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Limpet grazing on a physically stressful Patagonian rocky shore

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Abstract

Many theories of consumer control of communities have come from studies conducted in relatively benign, temperate zone rocky intertidal systems. Here, we examine gastropod grazing and the maintenance of bare space on a dry, wind-swept rocky shore of Patagonia, Argentina. Two limpet species are the primary intertidal grazers. *Siphonaria lessoni* dominates mid and high intertidal zones, while *Nacella magellanica* dominates the lower zone. In all zones, limpet densities are positively correlated with bare space and the occurrence of cracks. Tethering experiments revealed that: (1) physical stress sets the upper distribution limit of both limpets, (2) predators, such as oyster catchers, regulate *Nacella* populations and may restrict them to cracks and vertical surfaces, and (3) desiccation stress appears to drive similar crack distribution patterns of *Siphonaria* in the upper intertidal. Experimental removal of limpets in each intertidal zone indicated that limpets have: (1) no detectable effect in the high intertidal where physical forces dominate community organization, (2) weak impacts at mid-elevations as grazing only limited the abundance of fleshy algae with physical forces again dominating community structure, and (3) relatively stronger, but still weak impacts in the low zone. These results suggest that grazing impacts on Argentine rocky shores are weak in comparison to the physical stresses (e.g. high winds, low humidity) that largely determine structure in this system. The dominance of physical forcing in this system occurs despite having similar grazer densities to other temperate, but comparatively wet, rocky shorelines (e.g. British Isles) where top-down control is strong.

Keywords: Community structuring forces; Consumers control; Extreme physical conditions; Limpet grazing; Patagonian shorelines; Rocky shores

1. Introduction

In marine environments consumers can exert strong control over ecosystem structure and process, including regulation of primary productivity (Heck and Valentine, 1995; Silliman and Zieman, 2001; Duffy and Hay, 2002), biodiversity (Paine, 1966; Estes and Palmisano, 1974), decomposition (Newell and Bärlocher, 1993;

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Kemp et al., 1990), transfer of energy across ecosystems (Schindler and Lubetkin, 2004; Winemiller and Jepsen, 2004), and recovery after disturbance (Sutherland, 1974; Bertness et al., 2002). The role of consumers in regulating community structure has been particularly well studied in rocky intertidal systems, where many theories on consumer control were first demonstrated in the field, e.g. interspecific competition among grazers (Haven, 1973), keystone predation (Paine, 1966) and intermediate disturbance effect of grazers (Lubchenco, 1978). Most of these studies were conducted on temperate shorelines characterized by ample rainfall and moderate to high humidity (e.g. Northeast and Northwest U.S.: Lubchenco, 1980; Menge, 1983; Farrell, 1988; Wootton, 1991; Australia: Underwood, 1980; New Zealand: Schiel and Taylor, 1999; Northern Europe: Southward, 1958; Hawkins and Hartnoll, 1983; and the Chilean coast: Durán and Castilla, 1989; Santelices, 1990). Fewer studies have examined consumer impacts in systems exposed to extremely harsh physical environments, like the tropics or systems characterized by strong winds, and low precipitation and humidity (Bertness, 1982; Lubchenco et al., 1984; Menge, 1986; Williams et al., 2003). Investigating consumer impacts in such systems may provide insight into how consumer-driven processes are linked to climatic stress.

In the Southwestern Atlantic, rocky shores in Argentinean Patagonia (41–55° S; 63–70° W) are exposed to some of the most intense physical stress known for intertidal rocky environments (Bertness et al., 2006). These shorelines are exposed to dry, desiccating winds, the Roaring 40s, with daily speeds averaging >50 km/h. These winds at latitudes of 40–50° S, flow around the globe relatively unimpeded by continents and, combined with annual rainfall less than 18 cm/yr and humidity routinely below 40%, result in desiccation stress higher than any previously studied rocky shore system (Bertness et al., 2006). Nonetheless, a community of rocky shore organisms, dominated by the presence of two foundation species (mussels and coralline algae: Bertness et al., 2006; Silliman et al., in review) copes with this stress. Almost the entire assemblage (>90%), including chitons, amphipods, isopods, sea stars, brittle stars, worms, anemones, and crabs, from the low to high intertidal zone, live inside foundation species' matrices (Bertness et al., 2006) or rapidly succumb to desiccation (Silliman et al., in review).

On wave-protected shorelines, zonation of foundation species is pronounced. Bare rock dominates the high zone, covering >80% of the surface with the mussel, *Perumytilus purpuratus* Lamarck, 1819, and the invasive barnacle, *Balanus glandula* Darwin, 1854, inhabiting cracks and crevices. Bare space still comprises >40% of the surface in the mid zone, but mussel beds cover ~60% of the surface, associated with heterogeneous rock surfaces. In the low zone, mussels are overgrown and displaced by a thick mat of the coralline alga, *Corallina officinalis* Linnaeus, 1758, with bare rock covering only ~15% of surfaces (Bertness et al., 2006). Marine predators live almost exclusively associated with the foundation species for protection from desiccation. Only small crabs and intertidal fishes forage outside of these matrixes during evening high tides (Hidalgo et al., in press). The only marine consumers that routinely occur outside of foundation species matrices are two limpets: a small pulmonate, *Siphonaria lessoni* Blainville, 1826, in the high and mid zones, and a larger patellid limpet, *Nacella magellanica* Gmelin, 1791, which is limited to the low zone. In many other intertidal systems, limpets have been shown to be potent grazers that can retard community development and maintain bare space (e.g. Steneck, 1982; Farrell, 1991; Forrest et al., 2001; Jenkins et al., 2001; Jenkins and Hartnoll, 2001). Despite high limpet densities and their impacts in other systems, previous work on the organization and community structure of Argentinean Patagonia rocky shorelines has been completely descriptive (Ringuelet et al., 1962; Ringuelet, 1963; Olivier et al., 1966; Kühnemann, 1969; Otaegui and Zaixso, 1974; Zaixso et al., 1978; Zaixso and Pastor, 1977; but see Sánchez and Zaixso, 1995).

