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Limpet grazing on a physically stressful Patagonian rocky shore

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Abstract

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

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

1. Introduction

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

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

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

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

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