

ORIGINAL ARTICLE

## Succession and seasonal onset of colonization in subtidal hard-bottom communities off northern Chile

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### Abstract

Although there is extensive information concerning the colonization sequences of benthic communities, little is known about the successional development of subtidal hard-bottom habitats in highly productive coastal upwelling areas. In these systems, succession is predicted to be fast due to high growth rate of the later dominant colonizers. Using artificial hard substrata a field experiment was conducted in a rocky subtidal area off Northern Chile (Humboldt Current System) and monitored at 3-month intervals to test the following hypotheses: (i) epibenthic succession may proceed through consecutive replacement of species, (ii) there is a fast convergence rate towards natural communities, and (iii) different seasonal starting points for the colonization will produce different community structure over a 1-year period of exposure. Panels were installed on a vertical wall at 17 m water depth. Three replicate panels were sampled every 3 months over a period of 27 months. As a reference, six haphazardly selected plots from the surrounding natural community were surveyed at each sampling date. To evaluate how seasonally varying substratum availability affects community development, further panels were exposed for a 12-month period, starting in four different seasons ( $n = 3$  replicates per season). Community succession was slow and occurred through progressive changes, between early encrusting red corallines, middle *Balanus flosculus* and late *Lagenicella variabilis*. After 27 months, the community composition, but not its structure, was similar between experimental and reference communities on surrounding rocky bottoms. Seasonality had no effects and after 1 year of exposure the experimental communities converged towards a common structure. This study indicates that succession of subtidal epibenthic communities follows a slow and predictable pattern with a dominant late colonial species. In addition, aseasonal variability might be more relevant during colonization and succession in this upwelling ecosystem.

### Problem

Ecological succession of living communities is the process of a gradual change of species composition and abundance throughout time, better perceived when distur-

bance has removed biomass and/or created vacant habitats (Clements 1916; Gleason 1926; Connell & Slatyer 1977). The process is gradual, continuous and directional, involving colonization and extinction of species, increments of diversity, biomass, structure and shifts from

r-to K-life strategies (Odum 1969; Sousa 1980; Dean & Connell 1987a; McCook 1994). The occurrence of local disturbance of variable intensity resets the processes forming communities in different successional stages, creating the patch-mosaic pattern of biodiversity that characterizes many ecosystems (Sousa 2001).

Several studies have identified the biological processes explaining successional patterns of benthic marine communities. Colonization success is mediated by juvenile–adult interactions, e.g. rejecting or stimulating larval settlement (Osman & Whitlatch 1995a,b, 2004; Bullard *et al.* 2004). Succession also depends on the competitive interactions among species for the available space (Nielsen & Navarrete 2004; Valdivia *et al.* 2005) and the effects of animal predation (Day & Osman 1981; Himmelman *et al.* 1983; Osman *et al.* 1992) and grazing (Paine 1984; Farrell 1991; Benedetti-Cecchi 2000). Other studies have focused on the influence of the environmental variability on the pulses of settlement/recruitment, and the occurrence of disturbances which explain the successional pathway and outcome (Osman *et al.* 1992; Osman & Whitlatch 1998; Benedetti-Cecchi 2000).

Even though there is a good understanding of benthic succession, most of this knowledge has been gathered from intertidal rocky communities, where only organisms with specific habitat adaptations can thrive (Dean & Connell 1987a,b,c; Farrell 1991; Foster *et al.* 2003), or from fouling panels deployed on shallow floating structures such as rafts, pontoons, posts or piers, and docks (Osman 1977; Sutherland & Karlson 1977; Anderson & Underwood 1994; Brown & Swearingen 1998; Altman & Whitlatch 2007), which may not fully represent the conditions and communities occurring on natural subtidal rocky habitats (Connell & Glasby 1999; Glasby 2001; Glasby & Connell 2001). Comparatively less information is available concerning succession in rocky subtidal communities (Vance 1988; Watson & Barnes 2004a,b; Antoniadou *et al.* 2010). In addition, the vast majority of studies covering succession have been conducted in subtropical or temperate ecosystems where pulses of productivity are highly seasonal or less intense compared to intense coastal upwelling systems. Therefore, further information from deeper communities in highly productive systems is necessary to understand the general trend and core principles of community succession in the marine milieu.

In this study we examined succession in a subtidal hard-bottom habitat off Northern Chile, *i.e.* within the Humboldt Current System. In this system, communities are subject to the frequent occurrence of several types of disturbances at different scales. For example, the harvesting of macroalgae by artisanal fishermen leads to disturbance when kelp holdfasts are dislodged, creating spatially limited patches of bare rock (Vásquez & Santelices 1990;

Vásquez 1995). Such impacts usually occur on a much smaller spatial scale and at higher frequencies than disturbances recorded during strong El Niño events, when the combination of strong swell and higher temperatures sweeps away rocky biota (Vásquez *et al.* 2006; Thiel *et al.* 2007 and references therein). The successional recovery after El Niño on rocky shores communities is relatively slow and may take between 2 and 3 years (Arntz *et al.* 2006). In contrast, during cold La Niña conditions, the system is characterized by persistent upwelling that promotes high biological productivity (Escribano 1998; Wieters *et al.* 2003), which is reflected in high growth rates of the indigenous biota, and as a consequence succession is fast and leads to hierarchical competition between dominant sessile species (Navarrete & Castilla 2003; Nielsen & Navarrete 2004; Valdivia *et al.* 2005). Complete monocultures of typical late successional species (e.g. mussels or ascidians) can develop in about 6 months on shallow subtidal fouling panels (Valdivia *et al.* 2005; Cifuentes *et al.* 2007). Therefore, it is predicted that in deeper subtidal hard-bottom habitats succession may proceed through consecutive replacement of species in a relative short time.

