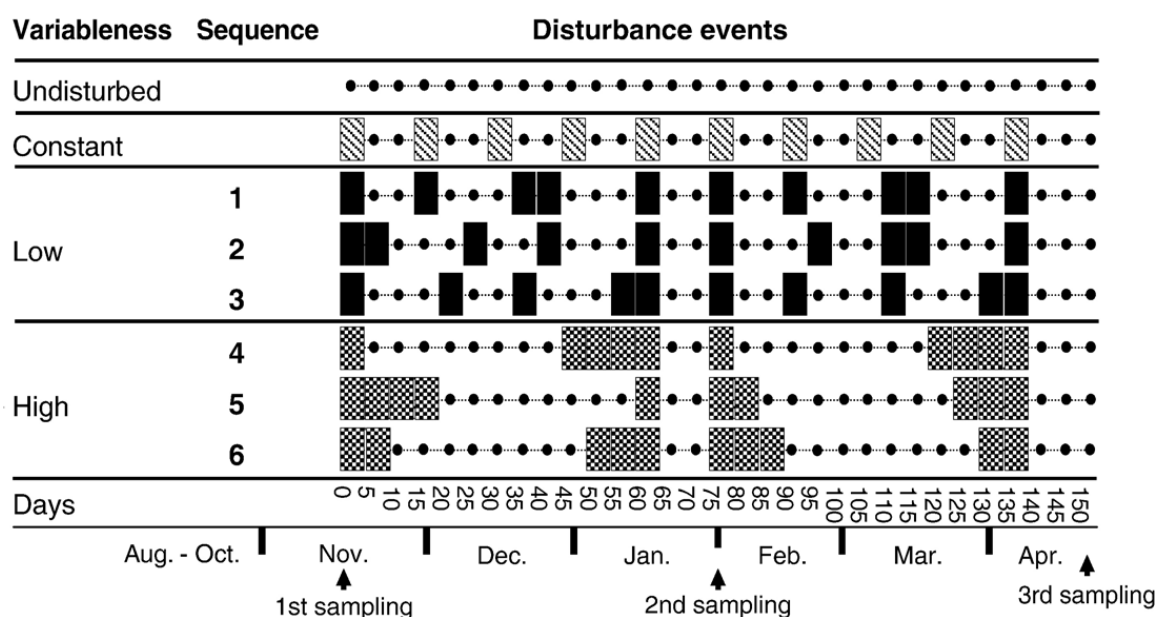

Fig. 2. Experimental time schedule, showing how the temporal sequences (a–g) of disturbance events are nested in two variable disturbance regimes (low and high). Rectangles represent disturbance events.

biomass is highly predictable. In our multi-factorial experimental design, the temporal variance of disturbance was the main fixed factor with two levels: low and high variableness (Fig. 2). The timing (sequence) of disturbance events was an additional random factor with three levels nested within the low and high variableness treatment level (Fig. 2). We treated the ring arrangement as a random factor (block), assessing spatial heterogeneity at the study sites. Each ring contained one replicate of each combination of variableness of disturbance with sequence, i.e. 6 treatment combinations plus one constantly disturbed assemblage and one undisturbed reference community. The two remaining positions within each ring were used to obtain a within-ring (i.e. within-block) replication of treatments that allowed assessing the variability among replicates at the lowest hierarchical level of the experimental design.

The size of the area affected, intensity, and overall frequency of disturbance events were the same for all treatment levels. We used high disturbance intensity, which means that all organisms present in the areas to be disturbed were removed. The overall frequency of disturbances was defined as the average number of disturbance events within a given time. All replicates were disturbed 10-times during the 150 days of the experiment, except the reference communities. In all treatment levels, the temporal intervals between disturbance events were arranged in such a manner, that the second and the third sampling could be done when (1) all communities had received the same number of disturbance events to avoid the confounding of the temporal variability of disturbance with its frequency (disrbance events per unit time) and (2) 2 weeks had passed after the last disturbance to avoid confounding the effect of temporal variability with time since last disturbance (Fig. 2).

2.3. Disturbance treatments

For the application of disturbances, the rings carrying the settlement panels were lifted out of the water and put into a boat. During the manipulation, the fouling communities were shielded from direct sunlight with a black plastic mesh. During each disturbance event, at two locations on each panel, the entire biomass was removed with a chisel. We used a PVC cylinder (4.6 cm diameter) to delimitate the areas to be disturbed (each representing 10% of the panel surface). The disturbance positions for each replicate were determined with a randomizer software using a grid of 36 intersection points (Geoffrey, Urbaniak and Plous, 2004; http://www.randomizer.org/). The first position was selected among all 36 possible points, while the second was restricted to points that would not lead to overlap with the first disturbed area. At subsequent disturbance events, the first position to disturb was again chosen freely among all 36 possible points, even when it coincided with a previously disturbed area.

