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ORIGINAL ARTICLE

Effects of physical disturbance on a sub-Antarctic middle intertidal bivalve assemblage

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Abstract

We present for the first time the vulnerability to disturbance of a bivalve assemblage situated in the middle intertidal zone of the Atlantic coast of the Southern South America (53°36'S, 67°58'W). This intertidal zone is characterized by a high level of sand movement preventing any establishment of sessile organisms on the vertical sides of rock outcrops. The coast is prone to potential spills from nearby hydrocarbon marine platforms, but this benthic assemblage has been poorly studied. In February 2001, we exposed the assemblage to two different experimental conditions: a complete removal of bivalves and a physical disturbance and tracked its recovery during the following 4 years. The disturbance lowered the diversity of associated fauna and made the sediment layer trapped among bivalves disappear, which was not restored. *Mytilus chilensis* was recruited into crevices or between byssi in the following settlement season, i.e. summer 2002. The recuperation of mussel coverage to predisturbance levels took 3 years after the total removal. In April 2004 the size frequency distributions, density and biomass/number ratio of *M. chilensis* were similar to those at the start of the experiment. *Perumytilus purpuratus* recovered more slowly than *M. chilensis*, probably due to its slower growth rate compared to *M. chilensis* and dependence on an adequate byssus matrix for settlement. The main apparent stressor was the irruption of sand, covering the bivalve assemblage for variable periods of time. This bivalve assemblage is characterized by low predatory pressure and therefore we hypothesize that it is predominantly controlled by competition for space.

Key words: South-Western Atlantic, mussels, Patagonia, Argentina, *Mytilus chilensis*, *Perumytilus purpuratus*, Tierra del Fuego, benthic resilience

Introduction

Physical stress is known as the prevailing environmental force structuring intertidal rocky communities of the southwest Atlantic. In Northern Patagonia, desiccation due to strong westerly winds is harsher than in any previously studied rocky intertidal system (Bertness et al. 2006). Intertidal predators – frequently responsible for the ‘top-down’ control of the community (e.g. Moreno et al. 1986; Menge 2000) – are very few or lacking, and are

found to be less important in the community structuring than in many other intertidal communities (Bertness et al. 2006; Bazterrica et al. 2007; Hidalgo et al. 2007). Along the southern South American Atlantic coast, the hard bottom intertidal zone is characterized by the predominance of bivalves *Brachidontes rodriguezii* (d’Orbigny, 1846) (north to 38°S), *Perumytilus purpuratus* (Lamarck, 1819) (= *Brachidontes purpuratus*, ca. 42–44°S) or *Mytilus chilensis* Hupé 1854 (south to 47°S) that form

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dense beds (Olivier et al. 1966; Penchaszadeh 1973; Zaixso & Pastor 1977; Zaixso et al. 1978; Sánchez & Zaixso 1995; Adami et al. 2004; Bazterrica et al. 2007; Hidalgo et al. 2007; Kelaher et al. 2007). Along the Patagonian coastline, *B. rodriguezii* or *P. purpuratus* dominate the mussel beds in warm temperate or in cold temperate waters, respectively (Liuzzi & López Gappa 2008).

In communities where mussels are the most abundant component and dominant in terms of biomass, knowledge of what occurs in the mussel zone provides a good idea of what happens in the community as a whole (McKindsey & Bourget 2001). It is well known that the presence of mussels increases the diversity of macrofauna over that of adjacent areas (Dye 1992; Tokeshi & Romero 1995; Günther 1996). In this context, the recovery of the bivalve matrix will produce an environmental alteration (Jones et al. 1994; Borthagaray & Carranza 2007) that promotes the settlement of the same or other species living in the interstices or within the accumulated sediment between the byssus and bivalve bodies (Suchanek 1985; Tsuchiya & Nishihira 1985, 1986; Jones et al. 1994; Alvarado & Castilla 1996; Thiel & Ullrich 2002; Kelaher et al. 2007). The concept of recovery after physical impacts differs between species, ecosystems and regions. For example, Underwood (1998, 1999, 2000) proposed that after a disturbance the recovery of communities to the original stage can take several years. Underwood (1998) studied the response to storms in 1974 in an intertidal community in New South Wales, where the recovery of algae took between 6 and 8 years, while other components of the assemblage showed no recovery at the time of the publication of his paper 24 years later (Underwood 1998). Yet, Thompson et al. (2002) generalized that after the collection of organisms or trampling, the recovery generally occurs rapidly once the disturbance has stopped. This seems to depend on the species involved and their individual growth rates (Thompson et al. 2002). For example, in the South African intertidal zone, cleared areas have the first sessile organisms returning after 2 years, with the mussel *Perna perna* particularly unable to recolonize up to 8 years (Dye 1992). Contrastingly, in northern Patagonia, Zaixso et al. (1994) demonstrated successful recruitment of the three mussel species after just 10 months of the removal of all mussels. Based on these previous studies and because the assemblage under investigation is dominated by *M. chilensis* and *P. purpuratus*, we will focus our analysis on the progression of these two populations following disturbance events of two different intensities.

Our knowledge of sub-Antarctic rocky intertidal communities is generally scarce. Particularly in the

southernmost part of South America, Tierra del Fuego, where previous studies only focused on the protected inner waters of the Straits of Magellan (Langley et al. 1980; Ríos & Gerdes 1997; Mutschke et al. 1998; Ríos & Mutschke 1999) or the Beagle Channel (Zaixso et al. 1978). Even studies in the Cape Horn Archipelago were done inside protected coves on a lee shore (Guzmán & Ríos 1981; Ríos & Guzmán 1982). All these previous studies were of a mostly descriptive nature and there is a lack of information of the intertidal community dynamics in open waters, with high-energy conditions like in the Atlantic coast. Compared to other coasts of the Atlantic Patagonia, the seashore of Tierra del Fuego is the least known (cf. http://atlas.ambiente.gov.ar/mapas/index_map.htm; Menge 2000; Bertness et al. 2006; Kelaher et al. 2007). The only geographically related study of subtidal macrobenthic assemblages was previously carried out in the sublittoral of Bahía San Sebastián (53°20'S, 68°30'W; López Gappa & Sueiro 2007).

Unlike cold temperate communities of the Northern Hemisphere, Pacific South America or other sub-Antarctic environments, Patagonian intertidal rocky shores are not subjected to the same structuring factors. Desiccation rates are the highest compared to other intertidal communities of the world (Bertness et al. 2006). Desiccation creates the harshest physical conditions in intertidal communities, and is assumed to be the main cause of physical stress in the Patagonian intertidal zone, affecting assemblage structure. The main consequences of the intense desiccation are low predatory pressure that exerts top-down control (Bertness et al. 2006; Bazterrica et al. 2007; Hidalgo et al. 2007), no recruitment in open spaces and reliance on ecosystem engineers for community recovery and extremely slow community restoration from disturbance (Bertness et al. 2006). Moreover, there is no ice as a factor of seasonal disturbance as in many littoral communities at a similar latitude in the northern hemisphere (cf. Archambault & Bourget 1983; Connell et al. 1997; Pugh & Davenport 1997; Belt et al. 2009; Scrosati et al. 2011). In southernmost South America, intertidal community recovery from a disturbance is scarcely understood. In Northern Patagonia (42°23'S) in an experiment of complete denudation (yet leaving bivalve byssii on the substrate), recruitment occurred within 10 months following bivalve removal whereas the biomass of 3 species of mytilids took 2 years to recover from denudation (Zaixso et al. 1994; Sánchez & Zaixso 1995). More recently, Bertness et al. (2006) pointed out the extremely slow recovery of the bivalve assemblage after its removal. This information, however, contrasts with the numerous studies on

the disturbance effect of ice to both soft and hard bottom communities in shallow Antarctica, where recovery times of the community to the original state can exceed decades (e.g. Barnes 1995, 2005; Peck et al. 1999, 2006; Gutt 2001).

