

# Green sea urchins structure invertebrate and macroalgal communities in the Magellan Strait, southern Chile

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**ABSTRACT:** Although sea urchins play a central role in determining the structure and functioning of macroalgal communities in many parts of the world, past research in southern Chile has failed to identify strong effects of urchin grazing, despite the prevalence of coralline-dominated communities and abundant urchins, which indicate a likely structuring role for urchins. Here, we conducted experimental removals of the most common urchin, the green sea urchin *Arbacia dufresnii*, on a single bedrock wall in the Magellan Strait, Chile. We monitored the responses of invertebrate and macroalgal communities relative to a control wall 6 times over 64 wk. The structure of macroalgal communities on each wall remained similar until more than 40 wk after urchin removal, at which time the community structure diverged, with significantly more macroalgae present on the urchin removal wall. These changes coincided with the onset of early summer and were likely driven by greater settlement, recruitment and growth of algae in the absence of urchins. After 64 wk, the abundance of chitons, bryozoans, mussels and the small bivalve *Hiatella solida* was also significantly greater on the urchin removal wall. Herbivory by *A. dufresnii* on these high latitude rocky reefs appears to have a potential structuring effect on benthic assemblages, although further replicated field experiments are required to document where and when these effects may occur.

**KEY WORDS:** *Arbacia dufresnii* · Macroalgae · Subantarctic rocky reef · Foliose coralline algae · Southern South America · Magellan region

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## INTRODUCTION

Sea urchins are among the most widely studied macroinvertebrates in rocky reef ecology. They play a central role in determining the structure and functioning of macroalgal forest communities (Lawrence 1975, Schiel & Foster 1986, Harrold & Pearse 1987, Steneck et al. 2002, Wright et al. 2005). Grazing by urchins removes encrusting algae, turf algae and invertebrates, creating 'coralline-urchin communities', while in areas devoid of urchins, communities are characterized by a high abundance of mature kelps and other macroalgae (Lawrence 1975, Schiel

& Foster 1986, Harrold & Pearse 1987, Andrew 1988, Steneck et al. 2002, Wright et al. 2005, Pearse 2006, Norderhaug & Christie 2009). Although transitions between communities dominated by macroalgae and those dominated by coralline crusts have been attributed to grazing by urchins in Canada (Foreman 1977), the Aleutian Islands (Konar & Estes 2003), the western Mediterranean (Palacín et al. 1998), Australia (Ling et al. 2010), New Zealand (Babcock et al. 1999), south central Chile (Dayton 1985, Jara & Céspedes 1994, Buschmann et al. 2004) and many other locations worldwide (Steneck et al. 2002), past studies in southern Chile (>50° S) have failed to detect

effects of urchin grazing on the structure of macroalgal communities (Castilla & Moreno 1982, Dayton 1985). Indeed, grazing by urchins is widely stated as having a limited role in structuring macroalgal communities (Castilla 1985, Harrold & Pearse 1987, Vasquez & Buschmann 1997). The apparent lack of an effect exists despite the prevalence of coralline-dominated communities (Alveal et al. 1973, Cárdenas 2008, Newcombe & Cárdenas 2011) and large numbers of urchins in some areas of southern Chile (Castilla & Moreno 1982, Vasquez et al. 1984, Cárdenas 2008), which suggest that urchins may have a significant structuring role.

In the Magellan region of southern Chile, the green urchin *Arbacia dufresnii* (Fig. 1A) is the numerically dominant urchin on deeper (>6 m) bedrock reefs (Newcombe & Cárdenas 2011). *A. dufresnii* has been described as largely carnivorous on northeastern Patagonian reefs (Penchaszadeh & Lawrence 1999) and omnivorous in southern Chile (Vasquez et al. 1984). Although the ecological role of *A. dufresnii* has not been examined in southern South America, the low coverage of sessile invertebrates and fleshy seaweeds, the dominance of en-

crusting corallines (Fig. 1B) and moderate densities of *A. dufresnii* (~2.5 ind. m<sup>-2</sup>) in the Magellan Strait (Cárdenas 2008, Newcombe & Cárdenas 2011) suggest that *A. dufresnii* may limit the abundance of both invertebrates and macroalgae. Other urchin species coexisting with *A. dufresnii* include the commercially exploited red urchin *Loxechinus albus* (Molina, 1782) and the small pink urchin *Pseudechinus magellanicus* (Philippi, 1857), neither of which occur in as great a density as *A. dufresnii* on reefs >5 m deep.