2.4. Sampling procedure

During the experiment, all communities were sampled three times in a non-destructive manner. The fouling communities that had developed on settlement panels after 3 months were sampled before applying the first disturbance event. A preliminary multivariate community analysis of the panels on the rings confirmed that there were no initial block effects, thereby assuring that no unintended "grouping-effects" among communities within the same ring were present as this could later on mask potential treatment effects. The second sampling was conducted 74 days after the first disturbance and the final sampling at day 150 (Fig. 2).

During each of the three community surveys, panels were detached from rings and then maintained in tanks ($40 \times 30 \times 25$ cm) with running seawater at the laboratory. The percent cover of macrobenthic fouling organisms >2 mm (height, length, or diameter) on each panel was first visually estimated and then a dissecting microscope was used to identify smaller organisms. The area surveyed per panel was 13×13 cm, excluding a 1-cm margin around the edges of the 15×15 cm tiles. After the first and second sampling, panels were returned to their initial positions at the study sites within 2 h. After the final sampling, the dry weight (drying at 60 °C for 48 h) of communities was measured from organisms scraped off the panels but excluding organisms, which were attached on the border and expanded >50% of their body mass outside the panel (e.g. ascidians growing on the edge).

2.5. Statistical analyses

The results from all three samplings were used to observe the effects of the disturbance itself and to document the process of succession. In order to evaluate the effects of variableness and sequence of time intervals between disturbance events, only the data collected during the third sampling were used for statistical analyses. All species found on the panels were included in the univariate analysis of species richness, while the other analyses were performed only with the 16 most common species, excluding rare species observed on less than 10 of all 60 panels at each site.

Within the multi-factorial, univariate analysis of variance (ANOVA) *a priori* contrasts between (i) undisturbed and disturbed communities and (ii) constantly and variably disturbed communities were conducted to test for the effects of disturbance and variability in a disturbance regime in general. The main factor in the ANOVA design was the variableness of disturbance regime (fixed factor), while the specific timing of disturbance events (i.e. sequence) was a nested factor. We also included the spatial heterogeneity at the study sites (block, random factor) and evaluated the effect on species richness, Pielou´s evenness, total percent cover (arcsine-transformed) and dry weight (ln-transformed). We evaluated normality using the Shapiro–Wilk's *W*-test and homogeneity of variances using Levene´s test. To calculate the lowest level of variance for the ANOVA model (error term) only the within-block replicates were used. Significant differences ($p < 0.05$) within treatments were identified using Tukey´s post-hoc test. Since Sequence was treated as a random factor, the error in the ANOVA was not the appropriate term for testing the significance of all main effects and interaction terms (Sokal and Rohlf, 1995). The construction of a quasi-F-test is an alternative to obtain an approximate *F*-ratio (Winer et al., 1991), but instead of using this quasi-F-test herein we decided to pool the mean squares of highly non-significant interactions terms (i.e. "post-hoc pooling procedure"; probability ≥ 0.25) with the error term to obtain a more adequate *F*-ratio (Winer et al., 1991; Underwood, 1997). This approach allowed us to test more accurately the main factor when the interaction terms were not significant.

We compared the structure (untransformed data) and composition (presence-absence data) of fouling communities with multivariate analyses of similarities (ANO-SIM; Clarke and Warwick, 1994). ANOSIM compares the ranking of Bray-Curtis similarities among different treatment levels and among all disturbed and undisturbed communities. If $R > 0.25$, we tested for differences with pair-wise comparisons. Additionally we identified the percentage of contribution of each species to these similarities using a SIMPER (Similarity Percentage) routine (Clarke and Warwick, 1994). PRIMER 5 from the Plymouth Marine Laboratory was used for ANOSIM and SIMPER analyses.

3. Results

3.1. General community characteristics and succession

We found 12 taxa of macroalgae and 28 taxa of invertebrates and identified them to the lowest possible taxo-nomic level. Bryozoans and hydrozoans were the most diverse groups with 9 and 8 taxa, respectively. We also recorded five species of ascidians, two barnacles, and one sponge. Before the application of disturbances started, the barnacle *Austromegabalanus psittacus* was the most abundant species, while the ascidian *Pyura chilensis* was rare (Fig. 3). Throughout the experiment, but only under undisturbed conditions, *P. chilensis* increased in abundance and became the dominant species by the end of the experiment. During this process it overgrew other organisms such as *A. psittacus*, which simultaneously decreased in abundance (Fig. 3). On the other hand, under constantly disturbed conditions, the abundance of *P. chilensis* remained low, while the abundance of *A. psittacus* decreased, similar to the trend in the undisturbed communities (Fig. 3).