The Atlantic coast of Tierra del Fuego has minimal human impact so far, but increasing activities entail risks of disturbances. Unfortunately, baseline surveys for this area are scarce and hence the need for knowledge about the vulnerability of intertidal communities and their capacity for recovery (Paine et al. 1996). The motivation for our study results from the possible anthropogenic factors of disturbance of the rocky shores as the result of several socio-economic activities in the area. First, potential oil spills (Bujalesky 2007; López Gappa & Sueiro 2007) are the principal threat of a massive mortality of the intertidal organisms (Paine et al. 1996 and references therein). Our study area is located 30 km south of the main operational area for offshore hydrocarbon extraction and the north-south coastal current is likely to disperse any spill along the coast of Tierra del Fuego. Second, mussel removal for human consumption can impact less severely, but will be sustained over time. Mussel harvesting may consist of extraction of small mytilids to be used as seeds in the nascent mytiliculture industry of the nearby Beagle Channel, or large individuals for retail, with the additional disturbance of trampling. Long-term studies with experiments being monitored are required to study the resilience of communities to such disturbances, as events that occur over a short period can have effects that are verified during the following years (Underwood 1998, 1999, 2000; Hawkins et al. 2009). The objective of this work was therefore to evaluate the effect of physical disturbance on the recovery of an intertidal bivalve assemblage located in the Atlantic shore of Tierra del Fuego, Argentina.

Materials and methods

Study area

This study was conducted in an intertidal rocky shore 30 km north of the city Rio Grande (53°36'S, 67°58'W), Tierra del Fuego, Argentina. This coast presents a slight slope compared to the typical Patagonian cliffs, and maximum tidal amplitude of 8.4 m, with an average of 5.5 m (Bujalesky 2007; Servicio de Hidrografía Naval 2010). The Atlantic coast of Tierra del Fuego is dominated by strong tidal currents, parallel to the coastline (NW-SE directions, respectively) and with maximum speed of 0.6 m s⁻¹ (Bujalesky 2007; Isla 2008; Servicio de Hidrografía Naval 2010). The coast is exposed to high-energy

waves, although prevailing strong westerly winds attenuate the wave regime in this area. The maximum significant wave height is 3.4 m and winds from NE to E produce a stronger swell, with extreme wave heights of 5.8–7 m (Bujalesky 2007). Tidal regime is semi-diurnal, with an amplitude of ca. 5.8 m and 9.2 m mean and maximum amplitude, respectively.

The studied beach has three distinct sections: the first of ca. 50 m is a reflective beach, has a slope of ca. 20° and is of gravel. In the next 300–400 m of the beach is subhorizontal with medium to coarse sand in the first 100 m and rocky outcrops for the next 200–300 m. The sampling area was located on the first 40–50 m of rocky outcrops, which are exposed at low spring tides throughout the year, i.e. at most 0.45 m above the chart datum. In this section of the beach, the studied assemblage is established on individual horizontal or subhorizontal rocks or outcrops of approximately 1–3 m² surface area and 0.5–0.7 m height, separated by 4–10 m and surrounded by sand. The assemblage is dominated by bivalves which settle on top of the rocks. Rock sides were free of organisms, probably due to sand erosion. Further down the beach, at 0.1–0.2 m above the chart datum, there are ca. 250–300 m of rocky outcrops, which are uncovered only during summer spring tides, and hold an assemblage mainly composed of colonial ascidians, sponges, barnacles, and anemones.

Experimental design

The experiment was started on 19–21 February 2001. A total of 29 rocks of similar size and shape and at the same tidal level were randomly selected and assigned to three treatments. (1) The total removal of all organisms or trace of organic structures living on the rock and the rock surface was cleared using a 20% HCl solution. This treatment was carried out for 9 different rocks. (2) Disturbance (also disturbed plots/trials hereafter): in order to simulate a physical disturbance, at the beginning of the experiment a rock of 10 kg, parallelepiped-shaped, that was dropped from a height of 1.8 m onto the rocky assemblage. This rock falling was one next to the other so that all the area of horizontal/subhorizontal surfaces of the treated rocks was impacted once. The disturbance was done in ten different rocks and resulted in many bivalves being crushed. The remaining empty shells (entire or fragments) and byssi were left on the rock without any further manipulation. (3) Control: no organisms were removed or disturbed from ten rocks. For their identification throughout the experimental study, all rocks were numbered with epoxy paint on the side margins.

The estimation of percentage cover was estimated from digital photos taken at each sampling date with

a quadrat of 0.15×0.15 m as reference. The same 225-cm^2 quadrat was used to take random samples from the rocks. All organisms found within the quadrat were removed from the substratum with a scraper and scrubbing brush. Samples were fixed in 5% formaldehyde and later preserved in 70% ethanol. In order to characterize the assemblage, a sample of 20 quadrats was taken at the start of the experiment from rocks different from those used in further trials. Thereafter, five samples from each treatment were taken during the low tide approximately every third month throughout 2001, 2002 and 2003 and once a year during 2004 and 2005. At each season rocks to be sampled were selected randomly. Because some of the five seasonal samples might have repeated the same rock, the location of the sample on the rock was recorded so that successive samples were not taken in the same place or within 0.15 m.

In the laboratory, the material was rinsed in sieves of different size mesh of 710, 1000, 1680 and 2000 μm . To determine the progress of the associated community of the bivalve assemblage, during the first year of sampling all organisms were separated and identified to the lowest taxonomic level possible. From the beginning of the experiment, the most abundant animals, the bivalves *Mytilus chilensis* and *Perumytilus purpuratus*, were separated. For each individual the wet mass was recorded to the nearest 0.0001 g using an analytical balance, and the length, width, and height were measured to the nearest 0.01 cm by means of a Vernier caliper.

Data analysis

To analyse the growth of the bivalves during the first year after settlement, the valve length of individuals in each quadrat was measured for each sampling date. Growth for a period was calculated as the ratio between the difference of two successive valve measurements and the elapsed time. At each sampling date the null hypothesis of equality of growth for the three different treatments was tested by a one-way ANOVA followed by Tukey's post-hoc comparisons (Sokal & Rohlf 1995). In order to meet the assumptions for normality and homogeneity of variance the Lilliefords and Bartlett tests were performed, respectively. Throughout the experiment and for total removal and disturbance plots, the increment of the percentage of bivalve coverage through time was represented by means of a linear regression.

During the first year of sampling of the community, the Species Richness index (R) was calculated as $R = \log_2 N$. The Shannon index for Diversity (H') was calculated as $H' = \sum P_i \log_2 P_i$ (N : total number of individuals; P_i proportion of individuals of species

i in the sample). Finally, the Equitability Index of Evenness was calculated as $E = H'/R$ (Magurran 1988; Krebs 1989). Null hypotheses of equality of diversity, richness or evenness indexes through treatments and sampling dates were tested with respective two-way ANOVAs followed by Tukey's post-hoc comparisons.

Furthermore, at selected dates the null hypothesis of equality of density was tested with a one-way ANOVA. A log-transformation of data was done when needed to meet ANOVA's assumptions (Sokal & Rohlf 1995). Densities of adults were compared with a Mann-Whitney U-test, because data were not normally distributed (Daniel 1978).

At the time of massive recruitment, Bhattacharya's (1967) method was applied using the FISAT package to the size frequency distributions of *Mytilus chilensis* to identify the mean sizes of the normally distributed cohort in the polymodal distributions. Further analyses were hampered by the high degree of overlapping of the different cohorts, probably due to continuous settlement during summer. Furthermore, throughout the study period, the trend and seasonality of the development of the bivalve assemblage in the three treatments was tested with a Cox-Stuart test (Daniel 1978), applied to the annual cohorts.

Results

Assemblage composition

The studied assemblage settled on top of rock outcrops and was dominated by bivalves *Mytilus chilensis* and *Perumytilus purpuratus* (Figure 1). At the start of the experiment, bivalves appeared in layers (of at least two), with *M. chilensis* occupying the top layer. Beneath the bivalves there was a layer of mud and sand, of variable height from a few mm to 10 cm, in which there were amphipods, isopods, polychaetes, gastropods, anemones, hydrozoans and small bivalves (Figure 1). In the control plots, this layer of mud remained during 2001 with the consequent occurrence of the mobile fauna associated with it. In the disturbed plots, the reduction of the mud layer was faster, with only 2–5 cm remaining in June 2001. In sampling events after February 2002, in all the assemblage the sediment layer associated with the mud bed was <5 mm or virtually absent including its associated fauna, and sampling was therefore discontinued.

