

## THE COMMUNITY STRUCTURE OF WESTERN ATLANTIC PATAGONIAN ROCKY SHORES

MARK D. BERTNESS,<sup>1</sup> CAITLIN M. CRAIN,<sup>1</sup> BRIAN R. SILLIMAN,<sup>1,2</sup> M. CIELO BAZTERRICA,<sup>3,4</sup> M. VICTORIA REYNA,<sup>3,5</sup>  
FERNANDO HILDAGO,<sup>3,4</sup> AND J. KONGO FARINA<sup>5</sup>

<sup>1</sup>Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912 USA

<sup>2</sup>Department of Zoology, University of Florida, Gainesville, Florida 32611 USA

<sup>3</sup>Facultad de Ciencias Naturales, Universidad Nacional de la Patagonia San Juan Bosco, Boulevard Alte. Brown 3700,  
C.P. 9120 Puerto Madryn, Chubut, Argentina

<sup>4</sup>Departamento de Ciencias Naturales, Universidad Nacional de Mar Del Plata, Mar del Plata, Argentina

<sup>5</sup>Center for Advanced Studies in Ecology and Biodiversity, Pontificia Universidad Católica de Chile, Alameda 340,  
C.P. 6513677 Santiago, Chile

**Abstract.** We examined the structure of rocky intertidal communities on the central Patagonian coast of Argentina. Extensive beds of the mussel *Perumytilus purpuratus* cover wave-exposed headlands from the low to extreme high intertidal (>95%), and a diverse assemblage of diminutive mobile invertebrates including limpets, starfish, and crabs live exclusively in the mussel bed matrix to avoid physical stress. On nearby wave-protected rocky shores, the high intertidal habitat is dominated by bare space (>85%) with mussels restricted to tide pools and crevices. Mussel beds cover the middle intertidal, while the low intertidal habitat is dominated by the erect coralline alga *Corallina officinalis*. These patterns are driven overwhelmingly by variation in extreme physical conditions. Desiccation stress generated by the dry southern trade winds is harsher than in any previously studied rocky intertidal system, including the Gulf of Panama, by >30% and is more severe on wave-protected than wave-exposed shores. Transplant experiments suggest that on wave-protected shores desiccation stress limits the upper distribution of mussels in the high intertidal and *Corallina* in the mid-intertidal, but at low intertidal elevations *Corallina* outcompetes mussels, restricting mussel distribution to mid-intertidal elevations. Transplant experiments also demonstrated that the coralline alga is precluded from wave-exposed shores by wave stress. Recovery from disturbance is unusually slow, ostensibly due to extreme physical stress. Consumer pressure is weak, with no common predaceous crabs or snails, and grazing by limpets showed limited control of community development, mostly by regulating ephemeral algae. Patagonian rocky shore communities are exposed to unusually harsh physical conditions and consequently are more strongly organized by physical stress than previously studied rocky intertidal communities.

**Key words:** community structure; *Corallina officinalis*; desiccation; mussels; Patagonia, Argentina; *Perumytilus purpuratus*; physical stress; rocky intertidal; zonation.

### INTRODUCTION

Because of strong gradients in physical conditions and dominance by slow moving or sessile organisms that are easy to experimentally manipulate, rocky intertidal communities have been valuable natural systems to experimentally explore the physical and biological forces that interact to shape natural communities. Studies on rocky shores have helped elucidate the roles played by interspecific competition (Connell 1961), predation (Paine 1966, Menge 1976, Lubchenco 1978), facilitation (Bertness 1989), disturbance (Dayton 1971, Sousa 1979), recruitment (Gaines and Roughgarden 1985), indirect interactions (Wootton 1992), and human exploitation (Castilla 1999) in influencing the organization of natural

communities. These studies have been particularly valuable in developing ecological theory because experimental work that would be difficult or impossible to carry out in many other systems can be extrapolated to systems less amenable to such approaches.

Experimental work to elucidate the structure of rocky intertidal communities began in England (Connell 1961) and on the Pacific (Paine 1966, Dayton 1971) and Atlantic (Menge 1976, Lubchenco 1978) coasts of North America and led to general conceptual models for the organization of natural communities (Menge and Sutherland 1976, 1987). Work in different geographic areas and habitats have helped refine, test, and in some cases to redefine these models (Schiel 2004). For example, ecologists in Australia realized that larval recruitment could be an important driver of community structure (Underwood and Denley 1984), because recruitment limitation is common in Australian inter-

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tidal systems. Earlier work in North America had been done in geographic regions where recruitment limitation was rare, so had underestimated the importance of recruitment limitation (Connolly and Roughgarden 1998). Similarly, while most early ecological theory assumed that natural communities were in equilibrium, work on rocky shores (Dayton 1971) and cobble beaches (Osman 1977, Sousa 1979) revealed the importance of disturbance in structuring natural communities. The physical stresses affecting intertidal organisms that researchers have generally focused on are desiccation risk and dislodgement risk due to wave exposure (McQuaid and Branch 1984, Denny and Wethey 2001, Tomanek and Helmuth 2002). However, with only a few exceptions (e.g., Menge and Lubchenco 1981, Dungan et al. 1982, Dungan 1986, Lively and Raimondi 1987), most experimental examinations of rocky intertidal community structure have been done in temperate zone intertidal habitats and not in more physically stressful intertidal habitats (i.e., desert coasts as well as tropical and subtropical areas) where physical stresses may play an overly dominant role in structuring resident biological communities.

Understanding how important structuring forces vary from well-studied temperate systems, to more stressful ones will not only provide important information on the generality of rocky shore ecological organization but may also inform our ability to predict how communities will respond evolutionarily and ecologically to elevated stresses. This could be particularly important given the accelerated pace of global change and the predicted rapid changes in physical conditions over the next century. Current theory predicts that under extreme physical stress consumers will play a diminished role in structuring communities (Menge and Sutherland 1976, 1987, Menge and Olson 1990, Schiel et al. 2004), while positive interactions driven by the amelioration of physical conditions will play an increasingly important role in structuring communities (Bertness and Callaway 1994, Bruno et al. 2003). These predictions, however, have not been well tested in communities that are chronically exposed to harsh physical conditions.

In this paper, we examine the organization of rocky intertidal communities on wave-exposed headlands and wave-protected bays in Central Patagonia in the Chubut Province of Argentina. There have been a number of descriptive studies on various aspects of these communities (Ringuélet et al. 1962, Olivier et al. 1966, Zaixso et al. 1978, López Gappa et al. 1990, Sanchez and Zaixso 1995). To date, however, no experimental work has examined the mechanisms underlying community structure. The intertidal communities on these rocky shores appear strikingly simple. Wave-exposed headlands are exclusively dominated by extensive beds of small (<2 cm in length) mussels, *Perumytilus purpuratus*, hereafter referred to as *Perumytilus*. Nearby wave-protected bays are dominated by bare rock and mussel cover at high and middle tidal heights, respectively, and a dense

coralline algal turf, *Corallina officinalis*, hereafter referred to as *Corallina*, entirely covers low tidal heights. Extreme desiccation is the most unique feature of these habitats. The southern trade winds average nearly 20–25 km/h (see *Results*) with low (<60%) humidity (Paruelo et al. 1998). These strong, dry winds combined with low rainfall make the desiccation potential on Patagonian rocky shores enormous, and high intertidal tide pools evaporated dry and coated with salt crystals during low tide are common. High desiccation rates make Patagonian rocky shores one of the most physically demanding rocky intertidal habitats that we are aware of. Thus an examination of the community structure and dynamics of Patagonian rocky shores is an examination of a rocky shore community that is shaped by and has evolved under extreme physical stress.

## METHODS

### *Field sites*

Our studies were conducted on wave-exposed headlands and wave-protected coastal bays of the Chubut Province, Argentina (see Plate 1). The region is characteristic of the arid Patagonian steppe where annual precipitation is <200 mm, mean annual temperature is 12°C, and predominant winds are from the southwest (Paruelo et al. 1998). Average monthly wind speeds range from 13 to 31 km/h and average tidal amplitude along the coastline is 4 m. In mid-latitude Argentinean coasts, intertidal shorelines are predominantly of consolidated limestone, locally known as *toba*. Shores of basaltic rock, where we conducted our studies, are scattered through the region and are common for ~200 km to the north of San Jorge Gulf, from Bustamante Bay in the south to Punta Tombo in the north. Our surveys and experimental studies were conducted between November 2001 and December 2004 at sites in Cabo Dos Bahias Park in Chubut, Argentina (44°54'34" S, 65°33'20" W). Two representative wave-exposed rocky headlands and adjacent wave-protected bays were chosen for our field experiments. Cabo Dos Bahias Park is a protected nature reserve and no collecting of intertidal organisms is permitted.

### *Descriptive data*

To describe the rocky intertidal community, we sampled 10 randomly placed 0.5 × 0.5 m quadrats in the high, middle, and low intertidal habitat at each study site. In each quadrat we estimated percent cover of all organisms and bare space using the point intercept method and a quadrat with 100 evenly spaced points. The high zone was defined as the elevation where the top vertical 3.5 m in the intertidal at wave-exposed headlands was covered with mussels. The middle intertidal zone was defined as the tidal height that was covered by mussel beds at wave-protected sites. The low intertidal zone was defined as the tidal height at wave-protected sites that was dominated by dense coralline algal cover. These zones were very clearly present at the study sites



PLATE 1. Tide pools on the central Patagonian coast of Argentina are frequently evaporated dry by constant southern trade winds, leaving them encrusted with salt—a striking demonstration of the high desiccation potential on these shores. Photo credit: M. Bertness.

used and at all wave-exposed headland and wave-protected bays in the Chubut Province of Argentina.

At wave-protected sites, microhabitat patterns in the distribution of mussels and coralline algae were conspicuous. In particular, in the high intertidal zone, mussels and coralline alga were restricted to crevices and tide pools, suggesting desiccation limitation. In the low intertidal zone, dominated by coralline algae, emergent surfaces were dominated by mussels, suggesting that coralline algae were limited from living at higher tidal heights by desiccation risk. We documented these patterns by quantifying percent surface cover in 10–20 randomly chosen microhabitat types in each zone.

In the extreme low intertidal or shallow subtidal habitat of wave-exposed shores, areas exposed only during extreme spring tides one to four days a month, the mussel bed gives way to a mixed community of mussels and fleshy and encrusting algae. To quantify this feature of exposed headlands we sampled 10 randomly placed  $0.5 \times 0.5$  m quadrats in the low intertidal fringe habitat for percent cover at each wave-exposed study site.

Most of the invertebrates in Atlantic Patagonian intertidal communities live inconspicuously in the interstitial spaces in mussel beds and coralline algal turfs where they are protected from wave and wind action (B. R. Silliman, M. D. Bertness, C. Bazterrica, V. Reyna, F. Hildago, and C. M. Crain, *unpublished manuscript*). To describe the organisms that live in mussel beds and coralline turfs we sampled eight randomly located  $10 \times 10$  cm quadrats at high, middle, and low elevations in the mussel beds at our two experimental sites on wave-exposed headlands. At our two wave-protected sites we sampled eight randomly located  $10 \times 10$  cm quadrats in mussel beds in the middle intertidal zone and eight randomly located  $10 \times 10$  cm quadrats in the coralline turfs in the low intertidal zone. In the laboratory, we identified and counted all invertebrates  $>1$  mm in length.