Here, in a 64 wk study, we examined the effects of grazing by *Arbacia dufresnii* on the structure of macroalgal communities at a site in Magallanes, southern Chile. We conducted experimental removals of *A. dufresnii* on a single bedrock wall and monitored effects on the structure of the invertebrate and macroalgal communities relative to a control wall. Our aim was to assess the potential, rather than generality, of *A. dufresnii* as a structuring force on rocky reefs. Accordingly, this is not a replicated field experiment because we aimed to document an effect rather than identify large-scale impacts. We first identified specific components of the community under-

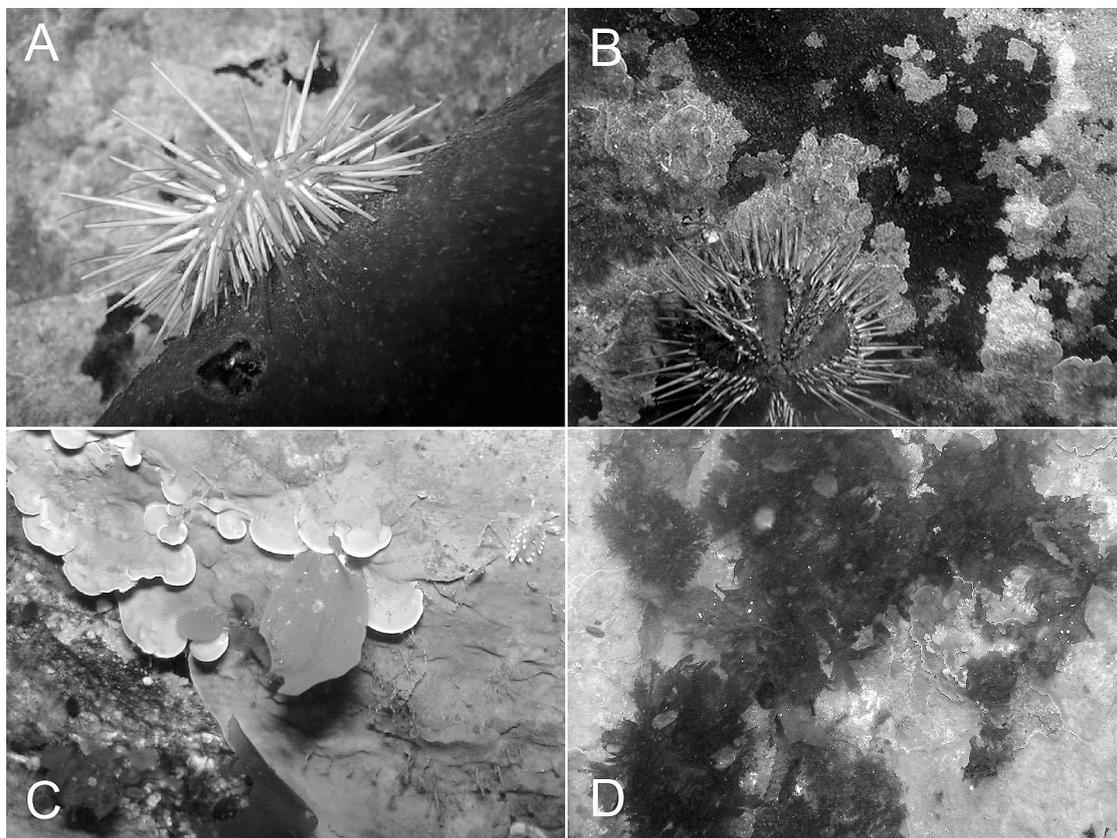


Fig. 1. (A) The green urchin *Arbacia dufresnii*; (B) smooth coralline algae-dominated reef surface; (C) apparent competition between raised coralline algae and fleshy algae; (D) recovery of fleshy macroalgae on the urchin removal wall

going change by examining the effect of urchin removal on (1) the percent coverage of brown, green and red macroalgae, (2) the biomass of brown, green and red macroalgae, (3) the abundance of *Macrocystis pyrifera* juveniles and (4) 13 components of the coralline algal community. We then analyzed macroalgal community structure as a multivariate matrix of distances (or dissimilarities) among observational units (either sampling dates or wall). Using this approach, we determined (1) whether the rate of change in macroalgal community structure differed between the control and urchin-removal walls and (2) whether the structure of macroalgal communities on each wall diverged following the removal of urchins. This study is one of the first ecological experiments undertaken on rocky reefs in the Magellan region.

## MATERIALS AND METHODS

### Study site

Our research site was located at Punta Santa Ana in the Magellan Strait (53° 37' 34" S, 70° 55' 13" W) on the eastern coast of mainland Chile. It is moderately exposed, with patchy rocky reefs extend from the intertidal to >20 m depth. The site consisted of 2 northeast-facing bedrock walls characterized by similar exposure, depth (7 to 16 m), inclination (see below) and macroalgal communities (ANOSIM  $R = -0.025$ ;  $p = 0.768$ , based on percent coverage of red, brown and green algae in 20 photoquadrats on each wall). *Arbacia dufresnii* was the most abundant mobile invertebrate, with nearly identical densities ( $\pm$ SE) on each wall (western wall:  $3.80 \pm 0.77$  ind.  $m^{-2}$ ; eastern wall:  $3.85 \pm 0.75$  ind.  $m^{-2}$ ; ANOVA:  $F_{1,38} = 0.004$ ,  $p = 0.948$ ; see Fig. S1 in the supplement at [www.int-res.com/articles/suppl/b015p135\\_supp.pdf](http://www.int-res.com/articles/suppl/b015p135_supp.pdf)). Walls were separated by ~200 m of boulders and gravel. The eastern wall ranged between 20 to 40 m wide and was surrounded by broken rock and gravel; the western wall was ~40 m wide, with areas of bedrock extending outward. At the top of each wall, *Macrocystis pyrifera* (hereafter *Macrocystis*) occurred on a section of reef with <45° slope to a depth of ~10 m, forming a thick surface canopy with understory algal growth constituting less than 20% of the aerial coverage. Coralline algae dominated the reef face. From 10 to 16 m on each wall, the reef was steeper (45 to 90°). Here *Macrocystis* was uncommon (less than 1 sporophyte in 100  $m^{-2}$ ), and other seaweeds covered less than 5% of the reef surface. Because inclination can have a significant effect on