A particular issue in the analyses of succession is that natural seasonal variability may mask underlying community trajectories, leading to confusion in the interpretation between patterns generated by succession or annual cycles (Osman 1978; Dean & Hurd 1980; Underwood & Chapman 2006). Succession can only be predicted when a consistent pattern of temporal changes in the composition or relative abundances of species is observed (Platt & Connell 2003; Hill *et al.* 2004). Thus community structure must be analyzed at different time intervals along the colonization process, allowing a distinction between the course of successional development and natural seasonal variability (Chapman 2002, 2007). Many studies have shown marked seasonal effects on the early colonization of hard substratum (Osman 1978; Dean & Hurd 1980; Anderson & Underwood 1994; Brown & Swearingen 1998; Watson & Barnes 2004a,b). Although there are seasonal fluctuations in the environmental conditions in shallow waters off Northern Chile, this signal is not always correlated with settlement and recruitment of benthic species inhabiting the rocky intertidal (Lagos *et al.* 2002, 2008), and subtidal soft sediments (Pacheco *et al.* 2010), contradicting the vast evidence previously found. Consequently, further studies are necessary to evaluate whether seasonality effects play an important role in the establishment of subtidal benthic communities.

The aim of this work is to provide comprehensive data on the structure of a successive developing subtidal (15–17 m) epibenthic community and to reveal the effect of the seasonal onset in the early pattern of colonization on

a temperate rocky wall using artificial substratum. The study was based on the following working hypotheses: (i) epibenthic colonizers exhibit predictable succession that proceeds through a consecutive replacement of species, (ii) the convergence rate (defined as the time necessary for developing communities to converge to the surrounding natural community) is comparatively short (*i.e.* months), and (iii) different seasonal starting points of the colonization end in a different community structure over a 1-year period of exposure. This is one of the first such studies to be conducted on hard substrates under conditions of intense eastern boundary upwelling, with sustained high productivity.

## Material and Methods

### Study site

This study was carried out in the northern-central region of the coastal Humboldt Current System (HCS) at a vertical rock face known as the 'Anemone Wall' (23°28' S; 70°37' W) off Peninsula Mejillones, located near Isla Santa María. The site is fueled by one of the most productive upwelling centers in Northern Chile (Escribano & Hidalgo 2000; Thiel *et al.* 2007) and thus the water is comparatively cold, nutrient-rich, and able to sustain high levels of primary production (Escribano 1998). Upwelling occurs year-round with maximum and minimum intensities in October and January, respectively, and results in comparatively low sea surface temperatures ranging from 14 to 20 °C (for more details see Escribano *et al.* 2002, 2004).

Anemone Wall forms part of a small embayment and extends from the shallow subtidal zone down to 50 m depth. The upper (down to 13 m) benthic assemblage is dominated by the kelp *Lessonia trabeculata* whose abundance is substantially reduced between 13 and 25 m where relatively small epibenthic taxa (*i.e.* filamentous and encrusting red algae, bryozoans, sponges and vermetid gastropods) dominate (Pacheco & Laudien 2008). Omnivorous fish such as *Pinguipes chilensis*, *Chromis crasma*, *Paralabrax humeralis* and *Cheilodactylus variegatus* are commonly present at the study site. A similar epibenthic community composition was observed in surrounding vertical rocky areas (A. Pacheco unpublished data), hence the community studied on Anemone Wall can be considered representative for the exposed coast of Peninsula Mejillones and other rocky subtidal sites along the coast of Northern Chile.

### Experimental set-up

In January 2006, 48 circular polyethylene panels (white color, 40 cm in diameter, 1.5 cm thick and 1256 cm<sup>2</sup> of

surface) were installed on Anemone Wall in an approximately horizontal row between 15 and 17 m depth along a 60-m transect. Thirty-nine panels were designated for the two experiments of this study (27 for the succession experiment and 12 for the seasonal experiment, see below); nine spare panels were placed to account for any losses. Polyethylene® was chosen to avoid selective larval settlement or substratum rejection as it has a neutral charge and thus does not influence natural biochemical conditions (Dexter & Lucas 1985). Panel surfaces were uniformly roughened with sandpaper (grading No. 60) to provide a more suitable surface (Bourget *et al.* 1994). The circular shape of the panels ensured that border effects were equal at the centered sampling area (38 cm in diameter).

To install the panels, holes were drilled into the bare rock and wall plugs inserted. Thereafter, adaptors (Polyethylene® cylinders 13.5 cm long and 4 cm in diameter) were screwed onto each wall plug. An external thread was used to fix the panels to the adaptors by screwing a nut adaptor, attached in the central rear part of the panel, to the adaptor thread. This allowed easy installation and removal of panels during the course of the experiment. The distance between the panels varied between 1 and 3 m depending on the relief of the rock wall. Panels were numbered and collected by SCUBA divers after 3, 6, 9, 12, 15, 18, 21, 24 and 27 months of exposure (treatments) for analysis. At each sampling date, three randomly selected panels were detached and carefully deposited into individual mesh bags. Each bag was placed into a distinct plastic container filled with filtered seawater to individually secure detached fauna.