3.2. Disturbance effects on dry weight, species cover and richness

Mean dry weight was strongly affected by disturbance at both study sites (Tables 1 and 2). The average dry weight of undisturbed communities was two times higher than that of disturbed communities (Fig. 4). Overall, the disturbed communities had a lower cover of organisms than the undisturbed communities (Fig. 4). These differences were highly significant, despite a significant block effect in the initial analysis (Tables 1 and 2). This block effect persisted after the pooling procedure for the southern site, where pair-wise comparisons revealed that percent cover in three rings was lower than in the other three rings (Tukey's HSD: $p < 0.05$).

Species richness at both sites was not affected by disturbance (Tables 1 and 2), but at the Southern site a significant block effect was observed and confirmed after having applied the pooling method (Table 2). In one ring (i.e. block), the species richness was higher than in the others, but pairwise post-hoc comparisons revealed no significant differences (possibly due to difference in statistical power between ANOVA and pair-wise comparisons, for details see Keppel, 1991). At both sites, the evenness of disturbed communities was significantly higher than those of undisturbed communities (Tables 1 and 2). This was possibly due to the removal of the solitary dominant ascidian *P. chilensis*.

3.3. Effects of variableness and specific timing (sequence) of disturbance on biomass, species abundance, and diversity

Disturbances applied at different time periods resulted in patches showing variable micro-successions in the disturbed communities. Disturbed areas could
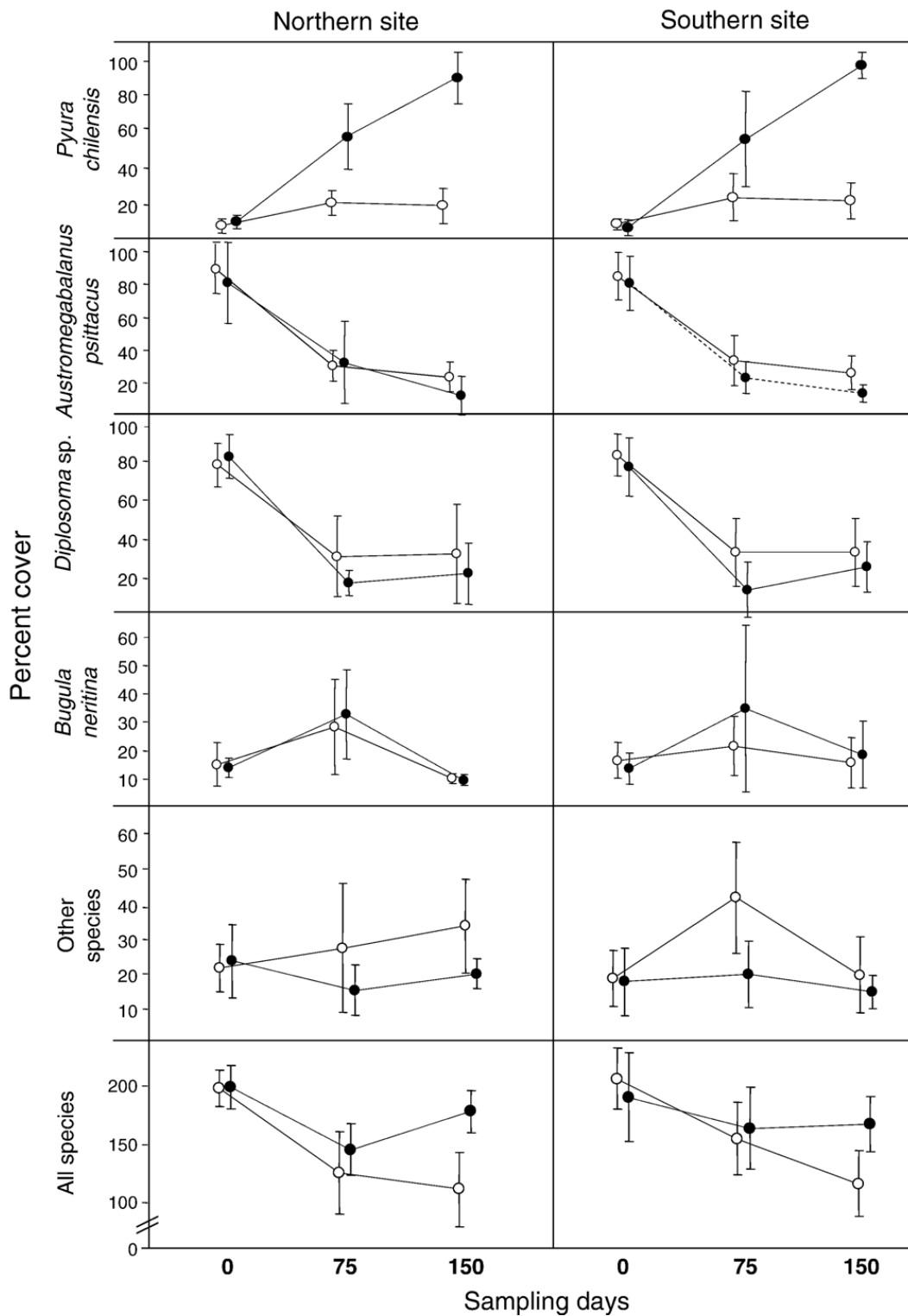
Fig. 3. Percent cover of principal species at the start, the middle and the end of the experimental phase, showing species cover on undisturbed (filled dots) and disturbed settlement panels (circles filled white); dots show the mean±S.D.