the establishment of macroalgal communities (Sommerhäuser et al. 2001), we divided each wall into 2 zones: the 'shallow zone' (7 to 10 m with *Macrocystis* forest) and the 'deep zone' (10 to 16 m with few *Macrocystis* individuals). We assigned the eastern wall to the urchin removal treatment.

### Changes in community structure resulting from urchin removal

In November (late spring) 2008, we haphazardly placed ten 50 × 50 cm quadrats in each zone on each wall ( $n = 40$  quadrats). The quadrats were not placed in cracks in the reef where sand and algal drift accumulated or over *Macrocystis* holdfasts >100 mm diameter. Each quadrat was photographed (5 megapixels), and urchins of all 3 species (*Loxechinus albus*, *Pseudechinus magellanicus* and *Arbacia dufresnii*) were counted in the adjacent 1  $m^2$ . All *A. dufresnii* on the whole 'removal' wall were then smashed. Subsequent sampling (photographs and urchin counts) was then conducted during Weeks 6, 16, 40, 54 and 64 (summer, February 2010). On all sampling dates, the 2 walls were sampled within 4 d of each other. The urchin removal wall was checked for urchins approximately every 5 to 7 wk between sampling dates and cleared as necessary. A statistically significant difference in the density of urchins was maintained for the duration of the study, with the abundance of *A. dufresnii* on the removal wall not greater than 12.5% of that on the control wall (repeated measures ANOVA:  $t_{188} = -11.498$ ,  $p < 0.001$ ; see Fig. S1 in the supplement).

Each photoquadrat was viewed in Adobe Photoshop and overlaid with a 10 × 10 grid to estimate the percent coverage (to the nearest 1%) of bare rock, sediment/sand, coralline algae, fleshy red algae, green algae, brown algae (excluding drift), sponges, bryozoans, ascidians and hydroids. Reef face hidden under algal fronds was not considered.

### Components of the community undergoing change

To identify specific components of the community undergoing change, we conducted 4 series of analyses examining the effect of urchin removal on the structure of invertebrate and macroalgal communities.

(1) We examined the effect of urchin removal on the percent coverage of red, green and brown macroalgae using the photoquadrats as described above.

(2) We examined the effect of urchin removal on the biomass of macroalgae in Week 64. We collected macroalgae from ten  $0.5 \times 0.5$  m quadrats in both zones on each wall. Samples were drained and frozen until processing, at which time they were defrosted and sorted into brown, green and red macroalgae, patted dry and weighed, with the weight of brown, green and red macroalgae used as the response variables. The red algae *Gigartina skottsbergii* was excluded from analysis because it is commercially exploited in the area; therefore, variation in its biomass could not necessarily be attributed to our experimental treatments.

(3) We examined the effect of urchin removal on the coralline algal community in Week 64. Coralline algae scrapings were taken with an adapted 42 mm diameter PVC tube; a straight cut was made at  $45^\circ$  from the widest section of the opening. The resulting apparatus was a concave blade over which the uncut section of the tube formed a hood. A plastic bag was wrapped over the other end of the tube, and 1 m of reef (clear of seaweeds) was scraped by running the apparatus over it once. This successfully sampled coralline substrate on steep walls (where fragments fell into the sampling bag), but not on more horizontal substrates, and was therefore only used on the deeper sections of the study areas ( $n = 5$ ). Samples were drained and frozen until processing, at which time coralline fragments were cleaned of attached growth and weighed, associated animals were sorted into the lowest possible taxonomic group, and individuals were counted (bryozoan colonies were counted as 1). The wet weight of coralline algae and the numbers of bryozoan colonies, amphipods, *Fissurella* spp., chitons, *Mytilus chilensis*, *Hiatella solida*, *Margarites* sp., *Eatoniella* sp., polychaetes, isopods, nemerteans and barnacles were used as the response variables.

(4) We examined the effect of urchin removal on the abundance of *Macrocystis* juveniles in Week 64. We counted the number of juvenile *Macrocystis* in ten  $0.5 \times 0.5$  m quadrats in both zones on each wall.