### Species identification and quantification

Colonizing organisms were identified to the lowest possible taxonomic level using a dissecting microscope. *Lithophyllum* sp. and *Lithothamnium* sp. were considered encrusting coralline algae because their taxonomic status is uncertain for Northern Chilean locations (Meneses 1993). Sponges were determined to genus level as detailed species information is not yet available for the locality (Desqueyroux & Moyano 1987). For all sessile taxa, percent cover was estimated by counting 136 intersection points from a circular grid (38 cm diameter) projected centrally onto the front of the panel. During counting, care was placed in determining the precise match between the intersection points and the counted taxa, as some taxa (*i.e.* colonial forms) can grow on top of other species. From 3 to 24 months, each intersection point corresponded to single taxon. After 27 months, panels showed a nearly complete cover of the arborescent bryozoan

*Lagenicella variabilis* over the barnacle *Balanus flosculus* (see Results), so an intersection point could correspond to both species. In this case, counts were attributed to *L. variabilis* as most barnacles were evidently dead. Free space was referred to the blank area without macroscopic taxa; however, that space was usually covered with a biofilm consisting mainly of benthic diatoms. Diatoms were identified at the beginning of the experiment but were excluded from analysis to avoid possible problems due to comparisons of species from very different size spectra. To reduce methodological bias, identification and estimates were always done by the same person, counting from a fixed position above the panel.

#### Successional pattern and convergence to the natural community

Communities sampled at 3-monthly intervals (3, 6, 9 ... 27 months) were used to study successional patterns over 27 months of exposure. It was hypothesized that the developing community on the panels would converge to the community structure of the surrounding reference communities. Thus, data from each time interval were compared with reference samples from the natural community. To describe the reference communities from the adjacent natural rocky habitat, six quadrats (43.5 cm side length and ~1890 cm<sup>2</sup> area) were photographed at each sampling date using a Nikonos V camera equipped with a 35-mm lens and a Nikonos SB-150 flash, installed on a frame designed to ensure a fixed distance of 64.5 cm from the lens to the target area. Random photo-quadrates of the natural surrounding wall habitat were taken at the depth similar to the experimental setup. Slides were projected onto a screen and adjusted to match a 1:1 projection so they could be quantified using the same projected grid used for the panels.

#### Influence of seasonality on the onset of colonization

To evaluate the effect of seasonality on the colonization process, for each season three replicate panels each were installed in March 2006, June 2006, October 2006 and January 2007. After 12 months of exposure, the communities were analyzed for differences between seasonal onsets. The hypothesis tested was that communities starting colonization at different seasons differ in structure and composition after 1 year of development.

#### Data analysis

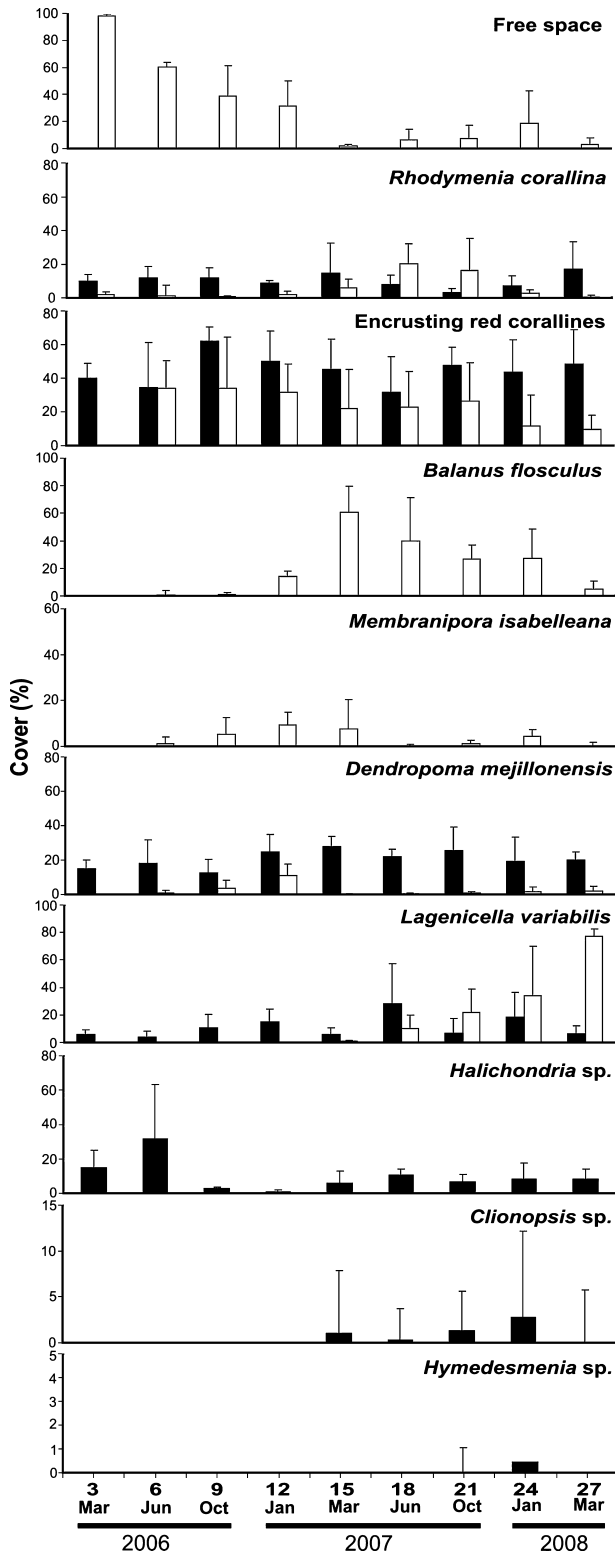
Canonical analysis of principal coordinates (CAP) (Anderson & Willis 2003; Anderson 2004) were used to build constrained canonical ordination plots calculated