either be colonized via settlement of planktonic propagules or from organisms growing into the area from the patch margins. When disturbances occurred in quick succession in adjacent areas larger open patches were created than when there were longer intervals between disturbance events and when they were more isolated. Larger open patches occasionally showed a higher tendency of being colonized from planktonic stages, while small open areas were frequently overgrown from already established organisms around the disturbed area.

Table 1
Northern site

	df	Dry weight			Percent cover			Richness			Evenness		
		MS	F	Rec. F	MS	F	Rec. F	MS	F	Rec. F	MS	F	Rec. F
D vs. $U^{B \times (D\ vs.\ U)}$	1	581293.45	239.32**	109.07**	0.00	116.49**	30.86**	6.57	5.02	3.689	0.14	29.14**	26.80**
C vs. $V^{B \times (C\ vs.\ V)}$	1	1434.77	1.03	0.25	0.00	0.87	0.97	2.10	0.78		0.00	0.45	0.68
$V^{B \times V}$	1	22.25	0.05	0.00	0.00	0.39		0.03	0.01		0.00	0.01	0.01
$S(V)^{B \times S(V)}$	4	3153.00	0.76		0.00	1.62	0.54	4.86	2.93*	2.59	0.00	0.60	0.36
$B^{B \times S(V)}$	5	5075.53	1.23		0.00	3.795*	1.28	4.23	2.54	2.26	0.01	1.65	0.98
$B \times (D\ vs.\ U)^{R}$	5	2428.91	0.16		0.00	0.08		1.31	0.51		0.01	0.41	
$B \times (C\ vs.\ V)^{R}$	5	1397.93	0.09		0.00	0.36		2.68	1.04		0.01	0.68	
$B \times V^{B \times S(V)}$	5	406.15	0.10		0.00	1.99	0.67	3.16	1.90	1.69	0.00	1.39	
$S(B \times V)^{R}$	20	4123.11	0.27		0.00	0.11		1.66	0.64		0.00	0.25	
R	6	15,045.85			0.00			2.58			0.01		
Transformation		None			Arcsin transformation			None			None		

Dry weight, total cover (%), species richness and evenness. Results of the multifactorial ANOVA. Degree of freedom (df), mean square (MS), Fisher ratio (F) and recalculated Fisher ratio after pooling procedure (Rec. F) for all sources of variation at both sites. Upper case letters on each source of variation indicate the term used as a denominator to obtain the F-ratio.

D = disturbed; U = undisturbed; C = constant disturbance regime; V = variable disturbance regimes; S = sequence; B = block; R = residual. Probability levels: * $p < 0.05$; ** $p < 0.01$.

Despite the effects of disturbance itself, no effects of the temporal variableness or the sequence of disturbance events on total abundance and biomass of the communities were observed at both sites (Tables 1 and 2). The average total abundance and biomass were similar between variability levels (i.e. constant, low and high variableness levels; Fig. 4) and between the different sequences of disturbance events nested in variableness (Tables 1 and 2).

Species richness was not influenced by the temporal variableness in the disturbance regime at both sites (Tables 1 and 2). The block effects on species richness detected at both sites were only confirmed at the Southern site after pooling non-significant terms in ANOVAs. Pair-wise comparisons showed that in one block the undisturbed communities were more diverse than the disturbed, whereas the reverse pattern was observed within the other five blocks. Nonetheless, neither the variableness of disturbance nor the sequence of disturbance events showed a significant effect on the mean number of species or on evenness at both sites (Tables 1 and 2).