The Menge-Sutherland environmental stress model (1987) predicts that the importance of consumers in controlling community structure should decrease as physical stress increases. This model is generally applied to comparing the relative importance of consumers along physical gradients within habitats, but can also be applied to compare communities across biogeographic and climatic gradients (e.g. Locke, 1996; Leonard, 2000; Jenkins et al., 2001; Bertness and Ewanchuk, 2002; Menge et al., 2002). On the physically stressful rocky shores of Patagonia, Argentina, we hypothesized that limpet grazing increases in relative importance moving down the intertidal, and is relatively less important than in previously studied rocky shore communities. We asked the following questions: (1) what is the impact of limpet grazing on community development and bare space maintenance across the intertidal on wave-protected Patagonian shorelines? and (2) what factors control limpet distribution along the intertidal gradient, and thus indirectly regulate their community impacts?

2. Methods

2.1. Study site

This study was carried out in the Natural Protected Area of "Cabo Dos Bahías" (44° 44' S, 65° 40' W), on the north end of the Gulf of San Jorge, Chubut, Argentina. This area is ideal for conducting experimental studies, as access is restricted and harvesting of marine life is prohibited. For experimental sites, we chose two representative protected rocky shores in a small, coastal embayment (~500 m in diameter). The two sites are separated by 10 m of sandy beach and had comparable abiotic environments, with similar bedrock and orientation to winds, sun, and waves. The close proximity of the two sites limited their independence, but logistic constraints prevented us from using more separate sites. Consequently, statistically we treat all experimental units as replicates from a single site, and our result must be interpreted with caution limiting our conclusions about other shores.

The climate is arid and desert-like with low precipitation (~18 cm/yr), mean temperatures of 12.5 °C (maximum of 39 °C and minimum of −7.5 °C), and strong, southwest winds, with mean velocity of 45 km/h and maximums routinely >130 km/h (Camacho, 1979). Desiccation stress is intense and among the highest recorded for rocky shore communities (Bertness et al., 2006). Tides are semi-diurnal, with an amplitude of 3.39 m (Servicio de Hidrografía Naval, 2002).

Intense desiccation stress limits most species (e.g. seastars, crabs, anemones, chitons) to living within the protective cover of two foundation species, the mussel, *P. purpuratus,* and the coralline alga, *C. officinalis*, or cracks, crevices and tide pools in the high elevation (Bertness et al., 2006). Two consumers, however, occur regularly outside of foundation species matrix: the limpets, *Siphonaria lessoni* and *Nacella magellanica* (referred to hereafter by genus names). *Siphonaria* dominates high and mid elevations, while *Nacella* occurs in the low zone. Potential predators of limpets include: oystercatchers, *Haematopus palliatus* Temminck, 1820 and *Haematopus ater* Vieillot et Oudart, 1825; the kelp gull *Larus dominicanus* Lichtenstein, 1823; fishes, mainly *Patagonotothen cornucola* Richardson, 1844 and *Helcogrammoides cunninghami* Smitt, 1898; the seastar *Anasterias minuta* Perrier, 1875; crabs, primarily *Cyrtograpsus altimanus* Rathbun, 1914 and *Cyrtograpsus angulatus* Dana, 1851 and the shell-drilling snails, *Pareuthria plumbea* Philippi, 1944 and *Trophon geversianus* Pallas, 1769.

Tidal heights were determined by the zonation of organisms that is striking (Bertness et al., 2006). The low intertidal zone was defined as the tidal height dominated by dense coralline algal cover, the middle intertidal zone as the tidal height covered by mussel beds, and the high zone as the elevation dominated by bare rock with mussels and barnacles present in crack and crevices.

2.2. Distribution patterns of *Siphonaria lessoni* and *Nacella magellanica*

To determine field distribution patterns of limpets, the number of individuals of each limpet species was recorded using ten 25 × 25 cm quadrats randomly placed along the three intertidal heights (low, medium and high) at each site in December 2003. Data were analyzed using a one-way ANOVA (intertidal elevations) with Tukey–Kramer comparisons. Data were checked for normality and homoscedasticity using Kolmogorov–Smirnov and Bartlett tests, respectively, and transformed the data as needed to meet ANOVA assumptions (Sokal and Rohlf, 1998).

Limpet densities were higher in areas with bare rock and negatively associated with foundation species. To quantify the relationship between limpet density and bare rock in mid and low intertidal elevations, 25 × 25 cm quadrats were randomly placed in the mid and low zone at each site ($n = 50$/zone/site). Within each quadrat, limpets were counted and percent cover of bare rock and mussels or coralline algae was estimated with a square grid of 50 equally spaced points. Regression models were then used to relate percent cover of bare rock to limpet densities. Besides regression analyses, significant differences were also assessed (one-way ANOVA; Sokal and Rohlf, 1998) between mean limpet densities and percent cover classes (0% and 100% of *Corallina officinalis*, 0%, 50% and 100% of *Perumytilus purpuratus*) at mid and low intertidal elevations, respectively.

2.3. Can limpets maintain recently created bare space?

To examine if limpets can maintain recently created bare space, we cleared 25 × 25 cm bare spaces at each tidal elevation and applied the following caging treatments ($n = 8$/treatment/site): (1) limpet exclusion cage, (2) cage control and (3) uncaged control. Intertidal areas designated for bare space treatment were initially cleared of all organisms using metal scrapers. Oven cleaner (see Cubit, 1984) was also applied to eliminate all organisms. Cages were 25 × 25 × 5 cm and made with a stainless steel, 0.7 cm mesh. Cage controls were cages with two sides removed. Cages were secured to the surface using 7 cm lag bolts. Uncaged areas had a single drill hole as a procedural control. To limit limpet access into exclusions, cage edges were sealed with epoxy putty (Z-spar) and painted with antifouling paint monthly. Tops of cages were brushed clean biweekly, and limpets inside cages were removed. The experiment began in December 2001 and ran for 2.5 yr. Each replicate was photographed in April 2004 to assess treatment effects. Percent cover of bare space, algae, and sessile organisms (barnacles and mussels) was determined using established random point distribution methods (Bertness et al., 2002).