After the start of the experiment and between June 2001 and February 2002, diversity was lower in the disturbed plots than in the control, since the null hypothesis of equality of the diversity index between treatments and dates was rejected (two-way ANOVA, $F_{\text{treatment}} = 6.9$; $p < 0.05$; Table I) and decreased with

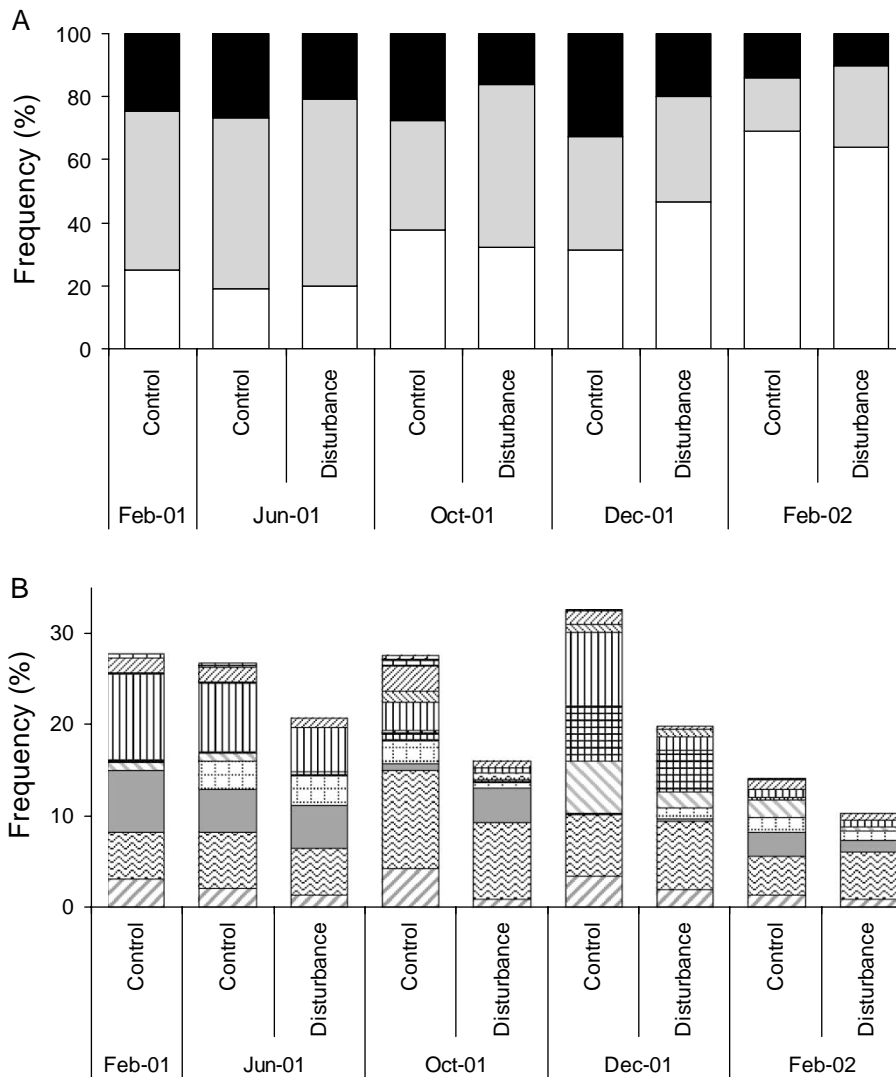


Figure 1. A. Relative frequencies of the three dominant species of bivalve mussels. \square *Mytilus chilensis* Hupé 1854, \square *Perumytilus purpuratus* Lamarck, 1819, \blacksquare others. B. Relative frequencies of the associated fauna. \square *Aulacomya atra* Molina, 1782, \square *Typosyllis amillaris* Müller, 1776, \square *Capitellides giardi* (Quatrefages, 1843), \square *Polychaeta*, \square *Edotia doellojuradoi* Giambiagi, 1925, \square *Exosphaeroma* sp.1 and sp.2, \square *Trophon geversianus* Pallas, 1774, \square *Notobalanus flosculus* Darwin, 1854, \square *Paramoera* sp., \square *Tryphosella schellengeri* Schellenberg, 1931, \square *Parafoxiophalus longicarpus* Alonso de Pina, 2001, \square *Anthozoa*, \square others.

time (ANOVA, $F_{\text{dates}} = 3.9$; $p < 0.05$). Species richness was also consistently lower in the disturbed treatment, as the null hypothesis of equality of the species richness index between treatments was rejected (two-way ANOVA, $F_{\text{treatment}} = 14.2$; $p < 0.001$). Evenness decreased in February 2002 as the null hypothesis of equality of this index between dates was rejected (two-way ANOVA, $F_{\text{dates}} = 9.44$; $p < 0.001$) with a concurrent increase in dominance of *M. chilensis* (Figure 1). *Perumytilus purpuratus* dominated the assemblage in June 2001 (Figure 1). The proportion of *M. chilensis* was higher than that of *P. purpuratus* in the disturbed plots in December 2001, and due to a recruitment event (see below). In February 2002, the proportion of *M. chilensis* in both the disturbed and control plots was $> 64\%$.

Notably, some common competitors for space (limpets) and predators (drilling snails, sea stars or seabirds) regularly present in other intertidal rocky shores are absent from this intertidal zone. A single individual of *Trophon geversianus* was found in June 2001 and there were no further signs of the presence of this or other drilling predators. We found no valves with the typical hole produced by predatory snails or seabirds (e.g. oyster catchers) in the experimental site or in the head of the beach where shells commonly accumulate.

In control plots, the percent coverage of bivalves varied between 82% and 97% during the period March 2001 to April 2004 (Figure 2). Only in March 2005 did coverage drop to values between 55% and 87%. In both disturbance and total

Table I. Diversity, richness and evenness during the first year of experiment after an experimental disturbance. Values are averages (± 1 standard deviation). For each index, respective two-way ANOVAs were performed to test null hypothesis of equality of the index between treatments and dates. Significant differences yielded by Tukey's multiple comparisons are noted by different letters ($p < 0.05$).

Date	Diversity		Richness		Evenness	
	Control	Disturbance	Control	Disturbance	Control	Disturbance
June 2001	1.94 ^a (0.33)	1.79 ^c (0.29)	3.28 ^a (0.20)	2.70 ^b (0.48)	0.59 ^a (0.07)	0.69 ^a (0.20)
October 2001	2.12 ^a (0.42)	1.50 ^c (0.27)	3.19 ^a (0.39)	2.43 ^b (0.35)	0.67 ^a (0.09)	0.62 ^a (0.05)
December 2001	2.07 ^a (0.53)	1.77 ^c (0.32)	2.99 ^a (0.43)	2.66 ^b (0.48)	0.68 ^a (0.11)	0.67 ^a (0.05)
February 2002	1.50 ^b (0.24)	1.35 ^d (0.33)	3.13 ^a (0.14)	2.85 ^b (0.55)	0.48 ^b (0.08)	0.47 ^b (0.04)

removal plots the percentage coverage of bivalves increased over time, although at different rates (Figure 2). Overall, total removal plots recovered at a higher rate than the disturbance plots ($F_{\text{equal slopes}} = 44.59$; $p < 0.0001$; Figure 2). However, the coverage of bivalves was variable and most evident among total removal plots. In the disturbance experiment the percent coverage of bivalves varied between 34% and 73% in June 2001 to 60–93% in March 2005, whereas in the total removal plots percent coverage varied between 0.2% and 9% in June 2001 to 9–80% in March 2005. In April 2004, i.e. 3 years after the total eradication of mussels, some of the total removal plots had a similar percent

coverage of bivalves to those of the disturbance experiment, although some other plots partially recovered to only $< 30\%$ of bivalve coverage (Figure 2). In March 2005, only half of the sampled outcrops had $> 40\%$ of bivalve coverage, coinciding with a decrease in bivalve coverage of control plots. During our study a few of the experimental outcrops (both from total removal and disturbance plots) were covered by sand and delayed, or never experienced, any recovery. Around some outcrops sand level varied up to 0.5 m in height, enough to cover or uncover the mussel bed, depending of the outcrop height. Movement of sand through the mid-intertidal, specifically during winter, appeared to be