from the Bray–Curtis similarity matrix using square root transformation of the data (*i.e.* to reduce the contribution of the most abundant species to the dissimilarity). Canonical ordination plots were used to resolve dissimilarities in community structure (*i.e.* percentage cover of all taxa) associated with different exposure times, reference communities and between seasons. Significant differences in community structure between successional times and seasons were tested using permutational multivariate analysis of variance (PERMANOVA; Anderson 2001, 2005). This is a robust analysis that compares an observed statistical test (pseudo *F*) generated under a null hypothesis using permutations and partition variation in multivariate community data. PERMANOVA also provides the calculation of Monte Carlo *P*-values in cases where there are a small number of possible permutations (*e.g.* small number of replicates such as in our design with three panels per sampling period), which allow statistical inferences at  $\alpha = 0.05$  during pairwise comparisons. Canonical ordination plots and PERMANOVA indicate the relative magnitude of community change between time intervals (*i.e.* exposure time, seasons) and whether communities are significantly different, respectively. However, they do not in themselves allow us to make a value judgment about changes, such as whether succession follows a consecutive sequence of changes through time. The ‘seriation with replication’ test of the RELATE analysis implemented in the PRIMER v6 software (Clarke & Gorley 2006) was used to test whether succession followed a constant trajectory or sequential pattern of change. This analysis uses the Spearman rank correlation ( $\rho$ ) between the community dissimilarity among samples and the dissimilarity model matrix that would result from the interpoint distances of the same number of samples equally spaced along a straight line. PERMANOVA was also used to identify after which time, the experimental communities became indistinguishable (in a statistically significant sense) from the surrounding natural community (*i.e.* convergence in structure). Because PERMANOVA works with balanced designs, three of the original six reference plots were randomly selected for comparison with panel’s data from each sampling date.

## Results

### Succession and convergence towards natural communities

After 3 months of exposure, benthic diatoms (*Navicula* sp., *Nitzschia* sp., *Cocconeis* sp., *Amphora* sp. and *Coscinodiscus* sp.) and small sporophytes of *Rhodymenia corallina* colonized the panels (Fig. 1). Encrusting coralline algae appeared after 6 months and persisted thereafter with similar cover (26%) throughout the experiment. After

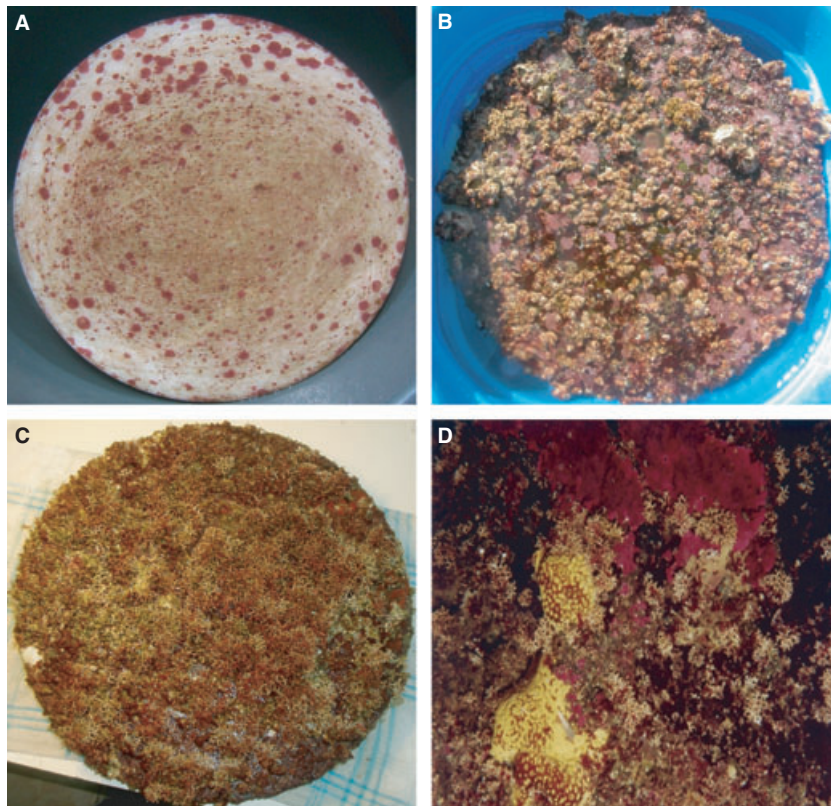


**Fig. 1.** Mean percentage ( $\pm$ SD;  $n = 3$ ) cover of epibenthic taxa from the community colonizing the panels (white bars) and the reference community (black bars), during the 27-month developing period. Numbers along the x-axis indicate the months after panel's exposure.

9 months, the bryozoan *Membranipora isabelleana* and the vermetid gastropod *Dendropoma mejillonensis* were found on the panels. One year after succession started, species richness appeared to be constant, although abundance continued to increase. After 15 months, the experimental panels were almost completely covered, mainly due to strong recruitment of the barnacle *Balanus flosculus* (61% of total cover), which overgrew *M. isabelleana*. Three months later (18 months of exposure), *B. flosculus* decreased in coverage to 40% and the bryozoan *Lagenicella variabilis* began to colonize. After 21 and 24 months, species coverage remained constant between surveys except in the case of *L. variabilis*, which increased considerably (up to 34%). Finally, after 27 months of exposure, *L. variabilis* dominated the community, covering >70% of the space (Figs 1 and 2). Variations in the percentage of available space during month 18, 21 and 24 resulted from variable predation pressure by the rock snail *Crassilabrum crassilabrum* and the sea star *Stichaster striatus* (A. Pacheco, personal observations) on *B. flosculus* and *M. isabelleana*. In general, colonial taxa (e.g. *L. variabilis*) dominated over solitary forms (e.g. *B. flosculus*) (Table 1) at the end of the experiment.