2.4. Do limpets maintain pre-existing bare space?

To examine if limpets can maintain pre-existing bare rock spaces, we identified >100 existing bare rock spaces >25 × 25 cm in the mid and low zones and applied the following treatments ($n = 11$/treatment/site): (1) limpet exclusion cage, (2) cage control and (3) uncaged controls. Cages and controls were as described above. The experiment began in December 2002 and ran for 2.5 yr. In April 2004, we quantified cover in all treatment plots as described above.

2.5. Data analysis for exclusion experiments

Differences in % cover among caging treatment and elevation were assessed using two-way ANOVA, with corresponding Tukey–Kramer multiple comparisons. Data were power transformed (Quinn and Keough, 2002) when necessary to meet assumptions of ANOVA.

2.6. What factors set intertidal distribution limits of limpets?

To examine the relative importance of physical stress and predation in controlling the lower and upper distribution limits of limpets, live specimens of *Siphonaria* and *Nacella* were tethered to rock surfaces at each elevation and assigned to one of the following treatments ($n = 20$ per treatment): (1) predator exclusion cage, (2) predator exclusion cage + shading, and (3) uncaged control. One limpet of each species was assigned to each treatment. Cages were 25 × 25 × 5 cm and made with a stainless steel, 0.7 cm mesh. To provide shading, 2 layers of black plastic vexar (0.7 cm mesh) were fastened to cage tops with cable ties. Animals of similar size were collected (~1 cm length for *Siphonaria*; ~4 cm for *Nacella*) from the study site and were placed in tide pools. We attached a 10 cm long fishing line to the apex of each limpet shell with epoxy putty. Animals were attached to rock in the assigned treatments by fastening the free end of the fishing line to the surface with epoxy. For 6 days, the number of dead limpets in each treatment was recorded daily. We also recorded whether or not soft tissue was present or missing in the dead limpet valves, indicating loss due to physical stress or consumers. The tethering experiment was repeated 3 times in summer 2002 (Dec., Jan, and

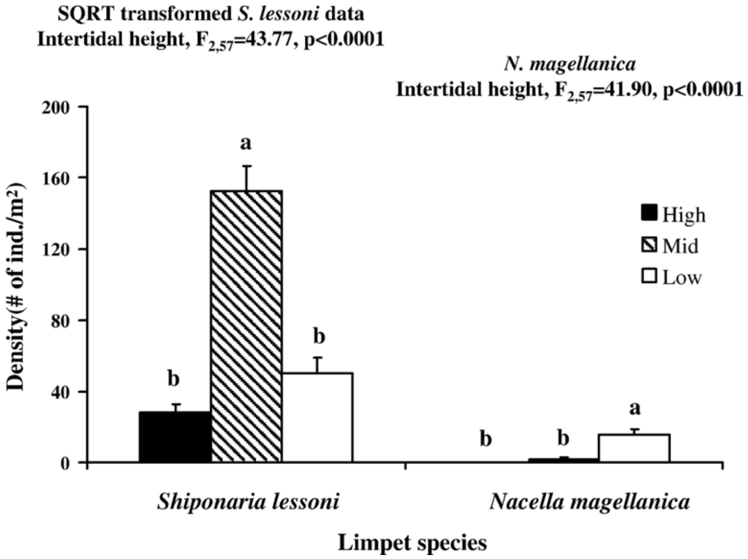

Fig. 1. Densities of *Siphonaria* and *Nacella* in the high, mid and low intertidal (Means + SE). ANOVA results are showed. Different letter means significant differences within species.