#### *Physical conditions*

To describe the physical conditions at our study sites we quantified wave forces, rock surface temperatures, and desiccation rates. Wave forces were quantified with

TABLE 1. Average climate data (sources are given in table footnotes).

| Location               | Temperature (°C) | Humidity (%) | Wind speed (km/h) | Air pressure (kPa) | Evaporation rate, mean $\pm$ SE (g·s <sup>-1</sup> ·cm <sup>-2</sup> ) | Rank |
|------------------------|------------------|--------------|-------------------|--------------------|--|------|
| Antofagasta, Chile†    | 16.8             | 76.4         | 12.6              | 101.55             | 0.01656 $\pm$ 0.001395   | 5    |
| Astoria, Oregon‡       | 10.5             | 81.6         | 13.7              | 101.71             | 0.00727 $\pm$ 0.00103  | 8    |
| Balboa, Panama§        | 26.8             | 76.6         | 6.8               | 100.90             | 0.02898 $\pm$ 0.00340  | 2    |
| Bodega, California#    | 11.7             | 85.7         | 16.4              | 101.61             | 0.00715 $\pm$ 0.000557   | 9    |
| Plymouth, England¶     | 6.2              | 88.1         | 9.3               | 101.67             | 0.00165 $\pm$ 0.000102   | 11   |
| Portland, Maine        | 6.6              | 70.5         | 16.2              | 101.58             | 0.01208 $\pm$ 0.00359  | 7    |
| Quillayute, Washington | 9.4              | 78.0         | 11.1              | 101.67             | 0.00483 $\pm$ 0.000742   | 10   |
| San Diego, California  | 17.9             | 69.5         | 11.2              | 101.61             | 0.02003 $\pm$ 0.00216  | 4    |
| Santo Domingo, Chile†  | 14.4             | 77.5         | 12.0              | 101.76             | 0.01267 $\pm$ 0.002260   | 6    |
| Sydney, Australia††    | 17.6             | 62.3         | 11.6              | 101.66             | 0.02259 $\pm$ 0.00275  | 3    |
| Trelew, Argentina‡‡    | 13.7             | 53.6         | 25.1              | 101.26             | 0.03950 $\pm$ 0.00912  | 1    |

† Center for Advanced Studies in Ecology and Biodiversity, Pontificia Universidad Católica de Chile ([www.bio.puc.cl/caseb](http://www.bio.puc.cl/caseb))

‡ Oregon Climate Service (<http://www.ocs.oregonstate.edu/index.html>)

§ Panama Canal Authority, Branch of Meteorology and Hydrology (<http://www.pancanal.com/eng/index.html>)

|| Climate Information Library, National Weather Service Forecast Office (<http://www.erh.noaa.gov/er/gyx/climate.shtml>)

¶ Weather Underground, Plymouth Airport, United Kingdom (<http://www.wunderground.com>)

# Bodega Marine Laboratory, University of California (<http://www.bml.ucdavis.edu/boon/>)

†† Bureau of Meteorology, Climate of Australia, Australian Government Printing Service, Canberra, Australia

‡‡ Centro Nacional Patagónico (<http://www.cenpat.edu.ar/>)

wave force dynamometers (see Bell and Denny 1994). Five dynamometer locations were installed in the middle intertidal zone at both wave-exposed headland study sites and both wave-protected bay study sites. Dynamometers were installed by screwing eyebolts into plastic anchors inserted into holes drilled in the beach rock with a rock drill. Each dynamometer was attached to an eyebolt with a key ring that allowed them to move freely in flow. During monthly trips to the sites, dynamometers were deployed and daily maximum wave forces were recorded.

Rock surface temperatures were measured with tidbit dataloggers (Onset Corporation, Onset, Massachusetts, USA). Dataloggers were attached to the rock surface with underwater epoxy (Z-spar Koppers Splash Zone compound, Carboline, St. Louis, Missouri, USA) and deployed over the summer (November–February) or winter (March–October) months. Replicate (3–4) dataloggers were deployed in both the wave-exposed and wave-protected habitats at both high and low tidal heights on bare rock surfaces and in mussel beds. Because all sites were presumably exposed to identical temperatures at high tide, we targeted low tide air temperature differences by extracting logger data for the two hours before and after low tide.

To examine differences in desiccation between wave-exposed and wave-protected study sites, we placed 10 weighed ( $\pm 0.1$  g), water-saturated sponges ( $5 \times 5 \times 2$  cm) at the middle tidal height at our wave-exposed and wave-protected study sites. Sponges were positioned at the same tidal height at both exposures just as the tide ebbed. Sponges were collected just before first wetting of the incoming tide and reweighed. This was replicated in spring, midsummer, fall, and winter, but the data for all seasons were pooled for final analysis because seasonal effects were not significant. For the same tidal height, rocks on the wave-exposed site were inundated on

average 1.42 h longer per tide than at the wave-protected site due to wave splash.

We also quantified the desiccation potential of central Patagonian rocky shores relative to other rocky intertidal sites that have been previously studied using local weather data. We obtained daily wind speed, air temperature, and humidity data from Trelew, Argentina; Plymouth, England; Portland, Maine, Quillayute, Washington, Astoria, Oregon, San Diego, California, USA; Balboa, Panama; Sydney, Australia; and Antofagasta and Santo Domingo, Chile (see Table 1 for sources). These specific sites were chosen because they were close to sites where earlier rocky intertidal studies had been done, and we were able to obtain the most complete climate data from these sites. From this data we calculated monthly desiccation potentials (general evaporation rates) for the 5–11 years of data available for each site using the general desiccation potential equation (Jones 1992:123–140):

$$E = (\rho r/P)(e_0 - e_z)(k^2 u_z)/[\ln(z/z_0)]^2$$

where  $E$  is evaporation rate (g·cm<sup>-2</sup>·s<sup>-1</sup>),  $\rho$  is air density (g/cm<sup>3</sup>),  $r$  is water/air molecular mass ratio (0.622),  $P$  is ambient pressure (mb),  $e_0$  is surface vapor pressure (mb),  $e_z$  is vapor pressure at elevation  $z$  (mb),  $k$  is the Von Karman constant (0.42),  $u_z$  is wind speed at elevation  $z$  (cm/s),  $z$  is elevation (cm), and  $z_0$  is a surface roughness parameter (cm).

For these calculations air density and water vapor pressure data were calculated using air temperature data from the sites and the standard relationships between these variables and air temperature. Vapor pressure at elevation  $z$  ( $e_z$ ) was calculated by multiplying the surface vapor pressure at the mean monthly temperature ( $e_0$ ) by the mean monthly relative humidity (Jones 1992). Mean monthly wind speed and mean monthly air pressure data

were inserted into the equation as variables  $u_z$  and  $P$  without any further modifications. For the surface roughness parameter we used 0.0256, which Conaway and van Bavel (1967) found to be a typical roughness parameter for wet soil and rock surfaces. The water/air molecular mass ratio ( $r$ ), the elevation ( $z$ ) at 100 cm above the surface, and Von Karman constant ( $k$ ), also known as the turbulent momentum coefficient, were all constants for all calculations. We analyzed the resulting evaporation potential data with an ANOVA comparing mean monthly evaporation rates among locations.

#### Recruitment

To quantify variation in the recruitment of benthic organisms with pelagic larvae we quantified mussel and barnacle recruitment to our wave-exposed and wave-protected sites (Leonard et al. 1998, Menge et al. 2003). Recruitment of the acorn barnacle *Balanus glandula*, hereafter referred to by generic name, was quantified in 10 25 × 25 cm quadrats in the middle intertidal zone at each site that were cleared of all sessile organisms in November 2001. Recruitment of barnacles was quantified annually in March 2001–2004. After monitoring annual recruitment, all recruits were removed to assess recruitment the following year. We quantified the recruit variation in the mussel *Perumytilus* in March 2002 by collecting 10 × 10 cm clumps of mussels from the middle and low intertidal zones at both our wave-exposed and wave-protected sites. In the laboratory we sorted and counted mussel recruits (mussels <3 mm in length) in the samples. In five years working in Cabo Dos Bahias Park and other rocky intertidal sites on the Patagonia coast of Argentina we never observed mussel recruits outside of mussel beds, while mussel recruits are always present in mussel beds.

#### Impacts of consumers and physical stress during secondary succession

To examine the role of consumers and physical stress in the development of intertidal communities on wave-exposed and wave-protected shores we ran a series of caging experiments. Our initial experiments included shading treatments to manipulate physical stress. The shaded treatments, however, were all lost at the wave-exposed sites due to the increased drag produced by the shade cloth. We have successfully used similar shades on the coast of New England, but the stronger wave stresses in Patagonia made the shading treatment unworkable at wave-exposed sites. Moreover, because physical stress on rocky intertidal organisms on the Argentinean coast of Patagonia appeared to be driven primarily by strong winds and not solar radiation, the shading treatment was not markedly ameliorating physical stress in this system. Due to these difficulties we abandoned the shading treatments at all sites.

At both wave-exposed and both wave-protected sites we established eight consumer removal cage plots, eight cage control plots, and eight control plots at three tidal

heights: the low zone, middle zone, and high zone. All plots were 10 × 10 cm and permanently marked with corner bolts on adjacent corners with one of the corner bolts labeled with a plastic numbered tag (McMaster Carr, Cleveland, Ohio, USA). Caged plots were covered with a 15 × 15 × 5 cm (length × width × height) stainless steel hardware cloth cage bolted to the substrate with a stainless steel center bolt. Cage control plots were covered with similar cages, but with two sides removed to give predators access. Control plots had no cage structures. All plots at each site and in all zones were randomly placed, and all live organisms in the plots were initially scraped from the surface with paint scrapers. In plots originally containing algal holdfasts, a propane torch was used to burn away holdfast remnants to prevent vegetative regrowth. All plots were established in November 2001 and were monitored photographically in April and November 2001–2004. Limpets were able to get into the caged plots by squeezing under cage edges or recruiting in as larvae. To deal with these problems we improved our control of limpets in April 2002 by painting a 3-cm strip of rock surrounding each caged plot with copper based antifouling paint that prevents limpets from crawling into the cages (Paine 1980). We also checked all cages monthly and removed limpets that had gotten into the cages. Damage to cages at both the exposed and protected sites forced us to abandon and collapse the experimental treatments. After three years nearly half of all cages, controls, and cage controls had been lost due to cage and/or tag loss, so we pooled the remaining plots from the two exposed and two protected sites for analysis.

Because abundance of the invasive barnacle *Balanus glandula* increased dramatically during the course of our experimental studies, we initiated a second succession experiment in 2003 to examine the effects of *Balanus* on the speed of system recovery. At both of our exposed sites, we established 16 20 × 20 cm clearings. Barnacle removal treatments were applied to half of the clearings by manually removing barnacle recruits twice a year. Percent cover and density of dominant organisms colonizing plots with and without barnacles were recorded and analyzed in 2004.

To quantify consumer pressure by shell-crushing predators such as crabs and birds, we did a series of tethering experiments similar to those we had previously done in New England (Leonard et al. 1999). In these experiments we attached small (15–20 mm in length) mussels on 5-cm fishing line, tethered to the substrate with marine epoxy at high and low tidal heights, at wave-exposed and wave-protected sites, both exposed to predators and in stainless steel cages (see previous description) that protected them from predators. This experiment was replicated monthly from November to January 2002 and 2003. For each replicate run, two sets of 20 tethered mussels were set up in each treatment type and examined daily for 4–5 days for signs of predation, e.g., crushed or missing mussels.

### *Mussel and coralline algae transplants*

One of the most striking contrasts between wave-exposed headlands and the wave-protected bay in Cabo Dos Bahias is the distribution of mussels and coralline algae. Wave-protected bays are characterized by distinct zonation of organisms across intertidal elevation, with space predominantly bare in the high zone, mussels in the mid-zone, and coralline algae in the low zone. In contrast, wave-exposed headlands are near monocultures of mussels across all tidal heights and coralline algae are rare. We conducted a series of transplant experiments to (1) determine the factors driving zonation within protected bays and (2) examine why coralline algae are absent from exposed headlands.

*Protected bay zonation experiments.*—Within protected bays, two transplant studies were conducted to examine the factors controlling the distribution of the two dominant species, the algal turf *Corallina* and the mussel *Perumytilus*. Experimental transplants were established in December 2002 and were destructively sampled in November 2003 and December 2004 for algae and mussels, respectively.