The canonical plot shows that community structure changes gradually from an early to an advanced successional stage (Fig. 3). This pattern was further supported by the results from the seriation analysis (RELATE:  $\rho = 0.715$ ,  $P < 0.01$ ). Significant differences between sampling times were detected (PERMANOVA:  $F_{(8, 26)} = 8.99$ ,  $P < 0.01$ ), thus indicating distinct changes in community structure during succession. Pairwise comparisons (Table 2) showed clear differences between communities that are well separated in time (e.g. 6 versus 15 months, 9 versus 27 months), whereas communities from consecutive sampling periods overlapped in structure (e.g. 12 versus 15 months, 18 versus 21 months), with the 24- and 27-month intervals showing greatest dissimilarity to the rest.

After 27 months, species composition on experimental panels was close to the natural community, but had not yet reached the same community structure (Figs 2 and 3, Table 1). The presence of three sponge genera and the absence of *M. isabelleana* and *B. flosculus* in the natural reference community accounted for the differences in species composition in comparison to the developing community (Table 1). All reference community samples clustered together, suggesting little temporal variation (Fig. 3). PERMANOVA comparisons of experimental communities with the respective natural references showed significant differences in community structure, confirming that experimental and natural communities had not yet fully converged after 27 months (in all cases  $P < 0.05$ ).



**Fig. 2.** Representative pictures of the successional experiment. (A) Panel after 6 months of exposure showing early patches of encrusting corallines. (B) Abundant cover of barnacles after 15 months. (C) 27-month panel completely covered with the arborescent bryozoan *Lagenicella variabilis*. (D) Natural reference plot showing patches of *L. variabilis*, the yellow sponge *Clionopsis* sp. and the reddish cover of encrusting corallines over the natural rock.

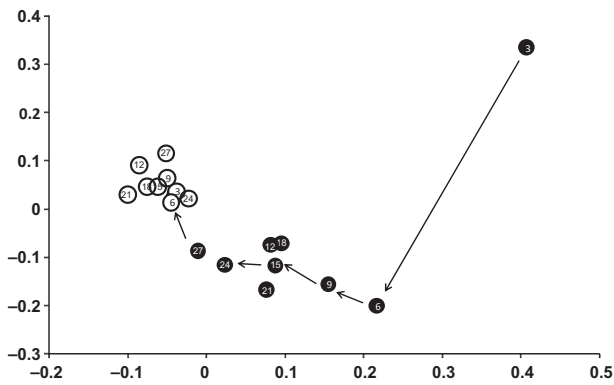
**Table 1.** Biological traits of taxa encountered (x) on experimental panels and in the natural reference community (NRC). A, Feeding mode (primary producer: pp, suspension feeder: sf). B, Growth form (solitary: sol, colonial: col). C, Fertilization (external: ext, internal: int). D, Development (spores: spo, larva: la, direct: di). E, Dispersal mode (pelagic: pe, pelagic/benthic: pebe, benthic: be). Dates: 3 (March 2006), 6 (June 2006), 9 (October 2006), 12 (January 2007), 15 (March 2007), 18 (June 2007), 21 (October 2007), 24 (January 2008), 27 months (March 2008).

	A	B	C	D	E	3	6	9	12	15	18	21	24	27	NRC
<i>Rhodomenia corallina</i>	pp	sol	ext	spo	pe	x	x	x	x	x	x	x	x	x	x
Encrusting red corallines	pp	sol	int	spo	pebe		x	x	x	x	x	x	x	x	x
<i>Balanus flosculus</i>	sf	sol	int	la	pe				x	x	x	x	x	x	
<i>Membranipora isabelleana</i>	sf	col	int	la	pe		x	x	x	x		x	x	x	
<i>Dendropoma mejillonensis</i>	sf	sol	int	di	be		x	x	x			x	x	x	x
<i>Lagenicella variabilis</i>	sf	col	int	la	pe						x	x	x	x	x
<i>Halicondria</i> sp.	sf	col	ext	la	pebe										x
<i>Clionopsis</i> sp.	sf	col	ext	la	pebe										x
<i>Hymedesmenia</i> sp.	sf	col	ext	la	pebe										x

**Seasonal onset of colonization**

After 1 year of exposure, the structure of the community was similar regardless of the season colonization started (Fig. 4A). Percentage cover of *M. isabelleana* and *B. flosculus* differed among seasons, whereas the rest of the taxa were fairly similar (Fig. 5); however, the PERMANOVA did not detect significant differences among community structures with regard to seasonal onset after 12 months

of exposure ( $F_{(3, 11)} = 2.12, P > 0.05$ ). When community data from the developing communities were plotted together with the seasonal data, community structure from both experiments converged around the interval among 15 and 21 months of exposure, except for the winter data, which remain dissimilar to the main group (Fig. 4B). PERMANOVA detected significant differences among the pooled dataset ( $F_{(12, 38)} = 7, P < 0.05$ ) and pairwise comparisons confirmed the pattern shown in the



**Fig. 3.** Canonical ordination plot of community structure calculated from Bray–Curtis similarity/dissimilarity measures with square root-transformed data of the average (i.e. centroids) of communities from panels (filled dots) and the reference community (open dots). Numbers indicated the time interval of sampling in months.

ordination plot, with early (3, 6, 9) months, winter and late (24, 27) months being significantly different ( $P < 0.05$ ) from the rest of the treatments.