For the first 3 analyses incorporating multiple response variables, we conducted multivariate analyses of variance (MANOVA) to test for the effects of treatment, depth and their interaction. We  $\ln(x + 1)$ -transformed data to improve assumptions of multivariate normality and heteroscedasticity. We used likelihood ratio tests to determine the significance of including the interaction term and the main effect of depth in the models (except in Analysis 3, in which only one depth was sampled). When the interaction term and/or depth did not significantly contribute to the model ( $p > 0.005$ ), they were removed, and we

focused on the remaining main effect(s). In the fourth analysis in which there was a single response variable, we conducted a 1-way analysis of variance (ANOVA) to test for differences in the abundance of juvenile *Macrocystis* between the control and urchin removal wall.

#### Rate of change in macroalgal community structure

If urchin removal results in a transition from a coralline crust community to a community dominated by fleshy macroalgae, we may expect the structure of macroalgal communities on the urchin removal wall to change at a different rate than that on the control wall. To assess this, we used the percent coverage of fleshy green, brown and red macroalgae and *Gigartina skottsbergii* (which was treated separately from other fleshy red algae because it is commercially exploited in the area) as a multivariate measure of macroalgal community structure. For each depth on each wall, we analyzed changes in macroalgal community structure as a matrix of dissimilarities among sampling dates. We used Bray-Curtis distances to calculate dissimilarities and non-metric multidimensional scaling (nMDS) to graphically display, in 2 dimensions, relationships between quadrats from consecutive sampling dates, and we plotted centroids for (1) quadrats from time  $t$  and (2) quadrats from time  $t + 1$ . We then calculated the Euclidean distance between centroids, which we standardized as a rate of change per week (see Fig. S2 in the supplement).

We conducted an ANOVA to test for the effects of depth and wall on the per-week rate of change in the structure of macroalgal communities. Analysis was performed on untransformed data because there was no evidence of heteroscedasticity and non-normality. We used likelihood ratio tests to determine the significance of including the interaction term and the main effect of depth in the model. Neither the interaction ( $F_{16,17} = 0.511$ ,  $p = 0.485$ ) nor depth ( $F_{17,18} = 0.183$ ,  $p = 0.674$ ) significantly contributed to the model; we therefore focused on the main effect of treatment.

#### Divergence in macroalgal community structure

If urchin removal affects the structure of macroalgal communities, the composition of macroalgal communities on the urchin removal wall should, through time, diverge from macroalgal communities on the control wall. To assess this, we used the same multivariate measure of macroalgal community structure

and statistical procedure as above; however, this time, we analyzed changes in macroalgal community structure as a matrix of dissimilarities among walls for each sampling date (see Fig. S3 in the supplement).

We conducted an analysis of covariance (ANCOVA) to test for the effects of depth (categorical) and sampling date (continuous) on changes in the structure of macroalgal communities between the urchin removal wall and the control wall. The analysis was performed on untransformed data because there was no evidence of heteroscedasticity and non-normality. We tested for influential observations (i.e. outliers) using Cook's distance; no influential observations were detected (Cook's distance < 0.5 for all data points). We used likelihood ratio tests to determine the significance of including the interaction term and the main effect of depth in the model. Neither the interaction ( $F_{8,9} = 0.452$ ,  $p = 0.520$ ) nor depth ( $F_{9,10} = 0.461$ ,  $p = 0.515$ ) significantly contributed to the model; we therefore focused on the main effect of time.

Because an obvious breakpoint in the scatterplot between the sampled week and community divergence could be seen using a lowess smoothing function, we also used a segmented regression to examine the effect of time on changes in the structure of macroalgal communities between the urchin removal and the control wall (see Muggeo 2003). A segmented relationship between the mean response  $\beta = E[Y]$  and the variable  $z$ , for observation  $i = 1, 2, \dots, n$ , is modeled by adding in the linear predictor the following terms:

$$\beta_1 z_i + \beta_2 (z_i - \Psi)_+ \quad (1)$$

where  $(z_i - \Psi)_+ = (z_i - \Psi) \times I(z_i > \Psi)$ , and  $I(\cdot)$  is the indicator function equal to one when the statement is true.  $\beta_1$  is the left slope,  $\beta_2$  is the difference-in-slopes, and  $\beta$  is the breakpoint (Muggeo 2003). We visually inspected the lowess smoothing function to determine the initial estimate of  $\Psi$  (smoothing parameter = 0.67) and then calculated maximum likelihood estimates of  $\Psi$  and  $\beta$ . Standard errors and confidence intervals of  $\Psi$  were obtained with linear approximation for the ratio of 2 random variables (Muggeo 2003). We used Akaike's information criterion (AIC) to determine if the simple linear model or the piecewise regression model fit the data better.

All analyses were performed in R 2.11.1 (R Development Core Team 2010). We conducted nMDS using the Vegan package (Oksanen et al. 2005). We used the package segmented 0.2–7.1 (Muggeo 2004) for the piecewise regression.

## RESULTS

The abundances of the 2 other locally found urchins (*Loxechinus albus* and *Pseudechinus magellanicus*) showed no response to removal of *Arbacia dufresnii* and remained at very low densities for the duration of the study. Neither species was recorded at densities >0.1 ind. m<sup>-2</sup> (SE = 0.1), and they were generally not present in our surveys.