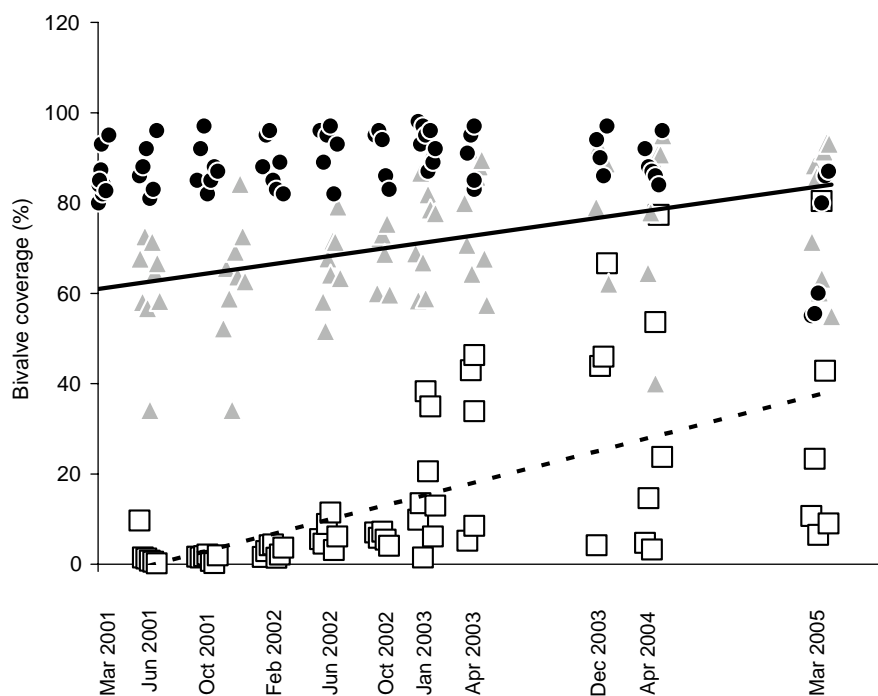


Figure 2. Percent of bivalve coverage in the treatments. Traingle: Disturbance. Box: Total Removal. Full line represents a linear function for disturbance plots as Coverage (%) = 0.015 days - 521.5 (R^2 : 0.195) and the dotted line is a linear function for the Total Removal plots as Coverage (%) = 0.027 days - 1025 (R^2 : 0.327)

the main factor of disturbance in this assemblage that could be only detected by the periodic sampling.

Mytilus chilensis

The disturbance treatment produced a loss of individuals of all size ranges, as evidenced by the size frequency distributions (SFDs) of June and October 2001, when compared to the control (Figure 3). Concurrently, density was also reduced in June and October 2001 (Figure 4). For both dominant species *M. chilensis* and *P. purpuratus*, percentage coverage was also reduced (Figure 2).

Over the total study period, two events of massive recruitment were clearly recorded in December 2001 and March 2005, and were independent of the experimental treatment (Figures 3 and 4). Chronologically, in the period March–December 2001 the SFDs of *M. chilensis* were biased to large animals and characterized by a modal group around 34–37 mm length. Recruitment, as the first occurrence of *M. chilensis* specimens <2 mm, was first detected in both total removal and disturbance plots in December 2001 (Figure 3). In both treatments SFDs showed two clear modes at 2 and 35 mm length. In February 2002, SFDs of the control and disturbance treatments were dominated by a modal group with a mode of 3–4 mm length that represented 74–79% of the total sampled individuals, respectively (Table II). In February 2002, densities of recruits in the three treatments appeared different ($F = 6.6$; $p < 0.05$, Figure 3, Table II) because recruits occurred at lower density at the total removal plots (Tukey's multiple comparisons $p < 0.05$). Also in February 2002, densities of adults were similar in both the disturbance and control plots (Table II; Mann–Whitney U-test_{adults} $p = 0.3$). These recruits of February 2002 could be traced in time until January 2003. During the period February 2002–January 2003 the disturbance and control plots exhibited bimodal SFDs with a main modal group of the recruits settled in February 2002, and a minor modal group of ca. 40 mm length of older animals that had dominated the SFDs in 2001. The only modal group of the total removal plots that appeared during 2002 likely corresponded to the recruits of February 2002. The massive recruitment of February 2002 was also detected by means of the Biomass/N relationship, which in 2001 increased to a maximum in October and in February 2002 Biomass/N values of all treatments were minimal (Figure 5A). Other maxima of Biomass/N and with values similar to those of the end of 2001 were recorded in April 2004.

Between January and April 2003 another recruitment event probably occurred but was only detect-

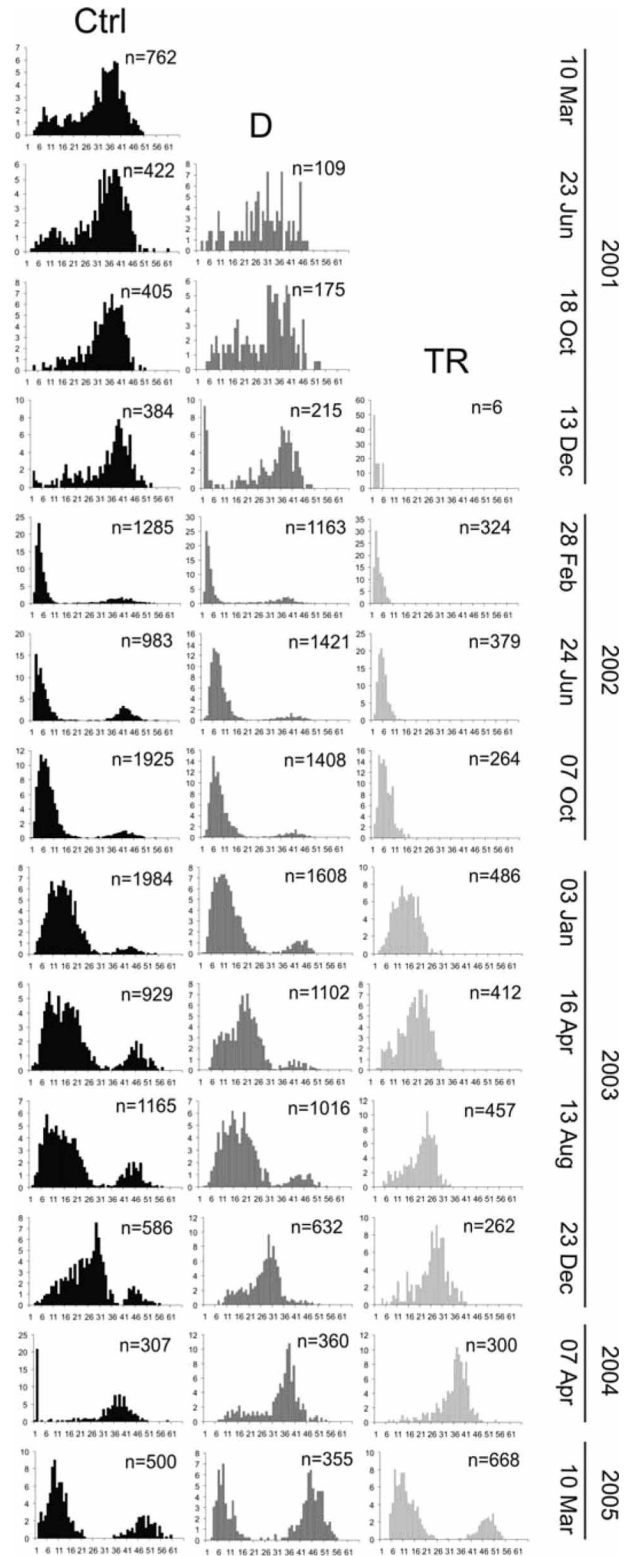


Figure 3. Frequency distributions of *Mytilus chilensis* sizes for the three treatments. Control (Ctrl), Disturbance (D) and Total Removal (TR). In June and October 2001 size frequency distributions of the total removal treatment are lacking because there were no animals settled on the experimental rocks.

able by indirect means: (i) the density in the control plots increased from ca. 16,000 in October 2002