### Discussion

#### Timing and pattern of successional development

Observations made during the development of subtidal hard-bottom communities off Northern Chile over an experimental period of 27 months showed that succession started with a film of benthic diatoms, followed by encrusting red corallines. A subsequent recruitment pulse of the barnacle *Balanus flosculus* partly replaced the encrusting corallines and the encrusting bryozoan *Membranipora isabelleana*. The arborescent colonial bryozoan *Lagenicella variabilis*, which appeared later during succession, overgrew space between the barnacles and subsequently replaced earlier colonizers. Thus, a competitive hierarchy was apparent: encrusting red corallines  $<$  *B. flosculus*  $<$  *L. variabilis*. Comparable sequences of competitive exclusion between species are commonly observed

during community development and have been described previously for intertidal hard-bottom systems: from the HCS off Chile and Peru a sequence comprising early species (e.g. ephemeral algae, barnacles), middle (e.g. turf algae, barnacles, gallery-building polychaetes) and late (kelp or mussel beds) has been documented frequently (e.g. Tokeshi & Romero 1995; Tarazona & Arntz 2001; Arntz *et al.* 2006; Thiel *et al.* 2007).

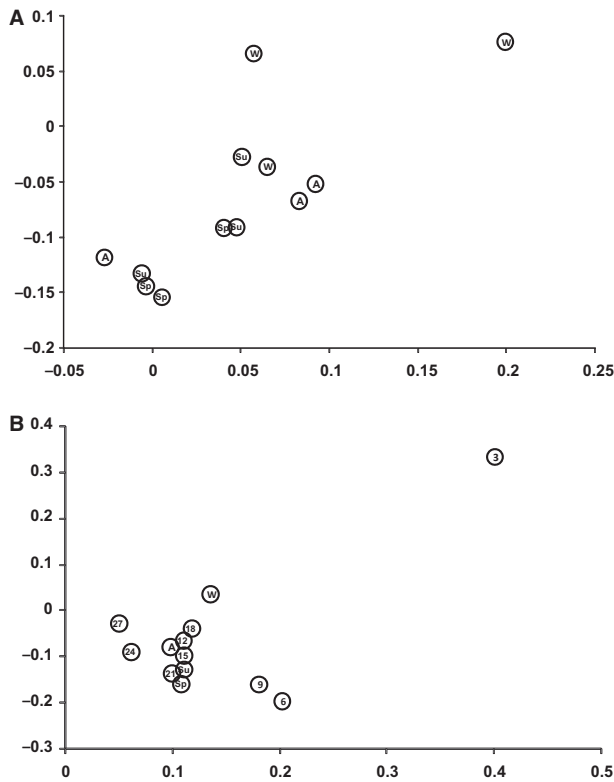
The succession sequence described in the present subtidal study is in line with those observed from fouling and rocky intertidal systems off central Chile, where high levels of primary production permit dominance of superior competitors due to high growth rates and rapid exclusion of inferior competitors (Navarrete & Castilla 2003; Nielsen & Navarrete 2004; Valdivia *et al.* 2005). However, our results show striking differences in the much slower development compared to the fouling and rocky intertidal communities in the same upwelling ecosystem. In central Chile, fouling communities on PVC panels, developed at ~0.5 m below the water surface, can fully occupy space and generate complete monocultures in just 6 months of exposure (Valdivia *et al.* 2005; Cifuentes *et al.* 2007). In contrast the present panels installed in the subtidal were poorly colonized for nearly a year and 15 months of exposure were necessary to achieve considerable cover caused by barnacle’s main recruitment.

Reasons explaining temporal differences in community succession may be attributable to strong upward transport of propagules and their preference for nutrient-rich and well illuminated shallow waters. In addition, the presence of a very shallow oxygen minimum zone might constrain the distribution of propagules in superficial layers (e.g. Escribano *et al.* 2002). Other studies have suggested that rapid community development would occur in shallow and protected embayments, as water retention mechanisms may enhance the supply of colonizers to benthic habitats (Watson & Barnes 2004a,b). Although Anemone Wall is not fully exposed, it forms part of the main exposed coast line where important retention processes are unlikely. In any case, the time of successional

**Table 2.** PERMANOVA t-values of pairwise comparisons among community structures at different stages of successional development (3–27 months of exposure).

	3	6	9	12	15	18	21	24
6	7.69*							
9	3.26*	0.79						
12	10.5*	2.80*	0.93					
15	5.97*	3.16*	1.76	2.20*				
18	4.83*	2.86*	1.76	2.40*	0.96			
21	7.02*	2.99*	1.65	2.46*	1.60	0.63		
24	8.66*	4.93*	2.42*	3.95*	2.07*	1.82	1.29	
27	7.35*	4.02*	2.23*	3.87*	3.41*	2.60*	2.25*	1.98

