



Top-down and bottom-up community regulation in marine rocky intertidal habitats

Bruce A. Menge

Department of Zoology, Oregon State University, Corvallis, OR 97331-2914, USA

Abstract

Strong top-down control by consumers has been demonstrated in rocky intertidal communities around the world. In contrast, the role of bottom-up effects (nutrients and productivity), known to have important influences in terrestrial and particularly freshwater ecosystems, is poorly known in marine hard-bottom communities. Recent studies in South Africa, New England, Oregon and New Zealand suggest that bottom-up processes can have important effects on rocky intertidal community structure. A significant aspect of all of these studies was the incorporation of processes varying on larger spatial scales than previously considered (10's to 1000's of km). In all four regions, variation in oceanographic factors (currents, upwelling, nutrients, rates of particle flux) was associated with different magnitudes of algal and/or phytoplankton abundance, availability of particulate food, and rates of recruitment. These processes led to differences in prey abundance and growth, secondary production, consumer growth, and consumer impact on prey resources. Oceanographic conditions therefore may vary on scales that generate ecologically significant variability in populations at the bottom of the food chain, and through upward-flowing food chain effects, lead to variation in top-down trophic effects. I conclude that top-down and bottom-up processes can be important joint determinants of community structure in rocky intertidal habitats, and predict that such effects will occur generally wherever oceanographic 'discontinuities' lie adjacent to rocky coastlines. I further argue that increased attention by researchers and of funding agencies to such benthic–pelagic coupling would dramatically enhance our understanding of the dynamics of marine ecosystems. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Top-down; Bottom-up; Rocky intertidal; Oceanography; Community dynamics

1. Introduction

As in most sciences, ecologists are concerned with attempting to discern order from the seeming chaos present in natural ecosystems. Milestones in the search for order

E-mail address: mengeb@bcc.orst.edu (B.A. Menge).

include: Darwin's (1859) perception of ecological and evolutionary order in a chaotically diverse world; the birth of plant community ecology in the first decades of the 20th century with the development of the theory of succession (e.g. McIntosh, 1985); the concept of food webs and the potential impacts of species interactions (e.g. Elton, 1927); the perception that populations must in some sense be regulated, with the development of an underlying theoretical framework for this phenomenon (e.g. Kingsland, 1985); and the trophic-dynamic concept with its intellectual offspring, ecosystem ecology (Cook, 1977). Despite these achievements, much early ecological research concentrated on natural history and description at the expense of searching for order and generality in nature. Community ecology in particular seemed excessively focused on idiosyncratic aspects of natural systems and the uniqueness of each system, rather than perceiving the general principles that structured natural communities.

This 'order vs. chaos' conundrum in community ecology was addressed by Hairston et al. (1960; hereafter HSS), who proposed a simple conceptual model for the dynamics of terrestrial communities. HSS suggested that communities consisted of four groups of organisms (carnivores, herbivores, plants, and detritivores), and that their trophic interactions explained why green plants dominate the earth and why organic biomass does not accumulate. Briefly, HSS argued that plants dominate natural communities because carnivores control herbivore abundance, thereby freeing vegetation from herbivore control. HSS also suggested that detritivores were resource-limited, thus preventing accumulation of organic matter on a global basis. This simple framework therefore suggested that carnivores and detritivores were regulated by competition, that herbivores were controlled by direct predation, and that carnivores indirectly regulated plant abundance. The overall perspective was that communities are regulated by processes whose effect flowed down the food chain; this was later termed 'top-down' control (Hunter and Price, 1992). Other inferences of HSS included: (1) exceptions might exist (e.g. impacts of species interactions might differ among species within groups) but these were balanced or overridden by the overall regulatory process inferred for each trophic group; (2) all communities consisted of three trophic levels (plus detritivores); (3) omnivory was unimportant (consumption of plants by carnivores was functionally insignificant); and (4) external, abiotic forces did not exert controlling influences on the biota.

Predictably, these simple arguments proved highly controversial and sparked debates that have continued to the present (e.g. Hairston and Hairston, 1993, 1997; Pimm, 1991; Polis and Strong, 1996). It seems undeniable, however, that HSS shifted the focus of community ecology sharply away from an emphasis on 'chaos' toward the discernment of 'order.' At the same time, critics argued that the HSS model was too simple, and identified several legitimate areas of concern (Ehrlich and Birch, 1967; Murdoch, 1966). The most fundamental of these were that species differences mattered, so the concept of homogeneous trophic levels was flawed, and that plant dominance could alternatively be explained to be a result of effective plant defenses. These criticisms helped spark an upswing in field experimental studies that, among other things, investigated the influence of consumers on prey populations and communities. Major steps were made in all habitat types (e.g. Sih et al., 1985), but research in marine benthic communities on effects of herbivores and predators generally led the way.