3.4. Effects of disturbance and its variability on community structure and composition

One-way ANOSIM on abundances of species revealed no significant differences in community structure among constant, low, and high variableness levels at both studies

Table 2
Southern site

	df	Dry weight			Percent cover			Richness			Evenness		
		MS	F	Rec. F	MS	F	Rec. F	MS	F	Rec. F	MS	F	Re. F
D vs. $U^{B \times (D\ vs.\ U)}$	1	377,652.42	82.69**	58.48**	0.00	14.60*	24.14**	9.00	0.72		0.12	28.55**	22.18**
C vs. $V^{B \times (C\ vs.\ V)}$	1	164.98	0.06	0.02	0.00	0.06	0.03	0.25	0.07	0.11	0.00	0.97	0.24
$V^{B \times V}$	1	18,509.60	3.01		0.00	0.07		1.00	0.40		1.00	0.40	
$S(V)^{B \times S(V)}$	4	3229.06	1.33	0.43	0.00	1.93	1.25	2.72	2.23	1.30	2.72	2.23	
$B^{B \times S(V)}$	5	6559.08	2.69	0.87	0.00	5.18**	3.35*	6.31	5.16**	3.01*	6.31	5.16**	
$B \times (D\ vs.\ U)^{R}$	5	4567.30	0.19		0.00	0.76		12.54	2.51		0.00	0.43	
$B \times (C\ vs.\ V)^{R}$	5	2849.01	0.12		0.00	0.18		3.70	0.74		0.00	0.16	
$B \times V^{B \times S(V)}$	5	6153.70	2.53	0.82	0.00	1.58	1.02	2.47	2.02	1.18	2.47	2.02	
$S(B \times V)^{R}$	20	2434.30	0.10		0.00	0.30		1.22	0.24		1.22	125.19**	
R	6	24,450.34			0.00			5.00			0.01		
Transformation		None			Arcsin transformation			None			None		

Dry weight, total cover (%), species richness and evenness. Results of the multifactorial ANOVA. Degree of freedom (df), mean square (MS), Fisher ratio (F) and recalculated Fisher ratio after pooling procedure (Rec. F) for all sources of variation at both sites. Upper case letters on each source of variation indicate the term used as a denominator to obtain the F-ratio.

D = disturbed; U = undisturbed; C = constant disturbance regime; V = variable disturbance regimes; S = sequence; B = block; R = residual. Probability levels: * $p < 0.05$; ** $p < 0.01$.
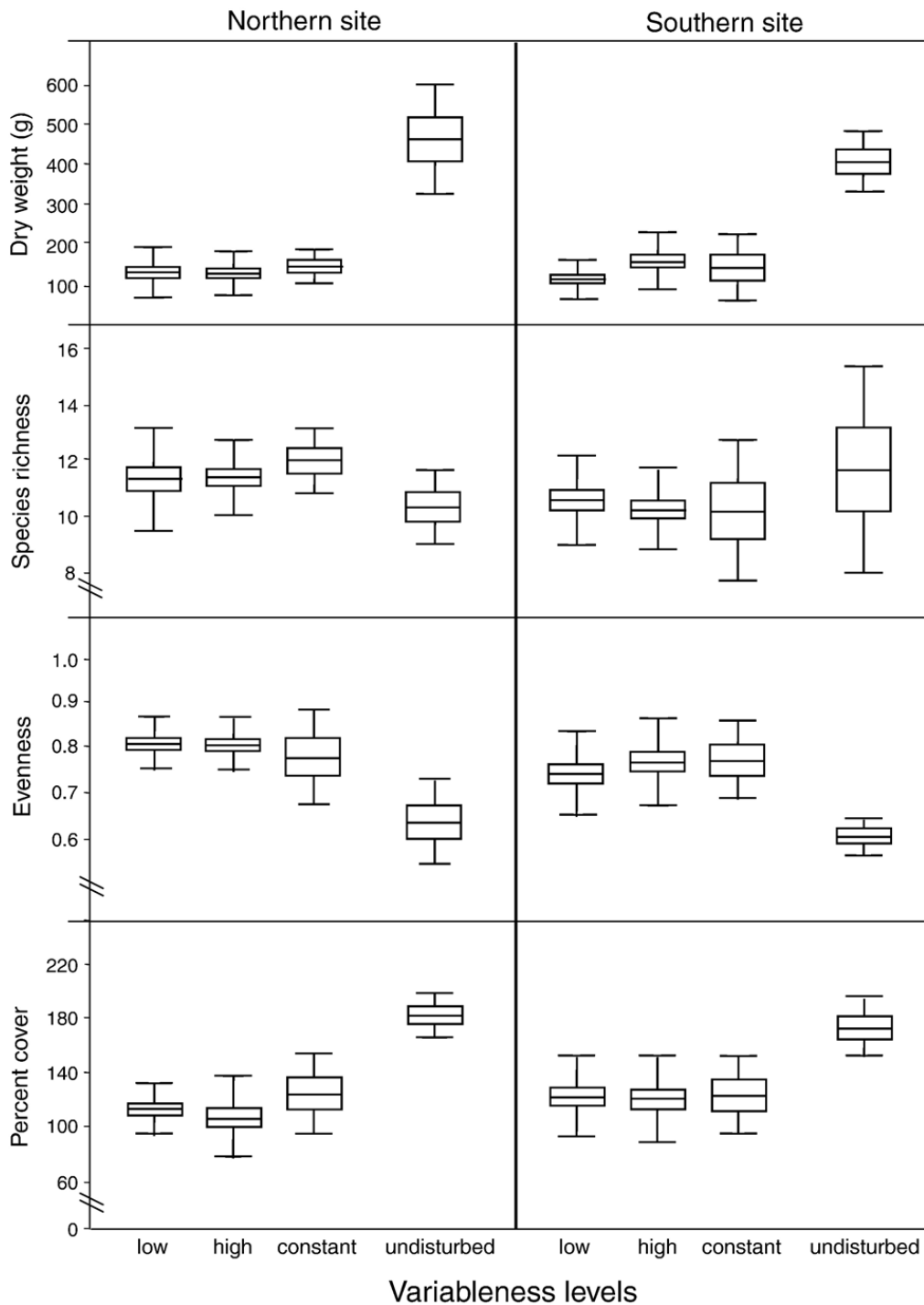
Fig. 4. Effects of the disturbance regimes on dry weight, species richness, evenness and total cover. Lines indicate the mean, ±S.E. (box) and ±S.D (whisker).