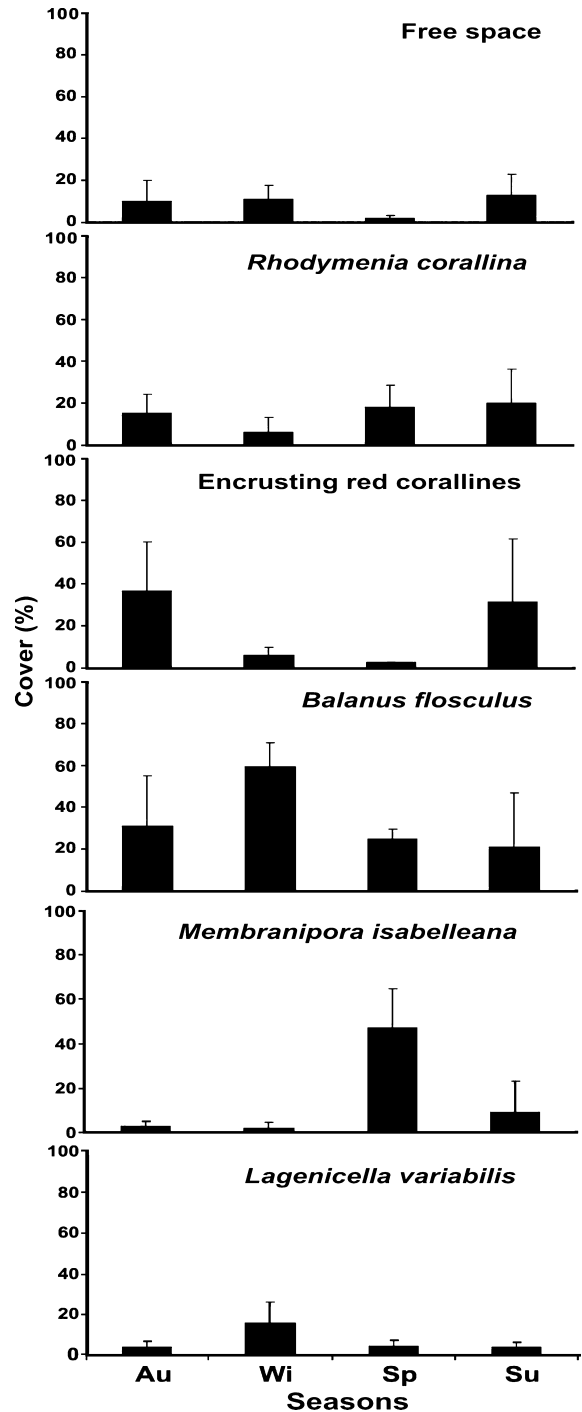
\*Significant Monte-Carlo P-values at 0.05 level.



**Fig. 4.** Canonical ordination plots derived from Bray–Curtis similarity distances of square root-transformed data. (A) Community structure from different seasonal onset (Su: summer; W: winter; A: autumn; Sp: spring). (B) Centroids of seasons and after a certain exposure time (in months).

development registered here is in line with observations (~15 months) from other subtidal hard-bottom communities in temperate regions (Vance 1988; Antoniadou *et al.* 2010). Thus it is worth noting that succession in subtidal communities appears to differ from that of other systems (*e.g.* intertidal or very shallow subtidal) and therefore caution must be taken when extrapolating or making predictions from those systems. For example, intertidal succession in large areas after strong disturbance caused by El Niño takes between 2 and 3 years (Tarazona & Arntz 2001; Arntz *et al.* 2006), whereas succession in a subtidal small patch may take nearly as long, as shown here.

Several studies (*e.g.* Sebens 1982; Osman & Whitlatch 2004) of benthic colonization supported predictions made by Jackson (1977) stating that colonial forms generally dominate over solitary ones in subtidal rocky communities during the course of succession. However, in some systems solitary species such as oysters or mussels are conspicuous space dominants (Greene *et al.* 1983; Witman & Dayton 2001). At Anemone Wall the early and



**Fig. 5.** Mean percentage ( $\pm$ SD;  $n = 3$ ) of taxa cover after different seasonal onsets of succession.

colonial *M. isabelleana* was displaced by the solitary barnacle *B. flosculus*, which was later overgrown by the bryozoan *L. variabilis*. Even though the latter dominant was a colonial species, there was a temporary dominance of a solitary one. In Central Chile, the solitary ascidia

*Pyura chilensis* dominates the space at the late successional stages in shallow-water fouling communities (Valdivia *et al.* 2005; Cifuentes *et al.* 2007). However, this species may behave like a colonial organism in the sense that dense agglomerations show dramatic lateral expansion during growth (Valdivia *et al.* 2005; Cifuentes *et al.* 2007; see also Alvarado *et al.* 2001 for an example with *Pyura praeputialis*). Species dominance during succession may not be related to this particular life-history trait in systems where competitive interactions are strong; there, a dominant species would lead the succession regardless of whether it is colonial or solitary.

Predators play an important role in the dynamics of space occupancy by removing the biomass of their prey selectively or non-selectively (Dean & Hurd 1980; Osman & Whitlatch 2004). We observed the rock snail *Crassilabrum crassilabrum* and the seastar *Stichaster striatus* preying on *B. flosculus*, thus potentially explaining its decrease in cover after 15 months of panel exposure. This might have opened the possibility of colonization and spread of the bryozoan *L. variabilis*. Omnivorous–carnivorous fish present at the study site do not appear to consume bryozoans (Medina *et al.* 2004; Berrios & Vargas 2004), which may further explain the increasing dominance of *L. variabilis* towards the end of the experiment.