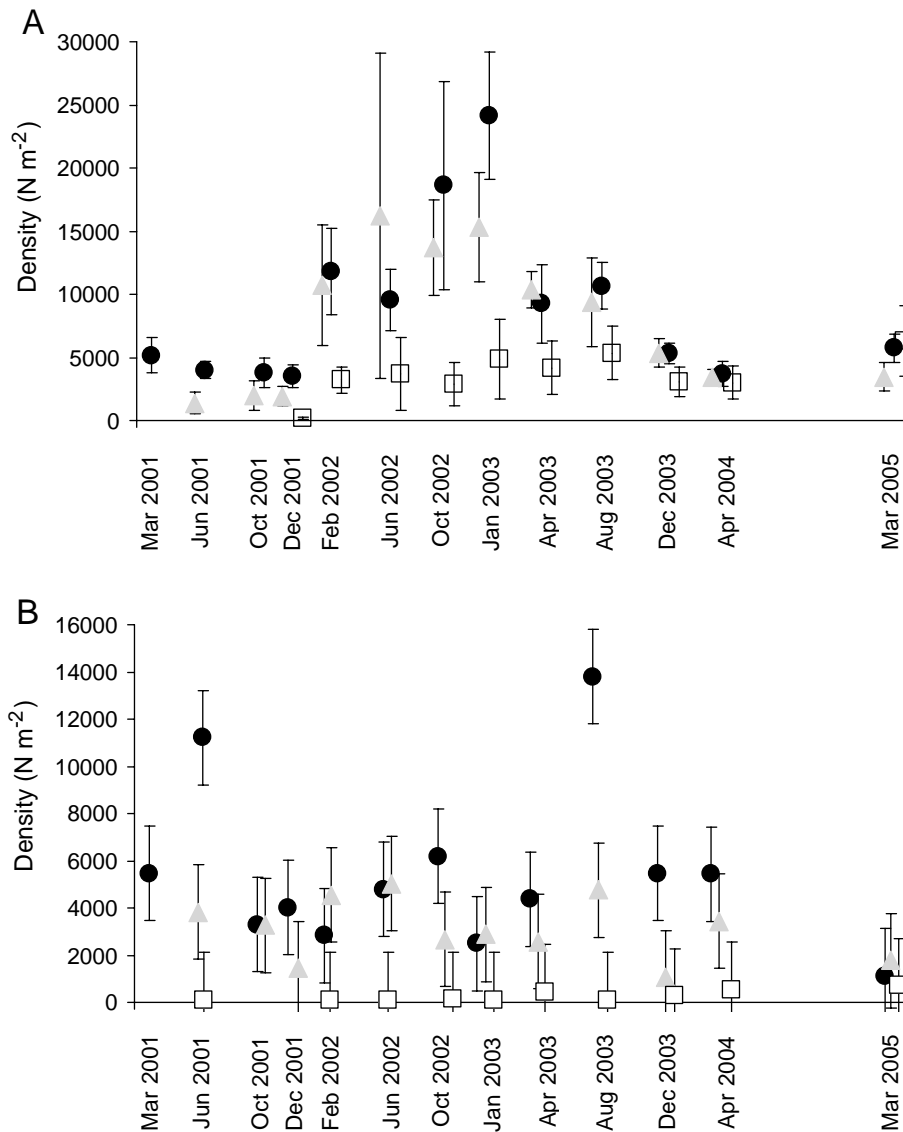


Figure 4. A. Density of *Mytilus chilensis* as individuals m^{-2} . B. Density of *Perumytilus purpuratus* as individuals/ m^2 . Triangle: Disturbance, Box: Total Removal; Circle: Control.

to ca. 25,000 individuals m^{-2} in January 2003 (Figure 4A). However, in contrast to the recruitment of February 2002, the B/N relationship for January and April 2003 exhibited no decrease (Figure 5A). (ii) In April 2003 very few (<2% of *M. chilensis* of ≤ 4 mm length) recruits were detected in all three treatments (Figure 3). Moreover, individuals of ca. 7 mm length (the second smallest modal group in the control plots, Figure 3) could account for the new recruits settled in January or February 2003, which at a growth rate of 0.15 mm per day (Figure 6) would have grown 7.5 mm in length in 50 days. In August 2003 the different modes of animals <25 mm length became indistinguishable (Figure 3).

Another recruitment event was detected in April 2004, but only in the control plots. Twenty-one percent of individuals were ≤ 4 mm in length while

the SFDs of the disturbance and total removal plots were biased to large animals of ca. 35 mm length (Figure 3). In April 2004, the size structure of the disturbance and total removal plots resembled that recorded in March 2001, the time of the initiation of our experiment. In March 2005 SFDs of the three treatments were clearly bimodal, with a smaller group with a mode ca. 5–7 mm length that presumably settled immediately before the latest sampling event and a larger group with modes at 45 or 50 mm length.

Immediately after the experimental disturbance and during June–December 2001, the density of *M. chilensis* of the control plots was higher than in the disturbance plots (Figure 4A). In December 2001 a very low density was recorded in the total removal plots. In February 2002 all densities increased and those of both control and disturbance plots were

Table II. *Mytilus chilensis*. Density (individuals m^{-2} , and 1 standard deviation) of recruits and adults of mussels and parameters of their size frequency distributions at the 28 February 2002. Different letters represent significant differences (ANOVA $F = 6.9$; $p < 0.05$, followed by Tukey's multiple comparisons $p < 0.05$).

28 FEB 2002	Control	Disturbance	Total removal
Density recruits \pm SD	8978 ^a \pm 3332	7582 ^a \pm 4517	2880 ^b \pm 929.30
Density adults \pm SD	2333 \pm 242	2755 \pm 303	–
Size classes			
Average length (SD)	3.49 (0.97)	3.62 (1.14)	2.89 (1.34)
<i>N</i>	796	811	292
Average length (SD)	6.06 (1.18)	5.88 (2.31)	5.89 (1.140)
<i>N</i>	249	131	69
Average length (SD)	35.31 (1.88)	33.03 (2.68)	
<i>N</i>	86	110	
Average length (SD)	39.28 (1.25)	38.33 (2.09)	
<i>N</i>	60	130	
Average length (SD)	43.34 (2.04)	44.57 (1.68)	
<i>N</i>	71	20	

higher than the density of the total disturbance plots (Table II; Figure 4A). In January 2003 the density of the control plots was at a maximum, and higher than the density of the disturbance plots (ANOVA $F = 22.53$, $p < 0.01$, Tukey $p < 0.01$).

During the first year after the massive settlement, the growth rate of *M. chilensis* from control and disturbance plots decreased with time while the growth rate of mussels from total removal plots remained constant (Figure 6). The growth rate of *M. chilensis* from the total removal plots was significantly lower than the growth rate of the other two treatments at days 76, 161, and 266 from recruitment ($p < 0.001$), while at day 354 the growth rates in the three treatments were similar. However, throughout the experiment growth was unaffected by treatments because the Cox–Stuart test showed that *M. chilensis* grew similarly in the control, disturbance and total removal plots (all treatments $p < 0.05$).

Perumytilus purpuratus

Unlike *M. chilensis*, the disturbance treatment did not have an effect on the *P. purpuratus* fraction of the bivalve assemblage. During the following samplings after the experimental disturbance there was no lack of individuals in the SFDs (Figure 7) and density remained constant compared to that of the control plots at the start of the experiment or in October 2001 (Figure 4).

Between March 2001 and January 2003, control and disturbance plots showed SFDs with animals of a wide range of sizes and biased towards small sizes, with modes varying between 4 and 14 mm length (Figure 7). For the complete removal plots and for the same period, there were few animals (always < 10) that ranged in size from 1 to 12 mm length. In the period March 2001–January 2003 no recruits were recorded, with the exception of a few of the smallest mussels sampled in June 2001, October 2002 and January 2003 in the total removal plots and in October 2002 in the control plots (Figure 7). Contrastingly, SFDs of control plots from April 2003 to April 2004, disturbance plots of August 2003 and total removal plots from April 2003 had SFDs dominated by the smallest individuals, i.e. *P. purpuratus* < 3 mm length (33–49% in the control; 3–25% in the disturbance; 16–75% in the total removal plots).