### *Algae transplants*

To examine the importance of physical stress and herbivory in controlling algal distribution, we conducted a transplant experiment manipulating tidal height, herbivory, and solar intensity and measured relative algal performance in various treatments. Seventy-two algal mats of standard size (15 × 15 cm) were harvested from continuous healthy beds in the low intertidal. All transplants were wrapped in fishnet (clear plastic, 50 μ, 1.2-cm mesh size) to maintain mat integrity without creating a substantial barrier to herbivores (once established, algae grew easily around and over the mesh). Twenty-four mats were transplanted to three intertidal levels (high, mid, and low) and randomly assigned to one of three caging treatments (cage, shade cage, and cage control, N = 8 replicates). Cages and cage controls were the same as described above, and shade cages had two sections of black plastic mesh (Vexar, 20 × 20 cm) placed within the top of the cage and secured with cable ties to reduce evaporative water loss due to solar irradiation. Transplants were placed on bare rock that was scraped clean of all organisms. Non-caged controls were lost within days of transplantation due to wind and wave stress and were therefore omitted from the design. Transplants were monitored monthly for nine months and scored for percentage of original transplant alive (percentage survivorship). At the end of the experiment, transplants were harvested and given a final percentage survivorship score.

### *Mussel transplants*

To examine the roles of physical stress, competition, and predation in driving mussel bed distribution, we conducted a similar transplant experiment with mussels. Mussels were removed from dense beds in the lower

mid-intertidal, and transplant biomass was standardized by removing 15 × 15 cm in beds of 4 cm depth. Transplant units were wrapped in fishnet mesh (see previous description) to minimize mussel loss while byssal threads reattached without excluding predators. Mussels were transplanted to high, mid-, and low intertidal zones within cage, shade cage, and cage control (N = 8) treatments. Again, non-caged controls were lost quickly, even given acclimation periods under cages that were later removed, so cage controls served as effective controls. Transplant area and caging treatments were prepared and placed as described before. Transplants were monitored monthly throughout the study period, and at the end of the experiment mussels were harvested and survivorship recorded. When algal biomass was present (low zone), the percent cover of algae both below and above transplanted mussels was measured.

In order to determine where mussels performed best in the absence of competitors, we conducted mussel growth experiments across tidal height. Twenty juvenile mussels between 8 and 12 mm in length were placed with 10 large mussels (>20 mm length) in 5-mm mesh nylon bags. Ten bags were placed at low, mid-, and high tidal elevations under cages to minimize mussel bag loss from wave stress in plots scraped clean of all inhabitants. Mussels were collected after 12 months, before algal competitors were able to invade the bare areas. The number of surviving juveniles was counted and juvenile valve length measured with digital calipers to calculate growth. The number of new mussels (<5 mm) recruiting into the bags was also recorded.

*Wave exposure transplant experiment.*—We hypothesized that coralline algae is absent from wave-exposed headlands because it is vulnerable to being torn from the substrate by heavy wave forces. We based this hypothesis on two observations. First, coralline algae were commonly found washed up on shore apparently after being torn from the substrate. Second, on wave-exposed headlands coralline algae are found in deep pools and behind emergent rock that dissipate wave energy, both microhabitats with reduced wave forces. To test the hypothesis that wave stress limited the distribution of coralline algae on wave-exposed headlands, we transplanted 15 × 15 cm sections of mussels covered with coralline algae (~80% cover) in stainless steel (1-cm mesh) cages to identical intermediate intertidal heights on wave-exposed shores (N = 10) and wave-protected shores (N = 10) in November 2003. In March after four months we scored the cages for algal cover.

### *Mussel bed dynamics*

One of the most striking characteristics of the mussel beds on wave-exposed shores in Cabo Dos Bahias Park is how rare disturbance-generated bare space is. In spite of the large waves that routinely hit these headlands, bare space is not common. To examine the stability and resilience of *Perumytilus* beds we: (1) quantified the

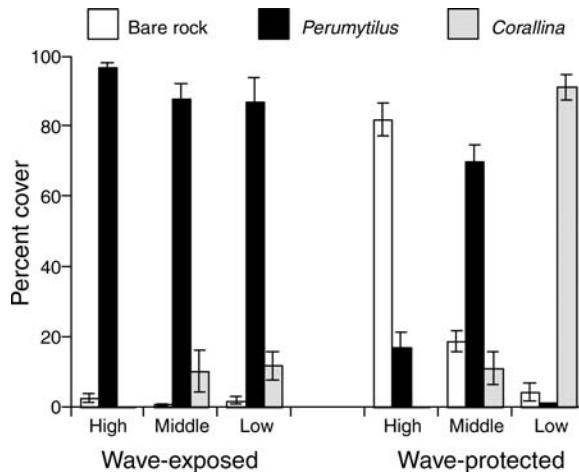


FIG. 1. Percent cover (mean  $\pm$  SE) of primary space occupants at the wave-protected and wave-exposed study site at Cabo Dos Bahias Park on the Patagonian coast of Argentina. Data from two wave-protected and two wave-exposed sites were pooled.

attachment strength of *Perumytilus* in wave-exposed and wave-protected habitats to compare with attachment strengths of well-studied North American mussels, (2) made clearings in *Perumytilus* beds to examine the hypothesis that these mussel beds appeared to experience little disturbance because disturbances recovered rapidly, and (3) marked random locations in mussel beds in wave-exposed habitats and marked edges of mussel beds in wave-protected habitats to detect changes in the mussel beds.

To quantify *Perumytilus* attachment strength we located representative mussels of a range of sizes in natural beds, attached them to a Pesola spring scale (Forestry Suppliers, Jackson, Mississippi, USA) and slowly pulled them from the bed at a 90° angle. When their byssal thread attachment broke, we measured mussel length in millimeters with calipers and recorded byssal thread attachment strength in grams. We repeated this on 30 mussels at both wave-exposed and wave-protected sites. To compare the attachment strength of *Perumytilus* with a well-studied Northern Hemisphere mussel, in February of 2005 we took identical measurements on *Mytilus edulis* individuals at two wave-exposed headland sites (25 mussels at each site) at Nahant, Massachusetts, USA (see Menge 1976 for site description). Dense *Mytilus* mussel beds annually colonize the area sampled at Nahant during the summer months, but over the winter most mussels are torn from the site by heavy waves and few mussels over two years old are found at the site (M. D. Bertness and G. C. Trussell, *personal observations*). Thus, the *Mytilus* sampled are likely living near the upper end of the ability of *Mytilus* to withstand wave stress.

To quantify recovery from disturbance at our Patagonian study sites five 25  $\times$  25 cm clearings were made in mussel beds in the middle intertidal zone at two

wave-exposed and two wave-protected sites in November 2001. These areas were cleared with paint scrapers, corner marked with stainless steel bolts and numbered tags, and photographed in November and April 2001–2004. The photographs were used to quantify mussel bed recovery. To quantify natural mussel bed dynamics, 50 random locations in the middle intertidal zone at wave-exposed sites were marked by drilling a hole in the substrate, inserting an anchor, and attaching a numbered tag and 25 cm long cable tie in the anchor with a stainless steel bolt. The cable ties made finding the numbered tags possible. At 50 locations at middle intertidal zone locations on the border of mussel beds and bare rock substrate, 15  $\times$  15 cm plots were marked with stainless steel screws and numbered tags. These marked locations were photographed in November and April 2001–2004, and the photographs were examined for changes in mussel cover.

#### Data analysis

All data from our descriptive studies, physical parameter measurements, barnacle and mussel recruitment assays, mussel density manipulations, and coralline algae transplants, were analyzed with fully factorial Model 1 ANOVA using JMP software (SAS Institute 2000) for Macintosh. Data were transformed as necessary to meet the assumptions of parametric statistics. Any post hoc comparisons were performed using Tukey's hsd or the linear contrast feature of JMP. For the long-term caging experiment, because many experimental plots were lost over the three-year time course of the experiment, we pooled data from wave-exposed and wave-protected study site replicates and analyzed the final data to compare experimental treatments. Mussel attachment strength measurements were analyzed with ANCOVA comparing *Perumytilus* with *Mytilus* attachment strengths.

## RESULTS

### Zonation at the study sites

The vertical zonation of rocky shores on the central Patagonian coast of Argentina is striking (Fig. 1). On wave-exposed headlands, dense beds of the mussel *Perumytilus* cover nearly the entire intertidal habitat from the extreme high intertidal to the low intertidal zones. Unoccupied bare space is rare on wave-exposed headlands in spite of the strong wave forces in these habitats and the potential for wave-induced disturbance. The mussel dominance of wave-exposed headlands decreases at lower tidal heights with the coralline algae, *Corallina*, occupying 10–15% of available space at middle and low tidal heights (Fig. 1). The distribution of *Corallina* at wave-exposed headlands does not appear to be random. In these habitats, *Corallina* is typically found in tide pools or other microhabitats with reduced exposure to wave forces (M. D. Bertness et al., *personal observations*). At the lowest levels of the intertidal, at heights only exposed during extreme low tides just a few

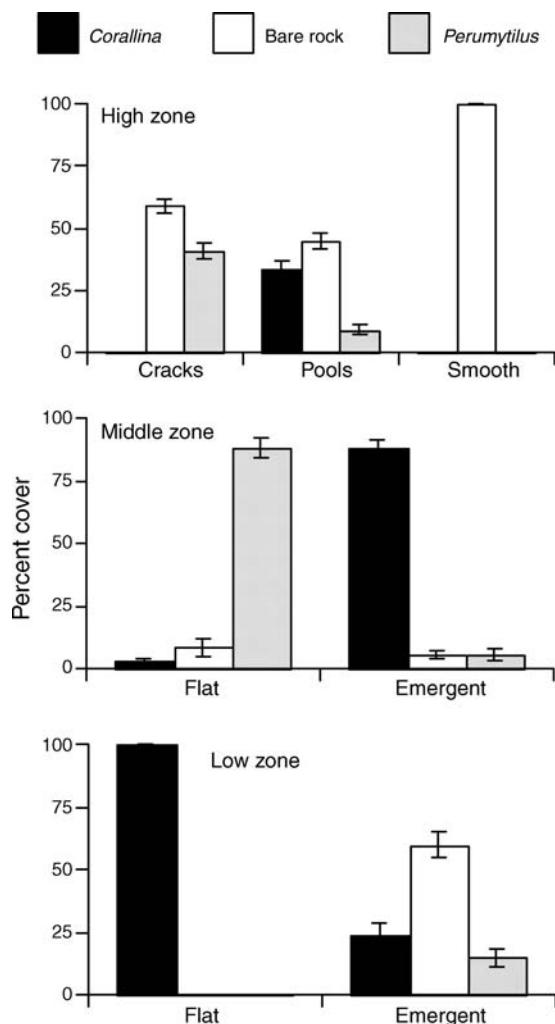


FIG. 2. Percent cover (mean  $\pm$  SE) of primary space in microhabitats on wave-protected shores in Cabo Dos Bahias Park, Patagonia.

times a year, mussel bed dominance gives way to a mixed assemblage of seaweeds, mussels, and barnacles, including *Ulva* (8.5%  $\pm$  6% cover) and *Porphyra* (4.4%  $\pm$  1.8% cover), *Corallina* (10.5%  $\pm$  3.2% cover), *Perumytilus* (34.1%  $\pm$  10.8% cover), *Balanus* (8.0%  $\pm$  2.2% cover), and bare space (33.3%  $\pm$  6.1% cover).

On adjacent wave-protected rocky shores high intertidal elevations are dominated by unoccupied bare space with mussel cover <20%, >70% of middle elevation space is covered by *Perumytilus* beds, and the low intertidal habitat is dominated by >90% cover of the coralline algae *Corallina* (Fig. 1). Microhabitat patterns in the distribution of sessile organisms on these wave-protected shores are conspicuous (Fig. 2). At high elevations smooth rock surfaces are bare with no macroorganisms, and *Corallina* and *Perumytilus* occur exclusively in tide pools, cracks, and crevices. In the middle intertidal of wave-protected shores, *Perumytilus* domi-

nates most flat rock surfaces but *Corallina* dominates tide pools. *Corallina* dominates virtually the entire low intertidal zone as a dense, thick (5–10 cm), spongy mat. The only exception to the complete *Corallina* cover in the low intertidal zone at wave-protected sites is on emergent substrate like large boulders or other rock features that expose substrate to more frequent aerial exposure. Bare space as well as *Corallina* and *Perumytilus* dominate these emergent substrates. *Corallina* continues to dominate wave-protected shores at the extreme low intertidal and shallow subtidal heights.