#### Convergence with the surrounding community

The developing community showed variation in structure compared with the reference community. However, fundamental differences in this parameter suggesting different successional directions (*i.e.* contingent succession, Berlow 1997) seem to be unlikely in the study system. The observation of a persistent natural community structure over time (Fig. 3) supports this notion. Although substratum heterogeneity is an important factor during settlement and recruitment of epibenthic species (Bourget *et al.* 1994), and even though the panels were elevated above the natural rock (thus lateral ingrowth was hindered and possibly benthic predation reduced), the observations on succession can be considered representative for the natural community. With the exception of two species only found on the panels (*B. flosculus* and *M. isabelleana*), the main species recorded from natural reference communities were also present on the artificial substrata. Sponge species were the only taxa present in the reference community but absent on the panels; This may be due to the comparably short time allowed for development (27 months), as sponges have been documented to appear generally at late stages of succession (Vance 1988; Roberts *et al.* 2006; Walker *et al.* 2007). In contrast, the barnacle *B. flosculus* was only recorded in the developing community, which may indicate that this species is a

comparatively weak competitor and requires disturbance to colonize newly available substratum. *Balanus flosculus* was not found in the natural reference community, and decreased substantially in abundance on the panels between month 15 and 27, implying an inability to colonize or persist in more mature natural communities. This is in line with observations concluding that barnacles commonly appear in the mid stage of succession, but disappear later when overgrown by dominant colonizers (Paine & Suchanek 1983; Yakovis *et al.* 2008). The colonization of small patches by lateral growth of dominant species accelerates convergence to the resulting community (Osman & Whitlatch 1998; Watson & Barnes 2004a).

Further differences between the experimental and the natural reference communities, are due to the variation in the cover of encrusting red corallines. On the natural rock the bare space was always covered with red encrusting corallines, which contrasted with the experimental panels that showed major proportions of open space during the first year (Fig. 2). As substantial areas of the natural rock are covered with corallines, reference communities may experience more frequent, stronger disturbances caused by more predation, compared to panels, which were less accessible to benthic predators. Likewise, *Dendropoma mejillonensis* was more abundant on the natural rock compared to the panels. Juveniles of *D. mejillonensis* leave the mantle cavity of the adult and crawl for <1 h before cementing themselves to the substratum (Pacheco & Laudien 2008). It may have been relatively difficult for this species to reach the panels, and those that did colonize successfully may have been overwhelmed by the large settlement of barnacles after 12 months. The pictures of the reference communities show that this species formed dense agglomerations of adults, which may resist colonization by others; small juveniles of *D. mejillonensis* found on the panels may not be able to suppress other colonizers at large. The present data do not allow us to predict when convergence between experimental and natural communities is completed, but based on the preceding considerations it is suspected that full convergence is achieved within 3–4 years after succession started.

#### Effects of seasonal onset of colonization

In contrast to the many studies on fouling communities showing significant seasonal effects in settlement, recruitment and early succession (Anderson & Underwood 1994; Brown & Swearingen 1998; Watson & Barnes 2004a,b), our experiment did not detect seasonal variability related to the onset of early colonization. Differences may be due to our temporal sampling design. Studies searching for seasonal pattern often quantified communities after 1 or

3 months of exposure. In contrast, we sampled after 1 year of exposure so it could be argued that panels were exposed for too long to detect seasonally dependent colonizers, as older communities tend to converge into a similar structure regardless of the season of initiation (Dean & Hurd 1980; Anderson & Underwood 1994; Brown & Swearingen 1998).

In Central Chile, studies trying to find a link between monthly larval settlement and seasonal upwelling and relaxation events acting as onshore transport mechanisms have shown that settlement of several species on intertidal rocky shores is not correlated with the seasonal variation of those processes (Navarrete *et al.* 2002; Lagos *et al.* 2007), but rather settlement is related to aseasonal warming events (Narváez *et al.* 2006). Seasonal upwelling and relaxation events are important processes retaining the larval pool close to the shore, but they cannot fully explain patterns of settlement and recruitment of many taxa (Lagos *et al.* 2005). Such mechanisms cannot explain the variability in the colonization of taxa with short-lived larva such as the bryozoans *Membranipora isabelleana* and *L. variabilis* (see also Osman & Whitlatch 1998), or the brooding vermetid gastropod *D. mejillonensis*. For example, there was a higher abundance of *M. isabelleana* in spring than during the rest of the seasons and so the appearance in a particular season appears to reflect peaks in reproduction, rather than a dispersal process. These results are in line with observations of lack of seasonal effects in the dynamics of soft-bottom benthic communities in the region (Carrasco & Moreno 2006; Pacheco *et al.* 2010); for these communities, aseasonal variability may be more relevant.

Regardless of the supply of colonizers, the establishment of the subsequent community structure also depends on the ability of certain species to occupy and monopolize space (Sebens 1982; Walker *et al.* 2007). As observed in the present experiment, the more advanced community is dominated by late, but apparently competitively superior colonizers. This is especially true for *L. variabilis*, which overgrew other colonizers and dominated the community (achieving 70% coverage) towards the end of the experiment. Thus, although seasonality generates high variability during the early colonization process, the effect is eventually overridden by biological interactions such as competition and growth performances, which determine the structure and composition of the advanced community.

## Conclusion

The observed pattern of succession in our study suggests a slow capacity of recovery of the subtidal hard-bottom community during cold upwelling conditions. During

strong El Niño events, variations in community composition and structure occur, but our ability to predict those changes is still very limited (Camus 2008). Therefore, we recommend conducting similar experiments during El Niño conditions to obtain a full understanding of the mechanisms that permit community recovery and persistence in this ecosystem.

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