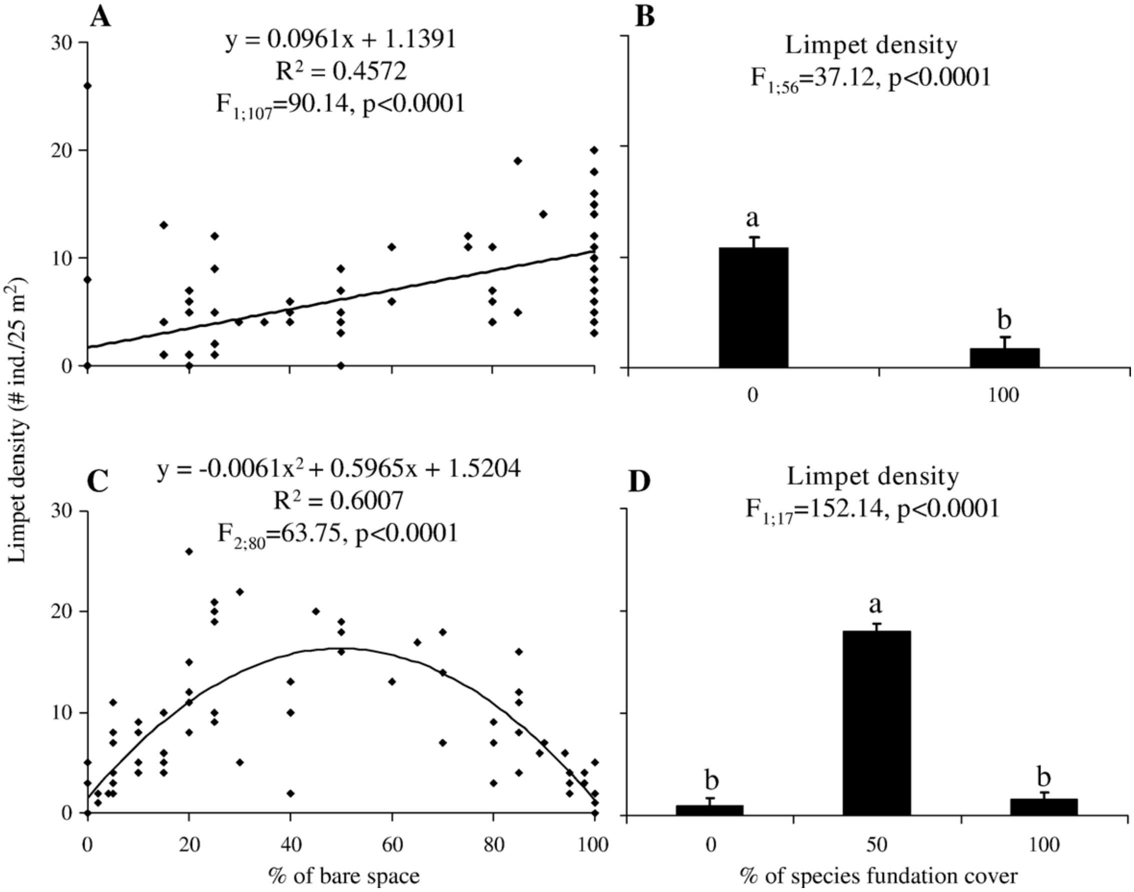

Fig. 2. (A) Least squares linear model of limpet density and percent bare space in the coralline-algae dominated low zone. (B) Survey results of limpet density in the low zone on 0 and 100% coralline algae cover (Mean + SE). (C) Polynomial second order model of limpet density and percent bare space in the mid zone. (D) Limpet density in the mid zone on 0, 50 and 100% mussel covers (Mean + SE). Regression analysis and ANOVA results are showed in the respective figures. 0% of *Corallina officinalis* and mussel cover are equivalent to a 100% of bare rock surface.

March). For analysis, we treated each experimental run (i.e. Dec., Jan, and March) as a replicate. The response variable was the number of dead limpets in each treatment on day six. Data were analyzed for each species using a two-way ANOVA (treatment × elevation), with Tukey-Kramer multiple comparisons. To compare the cause of limpet mortality along tidal heights, we estimated the proportion of limpet deaths due to desiccation (shells with soft tissue intact) or predation (empty shells), in uncaged treatments in the high, mid and low intertidal zones.

During the experiment, we observed two main features in *Nacella* and *Siphonaria* distribution within intertidal zones. In the low zone, *Nacella* tended to occupy vertical rather than horizontal surfaces. In the high and mid zone, *Siphonaria* congregated in cracks or similar microhabitats. To quantify the distribution pattern of *Nacella* in the rocks surfaces from the low zone, we walked a 300 m long, 1 m wide transect through the low intertidal of both sites and scored whether or not all *Nacella* encountered were oriented on relatively flat, accessible surfaces (0–70°) or vertical (80–120°) surfaces. Significant differences among categories in both surveys were assessed using a Chi-square test (Conover, 1999). To quantify the distribution pattern of *Siphonaria* within zones, we randomly placed ten 25 × 25 cm quadrats in each intertidal height and both sites and recorded the number of limpets situated in cracks or on flat surfaces. We analyzed the effect of microhabitat and zone using two-way ANOVA and Tukey–Kramer comparisons (Sokal and Rohlf, 1998). Data were power transformed (Quinn and Keough, 2002) to meet assumptions of ANOVA. To explore the relationship between *Siphonaria* and *Nacella*, we randomly placed ten 25 × 25 cm quadrats in the low zone at each site and recorded the number of each limpet

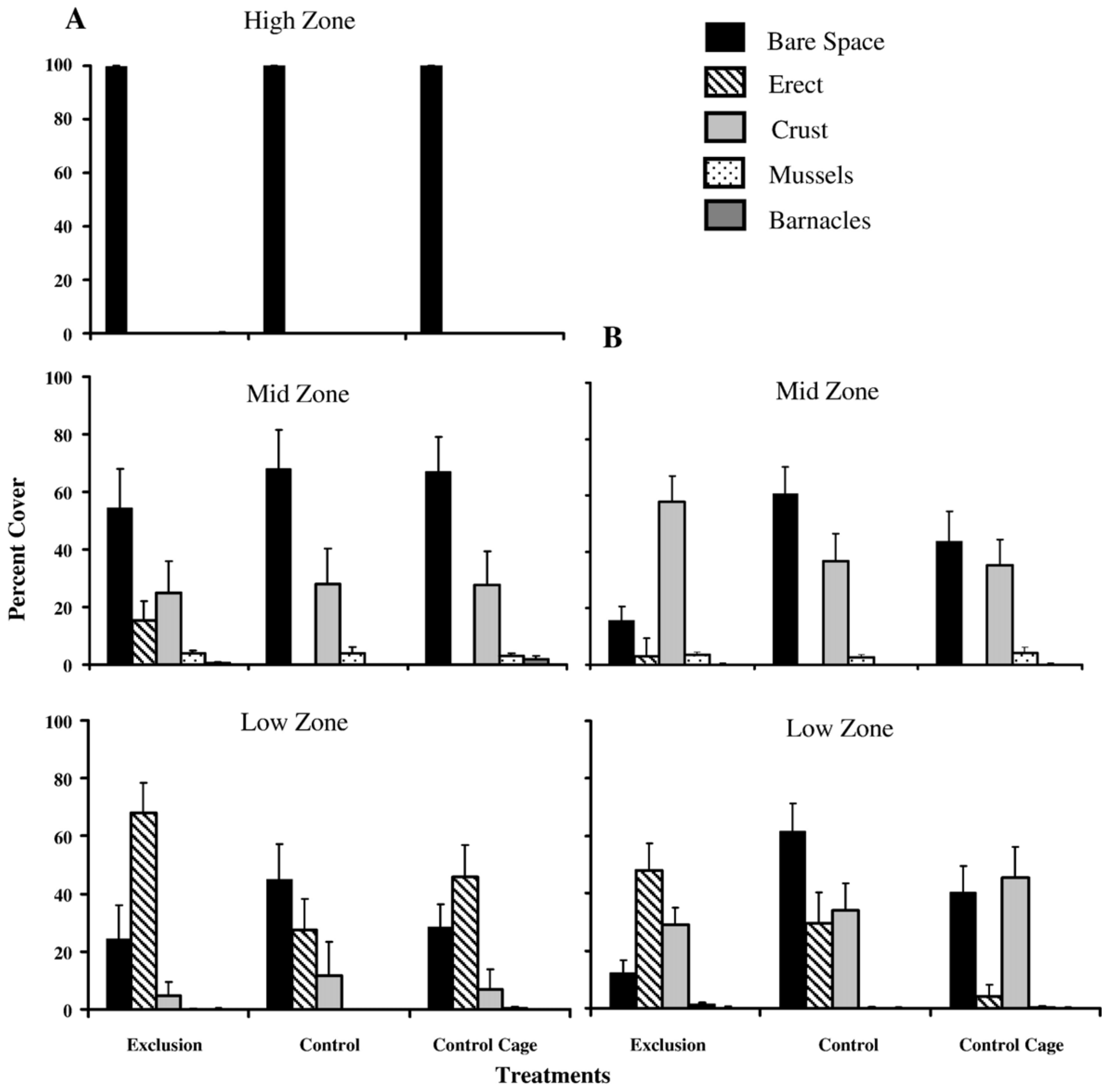

Fig. 3. Percent cover of bare space, algae (crusts and erects) and sessile organisms (barnacles and mussels) in (A) recently created and (B) pre-existing bare space limpet exclusions within intertidal heights (Mean+SE).