Quantification of the invertebrates living in mussel beds and coralline algae turfs revealed a rich diversity of organisms that differed markedly between wave-exposed and wave-protected shores and generally increased with decreasing tidal height. At wave-protected sites amphipods, insect larvae (Chironomidae), and polychaete worms (*Marphysa aenea*, *Platyneries australis*) were particularly abundant in the coralline turfs at low tidal heights, while isopods (*Exosphaeroma* sp.) and limpets (*Siphonaria lessoni*, *Nacella magellanica*) were more abundant at intermediate and high tidal heights in mussel beds (Fig. 3). A very different assemblage of invertebrates is found in the mussel beds at wave-exposed sites (Fig. 3). Wave-exposed sites can have as many as 600 anemones/m<sup>2</sup> (*Ovulactis mucosa*, *Bunodactis reynaudi*), >200 *Balanus*/m<sup>2</sup>, >200 limpets/m<sup>2</sup> (*Siphonaria lessoni*, *Nacella magellanica*), >100 chitons/m<sup>2</sup> (*Tonicia lebruni*, *Plaxiphora aurata*), and >80 starfish/m<sup>2</sup> (*Anasterias minuta*). As substrate at wave-exposed and wave-protected sites without mussels or coralline algae cover is bare and lack invertebrates, foundation species provide refuge to a diverse and abundant intertidal invertebrate assemblage.

#### Physical stress

Rock surface temperature data showed that in the high intertidal zone temperatures are markedly higher at wave-protected than wave-exposed sites, that temperature differentiation among sites was greatest during the summer months (November–March), and that temperatures generally increase with increasing tidal height and exposure to low tide aerial exposure (Fig. 4). The most significant feature of the temperature data was that the high intertidal habitat at wave-protected sites was 2–5°C higher than all other locations during the summer months including the same elevation on exposed shores ( $F_{1, 8626} = 375.8$ ,  $P < 0.0001$ ). Another interesting aspect of the data was that in wave-protected low intertidal habitats, rock surface temperatures were consistently 2°C cooler from August to November than at all other locations (Fig. 4). This apparent anomaly is likely a consequence of rock surfaces in this habitat covered by a dense waterlogged *Corallina* turf.

Desiccation was >50% higher at wave-protected sites than at wave-exposed sites. At wave-protected sites, sponges lost  $>40.7 \pm 4$  g of water mass during low tide

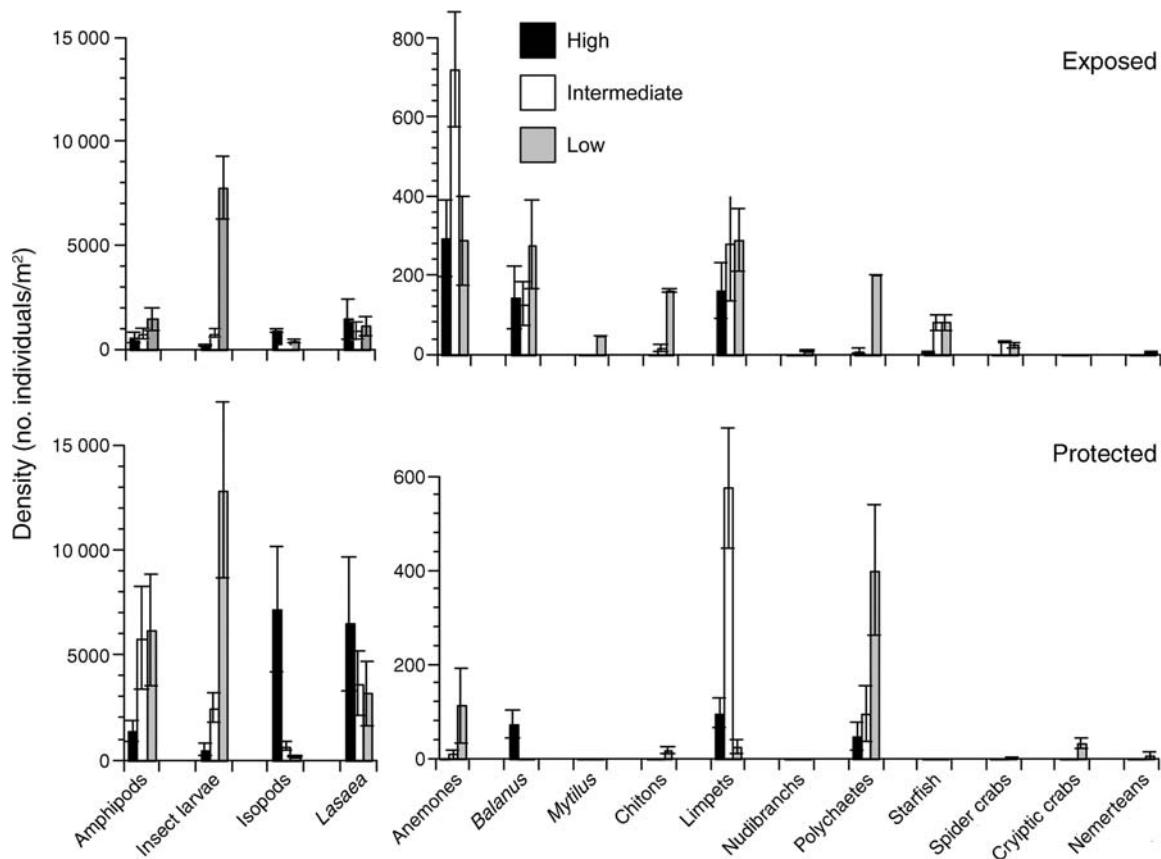


FIG. 3. Invertebrate densities in mussel beds and coralline turfs at wave-protected and wave-exposed sites. Data from wave-protected sites at low intertidal heights are from coralline turfs. All other data are from mussel beds. Common assemblage members include *Halosydna* sp., scale worm; *Marphysa aenea* and *Platynereis australis*, polychaetes; *Plaxiphora aurata* and *Tonicia lebruni*, chitons; *Ovulactis mucosa* and *Bunodactis reynaudi*, anemones; *Trochon geversianus* and *Pareuthria plumbea*, snails; *Anasterias minuta*, starfish, *Cyrtograpsus altimanus* and *Halicarcinus planatus*, crabs; *Lasaea* sp., viviparous clam; *Mytilus edulis* and *Aulacomya ater*, mussels; *Exosphaeroma* sp., isopods; *Siphonaria lessoni*, pulmonate limpet; *Nacella magellanica*, prosobranch limpet.

exposure, while at wave-exposed sites sponges lost only  $26.6 \pm 2.6$  g of water mass ( $F_{1,42} = 7.6$ ,  $P = 0.0085$ ).

Evaporation rates calculated from local weather station data confirm that the high winds and relatively low humidity on the Patagonian shores of Argentina lead to higher desiccation rates than in other previously studied rocky intertidal systems (whole model,  $F_{10,121} = 11.03$ ,  $P < 0.0001$ , Tukey's hsd; Trelew significantly greater than all others at  $P < 0.05$ , Table 1). Desiccation was over an order of magnitude higher on the Patagonian coast of Argentina than on the open coasts of Washington State and Oregon, central California, and Maine, USA, and England. Lower latitude and/or desert-coast sites in southern California USA, Australia, and Chile had desiccation rates approaching those of our Patagonian sites, but the desiccation rate in Balboa, Panama, which had the second highest desiccation potential, was still 30% lower than that found for the Patagonian coast of Argentina.

Average wave forces did not differ between our wave-protected sites ( $P > 0.50$ , ANOVA) or between our

wave-exposed sites ( $P > 0.80$ ), but were over four times higher at our wave-exposed ( $6.67 \pm 1.75$  m/s, mean  $\pm$  SE) than at our wave-protected sites ( $1.36 \pm 0.75$  m/s,  $F_{1,250} = 378.7$ ,  $P < 0.0001$ ). Maximum wave forces recorded at both wave-exposed sites were  $>15$  m/s, comparable to maximum wave forces on wave-exposed headlands in California, Washington State, and central Chile (E. Carrington, *personal communication*; Guíñez and Castilla 1999), whereas maximum wave forces recorded on wave-protected sites (3 m/s) were lower than the one reported in previous studies on the Pacific South American coast (Alvarado and Castilla 1996).

#### Recruitment

*Perumytilus* recruitment was over twice as great at wave-exposed ( $P < 0.001$ ) than on wave-protected sites and twice as great at low tidal heights than at high tidal heights ( $P < 0.001$ , Fig. 5). We express the data as potential recruitment, or the number of recruits counted in our sampling and also as actual recruitment, or the

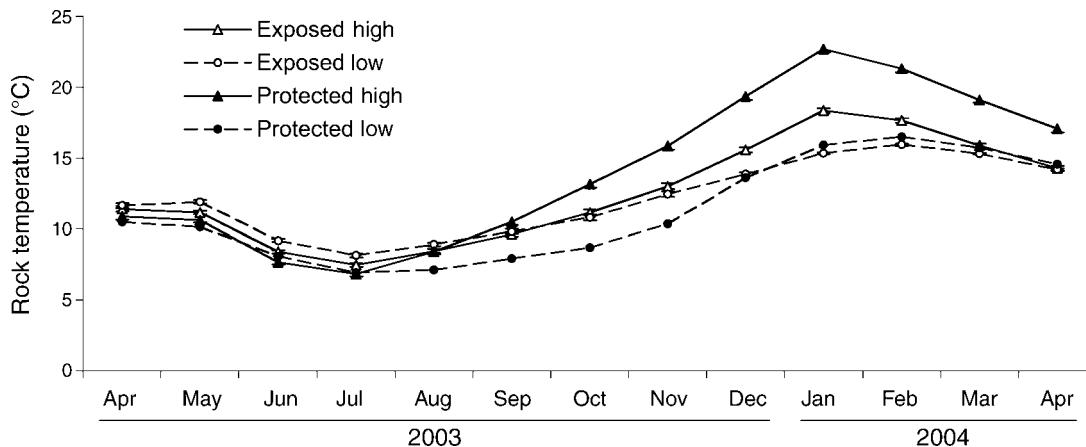


FIG. 4. Rock surface temperatures (mean  $\pm$  SE) during low tide aerial exposure at the wave-protected and wave-exposed study sites in Cabo Dos Bahias Park. (Error bars are smaller than the symbols.)

potential recruitment adjusted for the percent cover of mussels in a given habitat.

Differences in recruitment between wave-exposed and wave-protected habitats were more striking with *Balanus*. No *Balanus* recruits were found in any of our barnacle recruit monitoring plots in wave-protected habitats. Because *Balanus glandula* has a calcareous basal plate cemented to the surface, this pattern does not represent high barnacle mortality at wave-protected sites unless mortality is occurring at the early recruit stage before they leave a calcareous basal plate scar on the substrate. *Balanus* recruitment at the wave-exposed sites was slightly higher at high intertidal than middle intertidal sites and increased each year. *Balanus* is a recent invader from the west coast of North America. We did not notice them or find them in our initial surveys in 2001. Since then, however, it has become a conspicuous component of wave-exposed shores.