Throughout the sampling period, densities in the control and disturbance plots were fairly constant with the exception of two maximal densities of ca. 11,700 and 14,000 individuals m^{-2} in June 2001 and August 2003 in the control plots, respectively (Figure 7). Otherwise, densities varied between 1000 and 5000 individuals m^{-2} . In the control plots the maximum density of *P. purpuratus* in August 2003 was coincident with the occurrence of recruits (Figure 4B and 7). The maximum density in June 2001 seemed not to correspond to a recruitment event as there were only 3% of individuals < 3 mm length. Densities in the total removal plots remained below 500 individuals m^{-2} throughout the experimental period (Figure 4B). The lack of a massive recruitment of *P. purpuratus* was also reflected in the Biomass/N relationship, as there was no correspondence of the occurrence of small individuals in the SFDs (Figure 7) with a low Biomass/N relationship (Figure 5B). Clumps of *M. chilensis* likely provide an appropriate matrix for *P. purpuratus* settlement, as detected in the SFDs after April 2003 (Figure 7), and demonstrated by an increase of both the Biomass/N ratio in the total removal plots after August 2003 (Figure 5) as well as density in the control plots in August 2003 (Figure 4B). Throughout the experiment, growth was unaffected by treatments because the Cox–Stuart test showed that *M. chilensis* grew similarly in the control, disturbance and total removal plots (all treatments $p < 0.001$).

Discussion

Timeline of recovery from disturbance

We propose the recovery sequence of the bivalve assemblage in the Atlantic Southern Patagonia

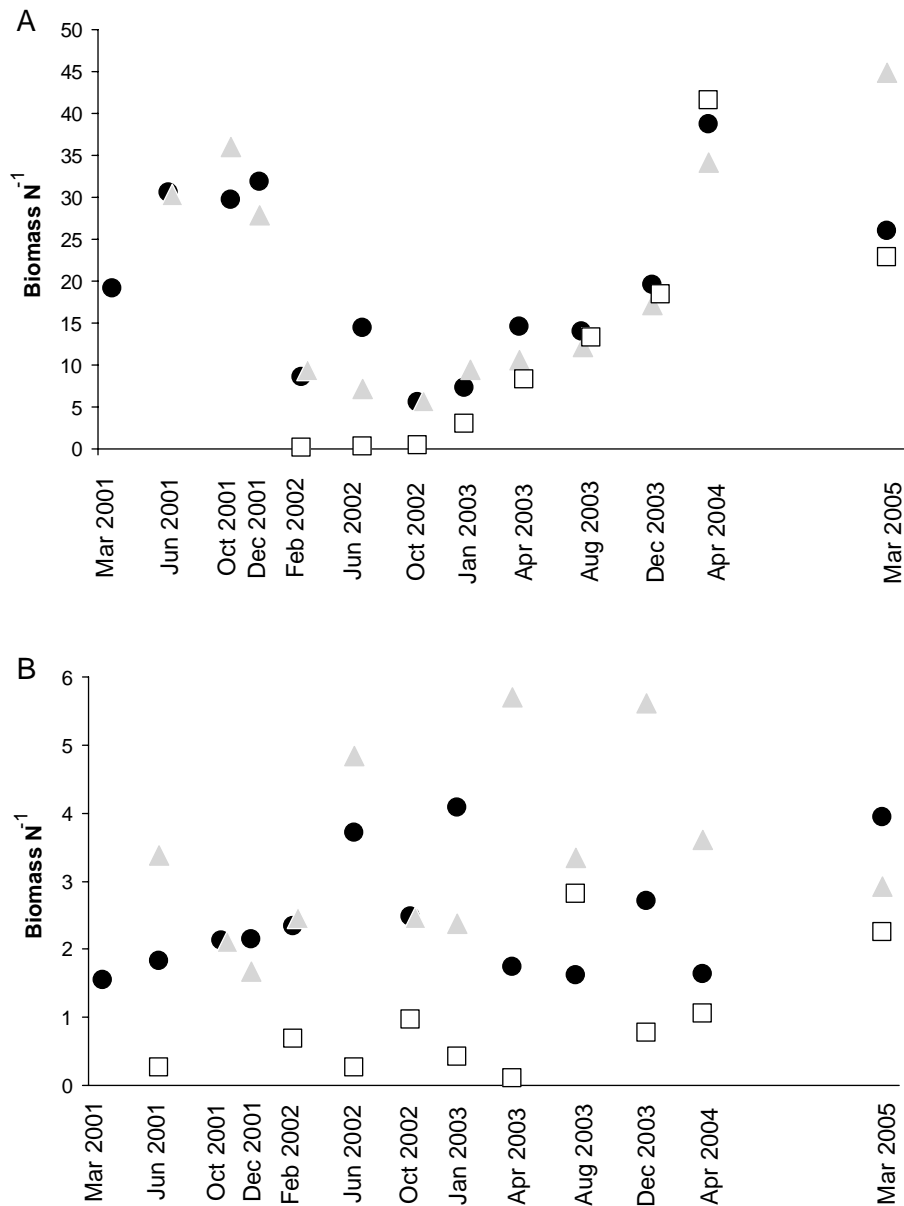


Figure 5. A. Biomass (g m^{-2})/ n of *Mytilus chilensis* recruits versus time. B. Biomass (g m^{-2})/ n of *Perumytilus purpuratus* recruits versus time. Triangle: Disturbance, Box: Total Removal; Circle: Control.

region is as follows. A massive recruitment of *Mytilus chilensis* occurs in the following summer of our disturbance experiments. Albeit a few *Perumytilus purpuratus* were detected on bare substrate in April 2001 and some recruits in June and October 2002, a massive recruitment of this species was recorded in the control plots since April 2003, approximately 2 years after disturbance. The size frequency distributions of *M. chilensis* in control and disturbed plots were similar right after the massive settlement, 12 months after the start of the experiment. The disturbance clearly produced the loss of many individuals, since in June 2001 the density in control plots increased fourfold that of the disturbed plots,

yet density became similar in both treatments after the massive recruitment of December 2001–April 2002. In April 2004, ca. 37 months after experimental disturbances, the SFDs of *M. chilensis* of the three treatments were similar to those recorded previous to the experimental trials. The restoring of the coverage by mussels was very variable: whereas the disturbed plots showed a clear increase in bivalve coverage during the period June 2001–April 2004, the recovery of the assemblage of total removal plots was uneven. In these latter plots and in a few cases (rocks) the bivalve matrix recovered to similar levels of coverage to the disturbance plots, yet only in those rocks with crevices where the bivalves settled and

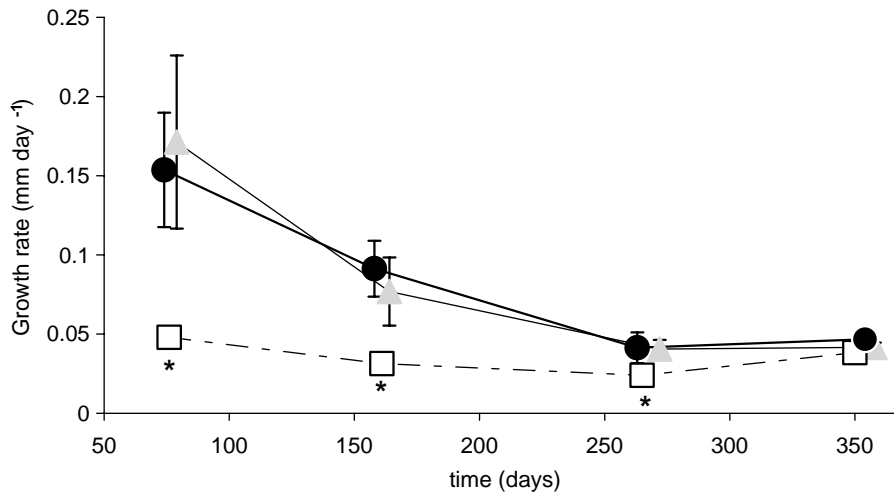


Figure 6. Growth rate of *Mytilus chilensis* recruits versus time during the first year of experiment. Asterisks mark significant differences between treatments for each date. Triangle: Disturbance, Box: Total Removal; Circle: Control.

grew. In March 2005 and in some total removal outcrops, coverage attained ca. 80% of rock surface that compares with the 90% of coverage of the rocks with a single disturbance or control. Therefore, after a total removal, depending on the rugosity of the substrate and the sand irruption, the bivalve assemblage of the Atlantic coast of Tierra del Fuego likely takes 36 months to recover to a stage of >70% coverage and *M. chilensis* individuals of ca. 35 mm.