species and performing correlation analysis on transformed data.

3. Results

3.1. Distribution patterns of *Siphonaria lessoni* and *Nacella magellanica*

Our survey of the limpet density showed differences across tidal elevation for both species (Fig. 1). *Siphonaria* was found at all tidal elevations, with highest densities in the mid zone ($p<0.05$; Fig. 1). *Nacella*, was absent from the high zone, and had its highest density in the low intertidal ($p<0.05$; Fig. 1). *Siphonaria* was always more abundant than *Nacella*. In the low coralline algae zone, limpet density increased with the availability of bare rock with ∼45% of the variation in limpet density explained by percent bare space (Figs. 2A and B). In the mid zone, dominated by mussels, limpet density in relation to mussel cover was explained best with a polynomial, second order regression (Fig. 2C). Peak limpet density occurred at ∼50% bare space and decreased to near zero approaching either 0 or 100% bare space ($p<0.05$, Fig. 2D).

Table 1
ANOVA results for percent cover of bare space, algae (crusts and erects) and sessile organisms (barnacles and mussels) in (A) recently created and (B) pre-existing bare space limpet exclusions within intertidal heights

	Bare space	Erect algae	Crustose algae	Barnacles	Mussels
A) Recently created bare space					
Intertidal heights	$F_{1;42}=8.89$, $p<0.01$	$F_{1;42}=59.3$, $p<0.0001$	$F_{1;42}=1.37$, $p=0.259$	$F_{1;42}=4.67$, $p<0.05$	$F_{1;42}=43.16$, $p<0.0001$
Cages treatment	$F_{2;42}=1.66$, $p=0.20$	$F_{2;42}=6.75$, $p<0.001$	$F_{2;42}=0.96$, $p=0.39$	$F_{2;42}=4.70$, $p<0.05$	$F_{2;42}=0.59$, $p=0.56$
Heights × Cages treatment	$F_{2;42}=0.06$, $p=0.94$	$F_{2;42}=2.08$, $p=0.14$	$F_{2;42}=0.59$, $p=0.56$	$F_{2;42}=2.18$, $p=0.13$	$F_{2;42}=0.95$, $p=0.40$
B) Pre-existing bare space					
Intertidal heights	$F_{1;60}=0.08$, $p=0.77$	$F_{1;60}=14.09$, $p<0.001$	$F_{1;60}=0.87$, $p=0.35$	$F_{1;60}=0.91$, $p=0.34$	$F_{1;60}=9.56$, $p<0.01$
Cages treatment	$F_{2;60}=15.52$, $p<0.0001$	$F_{2;60}=9.90$, $p<0.001$	$F_{2;60}=0.38$, $p=0.69$	$F_{2;60}=1.38$, $p=0.26$	$F_{2;60}=0.85$, $p=0.43$
Heights × Cages treatment	$F_{2;60}=0.04$, $p=0.97$	$F_{2;60}=1.39$, $p=0.07$	$F_{2;60}=2.27$, $p=0.11$	$F_{2;60}=0.38$, $p=0.69$	$F_{2;60}=0.79$, $p=0.46$

3.2. Can limpets maintain recently created bare space?

Limpet grazing slowed, but did not prevent algal recolonization of artificial bare space. In the high zone after 2.5 yr, bare rock accounted for >99.5% of cover regardless of caging treatment. Algae, barnacles, and mussels were sparse or undetectable in all treatments (Fig. 3A). Consequently, the high zone was excluded from subsequent analysis of limpet grazing impacts. Between mid and low levels, there were no significant caging effect on bare space, but there was significantly more bare space in the mid zone than in the low zone (Table 1A; Fig. 3A). Erect algae cover varied with tidal height and limpet exclusion (Table 1A). Erect algae cover was higher in the low zone (Fig. 3A) and in limpet exclusion cages ($p<0.05$; Fig. 3A). In the mid zone, limpet grazing suppressed erect algae, and was only found in limpet exclusion cages. In the low zone, percent cover of erect algae (coralline and fleshy) was ~20% highest in exclusions and cage controls ($p<0.05$; Fig. 3A), suggesting a strong artifact of caging on erect algae growth. There was no effect of limpet removal or elevation on crustose algae (Table 1A). Overall, limpets were not effective at maintaining experimentally generated bare space in the low zone, as intertidal plants and animals covered ~60% of the rock surface in uncaged areas after 2.5 yr and only ~40% remained bare space (Fig. 3A). Barnacles and mussels were extremely low in cover in all experimental plots after 2.5 yr of recovery (Fig. 3A). For barnacles, there was a significant effect of tidal height and treatment (Table 1A). Barnacle cover was higher in the mid zone and in both limpet exclusion cages and cage control areas in comparison to uncaged areas ($p<0.05$; Fig. 3A). There was no significant effect of limpet removal on barnacle abundance. For mussels, intertidal height, but not the presence of limpets, was the primary factor driving patterns of abundance, as mussel cover was highest in cleared areas in the mid zone (Table 1A; Fig. 3A).