*Role of consumers and physical stress in Patagonian rocky shore communities*

Recovery from the experimental disturbances has been extremely slow, even in the absence of consumers, ostensibly due to the extreme desiccation stress affecting these communities. Recovery from disturbance (cover of bare space and *Corallina*) in wave-protected sites after three years was significantly influenced by tidal height, caging treatment, and their interaction ( $P < 0.001$  main effects and interaction for both responses). Mussels did not recruit enough to analyze. At high intertidal elevations, plots remained almost entirely bare regardless of caging treatment, while in middle intertidal elevations plots were predominantly bare when consumers were present (control and cage control), but when mobile consumers were excluded, non-coralline crustose algae dominated plots (Fig. 6). At low elevations, considerably more recovery occurred, even in control plots exposed to consumers where coralline algae and algal crusts colonized >20% of the available space. Cage

controls and cages were exclusively colonized by coralline algae (40% and 80%, respectively). The cage artifact apparent in the low elevation recovery plots could be due to many factors, including cage controls limiting the access of larger herbivores or bulldozing mobile

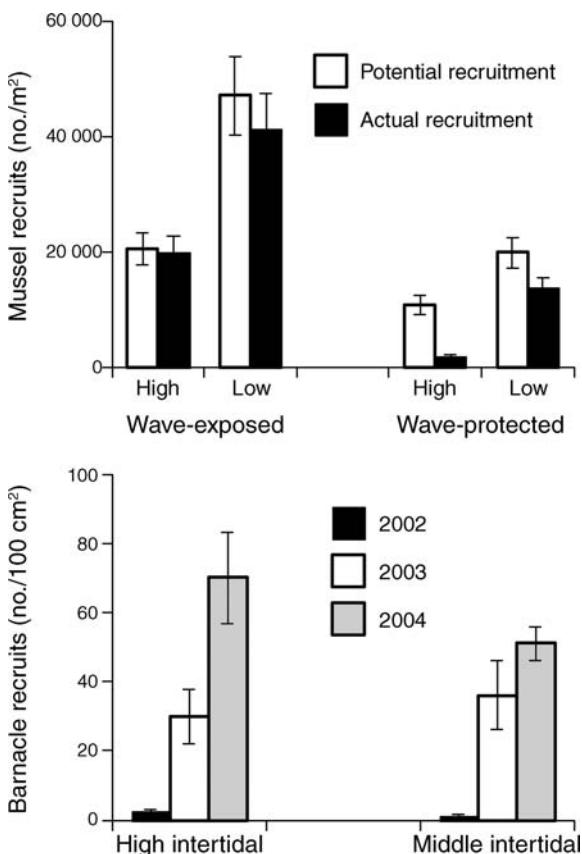


FIG. 5. Recruitment of *Perumytilus* mussels and *Balanus* barnacles to wave-protected and wave-exposed study sites in Cabo Dos Bahias Park. No *Balanus* recruits were found in the sampling plots at wave-protected sites.

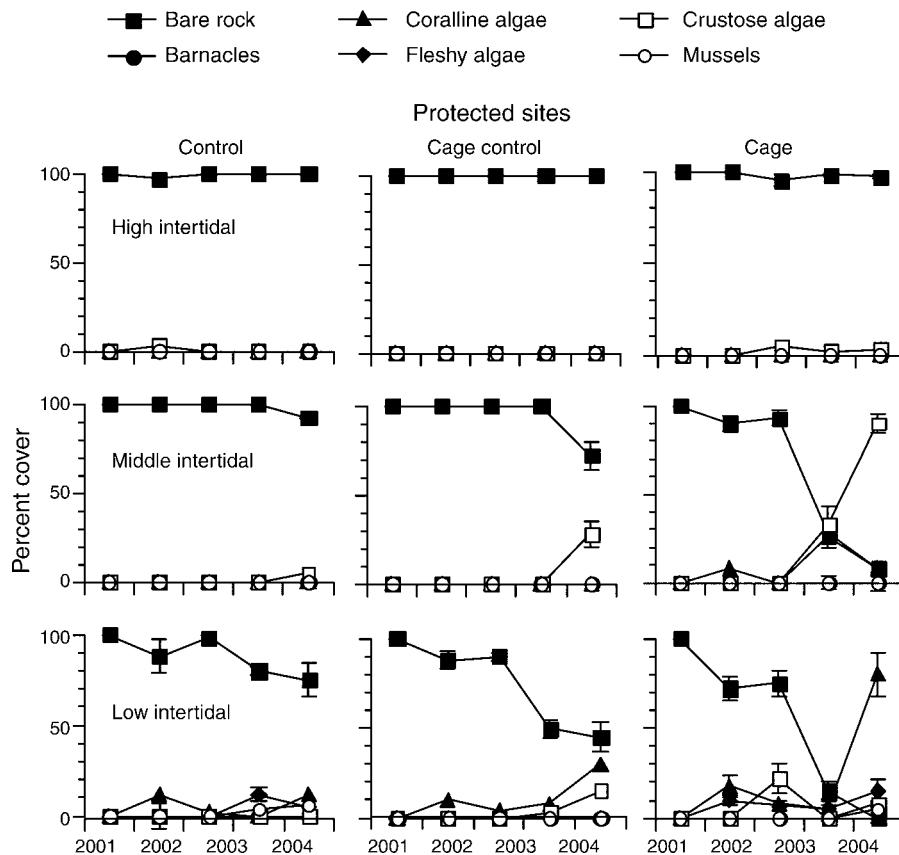


FIG. 6. Recovery from disturbance in control, cage control, and cage plots at wave-protected sites at three intertidal levels (high, middle, and low) at Cabo Dos Bahias Park. Recovery is measured as percent cover (mean  $\pm$  SE).

consumers, or cage controls ameliorating physical conditions of heat and desiccation. Previous work in this system has consistently shown mobile consumers to be uncommon and with little effect on these shores (Paruelo et al. 1998; F. Hidalgo, B. R. Silliman, and M. D. Bertness, *unpublished manuscript*). Additionally, because the strongest cage control artifacts occurred in the corners where physical stress amelioration would be expected to be the greatest due to the largest wind-block effect in cage corners, we suspect that artifacts are due to some stress amelioration in cage controls compared to uncaged controls.

At wave-exposed sites, recovery from disturbance was also slow but not as strongly limited by desiccation stress (Fig. 7). After three years of recovery, plots in the high intertidal of wave-exposed sites were colonized by barnacles ( $\sim 50\%$  cover in all caging treatments) and mussels ( $5\% \pm 3\%$ ,  $8\% \pm 4\%$ ,  $13\% \pm 5\%$  mussels in control, cage control, and cage, respectively). Recovery of barnacles and mussels in the middle intertidal was nearly identical to the high zone. However, in addition, crustose algae and fleshy algae (dominated by *Porphyra*) also recruited into caged plots at middle intertidal heights. At low elevations, control plots were still dominated by bare space after three years of recovery.

When consumers were removed, however, low intertidal caged plots were dominated by crustose and coralline algae after recovering for two and three years, respectively. In contrast to higher elevations at wave-exposed sites, neither barnacle or mussel recruitment were conspicuous after three years of recovery at the low intertidal elevations. Bare space, barnacle, and mussel cover after three years of recovery on wave-exposed sites were significantly influenced by tidal height, caging treatment, and their interaction ( $P < 0.0001$  for main effects and interaction for all response organisms).

Tethering mussels at wave-protected and wave-exposed sites revealed little evidence of shell crushing predation,  $<0.25\%$  per day with no difference between wave-exposed and wave-protected locations ( $P > 0.80$ , ANOVA). The few mussels that were crushed appeared to have been crushed by oystercatchers. These low predation rates reflect that there are no common native shell-crushing crabs or fish in the system.

Removing barnacles from middle intertidal elevation plots revealed that barnacles dramatically facilitated *Perumytilus* recruitment. After one year, barnacle removal plots had  $1.3 \pm 0.5$  mussel recruits/plot ( $N = 17$  plots), while control plots with barnacles present ( $50-$

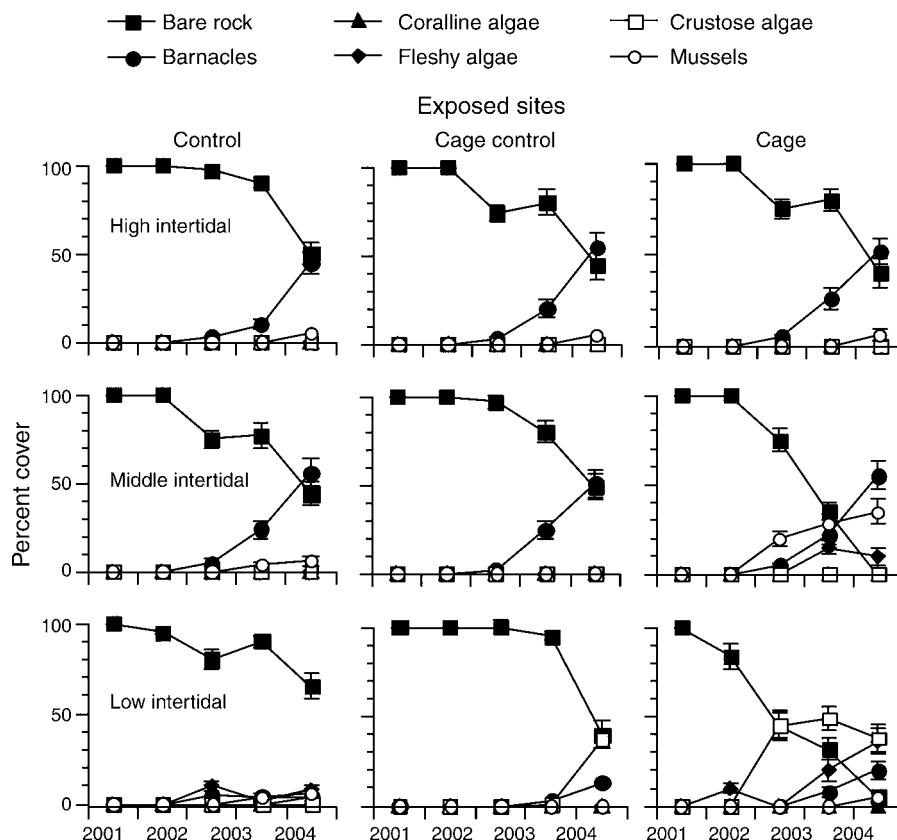


FIG. 7. Recovery from disturbance in control, cage control, and cage plots at wave-exposed sites at three intertidal levels (high, middle, and low) at Cabo Dos Bahias Park. Recovery is measured as percent cover (mean  $\pm$  SE).

75% cover) had  $70.3 \pm 23.5$  mussel recruits/plot ( $N = 18$ ;  $P < 0.009$ , ANOVA).

#### Transplant studies

For coralline algae transplants within protected bays, the effect of caging on algal survivorship varied significantly with tidal height ( $P < 0.001$  for height, cage, and height  $\times$  cage interaction, Fig. 8A). In the low zone, algal survivorship was high in cages and cage controls, but was reduced by shading. Initially, shading offered some benefit to algae transplanted to the high and mid-zones, but these differences were quickly negated by nearly complete mortality in these zones. Regardless of caging treatment, algal survivorship decreased substantially with increasing tidal height.

The success of transplanted mussels varied significantly with height alone ( $F_{2,58} = 532.04$ ,  $P < 0.001$ ), but was unaffected by caging treatment or cage by height interaction (Fig. 8B). Mussel performance was best in the middle intertidal where survivorship was close to 100% in all cage treatments (Fig. 8B). While mussels performed better under shade cages in the high intertidal, mussel mortality was high in all caging treatments in the high intertidal (Fig. 8B). Mussel survivorship was also reduced in all caging treatments in the low zone because the apparent source of mortal-

ity, competition from algal mats, was not eliminated by our caging treatments. While mussel transplants appeared healthy in the low zone, after two years they were significantly overgrown by invading algae (Fig. 9). Algae forcefully invaded mussel transplants from all sides, overgrowing the top of mussel transplants, and additionally recruiting under and growing up within mussel transplants. Mussel survival in cage controls vs. full cages was not significantly different, indicating that predation did not significantly influence mussel distribution in this system.

When coralline algae was removed, results from transplants of juvenile mussels to different tidal elevations showed that mussel growth decreased significantly at higher elevations (Tukey's hsd, low > mid > high at  $\alpha = 0.05$ ) and additionally, that recruitment was highest in the lowest zone (LS means contrast, low vs. mid- and high  $F_{1,26} = 40.63$ ,  $P < 9.4 \times 10^{-7}$ ).