Time of recruitment and post disturbance recovery

In southern temperate communities recruitment of bivalves is restricted to the summer season and the time of recovery will depend on whether the disturbance occurs before or after the recruitment season (Dayton et al. 1984; Breitburg 1985; Benedetti-Cecchi 2000). The recruitment success is driven by either the larval supply or space availability (Menge et al. 2010). The massive recruitment of *Mytilus chilensis* in the austral summer 2002–2003 occurred when individuals were ca. 30–40 mm length, leaving space for new recruits. This recruitment was independent of the open spaces left by our experiment because densities in the disturbed and control plots were similar. Although there is no information on the temporal or spatial distribution of bivalve larvae off Tierra del Fuego, larval supply seems not to be limiting. *M. chilensis* >22 mm total length and *Perumytilus purpuratus* >10 mm total length are sexually mature, can spawn mainly between December and February of each year (Vinuesa 1978; Alvarado & Castilla 1996; Gray et al. 1997) and were present in our samples throughout the study period. However, because of

strong currents prevailing in the area, larvae are likely to arrive from northern sites with similar reproductive timings. In our study, the disturbance was initiated in March and no recruitment occurred until the next reproductive season, 9 months later, in December 2001. As a result, the recovery time would have likely been shorter if the disturbance had been made immediately prior to the recruiting season.

Factors of disturbance in the Patagonian intertidal

One of the indicators of harshness of the studied assemblage is the strong coastal current of ca. 3.6 km·h⁻¹ of speed (Bujalesky 2007). This current along with waves can move pebbles up to 20 cm in diameter (Bujalesky 2007) and are responsible for the displacement of the nearby sand between and above the outcrops. Sand beds can remain stable for several months, especially during winter, to the point that permanent sand cover can cause mass mortality of mussels or impede the settlement of new individuals. As a result, some of the experimental outcrops showed a slow increase in bivalve coverage, as in case of the total removal plots with <10% of coverage (Figure 2). This sand deposit was not reported previously and was unexpected, and can be considered as the main disturbance factor along the Atlantic coast of Tierra del Fuego. This disturbance feature most likely differentiates the assemblage studied here from other localities on the Patagonian coast. In northern Patagonia, summer temperatures can be very high and combined with strong westerly winds produce the intertidal desiccation which is a major factor of disturbance (Bertness et al. 2006; Bazterrica et al. 2007; Silliman et al. 2011). Further

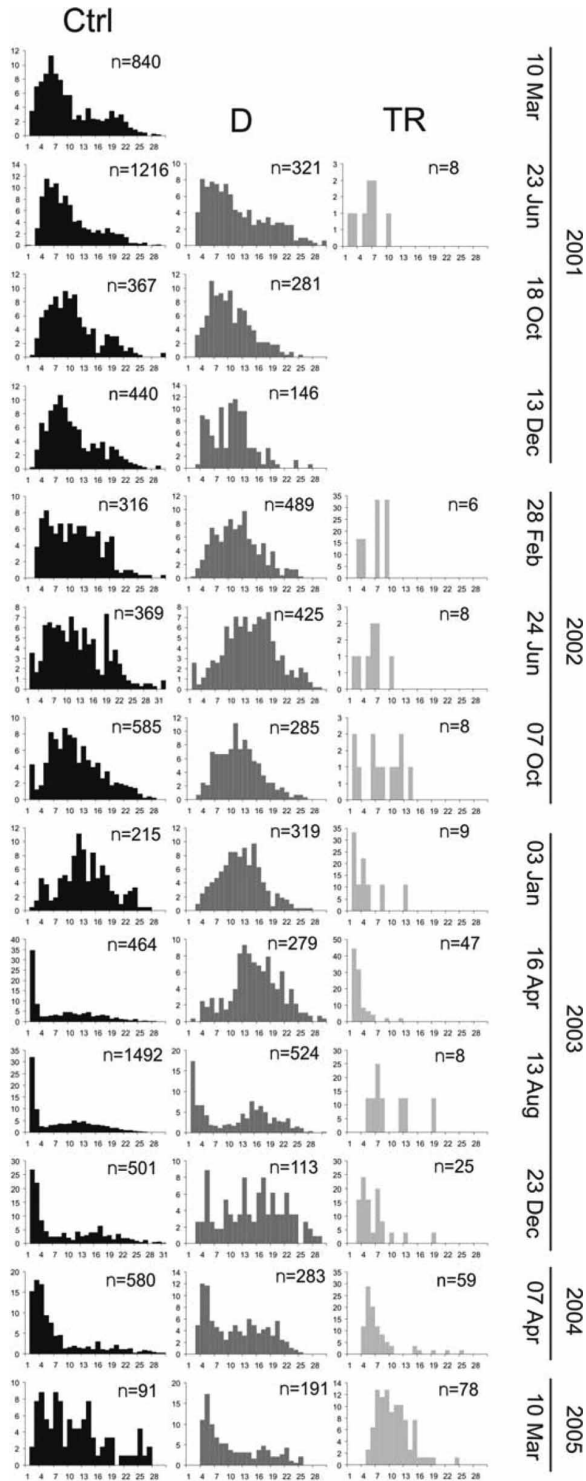


Figure 7. Size frequency distributions of *Perumytilus purpuratus* for the three treatments. Control (Ctrl), Disturbance (D) and Total Removal (TR). In October 2001 and December 2001, size frequency distributions of the total removal treatment are lacking because there were no animals settled on the randomly selected plots of the experimental rocks.

south in Tierra del Fuego, westerly winds can also be strong, since in Patagonia desiccation is wind-driven rather than temperature-dependent (Silliman et al.

2011), it is likely that extreme desiccation is an additional physical stress factor that affects the studied intertidal zone.

Destruction of the physical structure provided by the bivalve bed causes the loss of the infauna inhabiting the sand accumulated in the bivalve interstices. At the beginning of our experiments, mussels occurred in a stratified structure, with *Perumytilus purpuratus* in the lowest layer with sediment in between their byssi, with thriving infauna (Prado & Castilla 2006) and *Mytilus chilensis* on top. Within the following year following the start of our experiment, this structure of multiple layers gradually disappeared coincidentally with a massive recruitment of *M. chilensis* (see below), with the consequent decrease in diversity and evenness, in both control and disturbance plots (Prado & Castilla 2006; Kelaher et al. 2007), but more pronounced in the latter treatment. Once gone, this structure of two layers of bivalves and sediment was not longer found during our 4 years of the experiment. The cause of the natural thinning of the sand layer is unknown and deserves further studies. Although sand interrupted the studied site several times between 2002 and 2005 covering the rocks totally or partially, it was not retained by the bivalve matrix, which was dominated by *M. chilensis*. Moreover, at the time the sand layer was recorded in our studied community (2001) *P. purpuratus* was dominant, a fact that did not occur in the following years, at least until 2005 (Figure 1A). Hence it is probable that the retention and growth of the sand layer in this system is related to the interstitial space left by *P. purpuratus* and their position in respect to the substrate (not measured in this study) when it is abundant. *M. chilensis* grows faster than *P. purpuratus* and/or its position in respect to the substrate probably (e.g. Seed & Suchanek 1992) is less efficient in providing such interstitial spaces for sand retention, and sediment is only retained for short periods. Either the disturbance that destroyed the layer structure of the assemblage, the reduction of the sand layer, or the massive recruitment of *M. chilensis* that monopolize the space on the rock caused a comparable loss of diversity (Borthagaray & Carranza 2007).