### Components of the community undergoing change

The dominant macroalgae in the photoquadrats across all sampling dates were brown and red. The percent coverage of macroalgae did not differ between the walls in Weeks 0, 6, 16 and 40 (MANOVA:  $p > 0.05$  in all cases); however, in Weeks 54 (spring/summer) and 64 (mid-summer), there were significant differences (MANOVA:  $F_{3,35} = 6.899$ ,  $p < 0.001$  and  $F_{3,35} = 6.16.722$ ,  $p < 0.001$ , respectively), with the percent coverage of brown and red macroalgae significantly greater on the urchin removal wall than the control wall (Table 1, Fig. 2). On all sampling dates, the percent coverage of red macroalgae was greater in the shallow zone than in the deep zone. There was also a marginally significant effect of wall on the percent coverage of red macroalgae in Week 16 (Table 1).

Relative to the control wall, macroalgal biomass was 2.74-fold greater on the urchin removal wall in Week 64. There were significant differences in the biomass of macroalgae between walls (MANOVA:  $F_{3,35} = 10.697$ ,  $p < 0.001$ ) and depths (MANOVA:  $F_{3,35} = 3.766$ ,  $p = 0.019$ ). The biomass of red macroalgae was significantly greater on the urchin removal wall and in the shallow zone than the deep zone (Table 2). The biomass of both brown and red macroalgae was significantly greater on the urchin removal wall than the control wall (Table 2).

On the control wall, the number of animals present in coralline scrapings was ~1% of the abundance on the urchin removal wall and 6% of the diversity of the urchin removal wall. Over 70% of the fauna collected were juveniles of the bivalves *Mytilus chilensis* and *Hiatella solida*. The abundance of 5 of the 13 taxonomic classes examined was significantly greater on the urchin removal wall (Table 3). The weight of coralline algae from scrapings on the urchin removal wall was 296-fold greater than that from the control wall (Table 3). Although chitons, bryozoans, *M. chilensis* and *H. solida* were absent in samples from the control wall, they occurred at

Table 1. Mean (SE) percent coverage of red, brown and green algae in ten 0.5 × 0.5 m quadrats on a control wall or wall from which the urchin *Arbacia dufresnii* had been removed for 64 wk, and the results from a multivariate analysis of variance examining the effects of treatment (categorical: 2 levels, control and urchin removal) and depth (categorical: 2 levels, shallow and deep) on the percent coverage of the 3 types of algae. df = 1,37 for all treatments. Significant values in **bold** (p < 0.05)

Response variable	Weight (g m <sup>-2</sup> )		Effect	F	p
	Control	Removal			
<b>Week 0</b>					
Brown algae	4.2 (2.3)	1.8 (1.2)	Wall	1.134	0.294
			Depth	0.229	0.635
Green algae	0.2 (0.3)	1 (0.8)	Wall	1.588	0.216
			Depth	1.588	0.216
Red algae	25.4 (10.9)	20.6 (8.1)	Wall	0.110	0.742
			Depth	18.759	<b>&lt;0.001</b>
<b>Week 6</b>					
Brown algae	5.4 (3.0)	3.2 (2.1)	Wall	0.681	0.415
			Depth	0.750	0.392
Green algae	0.4 (0.6)	0.2 (0.3)	Wall	0.095	0.760
			Depth	0.095	0.760
Red algae	15.2 (5.4)	22.8 (8.5)	Wall	0.677	0.416
			Depth	9.639	<b>0.003</b>
<b>Week 16</b>					
Brown algae	4.0 (2.3)	3.2 (1.1)	Wall	0.088	0.769
			Depth	3.446	0.071
Green algae	–	0.4 (0.4)	Wall	2.177	0.149
			Depth	2.177	0.149
Red algae	12.2 (5.1)	24.4 (11.0)	Wall	4.784	<b>0.035</b>
			Depth	12.588	<b>0.001</b>
<b>Week 40</b>					
Brown algae	1.2 (1.4)	0.8 (0.8)	Wall	0.142	0.906
			Depth	1.058	0.310
Green algae	–	–	Wall	–	–
			Depth	–	–
Red algae	7.4 (2.8)	9.4 (3.1)	Wall	0.611	0.439
			Depth	7.043	<b>0.012</b>
<b>Week 54</b>					
Brown algae	10.8 (5.6)	42.8 (14.9)	Wall	8.384	<b>0.006</b>
			Depth	0.024	0.879
Green algae	–	0.6 (0.8)	Wall	1.000	0.324
			Depth	1.000	0.324
Red algae	36.8 (14.7)	88.6 (18.6)	Wall	14.387	<b>&lt;0.001</b>
			Depth	9.210	<b>0.004</b>
<b>Week 64</b>					
Brown algae	8.0 (3.8)	26.6 (5.4)	Wall	18.575	<b>&lt;0.001</b>
			Depth	0.185	0.669
Green algae	–	0.4 (0.6)	Wall	1.000	0.324
			Depth	1.000	0.324
Red algae	21.6 (6.5)	78.8 (13.7)	Wall	29.673	<b>&lt;0.001</b>
			Depth	5.431	<b>0.025</b>