Results of the *Corallina* transplant experiment between wave exposure sites were dramatic. When *Corallina* was transplanted to wave-protected sites at low tidal heights, it survived and continued to thrive ( $60 \pm 8\%$  *Corallina* cover). In contrast, when transplanted to identical tidal heights in wave-exposed locations, it suffered 100% mortality. After six months all the mussels transplanted to wave-exposed locations were

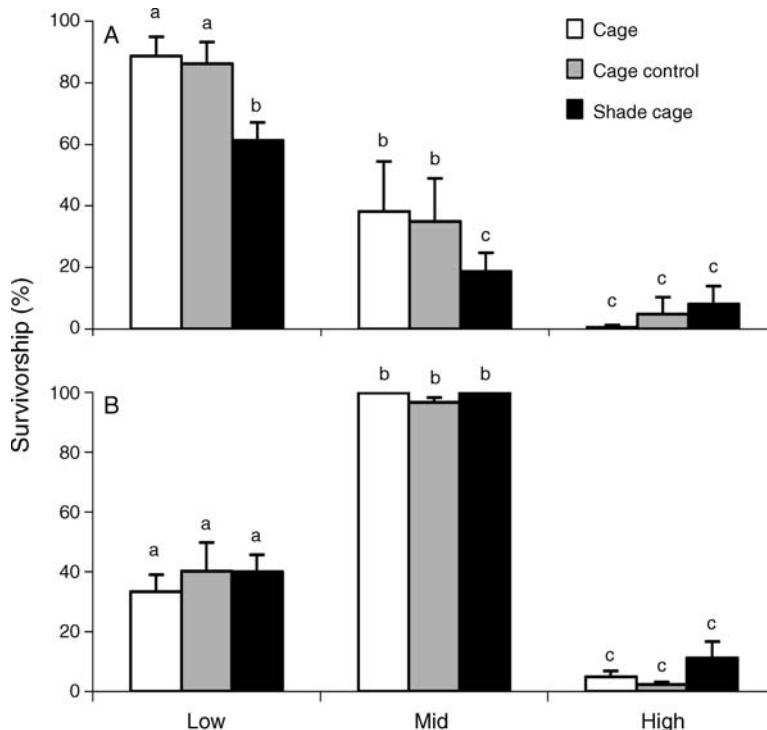


FIG. 8. Percent survivorship of (A) algae and (B) mussels in experimental transplants after eight months and two years, respectively. Data represent means + SE of eight replicate transplants in each height-by-treatment combination. Different letters indicate significantly different means from unplanned contrasts using Tukey's hsd.

alive and attached to the rock, but all of the *Corallina* was eliminated.

*Mussel bed dynamics*

Our examination of the dynamics of *Perumytilus* mussel beds revealed that, contrary to our initial hypothesis, they are highly static, resistant to natural disturbances and extremely slow to recover from disturbances. During the four years that we have been working at Cabo Dos Bahias Park we have not seen any

natural disturbances in the dense mussel beds at the wave-exposed headlands in spite of recording maximum wave water velocities of >15 m/s. In the winter of 2002 there was also a severe storm at our study sites with 15-m waves reported. Even after this storm we did not find any noticeable disturbances in the mussel beds at the study sites. None of the 50 locations we marked in the mussel beds at our two wave-exposed study sites showed any signs of disturbance from 2001 to 2004. Similarly, at our wave-protected study sites, *Perumytilus* beds are

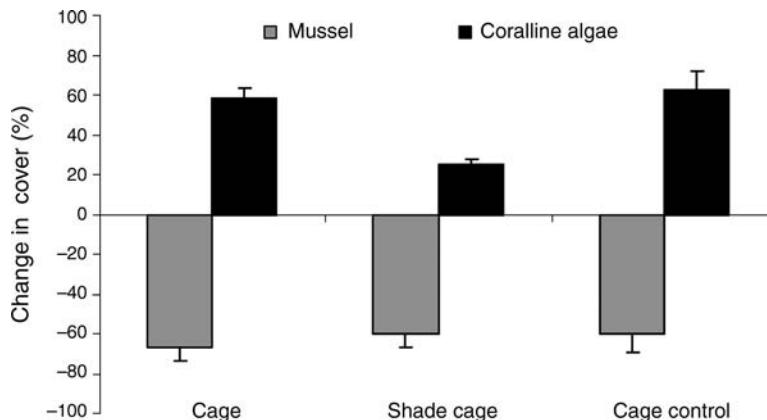


FIG. 9. Percentage change of dominant organism cover due to algal invasion and mussel death after two years in mussel transplants to low protected zones. Data represent means + SE in replicate transplants (N = 8).

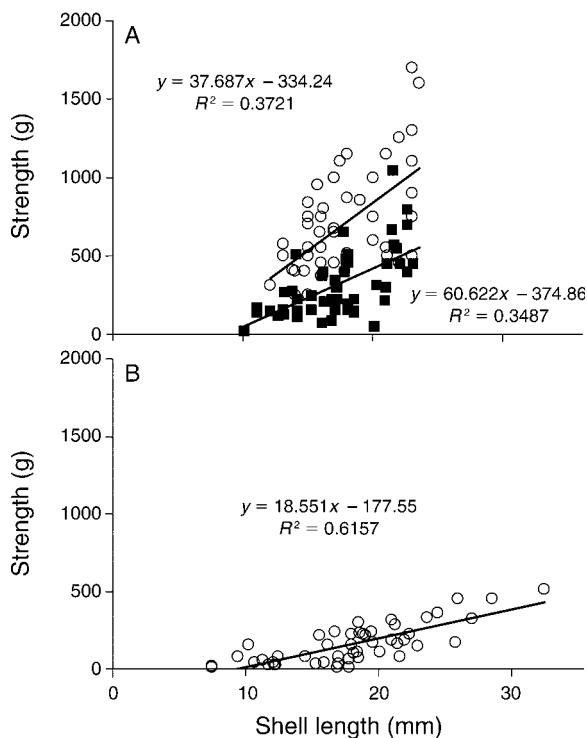


FIG. 10. Attachment strength, by size, of (A) *Perumytilus* from wave-exposed (open circles) and wave-protected (solid squares) locations at Cabo Dos Bahias Park, Chubut, Argentina, and (B) *Mytilus edulis* from wave-exposed and wave-protected locations at Nahant, Massachusetts, USA.

highly static. We did not detect any movement of mussels in crevices in the high intertidal zone ( $N=30$ ) or the edges of mussel beds abutting bare rock in the intermediate intertidal zone ( $N=30$ ) from 2001 to 2004.

The relationship between mussel length and attachment strength (Fig. 10) varied significantly among sites tested (Argentina exposed, protected, and Nahant, site  $\times$  length interaction, ANCOVA,  $F_{2,144} = 5.166$ ,  $P = 0.0068$ ). To compare attachment strength differences across sites, we compared mussels from a medium size class (between 15 and 20 mm) using a one-way ANOVA. Mussels of the same size had much higher attachment strengths in Argentina, particularly at exposed sites ( $F_{2,69} = 58.8061$ ,  $P < 0.0001$ ). For mussels of similar size, *Perumytilus* attachment strength was 3–4 times greater than *Mytilus edulis*. Attachment strengths at all sites were significantly different from each other (Tukey's hsd,  $P < 0.05$ ) with Nahant mussels having the weakest and Argentinean mussels at exposed sites the strongest attachment strengths.

*Perumytilus* recruitment to the large  $0.25 \times 0.25$  m experimental clearings made in the mussel beds at our two wave-exposed study sites at both high and intermediate tidal heights ( $N = 6$  clearings/site/height) has been negligible. After three years, mussel cover in all the clearings was  $<1\%$ . This is also the case for the large experimental clearings made in mussel beds at our two

wave-protected study sites at intermediate tidal heights. They are still dominated by  $>99\%$  bare rock.

## DISCUSSION

Patagonian rocky shore communities are exposed to harsher physical conditions than previously studied marine rocky intertidal communities due to the dry southern trade winds that blow year round in Central Patagonia, low local precipitation, and low humidity. Consequently, rocky intertidal communities on these shores are strongly structured by exposure to physical stresses. In particular, intense desiccation risk leads to: (1) suppression of the importance of consumers throughout the intertidal and across wave exposure gradients, (2) no recruitment to open surfaces by native animals, (3) extremely slow community recovery from disturbance, (4) complete reliance on ecosystem engineering by adult individuals of foundation species for community recovery, (5) reliance of intertidal organisms that typically live on open surfaces on the matrix of foundation species for protection from desiccation stress, and (6) reduction in the importance of recruitment variation on community structure. Foundation species dominance and facilitation of the invertebrate diversity by the amelioration of desiccation stress is the strongest biological process contributing to the structure and organization of these communities.

### *Physical stresses on Patagonian rocky shores*

A comparison with rocky shores where previous experimental community ecology has been performed revealed that Patagonian rocky shores are exposed to extreme desiccation rates (Table 1). Desiccation rates on Patagonian rocky shores are over an order of magnitude higher than the commonly studied temperate rocky intertidal shores of Washington, Oregon, central California, and New England in the USA, as well as in England, Australia, and Chile. High desiccation rates on Patagonian shores are the product of the strong, dry southern trade winds, low rainfall, and especially low humidity. These conditions produce higher desiccation rates than even warmer lower latitude subtropical and tropical sites in southern California, USA, Australia, and Central America.

In addition, physical stress on Patagonian rocky shores differs dramatically between wave-exposed headlands and nearby wave-protected bays. Desiccation at wave-protected sites is nearly twice as high as at wave-exposed sites. During the summer months, rock surface temperatures at high intertidal elevations on wave-protected sites are consistently higher by 2–5°C than at wave-exposed sites and preclude local intertidal organisms from recruiting into and inhabiting the high intertidal zone.

### *Horizontal zonation of Patagonian rocky shores*

Patagonian rocky shores exhibit conspicuous zonation patterns, both horizontally, reflecting gradients in

wave exposure and desiccation stress, and vertically, reflecting strong vertical gradients in physical stresses across the intertidal habitat. Wave-exposed headlands are almost entirely dominated by beds of the mussel *Perumytilus* due to a number of interacting factors. Wave splash amelioration of harsh physical conditions, particularly desiccation, has long been recognized to shift the high intertidal borders of intertidal fauna and flora to higher elevations at wave-exposed headlands (Stephenson and Stephenson 1971). On the wave-exposed shores of Patagonia, desiccation rates, rock surface temperatures, and stress due to the lack of immersion at high elevations (Fig. 4) are much lower than at the same elevations on wave-protected shores. Wave splash on exposed headlands thus enables mussel beds to dominate high intertidal elevations that are bare rock on nearby wave-protected shores.

Recruitment of barnacles and mussels at all intertidal heights is much higher on wave-exposed than on wave-protected shores (Fig. 5). Wave-exposed shores have higher fluxes of larvae, which translate into more larvae and recruits of organisms with planktonic larvae (Gaines and Bertness 1993). This flow effect on recruitment is particularly strong with the invasive barnacle *Balanus* that recruited heavily to our wave-exposed sites, while largely failing to colonize nearby wave-protected shores. While *Perumytilus* also had higher recruitment to wave-exposed sites, substantial recruitment did occur on protected shores in refuges from physical stress (both into mussel beds and cracks in rock), suggesting that recruitment limitation does not explain differential coverage of mussel beds on wave-exposed and protected shores. Experimental studies on the central coast of Chile have shown *Perumytilus* larvae are unable to settle directly on bare rock and instead depend on the presence of recruitment mediators such as mussel clumps, filamentous algae, or barnacle shells (Navarrete and Castilla 1990). This finding emphasizes that once mussel bed distributions are established, positive feedbacks between adult populations and recruits make bed expansion difficult. In addition, barnacles on exposed shores could aid in mussel bed development; however because this invader is so recent, facilitated succession alone does not explain greater mussel bed abundance on exposed shores.

The extensive mussel beds on wave-exposed headlands provide refuge habitat for a diverse suite of invertebrates, ranging from starfish and chitons to amphipods and clams (Fig. 3). Tethering experiments demonstrate that these organisms are entirely dependent on habitat amelioration of desiccation stress to survive and persist on these shorelines (B. R. Silliman, M. D. Bertness, C. Bazterrica, V. Reyna, F. Hildago, and C. M. Crain, unpublished manuscript). Without the buffering of physical stresses by the mussel bed, all these organisms, with the exception of the barnacle *Balanus* die within one tidal cycle exposure to low tide physical stress. Mussel beds are known to harbor interstitial commu-

nities (Suchanek 1986). For instance, on temperate and subtropical coasts of Chile and Peru, *Perumytilus* beds provide a favorable microhabitat for a large number of small-sized species, which are either found exclusively within the matrix or alternatively use mussel beds transiently as refuge or recruitment sites (Cancino and Santelices 1984, Castilla et al. 1989, Tokeshi et al. 1989, Alvarado and Castilla 1996). However, the Argentinean sites are unique in that none of the interstitial community and virtually no other intertidal organisms can persist outside of the mussel bed matrix, meaning that community structure, species diversity, and ecosystem function in this system are all obligately dependent on foundation species.

