



# Grazer impacts on algal community structure vary with the coastal upwelling regime

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## ABSTRACT

Community dynamics are often influenced by processes operating at large spatial scales. For example, the structure and dynamics of rocky intertidal communities depend not only on local factors, but also on the nearshore oceanic processes that affect the delivery of nutrients, propagules, and food particles. Conceptual models such as the grazer-reversal hypothesis predict that grazers will decrease the diversity of primary producers in nutrient-poor environments and increase diversity in nutrient-rich environments. To test this hypothesis, natural variation in the productivity of nearshore waters around the south island of New Zealand was used as a backdrop against which the occurrence of limpets, the dominant grazers, was experimentally manipulated. Limpets were either excluded or allowed access to replicate plots at five sites, two of relatively high nutrient availability and three of relatively low nutrient availability. Limpets had a negative effect on algal species richness and biomass at the nutrient-poor sites and little effect at the nutrient-rich sites, thus supporting the predictions of the grazer-reversal hypothesis. Results from this experiment suggest that in contrast to earlier results in the low zone, in the high zone of the rocky intertidal stronger bottom up effects (higher nutrients) did not “flow” up the food chain (to the herbivore level) to produce stronger top down effects. This finding is consistent with the idea that increasing environmental stress can alter the strength and direction of species interactions expected under a top-down/bottom-up scenario.

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## 1. Introduction

Ecologists have only relatively recently expanded their scale of inquiry to address linkages between adjacent ecosystems. These studies indicate that the supply of resources (Bustamante et al. 1995a, Polis and Hurd 1996, Wallace et al. 1997, Nakano and Murikami 2001, Menge et al. 2004, Pace et al. 2004, Menge and Menge 2013, Menge et al. 2015) and propagules (Gaines and Roughgarden 1985, Navarrete et al. 2005, Menge et al. 2003, Witman et al. 2010, Menge and Menge 2013, Menge et al. 2015) from one system can profoundly affect an adjacent system. Clarifying the role of subsidies from adjacent systems is an important step toward understanding large-scale variation in the abundance of, and interactions between, species.

Rocky intertidal communities are inherently linked to the larger oceanic context in which they occur. Although much attention has been focused on the effects of top-down processes such as predation and

grazing on structuring rocky intertidal communities (Paine 1966, 1974, Dayton 1971, Lubchenco 1978, Underwood 1980, Hawkins and Hartnoll 1983, Fairweather 1985, Williams 1993, Williams et al. 2000, Jenkins et al. 2001, 2005, Coleman et al. 2006), growing evidence from around the world demonstrates that large-scale oceanic processes can influence the structure and dynamics of these communities (Australia: Bulleri et al. 2012; Chile: Nielsen and Navarrete 2004, Navarrete et al. 2005, Wieters 2005; Ecuador: Witman et al. 2010, Vinueza et al. 2014; Europe: Jenkins et al. 2000, Coleman et al. 2006; New England: Bryson et al. 2014; New Zealand: Menge et al. 2003, Schiel 2011, Menge and Menge 2013, Schiel et al. 2016; South Africa: Bustamante et al. 1995b, US West coast: Menge et al. 1997, 2004, 2015, Freidenburg et al. 2007, Krenz et al. 2011, Menge and Menge 2013). Clearly, top-down and bottom-up factors both are important in marine, terrestrial, and freshwater communities (Hunter and Price 1992, Menge 1992, Hillebrand 2002, Vinueza et al. 2006, 2014).

Top-down and bottom-up factors can interact in a number of ways. Theoretical and empirical studies suggest that higher levels of nutrients support higher consumer biomass and/or more trophic levels (Fretwell 1977, Neill and Peacock 1980, Oksanen et al. 1981, Bohannan and Lenski 2000). Menge (2000a) summarized the roles of top-down and bottom-up effects in rocky intertidal habitats and concluded that in some cases these two forces can be tightly linked, with high levels of nutrients

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leading to greater per-population effects of consumers. Much of the work in this area has focused on understanding the effects of top-down and bottom-up factors on the abundance, biomass, or survival of benthic primary producers (algae) and/or prey (e.g. barnacles, mussels). However, these factors can also interact to yield different levels of diversity within ecological communities.

In contrast to these conclusions, the “grazer-reversal hypothesis” proposes that consumer control of diversity of primary producers in nutrient-poor environments should be strong, but weaker in nutrient-rich environments (Proulx and Mazumder 1998, Hillebrand 2002, Worm et al. 2002, Burkepile and Hay 2006). The proposed mechanism (Proulx and Mazumder 1998) was that the lack of nutrients in nutrient-poor environments hinders recovery of grazed plants, while recovery can be faster in nutrient-rich environments, enabling more species to coexist with their consumers. Another proposed possibility was that high grazing in nutrient-rich environments favored grazer-resistant plants, thereby allowing coexistence between grazers and high numbers of primary producers.

Previous research has documented large differences in rocky shore communities on the east and west coasts of New Zealand (e.g., Menge et al. 2003, Schiel 2011, Menge and Menge 2013). These differences have been attributed in part to differences in nearshore oceans—including upwelling and downwelling regions (Menge et al. 1999, Menge et al. 2003, Menge and Menge 2013) and climatic patterns (Schiel 2011, Schiel et al. 2016). Upwelling is the delivery of cold, nutrient-rich water from depth to the sea surface. Satellite imagery, intertidal air and water temperatures, monthly and daily upwelling indices, and water-sampling data (chlorophyll-*a*, particulates, and nutrients) all indicate that sites on the west coast of the South Island of New Zealand (hereafter SINZ) are characterized by intermittent upwelling, while sites on the east coast predominantly experience downwelling (Vincent et al. 1991, Menge et al. 2003, Menge and Menge 2013).