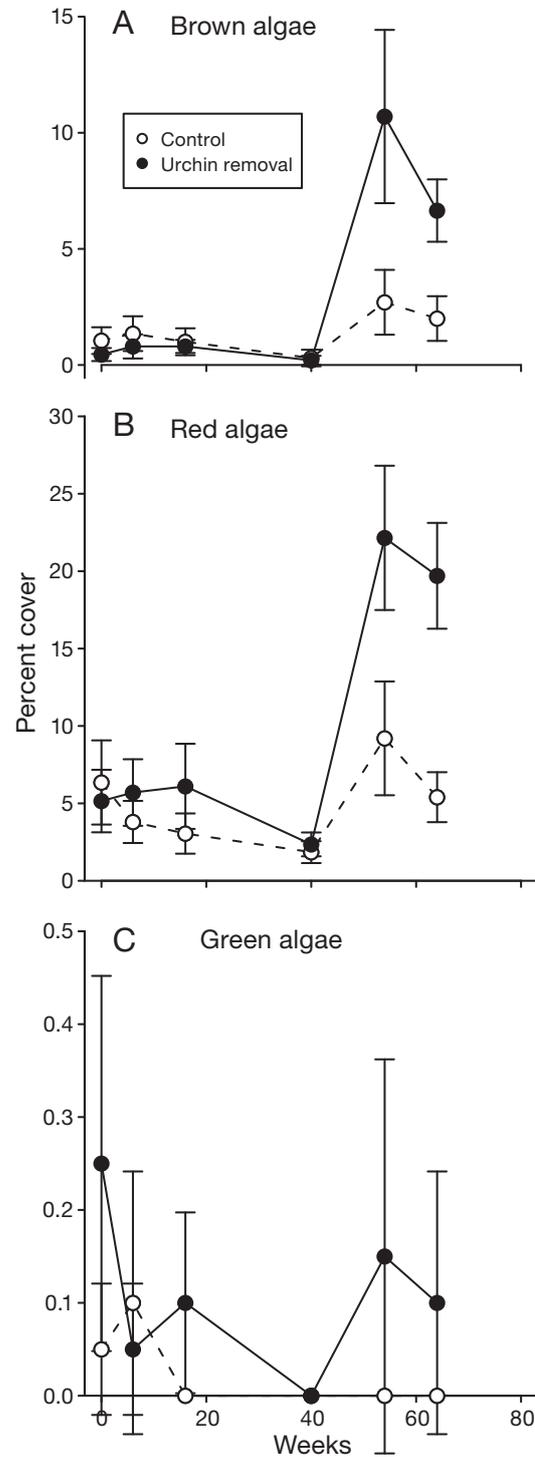


Fig. 2. Mean (± SE) percent coverage of (A) brown, (B) red and (C) green macroalgae from ten 0.5 × 0.5 m quadrats on a control wall or a wall from which the urchin *Arbacia dufresnii* was removed. Surveys of macroalgal communities and the removal of *A. dufresnii* occurred at Week 0, with subsequent surveys of macroalgal communities occurring in Weeks 6, 16, 40, 54 and 64. The urchin removal wall was periodically cleared between macroalgal surveys. Note: y-axis scales differ among panels

Table 2. Mean (SE) weight ( $\text{g m}^{-2}$ ) of red, brown and green algae in ten  $0.5 \times 0.5$  m quadrats on a control wall or wall from which the urchin *Arbacia dufresnii* had been removed for 64 wk. Also presented are results from a multivariate analysis of variance (MANOVA) examining the effects of treatment (categorical: 2 levels, control and urchin removal) and depth (categorical: 2 levels, shallow and deep) on the composition of the 3 types of algae. The overall MANOVA indicated that there were significant differences in algal composition between the control wall and urchin removal wall (MANOVA:  $F_{3,35} = 10.697$ ,  $p < 0.001$ ) and between the depths (MANOVA:  $F_{3,35} = 3.766$ ,  $p = 0.019$ ).  $df = 1,37$  for all treatments. Significant values in **bold** ( $p < 0.05$ )

Response variable	Weight ( $\text{g m}^{-2}$ )		Effect	<i>F</i>	<i>p</i>
	Control	Removal			
Red algae	39.1 (18.1)	110.4 (24.8)	Wall	20.254	<b>&lt;0.001</b>
			Depth	11.526	<b>0.002</b>
Brown algae	15.5 (11.1)	38.1 (14.8)	Wall	7.048	<b>0.012</b>
			Depth	1.046	0.313
Green algae	0 (0)	0.6 (0.5)	Wall	3.167	0.083
			Depth	0.013	0.910

