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Cross-scale variation in top-down and bottom-up control of algal abundance

Tess L. Freidenburg [a], Bruce A. Menge [a,*], Patti M. Halpin [b], Michael Webster [c], Ariana Sutton-Grier [d]

[a] *Department of Zoology, Oregon State University, Corvallis, OR 97331-2914, United States*
[b] *Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, United States*
[c] *Gordon and Betty Moore Foundation, San Francisco, CA 94129, United States*
[d] *University Program in Ecology, Nicholas School of the Environment, Box 90328, Duke University, Durham, NC 27708, United States*

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Abstract

Previous studies of top-down and bottom-up effects in Oregon rocky intertidal communities suggested that, unlike sea star–mussel dominated food chains, grazer-alga food chains deviated from simple food web predictions. However, this conclusion lacked generality due to limited replication at the site level. We explored how grazing and algal colonization and growth in different zones and multiple sites in intertidal communities varied in relation to processes varying on local to mesoscales, including oceanographic variation. Our approach employed the comparative-experimental method, in which identically-designed and replicated experiments are performed at multiple sites spanning the environmental gradient of interest. In a limpet–algae–barnacle interaction web, we tested the hypothesis that top-down and bottom-up effects were inversely related along the Oregon coast. To distinguish between the alternatives of large-scale oceanographic forcing vs. local control, our experiments spanned scales of meters (between mid and low zones), kilometers (seven sites), 10’s to 100’s of km (three regions), and ~ 260 km (central and southern coasts). Identically designed and executed experiments on effects and rates of grazing were conducted in a southern coast region of persistent upwelling and two central coast regions, one with intermittent upwelling in an area of weak offshore currents, and another with intermittent upwelling in an area of strong offshore currents. Grazer effects and grazing rates varied on all scales, indicating a complex interplay of processes operating at zone, site, regional, and coastal scales. Grazing was generally highest in all mid zones and in the low zone at the middle region (Cape Perpetua) on the central coast. Growth of early successional colonists tended to be higher at the northern and southern regions (Capes Foulweather and Blanco). Grazers had no effect on barnacle cover, but their foraging was inhibited by high densities of barnacles. Differences in grazing appear to be a complex consequence of direct and indirect effects of variable oceanographic conditions, limpet recruitment, and barnacle abundance. In contrast to positive associations between predation strength and the magnitude of prey subsidies, higher grazing strength was generally associated with lower magnitude of bottom-up effects and vice versa. Hence in this system predator–prey (sea star–filter feeder) and herbivore–plant (limpet–microalgae) interactions evidently respond differently to ecological subsidies.

Keywords: Algae; Bottom-up; Community structure; Early succession; Ecological subsidies; Grazing; Oregon; Rocky intertidal; Species interactions; Top-down; Upwelling

* Corresponding author.
E-mail address: mengeb@oregonstate.edu (B.A. Menge).

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1. Introduction

Since Hairston et al. (1960) proposed a top-down model of community regulation, ecologists have debated whether predation or primary productivity is most important in determining community structure and dynamics (Oksanen et al., 1981; Fretwell, 1987; Polis, 1999; Polis et al., 2000; Schmitz et al., 2000; White, 2001). However, in recent years ecologists have increasingly adopted an integrated perspective that recognizes the dynamic linkage between top-down and bottom-up processes (Hunter and Price, 1992; Menge, 1992, 2003, 2004; Menge et al., 1997a; Fraser, 1998; Leonard et al., 1998; Nielsen, 2001, 2003; Menge et al., 2003; Thompson et al., 2004). Determining the relative importance of, and linkages between, top-down and bottom-up processes is crucial to understanding variation in community structure.

Studies in marine intertidal systems have been fruitful in exploring the relative contributions of top-down and bottom-up processes. In South Africa, increases in nutrient supply from bird guano modified community structure through enhancement of algal production, leading to increased growth of limpets and greater abundance of algal-dwelling invertebrates (Bosman et al., 1986; Bosman and Hockey, 1986). Invertebrates associated with the algal turf in areas with inputs of guano provided food for small shorebirds. In unenriched areas, algal mats and their associated communities of invertebrates and shorebird predators were absent. In New England, differences in flow velocity influenced the delivery of subsidies such as nutrients, food and larvae to intertidal habitats (Leonard et al., 1998, 1999). In high flow environments, subsidy effects were stronger due to both higher delivery rates of planktonic larvae and food and to inhibition of foraging by predatory crabs. In low flow environments, consumer effects were stronger as foraging rates of crabs increased with reduced hydrodynamic forces.

1.1. Background

Research on the Oregon coast indicates that top-down effects (i.e. predation and grazing) and ocean-derived subsidies (i.e., phytoplankton concentrations and prey recruitment) affect intertidal community structure (Menge, 1992; Menge et al., 1994; Menge et al., 1997a; Menge, 2000). However, the magnitude of these effects differed substantially between two sites. Boiler Bay (hereafter BB) and Strawberry Hill (hereafter SH), 80 km apart on the Oregon coast, have contrasting patterns of community structure in the low intertidal zone. BB has a high cover of algae and low cover of sessile invertebrates while SH has the opposite (Menge, 1992; Menge et al., 1994). Observational and experimental studies have demonstrated that at SH, where phytoplankton productivity and recruitment rates were consistently higher, predation and grazing rates were also higher (Menge et al., 1997a; Menge, 2000). The greater top-down forces and subsidies at SH are thought to depend on differences in nearshore (0–10 km from shore) oceanographic patterns (Menge et al., 1997a,b).

Previous studies in Oregon have led to a seeming paradox (Menge, 2000). While both predation and grazing were strongest at SH, their association with their respective subsidies contrasted. As expected from simple food chain theory (Oksanen et al., 1981), mussels and barnacles, the primary prey of sea stars and whelks, were generally more abundant at SH, where predation was strong. The dynamics of the limpet–algal food chain, however, seemed more consistent with a simple top-down perspective. Benthic algae, the primary food resources of limpets, were generally less, not more, abundant at SH. Classically, inverse relationships between resource and consumer abundance have suggested that consumers were responsible for the low resource abundance (e.g., Hairston et al., 1960). The observation that field measurements of macroalgal (*Saccharina* [formerly *Hedophyllum*] *sessile*) growth did not differ between BB and SH (B. A. Menge, unpublished data) seemed consistent with this hypothesis. Thus, the interaction web topped by limpets evidently exhibited qualitatively different dynamics, suggesting that nutrient–macrophyte based interaction webs and nutrient–phytoplankton based interaction webs respond differently to oceanographic conditions. These studies were limited to a comparison between two sites, however, so whether these results were general, i.e., representative of larger, coast-wide patterns, was unclear.

1.2. Oceanographic scenario

As has recently been demonstrated for the sea star–filter feeder interaction web (Menge et al., 2004), regional differences in consumer effects and resource subsidies may stem from variability in the intensity of seasonal upwelling. A summary of key coastal oceanographic features characterizing the Oregon coast can be found in Menge et al. (2004). Briefly, on the US West Coast seasonal upwelling occurs during spring and summer when equatorward winds, combined with the Coriolis effect, drive surface water offshore. Displaced surface water is replaced by cold, nutrient-rich water from depth (Parrish et al., 1981; Brink, 1983; Huyer,