sites (Table 3), while pair-wise tests showed that there were consistent differences between all disturbed and undisturbed communities (Table 3; see also Fig. 4). However, the comparison of presence–absence data showed no significant differences (Table 3), revealing a similar community composition among the different treatments.

Differences in community structure are mainly caused by ascidians, namely the solitary ascidian *P. chilensis* and the colonial ascidian *Diplosoma* sp. In undisturbed communities the solitary ascidian *P. chilensis* contributed more than 60% to the similarity between communities at each site (Table 4), while in disturbed communities the same percentage was distributed among two or more

species, but in both sites *Diplosoma* sp. was the main contributor (Table 4).

4. Discussion

Since opened space generated at different time periods could potentially be colonized by different species, we expected that temporal distribution of disturbance events would have affected the assemblages. Although disturbance (i.e. removal of biomass) had a strong effect on the structure of the communities studied, neither variableness in the disturbance regime nor the sequence of disturbance events affected the diversity and structure of fouling communities in our study. Previous studies indicated that the temporal match/mismatch of principal ecological processes can have an important influence on the structure of benthic communities (Butler, 1989; Menge et al., 1994; Horne and Schneider, 1995; Navarrete, 1996; Chapman and Underwood, 1998). However, fouling communities, like those examined in our study system, may show a high degree of resilience, thereby being relatively unaffected by disturbances distributed in short periods of time.

4.1. Effects of disturbance on the fouling communities

The disturbance affected the biomass, total species abundance, evenness, and the structure of fouling communities. The ascidian *P. chilensis* contributed mainly to the high biomass and total abundance values, while it reduced evenness in the undisturbed communities. Under undisturbed conditions, *P. chilensis* completely overgrew the solid layer of the barnacle *Austromegabalanus psittacus*, very abundant at the beginning of the experiment, causing the death of the barnacles. As a consequence the whole community could become dislodged from the settlement panel. This process was never observed in disturbed communities where *P. chilensis* grew in the open patches on a more stable substratum.

The effects of the physical disturbance applied to the assemblages in this study correspond to the general view of disturbance as a structuring force in communities (Connell and Slatyer, 1977; Paine and Levin, 1981; Kondoh, 2001; Sousa, 2001). However, species richness was not affected, in spite of the removal of biomass creating opened space, which is often the limiting resource in fouling communities (Connolly and Muko, 2003; Platt and Connell, 2003). In fouling communities at our study site, Valdivia et al. (2005) found an increased species richness at a level of five disturbance events (of the same kind as those applied in our study) in 5 months. In our experiment, all disturbed communities

experienced 10 disturbance events in 5 months. This is similar to the highest disturbance frequency applied by Valdivia et al. (2005), who, at 12 disturbance events in 5 months, also observed species richness similar to that of undisturbed communities. This was presumably due to the harsh disturbance regime, so the high number of disturbance events used in our experiment might have overcompensated the positive effects of disturbance events on species richness.