Mechanisms modelling the bivalve assemblage

Our results suggest that the bivalve assemblage of the Atlantic coast of Tierra del Fuego is most likely controlled by competition for space rather than other biological interactions like predation, for the following reasons. First, in the total removal treatment, bivalve recruitment begins only in crevices and rough surfaces, and thereafter the mussel bed

progresses sideways through settling on the structure provided by the byssal threads of established mussels (Bourget et al. 1994; Nielsen & Franz 1995; Guichard et al. 2003). Attachment on a bare substrate is probably unsuccessful due to the physical stress produced by extreme desiccation (Silliman et al. 2011) and strong currents carrying sand with its consequent abrasive effect on the rock surface (cf. Bujalesky 2007). As a matter of fact, rocks that progressed towards a full coverage of bivalves were those with several crevices from which the assemblage grew. In the extreme case that a single crevice exists then the total coverage of the rock will be delayed compared to those rocks with more irregularities e.g. (Seed & Suchanek 1992; Bourget et al. 1994 and references therein). Second, massive recruitment only occurred when the size of bivalves was adequate to allow new individuals to settle and grow. Pioneer works have found that pediveliger larvae of *Mytilus edulis* settle preferentially on filamentous substrata, which provide physical protection (De Block & Geelen 1958; Dean 1981). If specimens already attached to the substrate are large enough, their bodies will leave interstices and new recruits will have the adequate space (and environment) to settle (Suchanek 1985; Seed & Suchanek 1992; Alvarado & Castilla 1996; Harris et al. 1998). For example, the massive recruitment of *Mytilus chilensis* occurred in summer 2002 (Figure 3) when modal sizes were ca. 35 mm length and *Perumytilus purpuratus* were ≥ 5 mm length. In *P. purpuratus* a detectable recruitment occurred during summer 2003 when modal sizes were ca. 15 mm and 11–14 mm length for *M. chilensis* and *P. purpuratus*, respectively. Crowding has been reported as a negative effect affecting bivalve growth (Kautsky 1982; Boromthananarat & Deslous-Paoli 1988; Frechette & Lefaiivre 1990). However, chemical or tactile signals associated to the presence of conspecific adults probably promotes recruitment of larvae, so that the gregarious habit may be a mechanism to maximize the recruitment where growth conditions are favourable (Nielsen & Franz 1995). Settlement among adult individuals could confer additional advantages that may help to avoid predation or reduce desiccation or thermal stress (Nielsen & Franz 1995; Silliman et al. 2011). Third, opening of interstitial spaces after a partial disturbance. Disturbance results in increasing rates of mortality (or emigration) of individual organisms, and also releases space-resources that can enhance the local density of populations by colonization (immigration or recruitment) (cf. Grime 1973; Connell et al. 1997; Bertocci et al. 2005). Disturbances in the intertidal zone vary in extent (area affected) and intensity (degree of damage). When space is scarce

or disadvantageous, bivalve assemblages can develop into a multi-layered structure (Alvarado & Castilla 1996), which would make them more vulnerable to disturbances and less stable than single-layered arrangements because a higher proportion of individuals are attached to their neighbors and not directly to the substrate (Paine & Levin 1981).

Nevertheless, in our study area the occurrence of a massive recruitment event of *M. chilensis* in the following season of the disturbance obscured the role of opening spaces we created in the disturbance plots, since density of recruits in February 2002 were similar in the control and disturbance plots. It therefore appears that in the present case, space as limiting factor was evidenced only at the start of the experiment, when bivalves were disposed in multilayers. Open spaces are probably originated by physical disturbances as, e.g. wave action or sand deposition. Through the 4 years of study we observed that waves can remove larger animals from the assemblage especially when they are disposed in several layers. This is probably the case of decreasing coverage in 2005. Deposition of sand can produce massive mortality if it remains for a long time or moves among rocks as it is the case for the vertical sides of the outcrops that are normally devoid of bivalves. If sand covers any horizontal part of the rock for a short time (equivalent to our disturbance treatment), it will produce mortality that opens patches in the bivalve assemblage, therefore allowing larger *M. chilensis* to move sideways occupying this new space, and therefore offering a new environment for settlement of new individuals.

The population of *P. purpuratus* seems to have been more affected by the total removal experiment than *M. chilensis* and its recovery was slower probably due to its slower growth rate and dependence of a mediator for its settlement. In the studied bivalve assemblage, clumps of *M. chilensis* most likely provide an appropriate matrix for *P. purpuratus* settlement, detected in the SFDs after April 2003 (Figure 7), as an increase of both the Biomass/N ratio in the total removal plots after August 2003 (Figure 5) and the density of the control plots in August 2003 (Figure 4B). On the other hand, although our results from the total removal plots show that *P. purpuratus* is able to attach to bare substrates, it seems to be at very low densities and only possible in irregularities and crevices. Moreover, in the recruitment season when there is a high number of recruits of *M. chilensis* (i.e. February 2002), recruitment of *P. purpuratus* was low and vice versa (i.e. in April 2003 many *P. purpuratus* recruits and few *M. chilensis* were recorded). Hence, the lack of an appropriate substratum or mediators, and the relatively slow growth of *P. purpuratus* compared with that of *M. chilensis*, hampers the

recovery of *P. purpuratus* in the intertidal assemblage of the Atlantic coast of Tierra del Fuego after a disturbance.

Role of mediators and predators in the intertidal communities of Patagonia

One of the striking differences of the studied assemblage with others of southern South America is the absence of barnacles as mediators for mussel recruitment and grazer/predators controlling open spaces. In Northern Patagonia or in central Chile recruitment mediators are key for the recovery of the assemblage, by providing an adequate substrate for larval settlement. In central Chile, *P. purpuratus* recruits only occur on the walls of adult barnacles that form patch borders and recover very slowly from disturbance on a bare substrate (Navarrete & Castilla 1990). In northern Patagonia and at the lower intertidal level, coralline algal turf or barnacles offer an adequate environment for *Perumytilus purpuratus* recruitment at lower or upper intertidal, respectively (Bertness et al. 2006). In most of the intertidal communities of Patagonia the occurrence of native barnacles is rare and they are only exceptionally present at the upper zones of certain communities (Ringuelet et al. 1962). In the Atlantic Tierra del Fuego region, barnacles were absent from the bivalve zone and never recruited to any of our plots. *Mytilus chilensis* recruited in cracks and crevices of the outcrops and in turn their byssi served as mediators for the massive recruitment of *Perumytilus purpuratus* (cf Figure 3 and 7). Moreover, similar to northern Patagonia, in the intertidal community studied here, bivalve predators, e.g. *Trophon* spp., are virtually absent. Predators could delay the recovery of the community as it occurs on the Pacific coast of SSA (Moreno et al. 1986), or be responsible for opening spaces for the lateral progress of the mussel bed and the consequent recruitment of new individuals (Connell et al. 1997; Bertocci et al. 2005). Grazers such as limpets can maintain bare spaces and keep them free of new recruits (Dayton 1971; Berlow & Navarrete 1997) but allow for the new settlement in the periphery of the already established bivalves. Both grazers and carnivores (sea stars or drilling whelks) were virtually absent from all our samplings or observations. These facts reinforce the idea that the natural recovery of the system depends on the settlement and growth of individual mussels and the associated bed expansion (Paine & Levin 1981).

For the intertidal zone of Tierra del Fuego we suggest that there is no selective mortality by predation on *M. chilensis*. This is supported by the shape of the size frequency distributions of the dominant *M. chilensis* showing a gradual increase in

size over time, especially in the total removal plots (Figure 3). In previous studies, bimodal size frequency distributions of *P. purpuratus* were attributed to mortality by predation (Alvarado & Castilla 1996). Here, the bimodal distributions are most likely the result of competition for space. After the massive recruitment of February 2002, these animals monopolized the space until April 2003 when some *M. chilensis* recruits were detected in the total removal plots but were not further traceable. In April 2003, a massive recruitment of *P. purpuratus* was detected (Figure 7) when practically all *M. chilensis* were > 8 mm with modal sizes ca. 9, 20 or 43 mm, leaving room for new recruits.

Conclusion

Our study is the first to show the recovery time of an intertidal assemblage in southern Patagonia, southwest Atlantic. We detected a massive recruitment of *Mytilus chilensis* 8 months after the start of our experiment, i.e. in the following settlement season. On bare surfaces recruitment occurs only in crevices whereas in open patches created by our disturbance treatment settlement takes place on the byssi of the settled bivalves. The percent coverage and the population structure of both bivalves were recovered 36 months after the experimental removal of all the assemblage. The initial structure of multilayers with sand, *Perumytilus purpuratus* and *M. chilensis* found at the start of the trial was never completely recovered by the end of the 4-year experiment. We detected that sand transported by the strong coastal current can cover the outcrops where bivalves thrive, and remain for a variable period of time, causing partial or total mortality. The rocky intertidal assemblage of the Atlantic southern tip of South America is characterized by very little predatory control and we hypothesize that this bivalve assemblage is predominantly controlled by competition for space.

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