3.3. Do limpets maintain pre-existing bare space?

The effectiveness of limpets in maintaining naturally occurring bare space and retarding community development was also weak, but more pronounced than for artificially bare space (Fig. 3B). There was no effect of tidal height on bare space, but there were strong caging effects (Table 1B). Bare space was greatest in uncaged control areas ($p<0.05$; Fig. 3B). Cage controls and limpet exclusion cages had significant organism colonization, with the impact of exclusion cages approximately twice that of cage controls. There was a significant effect of both tidal height and limpet exclusion on percent cover of erect algae (Table 1B). Cover of erect algae was significantly higher in the low zone and in limpet exclusions ($p<0.05$; Fig. 3B). Once again limpet grazing suppressed growth of erect algae in the mid zone that only grew in limpet exclusion cages and covered 12% of the surface (Fig. 3B). In the low zone, cover of erect algae was significantly higher in limpet exclusions in comparison to both cage control and uncaged treatments ($p<0.05$; Fig. 3B). Thus, as opposed to artificial bare space, there was a significant effect of limpet grazing suppressing erect algal in the low zone, but approximately half of this impact can be attributed to cage effects (Fig. 3B). As in the prior limpet exclusion experiment, there was no effect of limpet removal or tidal elevation on crustose algae (Table 1B; Fig. 3B). Overall, limpets were more effective in maintaining pre-existing than experimentally generated bare space in the low zone, as ~60% of the rock surface in uncaged control areas remained bare after 2.5 yr of recovery. For barnacles, there was no effect of either

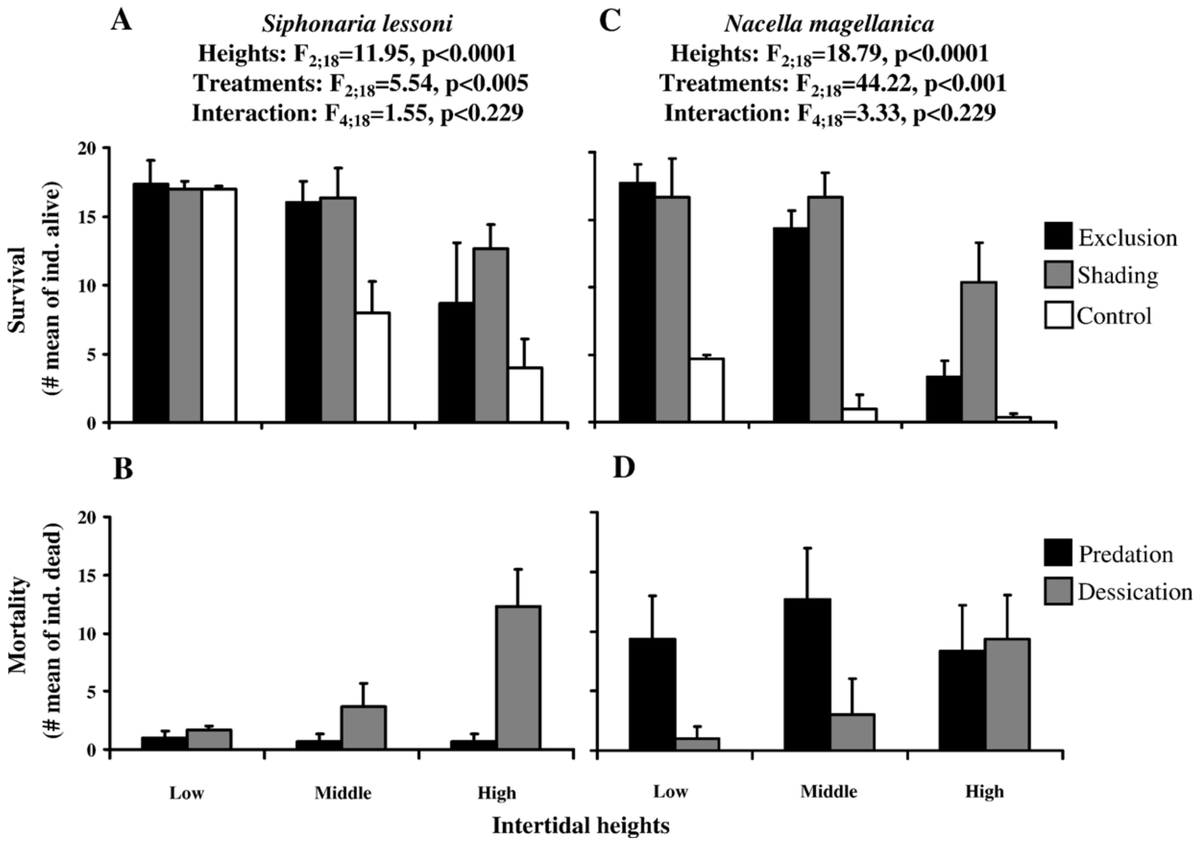

Fig. 4. (A) Effects of consumer and physical stress on survival of tethered *Siphonaria* in the high, mid and low intertidal and ANOVA result. (B) Causes of mortality (predation or desiccation) for *Siphonaria* dead across the intertidal zones in uncaged tethered treatments. (C) Effects of consumer and physical stress on survival of tethered *Nacella* in the high, mid, and low intertidal and ANOVA result. (D) Causes of mortality (predation or desiccation) for *Nacella* across intertidal zone in uncaged tethered treatments (Means+SE).

elevation or limpet exclusion (Table 1B; Fig. 3B). For mussels, however, as in the prior limpet exclusion experiment, percent mussel cover was significantly affected by tidal height, but not limpet grazing (Table 1B; Fig. 3B), as mussel abundance again was much higher in the mid vs. low zone.