Menge et al. (2003) documented dramatic differences in the rates of key ecological processes between sites around the SINZ characterized either by intermittent upwelling or persistent downwelling. They hypothesized that downwelling leads to lower inputs of subsidies (nutrients, particulate food, propagules), resulting in lower abundances of both predators and prey, ultimately leading to decreased impacts of predators on prey (here and subsequently, references to the strength of top-down, predation, or grazing effects mean per-population). As predicted, rates of key ecological processes such as recruitment and predation were higher at the intermittent upwelling-dominated west-coast sites than at the downwelling-dominated east-coast sites (Menge et al. 2003, Menge and Menge 2013).

Results linking nearshore oceanic conditions to the impacts of grazers on algae have been less clear. Guerry et al. (2009) tested the influence of nutrients and grazing on algal diversity and biomass of macroalgae at an east coast site in SINZ, finding that enrichment increased the biomass of foliose algae when grazers were excluded. By excluding limpets in the low intertidal zone on the SINZ, Menge et al. (1999) demonstrated that, unlike differences seen with predation, after 4 months limpet effects were similar and strong at intermittently-upwelled (higher nutrients) and downwelling-dominated (lower nutrients) sites. Because grazer-accessible space (bare rock, algal crust covered rock) was greater at their west coast sites, they concluded that grazing had an overall greater impact on community structure at the intermittently upwelled west coast sites. Notably, these experiments were carried out at closely adjacent locations at single sites on the east and west coasts and were thus limited in their ability to reflect oceanic differences between the coasts. One goal of the present study was to examine grazer impacts at larger spatial scales in the context of differing nutrient regimes.

The primary objective of this study was to test the grazer-reversal hypothesis by experimentally manipulating molluscan grazers against a backdrop of natural variation in bottom-up effects and invertebrate recruitment in nearshore waters of the SINZ. In this study, grazing

impacts in the high intertidal (not investigated in Menge et al. 1999), were investigated at much larger spatial scales and for a longer time scale (20 months). The “comparative-experimental approach” (e.g. Dayton 1971, Menge et al. 1994, McPeck 1998, Coleman et al. 2006, Rilov and Schiel 2011) was used to examine the effects of limpets in the high intertidal zone. That is, identically designed experiments were conducted at multiple sites ranging across distances of 100 s of km on each of the east and west coasts of the SINZ. Two sites were used on the intermittently upwelled, more productive west coast and three sites were used on the downwelling-dominated, less productive east coast. Natural variation in bottom-up inputs (e.g., nutrients) provided a backdrop against which to conduct identical experiments in which limpets were either excluded or allowed access to plots. Besides the larger spatial and longer temporal scales, this investigation built upon the previous research of Menge et al. (1999, 2003) by examining how the composition of high intertidal algal communities changes in relation to grazing. More broadly, it examined the role of the top-down force of grazing at sites with differing levels of nutrient inputs and tested the predictions of the grazer-reversal hypothesis. This hypothesis would be supported if limpets had positive or no effects on algal diversity at the more nutrient-rich west-coast sites, but negative effects at the less nutrient-rich east-coast sites.

## 2. Methods

### 2.1. Study sites

To facilitate interpretation and provide depth to the environmental context, this study was conducted on near-vertical walls in the barnacle-dominated high zone at sites used in our long-term research program in New Zealand. Three east coast sites include Raramai (RR) and Bird Rock (BR; 200 m apart, 43.5° S, 175.5° E) just south of the Kaikoura peninsula, and Box Thumb (BT; 45.5° S, 173.5° E) on the north side of the Banks peninsula (approximately 150 km south of RR and BR). Although BR and RR are near each other, we decided to add experiments at BR after noting that a gull colony nested on the outcrop above our study site to see if nutrients derived from gull feces might influence grazer-algal dynamics. A more southerly east coast site, Shag Point, was not used because prior experience showed that the substratum there was too erosive to accommodate long-term (many months) application of herbivore exclusion techniques (see below). Two west coast sites, Woodpecker Bay (WB; 41.5° S, 171.5° E), and Jackson Head (JH; 44.5° S, 167.5° E) are approximately 350 km apart. Another long-term west coast site, Twelve-Mile Beach, was not used because the high zone there is unconsolidated gravel/pebbles. All sites but BR have been the focus of previous research elucidating the link between nearshore oceanic conditions and community dynamics (Menge et al. 1999, Menge et al. 2003). All sites were moderately wave-exposed rocky reefs. The aspect of the vertical surfaces used for the experiment at each site varied. The wall at BR faces north, RR faces south, BT faces east, WB faces northwest, and JH faces southeast.

### 2.2. Nutrient levels

Background nutrient concentrations were monitored to ensure that previously documented differences in bottom-up inputs (Menge et al. 1999) persisted during the course of this experiment. Sampling was focused on the algal growth season (October through January) based on the assumption that most relevant nutrient variation would occur during spring and early summer, when upwelling (at least on the west coast) provides nutrient pulses to the photic zone. Methodology followed that used by Guerry et al. (2009). Water samples were taken (3 replicates/site/sample day) from a depth of approximately 1 m at the water's edge at low tide using a 250-ml acid-washed brown high-density polyethylene bottle attached to the end of a sampling pole. Nutrient samples (50 ml) were filtered through 25-mm combusted Whatman

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