4.2. Effects of the temporal variability of disturbance

In highly variable disturbance regimes, series of successive disturbance events that are clumped in time can open up large patches over a relatively short time period. Larger clearings presumably receive more colonists from the water column per unit time than smaller isolated patches (McCabe and Gotelli, 2000; Sousa, 2001). Furthermore, their smaller edge-area ratio may reduce the speed of re-colonization by vegetative growth (from the sides), and in turn favor colonizers from the water column. Temporal clumping of disturbance events should also massively reduce the abundance of dominant competitors, which would then favor competitively inferior species and thereby enhance evenness. In contrast, constant disturbance regimes, not showing temporal clumping of disturbances, create smaller patches with greater edge-area ratios, which should be more rapidly re-colonized by neighboring organisms, either by vegetative growth or larvae that are dispersing over short distances. Hence, variable disturbance regimes should rather favor colonizers, while constant disturbance regimes provide suitable conditions for competitors. Thus, the former should lead to an increase in species richness and evenness, as well as changes in the structure and composition of benthic communities. However, in our study, neither species richness and evenness nor structure and composition of the communities differed between constant and variable disturbance regimes.

All predictions on the effects of temporal variability in a disturbance regime on fouling communities assume that space is limited and therefore competitive exclusion exists. In our study competition for space could have been low, since the high frequency of disturbance could have generated open space in excess and therefore hidden potential effects of its temporal variability. The harsh disturbance regime might have removed such a high amount of biomass that the formation of different patches as a function of the clumping of disturbances in time was no longer decisive for the re-colonization process. Thus, recruits from the water column had access to

Table 3
One-way ANOSIM

| | (a) Community structure | | | | (b) Community composition | | | |
| | Northern site | | Southern site | | Northern site | | Southern site | |
	R	p	R	p	R	p	R	p
Global R	0.309	0.001	0.239	0.001	0.006	0.041	−0.001	0.047
Pair-wise comparisons								
low vs. constant	−0.038	0.66	0.012	0.42	−0.081	0.78	−0.007	0.503
low vs. undisturbed	0.923	0.001	0.78	0.001	0.044	0.32	0.085	0.211
low vs. high	0.015	0.25	−0.019	0.73	−0.019	0.74	−0.009	0.561
constant vs. undisturbed	0.969	0.001	0.893	0.001	0.06	0.2	0.025	0.316
constant vs. high	0.045	0.27	−0.034	0.62	−0.015	0.55	−0.067	0.779
high vs. undisturbed	0.953	0.001	0.723	0.001	0.173	0.077	−0.005	0.47

R-values (R) and significance level (p) based on matrices of similarities of (a) Community structure measured as species abundance and (b) Community composition based on presence–absence data, comparing constant, low, high variableness levels and undisturbed treatment for both sites (northern and southern site) with pair-wise comparisons.

all disturbed communities, since space was not limited and competitive pressure was low.

Bertocci et al. (2005) suggested that the interaction of the temporal sequence of events in a disturbance regime with temporal patterns in larval supply should influence marine hard-bottom communities. When a disturbance event coincides with or closely precedes the settlement phase of a fouling organism, it will enable this species to establish within a community. On the contrary, if the timing of disturbance events does not match its settlement period, the species might be excluded. Thus, each sequence of disturbance events in our study could, theoretically, allow different species to establish, depending on the match/mismatch of its settlement

activity and the timing of the disturbances. However, it seems that the recruitment of new colonizers in the disturbed communities was not limited by space, as previously discussed, and therefore should have been independent from the sequence of disturbance events.

Contrary to our results, a study by Navarrete (1996) revealed an effect of temporally variable biological disturbance regimes (i.e. predation) on the succession and composition of macrobenthic communities. In contrast to predation, which most often is selective, the disturbance we chose eliminated all organisms within a disturbed area. By this, it imitated a harsh physical disturbance such as the impact of strong waves, drifting logs, or ice scour (Dayton, 1971; Paine and Levin, 1981;

Table 4
SIMPER analysis results

Variableness	Northern site		Southern site	
Low	Average similarity: 58.62	Contribution (%)	Average similarity: 56.64	Contribution (%)
	Diplosoma sp. (25.91)	26.77	Diplosoma sp. (42.17)	44.11
	Pyura chilensis (20.50)	23.38	Austromegabalanus psittacus (15.65)	15.85
	Austromegabalanus psittacus (13.68)	14.37	Pyura chilensis (16.17)	13.93
High	Average similarity: 62.22		Average similarity: 54.64	
	Diplosoma sp. (23.64)	25.12	Diplosoma sp. (37.86)	39.30
	Pyura chilensis (17.05)	20.35	Pyura chilensis (17.67)	17.63
	Austromegabalanus psittacus (15.68)	19.56	Austromegabalanus psittacus (15.24)	14.46
Constant	Average similarity: 59.35		Average similarity: 59.15	
	Diplosoma sp. (32.22)	27.02	Diplosoma sp. (36.11)	39.50
	Pyura chilensis (18.89)	19.66	Pyura chilensis (22.22)	22.61
	Austromegabalanus psittacus (17.78)	19.64		
Undisturbed	Average similarity: 74.91		Average similarity: 81.74	
	Pyura chilensis (92.86)	64.60	Pyura chilensis (95.00)	66.81

Community similarity at the end of the experiment for communities with low variableness, high variableness and constant intervals between disturbance events, and undisturbed communities. For each factor the average similarity among all communities and the species that contribute ≥60% of the similarity at each factor level is shown. Mean percent cover of each species is given in parenthesis.