Table 3. Mean (SE) wet weight ( $\text{g m}^{-2}$ ) of coralline algae and the numbers of bryozoan colonies, amphipods, *Fissurella* spp., chitons, *Mytilus chilensis*, *Hiatella solida*, *Margarites* sp., *Eatoniella* sp., polychaetes, isopods, nemerteans and barnacles in five  $420 \text{ cm}^2$  scrapings of coralline algae from a control wall or wall from which the urchin *Arbacia dufresnii* had been removed for 64 wk. Also presented are results from a multivariate analysis of variance examining differences in the composition of the 13 taxonomic groups.  $df = 1,8$  for all treatments. Significant values in **bold** ( $p < 0.05$ )

Response variable	Abundance ( $\text{m}^{-2}$ )		<i>F</i>	<i>p</i>
	Control	Removal		
Corallines	<0.1 (<0.1)	3.5 (1.0)	15.564	<b>0.004</b>
Bryozoans	0	5.7 (1.6)	30.917	<b>&lt;0.001</b>
Amphipods	0	2.9 (1.4)	5.084	0.054
<i>Fissurella</i> sp.	0	1.0 (0.6)	2.667	0.141
Chitons	0	1.4 (0.6)	6.00	<b>0.040</b>
<i>M. chilensis</i>	0	13.8 (4.5)	13.471	<b>0.006</b>
<i>H. solida</i>	0	39.5 (21.4)	11.511	<b>0.009</b>
<i>Margarites</i> sp.	0	0.5 (0.5)	1.000	0.347
<i>Eatoniella</i> sp.	0	1.0 (0.6)	2.667	0.141
Polychaetes	0.5 (0.5)	1.4 (1.0)	0.674	0.435
Isopods	0.5 (0.5)	0	1.000	0.347
Nemerteans	0	0.5 (0.5)	1.000	0.347
Barnacles	0	5.7 (4.6)	2.168	0.179

densities ( $\pm$ SE) of  $1.4 \pm 0.6$ ,  $5.7 \pm 4.6$ ,  $13.8 \pm 4.5$  and  $34.5 \pm 21.4$  ind. per sample ( $420 \text{ cm}^2$ ) on the urchin removal wall, respectively.

The abundance of juvenile *Macrocyctis* on the urchin removal wall was 3 times greater than on the control wall (Removal:  $1.65 \text{ ind. m}^{-2}$ ; Control:  $0.55 \text{ ind. m}^{-2}$ ;  $F_{1,38} = 4.356$ ,  $p = 0.044$ ).

### Rate of change in macroalgal community structure

The weekly rate of change in the structure of macroalgal communities did not significantly differ between the urchin removal wall and the control wall (ANOVA:  $F_{1,18} = 0.805$ ,  $p = 0.382$ ; Fig. 3A).

### Divergence in macroalgal community structure

Although the structures of the macroalgal communities on both walls were changing at similar rates, their trajectories differed. The linear regression indicated significant divergence in the composition of macroalgal communities on the removal and control walls through time (ANCOVA:  $F_{1,10} = 6.458$ ,  $p = 0.029$ ). However, the piecewise regression gave a

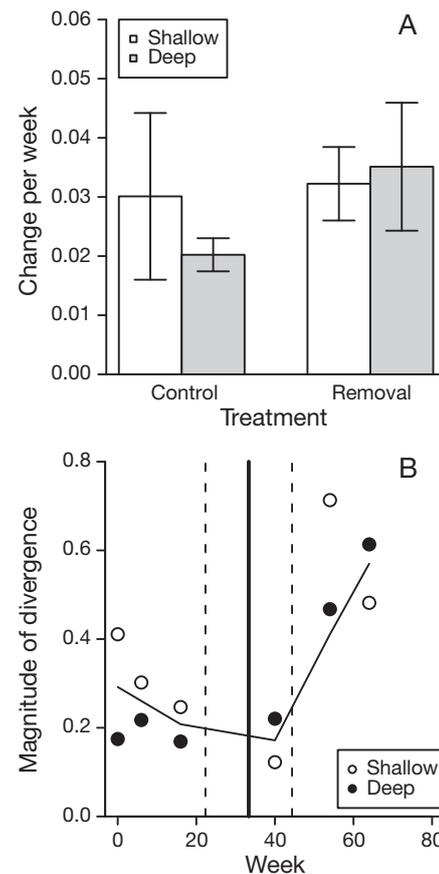


Fig. 3. (A) Mean ( $\pm$  SE) weekly rate of change in the structure of macroalgal communities on a control wall or wall from which the urchin *Arbacia dufresnii* was removed. (B) Magnitude of divergence in the structure of macroalgal communities on the urchin removal wall and the control wall through time, for shallow and deep zones. The lowest smoothing line is shown. The breakpoint of the best fitting model from a piecewise regression model is shown as a heavy solid vertical line ( $\pm$  SE, dashed vertical lines)

Table 4. Statistical relationship between the divergence in community structure and time since the removal of *Arbacia dufresnii* based on linear and piecewise regressions. For piecewise regression, slope parameter refers to the slope before the breakpoint. Standard errors are indicated in brackets. \* $p < 0.05$

AIC	AIC	Slope	Breakpoint (week)	Difference in slope parameter
Simple linear	-6.801	0.005 (0.002)*	-	-
Piecewise regression	-10.180	-0.005 (0.008)	33.34 (11.02)	0.022 (0.010)*

better fit to the model than the linear regression (Table 4). The breakpoint occurred approximately 22 to 44 wk after urchin removal (Table 4). Before the breakpoint, there was a slight convergence in community structure between the walls (although this was non-significant; Table 4, Fig. 3). There was a significant change in the slope of the piecewise regression before and after the breakpoint (Table 4, Fig. 3), characterized by a strong divergence in community structure between the urchin removal wall and the control wall after the breakpoint (Fig. 3).