#### *Vertical zonation of Patagonian rocky shores*

At the lowest intertidal levels at wave-exposed headlands, elevations on the subtidal fringe of the intertidal habitat, the *Perumytilus* mussel bed gives way to a zone dominated by a mixture of mussels, erect coralline algae, fleshy algae, and crustose non-coralline algae. While this zone was too low to practically conduct experiments (in many months this level is not exposed even during monthly maximum low tides), it is likely that at these elevations on wave-exposed shores, starfish predation on mussel beds is responsible for reduced mussel densities and the emergence of other primary space holders. Starfish control the lower intertidal distribution of mussels in temperate systems on the Pacific coast of Washington (Paine 1974), Oregon (Sanford 1999), and New England (Menge 1976), but their influence varies importantly depending on the species of starfish and prey and specific physical characteristics (Paine et al. 1985, Sanford 1999). In Patagonia, starfish predation is not strong enough to limit mussels in most of the intertidal. In the middle and lower intertidal of wave-exposed shores, starfish are only able to live in the intertidal habitat in the presence of mussels ameliorating physical stress (B. R. Silliman, M. D. Bertness, C. Bazterrica, V. Reyna, F. Hildago, and C. M. Crain, unpublished manuscript). At the lowest intertidal elevations and shallow subtidal, starfish appear to become less dependent on mussels for survival and become potentially limiting predators. This sort of switch in the nature of interactions across intertidal stress gradients, where positive associations prevail at stressful high intertidal heights, but switch to negative competitive or consumer interactions in more physically benign habitats has been found in a wide range of intertidal systems (Bertness and Hacker 1994, Bertness and Leonard 1997).

In contrast to the mussel bed monoculture that dominates wave-exposed headlands, strong vertical intertidal zonation is conspicuous on the nearby wave-protected shores. In the high intertidal of wave-protected shores, the majority of space is devoid of sessile organisms, with mussels and coralline algae only present in cracks, crevices, and tide pools, suggesting that extreme physical stress limits colonization of most rock

(Fig. 2). Desiccation is twice as great at wave-protected than wave-exposed sites, and rock temperatures show that the physical conditions at high elevations on wave-protected Patagonian shores are dramatically more stressful than on adjacent wave-exposed shores (Fig. 4). Indeed, transplants of both mussels and coralline algae to high elevations of protected bays were unable to survive even in shaded conditions. Shade blocks have previously been used successfully for alleviating physical stress and increasing survivorship of most intertidal organisms at high tidal heights on New England rocky shores where physical stress on intertidal organisms is driven by solar radiation (Bertness et al. 1999). In contrast, desiccation on the eastern Argentinean coast is primarily driven by the substantial and relentless Patagonian winds that were not effectively alleviated by our experimental manipulations.

Zonation patterns on protected Patagonian shores are thus driven by trade-offs in the dominant organisms between physiological tolerance to high desiccation stress and competitive ability. *Perumytilus* exhibited higher tolerance to desiccation stress than *Corallina* because *Perumytilus* transplants thrived in mid-intertidal elevations, where *Corallina* transplants were unable to survive and quickly became dry and brittle (Fig. 8). In contrast, *Perumytilus* was unable to survive in low intertidal elevations in the presence of *Corallina* which aggressively invaded mussel transplants (Figs. 8 and 9). Growth studies confirmed that mussels grew best in the low intertidal, likely due to increased feeding time with the greater time of tidal immersion (Bertness and Grosholz 1985). Stress for intertidal mussels in general (Gillmor 1982) and specifically *Perumytilus purpuratus* on the Chilean coast (Cancino and Rojas 1986) has been experimentally demonstrated to increase with elevation, mainly due to the reduction of immersion time that, in turn, reduces feeding and respiration. Mussels also had highest recruitment into the lowest intertidal zone suggesting optimal conditions in this zone (Leonard et al. 1999). Predation on mussel transplants in any tidal height was trivial (Fig. 8), and mussel tethering data confirmed low predation intensity in this system. Instead, mussel distribution was limited in low tidal elevations by competition with coralline algae. Algal overgrowth of invertebrates has been seen in coral reefs (Hughes 1989) and rocky intertidal (Paine 1984) and in the case of *Corallina officinalis*, superior competitive ability is likely due to quick growth and dense turf morphology, which captures sediments and likely fouls filter-feeding in mussels. In fact, when *Corallina* turfs were excavated, a dense coat of mud and mud-dependent organisms were invariably located at the turf base and any mussels encountered were dead intact shells (M. D. Bertness et al., *personal observations*).

#### *Comparison with zonation on other rocky shores*

The rocky intertidal communities of the Patagonian coast of Argentina superficially appear to be structured

like those in New England (Leonard et al. 1998). In New England, habitats exposed to high flows have high larval delivery of sessile organisms, high growth rates of sessile filter feeders due to high food fluxes, and low predation rates by mobile predators due to flow inhibiting predator foraging efficiency (Leonard et al. 1998). This leads to shorelines dominated by mussel beds. Conversely, in wave-protected New England shores, low larval and food delivery and intense grazing lead to an intertidal dominated by long-lived unpalatable seaweed (*Ascophyllum nodosum*). A similar pattern, likely driven by similar mechanisms, has been described for the temperate coast of the south Pacific, where barnacles (*Jehlius cirratus* and *Nothochtamalus scabrosus*) and mussels (*Perumytilus purpuratus*) dominate exposed coasts and algae (red and green) dominate wave-protected areas (Castilla 1981, Santelices 1991).

On Patagonian wave-exposed headlands, mussel beds dominate the landscape due to high larval delivery and reduced physical stress, similar to New England high flow shores. However, differences in consumer pressure between exposed and protected sites as seen in New England, do not play an important role on Patagonian shores because there are no important mobile predators that occur outside of foundation species in this system. Mussel tethering experiments in New England found that predation on small tethered mussels on wave-protected shores is relatively high, on the order of 20–40% mortality a day (Leonard et al. 1998). On wave-protected Patagonian shores, there is no native shell-crushing crab and predation on tethered mussels, mostly by oystercatchers, is extremely low, less than two orders of magnitude lower than in New England (0.25% per day) and similar on wave-exposed and wave-protected shores. Moreover, there is also no native drilling snail on Patagonian rocky shores that lives outside of the mussel matrix (and snails in the matrix are rare), reducing predation pressure on both mussels and barnacles. In Patagonia, limitation of sessile organisms on wave-protected rocky shores appears to be largely due to physical factors, rather than consumer pressure. This is supported by the restricted distributions at wave-protected sites of mussels at high elevation and limpets at mid-elevation to refuge habitats. Shading plots at wave-protected sites led to an increase in limpet densities of an order of magnitude (M. C. Bazterrica, B. R. Silliman, C. M. Crain, and M. D. Bertness, *unpublished manuscript*) and prolonged mussel survival at high intertidal elevations. Moreover, recruitment limitation does not appear to be important in structuring wave-protected rocky shores in Patagonia because recruitment of mussels is high on wave-protected shores, but entirely restricted to foundation species refuge habitats by severe desiccation stress. Thus, while wave-exposed, high flow sites in New England and Patagonia are superficially structured somewhat similarly, wave-protected sites are structured differently, with grazing and recruitment limitation the dominant forces on New England wave-

protected shores and physical stress the overwhelmingly dominant structuring force on wave-protected Patagonian shores.

Distributional patterns of *Perumytilus* and *Corallina* within and between our exposed and protected study sites have been reported previously along the Argentinian coast (Kühnemann 1969, Otaegi and Zaixso 1974, Zaixso and Pastor 1977, Escofet et al. 1978, Zaixso et al. 1978, Sánchez and Zaixso 1995), but differ somewhat from distributional patterns reported in the Chilean extent of their range (Santelices 1989). In Chile, *Perumytilus* has been shown to be the dominant competitor on protected shores whose lower distribution is limited by predation, rather than competitive dominance by *Corallina* on low intertidal shores found in our study. Species interactions are known to differ based on the environmental context within which they take place (Tilman 1982). Here we present abundant evidence that physical conditions on Patagonian shores are exceedingly stressful and drive the unique nature of species interactions. For instance, wave exposure on protected bays is lower at our study sites in Argentina (1.4 m/s) than ones studied in Chile (3.0 m/s, Guíñez and Castilla 1999) potentially driving a reversal in competitive hierarchies between the two dominant species on different coasts. Whether physical environment alone drives shifts in species ranges and interactions between the Atlantic and Pacific coasts of Patagonia remains to be tested.

#### *Secondary succession on Patagonian rocky shores*

Secondary succession on Patagonian rocky shores is extremely slow, particularly at physically stressful high intertidal elevations and wave-protected shores. In the most favorable conditions on wave-exposed shores, after three years there was very little recovery of the mussels that dominate undisturbed habitats at all tidal heights, even when consumers were excluded (Fig. 6). At high and intermediate tidal heights the barnacle *Balanus* recruited to our experimental disturbances and barnacles facilitated *Perumytilus* recruitment. Nonetheless, after three years none of the disturbance treatments at wave-exposed sites had >15% mussel cover (Fig. 6).

Secondary succession at intermediate and high elevations at wave-protected sites was even slower. At the wave-protected sites no mussel recruitment and only trivial barnacle recruitment has been detected in control or consumer removal treatments in three years (Fig. 6). Low intertidal plots at wave-protected sites were the only experimental disturbances that showed marked secondary succession to their original state in the three years of our experiment. In these plots, originally dominated by 100% *Corallina* cover, *Corallina* recolonized nearly 20% of control plots and >70% of consumer removal plots, demonstrating that *Corallina* recovery can occur within a few years, but is potentially kept in check by limpet grazers (Fig. 6).

Secondary succession leading to the recovery of the mussel beds that dominate undisturbed habitats at all elevations at wave-exposed sites and middle tidal heights at wave-protected sites (Fig. 1) appears to be entirely dependent on ecosystem engineering (sensu Jones et al. 1994) or habitat amelioration provided by mussel beds. With the exception of mussel recruits settling in the interstitial spaces between the invading exotic barnacle, *Balanus glandula*, mussel recruits are found exclusively in established mussel beds. This suggests that natural recovery of disturbances in mussel beds in an uninvaded system only occurs by growth of mussels within the bed leading to bed expansion (see Paine and Levin 1981). Thus, extreme desiccation stress, which forces recruits to live only within a foundation species matrix, leads to natural disturbance patch recovery that is obligately dependent on ecosystem engineering. Variation in recovery rate and foundation species dependency across climatic stress gradients has been seen in *Perumytilus* beds of the Chilean coast. In central Chile, *Perumytilus* beds are very slow to recover from disturbance particularly in the absence of recruitment mediators (Navarrete and Castilla 1990); however in southern Chile, the recovery rate was very fast when herbivores and carnivores were excluded because mussel recruits could persist outside of established beds in this more physically benign location (Moreno et al. 1986).

In New England recovery from disturbance in both wave-exposed and wave-protected habitats was slow in control plots, with little recovery seen in four years, but rapid when consumers were excluded, with complete recovery occurring in less than two years in consumer exclusion cages (Bertness et al. 2002, 2004). This is in stark contrast to our results from the Patagonian rocky shores of Argentina where recovery was slow whether or not consumers were present. This and the relatively high recruitment of mussels and other organisms within mussel and *Corallina* beds suggests that physical stress limits the slow secondary succession in this system.

#### *Mussel bed dynamics on Patagonian rocky shores*

The *Perumytilus* mussel beds on wave-exposed headlands in central Patagonia are superficially similar to intertidal mussel beds that have been studied on other coasts, but differ from previously studied mussel beds in a number of important respects. Like previously studied mussel beds (Paine 1974, 1976, Paine and Levin 1981, Castilla and Paine 1987, Leonard et al. 1998, Navarrete and Castilla 2003) *Perumytilus* beds dominate wave-exposed or high flow rocky shore habitats as the clear competitive dominant of these habitats. Mussel beds develop as a consequence of the strong gregarious settlement of mussels and the group benefits that individual mussels derive from living in dense aggregations including protection from desiccation, wave-stress dislodgement, and predators (Bertness and Grosholz 1985, Denny et al. 1985, Witman 1985, Alvarado and Castilla 1996). The group benefits of mussel aggrega-

tions also permit mussels to live at higher elevations than individual mussels can and lead to mussel beds having abrupt, rather than diffuse high intertidal borders (Bertness and Leonard 1997). Like other mussel beds, *Perumytilus* mussel beds serve as critical foundation species or ecosystem engineers in wave-exposed rocky intertidal habitats by providing protection from desiccation and wave-stress dislodgement to the wide variety of mobile and sessile organisms that live within the mussel bed matrix (Cancino and Santelices 1984, Witman 1985, Suchanek 1986).