Petraitis and Methratta, 2006). Different from this non-selective effect, a decrease in the abundance or the removal of a single species due to predation may facilitate or inhibit the recruitment and persistence of other species, regardless of the total amount of space available (Young and Gotelli, 1988). A study by Benedetti-Cecchi et al. (2006) revealed positive and negative effects of the more variable aerial exposition on the diversity and structure of algae and barnacle assemblages, respectively. However, the effects of exposition variability were opposite to the effects of the mean intensity of aerial exposition. The differential response of some species to similar frequency and variability of disturbance could shape the patterns of hard-bottom communities. Some species can spread and colonize free open patches when the disturbance condition are more variable, changing thus diversity, evenness, and structure of communities. In our communities with a single dominant competitor species, the non-selective variable disturbances affect the communities uniformly, offering similar opportunities for all potential colonizers. Interactions between the variability and mean intensity of disturbance may particularly occur in systems where disturbance affects only some species.

The presence of already established organisms in the communities may have caused both pre-and post-settlement mortality of larvae on newly opened space. This mechanism surely is, besides spatial and temporal patterns in the supply and recruitment of propagules, an important determinant for community composition and structure (Eckman, 1996; Sousa, 2001; Bellgrove et al., 2004). Additionally, the cumulative filtration of aggregated filter-feeders is known to reduce larval recruitment densities (Young and Gotelli, 1988; Bingham and Walters, 1989; Osman and Whitlatch, 1995; Navarrete and Wieters, 2000; Yakovis et al., 2004). The dominant filter-feeding invertebrates in fouling communities (here the ascidian *P. chilensis* and the barnacle *Austromega-balanus psittacus*) are characterized by high filtration rates (Osman and Whitlatch, 1995; Westheide and Rieger, 1996). Hence, their presence most likely decreased the number of recruits or even completely prevented the colonization of open space by species recruiting via planktonic larval stages. In our experiment, disturbed patches on the settlement panels were always surrounded by organisms, which competed for the provided space by vegetative encroachment (e.g. *Diplosoma* sp.), or by their capability to overgrow other organisms (e.g. *P. chilensis*). At many localities, ascidians are the dominant species on artificial surfaces (C. Lambert, 2005), because they are capable to support a wide range of environmental factors (C. Lambert, 2005; G. Lambert, 2005; Bates, 2005). In addition,

colonial ascidian species can respond quickly to environmental variations, triggering, suppressing or delaying their reproduction or development (Bates, 2005). In agreement with Jackson's (1977) prediction, in our experiment, the colonial ascidian *Diplosoma* sp. colonized the free space left after a disturbance event more rapidly than the solitary ascidian *P. chilensis*. The notorious dominance of *Diplosoma* sp. in disturbed communities is probably due to its high potential of vegetative growth (see also Valdivia et al., 2005).

5. Outlook

Our results suggest that the relevance of temporal variability of disturbance regimes for the structuring of marine fouling communities is restricted. Three main reasons may have been responsible for the absence of effects in this study, (i) the dominant filter-feeders already established on the panels before the start of the experiment eliminated new colonizers, (ii) many new colonizers were eliminated due to the harsh disturbance regime, (iii) Fouling organisms that were already established around disturbed patches might have quickly overgrown the newly available space, making the colonization process relatively independent from the temporal availability of propagules in the water column. We found some support for all three points in our study and conclude that temporal variability of non-selective disturbance may generally be of low importance for fouling communities that are similar to our study system. Effects of variable disturbance may occur when disturbances selectively affect particular taxa in the communities as found by Navarrete (1996) and by Benedetti-Cecchi et al. (2006). Fouling communities are dominated by opportunistic species, many of which are capable of asexual reproduction and clonal growth and thus can rapidly exploit available space (Braithwaite and McEvoy, 2005). Consequently, temporal variability in disturbance might become of minor importance in established fouling communities. Benthic communities (composed of non-clonal organisms) in which discrete settlement pulses occur at specific times of the year and in which space is a limiting resource may be more prone to variability of disturbance (Roughgarden et al., 1991; Sponaugle et al., 2002). This should be particularly true for systems with a high seasonality, in which rare but intense disturbance events occur either before or during periods of intense recruitment.

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