3.4. What factors set intertidal distribution limits of limpets?

In the *Siphonaria* tethering experiment, there were significant effects of tidal height and caging on survivorship (Fig. 4A). *Siphonaria* survival increased from the high to the low zone ($p<0.05$) and it was significantly higher in shaded treatments and exclusion treatments, then controls ($p<0.05$). In the low zone, survival was nearly the same across all treatments, but at mid and high elevations, shading significantly increased survivorship, and caged exclusions had the same positive effect (Fig. 4A). Examination of dead limpets

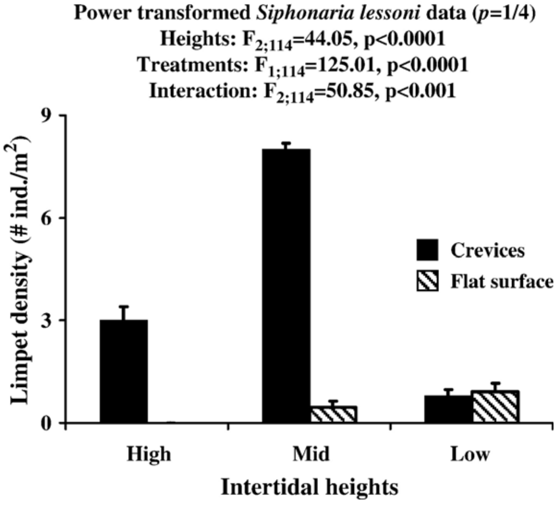

Fig. 5. *Siphonaria* density on flat surfaces and crevices in the mid and high intertidal elevations. ANOVA results are showed (Means+SE).

in uncaged control areas across tidal height revealed that desiccation was the main cause of mortality, even in the low zone where it represented 63% of the mortality. In the mid and high zones, mortality from desiccation increased to >80 and >90%, respectively. Predation mortality was low in all zones (Fig. 4B).

In the *Nacella* tethering experiment, there was a significant interaction between tidal elevation and caging treatment (Fig. 4C). In the mid and low zones, both shaded and exclusion cages significantly increased limpet survival similarly, but in the high zone, shading more dramatically increased *Nacella* survival (Fig. 4C). Examination of dead *Nacella* in uncaged controls, showed a markedly different pattern than that for *Siphonaria*. In the low and mid zone, >80% ($n=31$, $n=47$ respectively) of the dead limpets were void of soft tissue, indicating substantial predation, likely by oystercatchers (Fig. 4D), while in the high zone, the ratio was nearly 50/50 ($n=53$).

Our survey of flat and heterogeneous surfaces, revealed that >90% of pulmonate limpets were found in cracks and crevices rather than on flat surfaces during low tide (Fig. 5). No limpets were found in flat surfaces in the high zone while in the middle the limpets were mostly in crevices. This pattern did not occur in the low zone, where pulmonate limpet density in crevices or flat surfaces was similar (Fig. 5). Survey of *Nacella* orientation on rocks in the low zone at protected sites showed that >70% were found on vertical, rather than horizontal surfaces ($x_1^2=8.35$, $p<0.01$). There was no correlation ($r=0.31$; $p=0.18$) between density of *Siphonaria* and *Nacella* in the low intertidal zone.

4. Discussion

Patagonian shorelines of Argentina are some of the most physically extreme intertidal environments ever studied (Bertness et al., 2006). Experimental studies have shown that >90% of the marine species (e.g. starfish, keyhole limpets, anemones, crabs, chitons, polychaetes) occurring along these shorelines are obligately dependent on foundation species and must live inside mussel or coralline algae matrixes to persist in the face of intense desiccation stress (Bertness et al., 2006). Intertidal predators are also conspicuously lacking and only a small number of diminutives crab predators (1–2 cm in carapace width) forage over the surface at night (Bertness et al., 2006; Hidalgo et al., in press). Here we examine the importance of intertidal herbivores on community structure and found that consumer control is much less important than on previously studied coastlines (New England: Lubchenco and Menge, 1978; South Africa: Branch, 1976; Australia: Underwood, 1980; Europe: Hawkins and Hartnoll, 1983; Chile: Jara and Moreno, 1984; New Zealand: Creese, 1988). Two intertidal limpets, *Siphonaria lessoni* and *Nacella magellanica*, are the dominant grazers, reaching densities at lower intertidal elevations similar to that of gastropods in other temperate intertidal systems, but their impact seem to be generally less important than the extreme physical environment in driving community structure. Although our results must be discussed with caution because they were carried out on a single shore, this shore and the community is typical of sheltered shores in the region (Bertness et al., 2006).

4.1. Grazing impacts of limpets on bare space generation and maintenance

In our disturbance-recovery experiment, even with the removal of grazers, community development in bare areas was slow, with minimal recovery in 3 yr. These results are consistent with the exceedingly slow bare space colonization and secondary succession on these shorelines. For example, 5 yr after bare space was experimentally generated by removing 100% mussel cover in small 50×50 cm plots on wave-exposed headlands, only 15% of the cleared area has recovered (Bertness et al., 2006). Young mussel recruits cannot survive direct exposure to desiccation stress without protection from adult conspecifics. Consequently, recovery takes place slowly by the advancement of adults from disturbance edges (Bertness et al., 2006). This is in contrast to much faster community recovery in the absence of grazing on rocky shores on the Northwestern and Northeastern Coasts of the U.S. (e.g. Bertness et al., 2002) and in Chile (e.g. Jara and Moreno, 1984), where climates are relatively less physically stressful for marine organisms exposed at low tide.

The effect of limpet grazing also varied across with elevation. No detectable effect of limpet grazing was found in the high intertidal, while limpet removals in the most benign, mid and low, intertidal elevations led to small, significant increases in colonization. In the low zone, limpet removal led to substantially more colonization by coralline algae, the zonal dominant.

In the natural bare areas, limpets had a slightly greater impact in suppressing community recovery than in experimentally generated bare areas. Control plots in natural bare areas recovered less than in artificial bare areas. This may be due to the homing of limpets (Cook and Cook, 1978, 1981; Garrity and Levings, 1983) already present in or near natural bare areas. Olivier and Penchaszadeh (1968) and López Gappa et al. (1996), however, did not find homing in Argentinean *Siphonaria*. The artificial bare areas were also surrounded by space holders that limited limpet access to the newly created bare space. Some limpets, however, were able to recruit into the newly established bare areas (*pers. obs.*) and their grazing slowed but did not completely suppress community recovery in these areas. Since limpets were unable to completely maintain bare patches in the lower intertidal, the persistence of bare space in the low intertidal is likely due to a combination of factors, including: (1) top-down control by limpet grazing, (2) wave disturbance during storms, which can dislodge coralline algae (Bertness et al., 2006), (3) wind generated desiccation stress, which can kill coralline algae (bleaching events due to desiccation of low intertidal *Corallina officinalis* in Argentina were recorded by López Gappa et al. (1993)), and/or (4) wave-generated rock tumbling during storms (*pers. obs.*).