*Perumytilus* beds in Patagonia differ markedly from previously studied mussel beds because *Perumytilus* is highly resistant to heat and desiccation stress, is resistant to wave dislodgement, and is extremely slow to recruit to habitats not already dominated by conspecifics. Due to the high stress tolerance of *Perumytilus* to aerial exposure, *Perumytilus* beds cover all available substrate on wave-exposed headlands from the low intertidal zone all the way up to the highest reaches of the intertidal splash zone, typically considered competitive refuges occupied by acorn barnacles on other temperate coasts (Stephenson and Stephenson 1971, Santelices 1991). While our data suggest that the ability of *Perumytilus* to live at extremely high elevations on wave-exposed headlands is at least partially due to habitat amelioration group benefits, *Perumytilus* appears to be nearly as stress tolerant as the invading acorn barnacle and could potentially limit the success *Balanus* has invading Patagonian rocky shores. On the other hand, we have seen the beginnings of a high intertidal barnacle zone above mussel beds on shores subject to intermediate wave exposure, suggesting that with decreased recruitment and increased physical stress, mussels may lose their dominance leaving a high intertidal refuge for *Balanus*. Neither *Perumytilus* nor *Balanus* appear to be able to handle the increased physical stress of wave-protected bays.

*Perumytilus* beds also appear to be much more resistant to wave-generated disturbance than previously studied intertidal mussel beds. In four years we have never seen the kind of wave-disturbance bare patches that are common on the Atlantic and Pacific coasts of North America. There are a number of potential reasons for this. *Perumytilus* are small mussels, rarely reaching body sizes  $>2$  cm long, are extremely slow growing, and have a byssal thread attachment over twice as strong as similarly sized North American mussels (Fig. 6). The small size of *Perumytilus* likely leads to their being exposed to less drag from wave forces than a larger mussel would on the same shoreline (Denny et al. 1985). Slow growth of *Perumytilus* means that beds do not grow and expand as quickly as other mussel beds where higher individual growth rates lead to neighbor crowding and lateral expansion. In addition, high growth rates of other mussels leads to individual detachment from the primary substrate, making mussel beds more vulnerable to wave dislodgment (Paine and Levin 1981). While

wave disturbance to mussel beds on wave-exposed rocky shores in central Patagonia is not generally common, on headlands that have vertical rock walls (which are exposed to direct hits by oceanic swells) disturbances in mussel beds are more common (M. D. Bertness et al., *personal observations*) and could potentially serve as disturbance-generated refuge habitat for *Balanus*.

*Perumytilus* beds on the Patagonian coast of Argentina also appear to have particularly slow rates of secondary succession. Slow secondary succession in this system is likely the product of the slow growth rate of *Perumytilus*, the strong dependence of *Perumytilus* recruits on living in the adult mussel bed, and the extreme desiccation stress on these shores. The slow growth rate of *Perumytilus* results in mussel beds that show very little lateral expansion due to crowding of individuals in the beds. We have examined the recovery of artificial disturbances on both wave-protected and wave-exposed habitats for over three years and to date have seen  $<5\%$  recovery of the *Perumytilus* mussel beds. In *Mytilus californianus* beds on the coast of Washington, USA and *Mytilus edulis* beds on the coast of New England, USA lateral growth of mussel beds due to crowding is obvious and plays a large role in bare patch recovery. The strong desiccation stress of the Patagonian rocky shores of Argentina also dictates that *Perumytilus* recruits are largely restricted to living in refuge habitats, like cracks and crevices and established mussel beds. Thus, physical stress limits the *Perumytilus* recruitment and the rate of secondary succession.

The biogeographic distribution of *Perumytilus purpuratus* extends from mid-latitudes of Argentinean Patagonia, south around the Cape Horn, and north on the Chilean coast as far as Ecuador. Mussel bed dynamics of *Perumytilus* within the Chilean range have been experimentally investigated, demonstrating that *Perumytilus* is a dominant competitor on mid-intertidal levels, but that both its intertidal distribution and body size distribution are importantly affected by predation by mollusks and sea stars (Castilla 1999). Recruitment has been shown to be facilitated by adult populations and by other sessile organisms such as barnacles (Navarrete and Castilla 1990, Alvarado and Castilla 1996). In addition, *Perumytilus* beds practically disappear on the Chilean coast from  $18^{\circ}\text{S}$  to  $30^{\circ}\text{S}$  due to influence of higher water temperatures that affect this region periodically during ENSO years (Broitman et al. 2001). Argentinean range appears to be unique for several reasons likely due to the particular physical environment. As opposed to the dynamics on the Chilean coast, *Perumytilus* beds on the Argentinean coast reach the high intertidal levels on wave-exposed sites, are competitively displaced by *Corallina* at low intertidal levels of wave-protected sites, and lack any kind of influence by predation at their adult stages. Due to the importance of *Perumytilus* on rocky intertidal communities of South America, all these differences

should be addressed in future comparative studies covering the entire geographical range of this species.

*How will invaders impact Patagonian rocky shore communities?*

Possibly due to the remoteness of Patagonia and extreme physical stress, few exotic invaders have significantly impacted the Patagonian shores of Argentina. Recently, however, two prominent invaders have gained a foothold on Patagonian shores: the Northern Pacific acorn barnacle *Balanus glandula* (first reported in Mar del Plata in 1974 and first found in Cabo dos Bahias in 2001 and reported here) and the European green crab *Carcinus maenas* (first found in muddy bays near to our study sites in 2003 [F. Hidalgo, B. R. Silliman, and M. D. Bertness, *unpublished manuscript*]). Because we understand a great deal about the role that these common invertebrates play in their native communities, we may be able to predict the impact that they will have on Patagonian rocky shore communities.

*Balanus glandula* is a dominant space holder in its native community forming a high intertidal barnacle zone on both wave-exposed and wave-protected rocky intertidal habitats (Ricketts and Calvin 1985). Its native range is from Baja Mexico to Alaska. *Balanus* is a common prey organism for drilling snails and starfish in its native range and is competitively inferior to mussels because the mobility of mussels gives them an advantage over sessile barnacles. Acorn barnacles, however, can facilitate mussel dominance by providing rough surfaces that promote recruitment and protecting mussel recruits from physical stress and enemies (Menge 1976).

We suspect that one of the first impacts that *Balanus* will have on Patagonian rocky shores will be to accelerate secondary succession by facilitating mussel recruitment. As already discussed, secondary succession in this system is extremely slow and *Balanus* could significantly speed up secondary succession. We predict that *Balanus* will not form a high intertidal barnacle zone at wave-exposed shores due to the stress tolerance and competitive dominance of *Perumytilus*. Over time selection for thermal tolerance (Schmidt et al. 2000) could allow *Balanus* to form a high zone in wave-protected sites. There is some evidence that at sites exposed to intermediate wave stress *Balanus* may live at higher elevations and form a barnacle zone. This may occur because reduced larval supply, increased stress, and decreased positive feedbacks could lead to *Perumytilus* being unable to live at high heights, leaving high intertidal space suitable for *Balanus* to occupy. Without high recruitment and high adult densities, *Perumytilus* may not be able to live at intertidal levels. The impact of *Balanus* on Patagonian shores depends on species-specific interactions. For example, invasion by the tunicate *Pyura praeputialis* (Paine and Suchanek 1983) on *Perumytilus*-dominated shores of Chile, led to an opposite result from what is predicted with the *Balanus* invasion. Because invasive tunicates into the bay of

Antofagasta could outcompete *Perumytilus*, their introduction drastically changed the species composition and community structure of this intertidal system (Castilla et al. 2004).

The recent introduction of the European green crab, *Carcinus maenas*, could have a much larger impact on Patagonian rocky shores because these communities currently lack predaceous crabs and snails. On wave-exposed headlands *Carcinus* is predicted to have little impact because crab locomotion and foraging are both hampered by waves (Weissburg and Zimmer-Faust 1993). On wave-protected shores, however, *Carcinus* may have a large impact. *Carcinus* can control the abundance and distribution of barnacles on protected shores (Leonard et al. 1999), so could limit the success of *Balanus* invading wave-protected habitats in Patagonia. *Carcinus* is also a voracious predator of mussels (Hughes and Seed 1995), so could limit the abundance of mussel beds on wave-protected Patagonian shores. As a general omnivore and predator of crustaceans, *Carcinus* could have its largest impact by foraging in the *Corallina* matrix and destroying the matrix as a by-product of its foraging. Thus, the largest potential impact of *Carcinus* could be limiting the distribution and abundance of mussel and coralline algae foundation species, with a concomitant loss of all dependent organisms. This could dramatically reduce the species diversity of these shorelines.

*Lessons from Patagonian shores*

Our results have a number of messages of general interest. First, our results warn that similarities in patterns among communities do not necessarily mean that similar mechanisms generate them. Superficially, wave-exposed headland and protected bays of the Patagonian coast of Argentina appear to be structurally similar to high and low flow rocky shores in the Gulf of Maine (Leonard et al. 1998). Whereas most spatial patterns in the Gulf of Maine are driven by consumer pressure, however, on Patagonian rocky shores, similar patterns are driven largely by harsh physical conditions. This warns that even in well-studied systems like rocky intertidal communities, extrapolating causation based on similar appearances to unstudied systems may be entirely misleading.

Our results also support many predictions of general models of community organization. On Patagonian rocky shores consumers play a very small role ostensibly because consumers have not been successful ecologically or evolutionarily in these extremely physically stressful habitats. The desiccation potential of Patagonian shores is higher than in any previously studied intertidal community. Weak consumer effects in communities under strong physical stress are one of the main predictions of the Menge and Sutherland (1976, 1987) models of community organization. The most striking biological interaction shaping the intertidal communities of the Patagonian coast of Argentina is that the

invertebrate diversity in these communities is dependent on the group benefit of living in the foundation species mussel beds and coralline algal turfs where they are buffered from physical stress. This is consistent with recent models of community organization (Bertness and Callaway 1994, Bruno et al. 2003) that predict that group benefits or positive interactions will be the dominant biological interaction shaping communities exposed to severe physical stress. Thus the organization of Patagonian rocky shores supports many of the major predictions of how extreme physical stress will affect community structure and organization.

None of the existing models of community organization, however, predicted the extent to which we found Patagonian rocky shores to be ecologically and evolutionarily shaped by extreme physical stress. Ecologically, extreme desiccation stress has led to a system entirely dependent on habitat-ameliorating foundation species that provide shelter to virtually all organisms in the assemblage, including the native predators (B. R. Silliman, M. D. Bertness, C. Bazterrica, V. Reyna, F. Hildago, and C. M. Crain, *unpublished manuscript*), limit recruitment success, and control the rate of secondary succession and recovery from disturbance. Evolutionarily, extreme desiccation stress has led to an assemblage of diminutive mobile invertebrates that are obligately dependent on living within the foundation species mussel beds and coralline algal turfs for shelter. This leaves an evolutionary void or empty niche on open bare space exposed to extreme desiccation that lacks native organisms and a lack of significant consumers.

Understanding how communities respond ecologically and evolutionarily to increased physical stress, once a question of interest only to community ecologists, is becoming increasingly important to conservation biologists and resource managers due to the threat of global warming and predicted increased physical stress in many ecosystems. Our results suggest that as physical stresses increase in human modified ecosystems, the role played by habitat ameliorating foundation species in communities will increase. This suggests that in systems exposed to high physical stress and dominated by foundation species, conservation biologists need to focus their management and conservation efforts on foundation species rather than the often more charismatic organisms that are dependent on them.

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