## DISCUSSION

Local urchin species have not been considered a strong structuring force on rocky reef communities in the subantarctic waters of southern Chile (Castilla & Moreno 1982, Castilla 1985, Dayton 1985, Harrold & Pearse 1987, Vasquez & Buschmann 1997). Our results, however, suggest that the green sea urchin *Arbacia dufresnii* could play an important ecological role, as do urchins in similar latitudes in the northern hemisphere (Konar & Estes 2003). Although *A. dufresnii* may be omnivorous, feeding largely on animal prey (Castilla & Moreno 1982, Vasquez et al. 1984, Penchaszadeh & Lawrence 1998), our results suggest it can also be an important herbivore, directly influencing the structure of algal communities. These results shed further light on the equivocal findings of Jara & Céspedes (1994) from Seno Reloncavi, south-central Chile (41°S), where *A. dufresnii* influenced community structure by preventing the colonization of algae to artificial reefs at 16 m but not at 13 m.

*Arbacia dufresnii* may be widely important in Magellanic rocky reef ecology. The densities found here fall within the range (0 to 5.5 ind. m<sup>2</sup>) found at 8 sites in the nearby Bernardo O'Higgins National Park (sites at ~50°S), where *A. dufresnii* is usually the most common urchin at 5 and 15 m depth, and macroalgae were often scarce (E. M. Newcombe/Fundación

CEQUA unpubl. data). Although the density of urchins in our study (~3.5 ind. m<sup>-2</sup>) was lower than in many studies reporting structuring effects of urchins (e.g. Buschmann et al. 2004, Wright et al. 2005, Norderhaug & Christie 2009), our results are consistent with findings in the western Mediterranean (Palacín et al. 1998), where a similar effect was reported in communities with sea urchin densities of <5 ind. m<sup>-2</sup>. Similarly, *Heliocidaris*

*erythrogramma*, also an enigmatic and moderately abundant (~4 to 6 ind. m<sup>-2</sup>) urchin, was found to reduce the coverage of habitat-forming macroalgae in temperate Australia (Ling et al. 2010).

In southern South America, *Macrocystis* can grow much deeper than the depths found at the beginning of our experiment (Barrales & Lobban 1975), and our finding that more juvenile *Macrocystis* recruited in the absence of *Arbacia dufresnii* suggests that the urchin is limiting kelp recruitment below 10 m. *A. dufresnii* grazing reduced the growth not only of understory and canopy macroalgae (*Macrocystis*) but also of coralline algae. Coralline algae constitutes a high-value algal food source for herbivores (Manevelde et al. 2006), and grazing by urchins, parrotfish and gastropods is known to affect coralline growth forms (Adey 1965, Steneck & Adey 1976, Steneck 1985, Manevelde & Keats 2008). Under natural urchin densities, coralline algae tends to be largely restricted to an encrusting growth form (Fig. 1B); however, with grazing pressure removed, raised edges to coralline patches became much more common (Fig. 1C), resulting in the high biomass of coralline fragments in scraping samples. The raised coralline growth form may increase the settlement of invertebrates (Steller & Cáceres-Martínez 2009) and seaweeds (Scheibling et al. 2009). The invertebrate and algal taxa found in coralline scrapings were all found in stomachs of *Arbacia dufresnii* individuals collected from study sites, where algal material constituted 97% of organic material in the sampled guts (E. M. Newcombe unpubl. data).

Castilla & Moreno's (1982) experimental removal of all urchin species on natural reefs in the Beagle Channel did not identify a strong effect of urchins on community structure. Their experiment ran from April (as water temperatures are falling towards their winter lows) to December (early summer). In our study, understory macroalgae presumably settled across both experimental walls, but new recruits only survived in the absence of grazing by urchins. It may

be that a longer experimental period would have also produced similar results in Castilla & Moreno's (1982) study. The effects of urchin removal may take several years to fully manifest (Scheibling 1986), and it is possible that urchin grazing is a much more common structuring force on rocky reef communities in the extreme south of South America than previously thought. We were unable to continue maintaining and monitoring our sites, but it is likely that the effects of *Arbacia dufresnii* grazing would have strengthened had it been possible to maintain experimental conditions for several more years. The effect of urchin grazing on benthic communities can depend on variables such as depth (Ortega-Borges et al. 2009), water movement (Lauzon-Guay & Scheibling 2007) and urchin density coupled with algal palatability (Wright et al. 2005). Although we present data suggesting that grazing by urchins has a potential structuring effect on benthic assemblages, further replicated field experiments are required to document where and when these effects may occur.

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