The time course of our study, as on wave exposed Patagonian shores (Bertness et al., 2006) is much longer than in previously studied systems and will take more years of recovery to accurately predict trajectories and community assembly rules. Results from less stressful low elevations, however, suggest that limpets slow secondary succession in most habitats and have the potential to maintain bare rock in some areas. It is remarkable that our experimental cages impacted community recovery. Cage structures likely impacted community recovery in two ways: by buffering colonizing organisms from intense physical stress and reducing consumer pressure. Since almost all of the colonization of bare space in control cages occurred in the corners of cages that likely offered both amelioration of physical stress and protection from predators it is not possible at this point to interpret these cage artifacts. New experiments with cages without tops (e.g. only fences) are needed to differentiate the effect of grazer removal from solar and wind buffering by full cages.

4.2. Controls on limpet distribution

Tethering experiments show that the upper distributions of both *Siphonaria* and *Nacella* are limited by desiccation, as artificial shading enhanced the survival of both limpets. Factors that control the lower distributions of these limpets were not clearly identified so will not be discussed. Only the larger *Nacella* is significantly preyed upon and this pressure is consistent across the intertidal gradient. This is consistent with the fact that the genus *Siphonaria* was described as not palatable due the presence of polipropianates (Capon and Faulkner, 1984). Even when potential artifacts usually arise from tethering experiments (see Peterson and Black, 1994; Zimmer-Faust et al., 1994), it is assumed that if a prey species does not rely on active escape, but on passive escape, as is the case of limpets, then the bias introduced by tethering should be minimal (Barbeau and Scheibling, 1994). Hence, while tethering studies can not provide true estimates of mortality rates (see Peterson and Black, 1994; Zimmer-Faust et al., 1994), they are useful for comparing mortality due to different causes (Barbeau and Scheibling, 1994). Our observations of bird predation in the field and tethering evidence (i.e. empty shells containing small remnants of flesh, Hahn and Denny, 1989), suggest that predation losses were mainly due to oystercatchers, that routinely feed on *Nacella* on flat surfaces. *Nacella* have lower tolerance to physiological stress than *Siphonaria* since it only survives in the high intertidal when desiccation stress is ameliorated under a shading treatment. *Siphonaria* displacement to the mid zone could be explained by pulmonate adaptations to the high physical stress (e.g. Wolcott, 1973), interactions with other components of the community such as algal canopy (e.g. Jenkins et al., 1999), food supply (Worma and Chapman, 1998), and / or intraspecific interactions (e.g. Evans and Williams, 1991). There is likely no strong interspecific interaction between *Siphonaria* and *Nacella* since there was no significant correlation between their densities.

Factors that control the distribution of limpets across the intertidal also seem to constrain their distribution to “refuge” microhabitats that improve survival. In the high intertidal, where desiccation is highest, virtually all limpets are found in cracks and crevices and rarely on bare, flat surfaces, a behavior that has been shown to reduce water loss in snails (Garrity, 1984; Benedetti-Cecchi and Cinelli, 1993). In the low zone, *Nacella* are more often found on vertical surfaces, likely due to reduced physical wave and desiccation stress with vertical orientation (Garrity, 1984; Benedetti-Cecchi, 2001). It is also less likely for bird predators to encounter and successfully prey on limpets in this orientation (Wootton, 1990, 1992).

In the low zone, the dominant sessile space holder *Corallina officinalis* also impacts limpet distributions, as its hair-like surface is not conducive to limpet attachment, and there is a strong negative correlation between coralline algae and limpet density (*Nacella* is always found on bare surfaces and crawls off coralline algae if placed on it). In the mid zone, where physical stress increases, mussels engineer microhabitats and increase moisture retention and can provide refuge space on the edges of their beds on otherwise smooth rocks (Silliman et al., in review). At mid elevations, *Siphonaria* densities peak at intermediate mussel cover, likely due to maximized edge/crack spaces that occur at intermediate mussel densities.

4.3. Grazer impacts in stressful environments

Environmental stress models (Menge and Sutherland, 1987) predict that grazer impacts will be greatest in the least stressful habitats. Our results support these predictions. Across the intertidal, both herbivores effects and potential community recovery are limited at higher elevations. Our results show that abiotic factors, such as desiccation, largely drive limpet distributions, and subsequently determine where grazing can potentially drive community patterns and secondary succession. Limpets reach their highest densities in low bare areas and mid elevations and could thus exert top-down control in these environments. In addition, physical drivers determine in which environments dominant sessile organisms can recover in high enough densities so that herbivores have the potential to exert top-down control.

Compared to previously studied shorelines where grazers of similar sizes occur at similar densities (e.g. 80–160 limpets/m^2 in Patagonia and 50–90 snails/m^2 on the coast of Maine; this study and Leonard et al., 1998), limpets have a relatively small impact on Patagonian rocky shores. For instance, in Argentina, limpets simply slow community development, while on rocky shorelines of estuarine rivers and coastlines of Maine and England, snails and limpets can completely suppress community development at high densities (200–400 individuals/m^2) and determine when and where erect algal canopies can emerge and dominate at moderate densities (50–150 individuals/m^2) (Leonard et al., 1998; Bertness et al., 2004). This qualitative, biogeographic comparison suggests that changes in per capita interaction strength (e.g. decreased overall movement of limpet to reduce desiccation), rather than change in grazer density, is the major mechanism by which elevated physical stress decreases top-down control by grazers in this system.

The Patagonian shores of Argentina have the harshest desiccation stress yet described for the rocky intertidal, including intertidal tropical systems (Bertness et al., 2006). The diminished role of grazers in driving community dynamics in these stressful habitats suggests that environmental stress models hold true across large-scale climatic gradients. This comparison aids in scaling-up community assembly rules to explain global patterns in community organization across large-scale environmental gradients. Our results also highlight that model systems in extreme environments can be useful for understanding community structure in increasingly harsh environments driven by climate change.

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