Table 1

Examples of top-down control by predators in marine rocky intertidal habitats

Location	Latitude, longitude	Predator	Prey	No. sites	Community effect	Ref.
1. Northeast Pacific, Makah Bay & Tatoosh I., Washington (WA), USA	48°19'N, 124°40'W & 48°24'N, 124°44'W	<i>Pisaster ochraceus</i>	Mussels, barnacles	2	Determines lower limit of mussels, maintains diversity and species composition of low zone	(Paine, 1966, 1974)
2. Northeast Atlantic, Scotland, UK	55°50'N, 5°W	<i>Nucella lapillus</i>	Barnacles	1	Determines lower limit of <i>Semibalanus balanoides</i> , controls barnacle abundance on mid shore	(Connell, 1961)
3. Northeast Pacific, San Juan Islands, WA, USA	48°32'N, 123°05'W	<i>Nucella lamellosa</i> , <i>N. ostrina</i> , <i>N. canaliculata</i>	Barnacles	1	Controls abundance, size/age structure of <i>Balanus glandula</i> on midshore	(Connell, 1970)
4. Northeast Pacific, open coast and San Juan I., WA, USA	48°19'N, 124°40'W to 48°33'N, 123°0'W	<i>Pisaster ochraceus</i> , <i>Nucella</i> spp.	Mussels, barnacles	6	Control abundance of barnacles, mussels in upper low zone	(Dayton, 1971)
5. Southwest Pacific, North Island (west coast), New Zealand	37°20'S, 174°10'E	<i>Stichaster australis</i>	Mussels, barnacles	1	Determines lower limit of mussels, maintains diversity and species composition of low zone	(Paine, 1971)
6. Southwest Pacific, North Island (east coast), NZ	37°20'S, 174°40'E	<i>Lepsiella scobina</i>	Barnacles	1	Controls abundance of <i>Chamaesipho columna</i> , <i>Elminius plicatus</i> on mid shore	(Luckens, 1970, 1975)
7. Northwest Atlantic, New England, USA	44°10'N, 68°1'W to 42°25'N, 80°55'W	<i>Nucella lapillus</i>	Mussels, barnacles	6	In moderately sheltered environments, control prey abundance and distribution in mid zone, determine species composition	(Menge, 1976)
8. Northwest Atlantic, New England, USA	44°10'N, 68°1'W to 42°25'N, 80°55'W	<i>N. lapillus</i> , <i>Asterias</i> spp., <i>Carcinus maenas</i> , <i>Cancer</i> spp.	Mussels, barnacles	5	In moderately sheltered environments, control prey abundance and distribution in low zone, determine species composition	(Lubchenco and Menge, 1978)
9. Northeast Atlantic, Ireland	51°30'N, 9°25'W	<i>Carcinus maenas</i> , <i>Portunus puber</i> (crabs)	Mussels, whelks	2	Determine shell thickness, abundance of whelks in sheltered areas, abundance of mussels in sheltered areas	(Ebling et al., 1964; Kitching et al., 1959)
10. Northwest Atlantic, New Jersey, USA	39°50'N, 74°20'W	<i>Callinectes sapidus</i> (crab)	Mussels, barnacles	2	Control of mussel abundance in sheltered areas	(Peterson, 1979)

11. East Pacific, Panama	8°45'N, 79°30'W	<i>Purpura pansa</i> (whelk)	<i>Nerita</i> <i>scabricostata</i> (gastropod)	1	Directly and indirectly determines distribution and behavior of prey, indirectly affects abundance of algal crusts and barnacles	(Garity and Levings, 1981)
12. East Pacific, Panama	8°45'N, 79°30'W	Whelks, crabs, fishes, limpets	Barnacles, oysters, mussels, limpets, snails Barnacles	1	Control abundance, size, and microhabitat of prey	(Lubchenco et al., 1984; Menge and Lubchenco, 1981; Menge et al., 1986a, 1986b)
13. Gulf of California, Sonora, Mexico	31°20'N, 113°40'W	<i>Acanthina</i> <i>angelica</i> (whelk)	Barnacles	1	Controls abundance of <i>Chthamalus anisopoma</i> , indirectly determines community composition	(Dungan, 1986, 1987)
14. Gulf of California, Sonora, Mexico	31°20'N, 113°40'W	<i>Morula</i> <i>ferruginosa</i> (whelk)	Mussels, barnacles	2	Reduces abundance of mussels, enhances abundance of barnacles	(Lively and Raimondi, 1987)
15. Southeast Pacific, Chile, central coast	33°30'S, 71°38'W	<i>Concholepas</i> <i>concholepas</i> (whelk)	Mussels, barnacles	2	Controls abundance of prey, indirectly determines community composition in mid and upper low zone	(Castilla and Duran, 1985; Duran and Castilla, 1989)
16. Southeast Pacific, Chile, central coast	33°30'S, 71°38'W	<i>Helicaster</i> <i>helianthus</i> (sea star)	Mussels, barnacles	1	Reduces abundance of mussels	(Paine et al., 1985)
17. Southwest Pacific, New South Wales, Australia	34°0'S, 151°15'E	<i>Morula</i> <i>marginalba</i> , <i>Thais orbita</i> (whelks)	Barnacles, limpets	1	<i>Perumytilus purpuratus</i> , indirectly enhances abundance of barnacles	(Fairweather, 1985; Fairweather et al., 1984; Underwood et al., 1983)
18. Northeast Pacific, Santa Barbara, CA, USA	32°52' to 35°09'N, 118° to 121° W	<i>Ocenebra</i> <i>binaculoides</i> , <i>O. binaculatus</i> (octopuses)	<i>Tegula</i> <i>funeralis</i> (snails)	6	Control abundance, distribution of <i>Tegula</i>	(Fawcett, 1984)
19. Northeast Pacific, Catalina I., CA, USA	33°25'N, 118°30'W	<i>Pandirus</i> <i>interraptus</i> (lobster), <i>Haliçhoeres</i> <i>semisinctus</i> , <i>Oxydolis</i> <i>californica</i> (fishes), <i>Cerastoma</i> <i>nuttalli</i> , <i>Maxwellia</i> <i>gemma</i> (whelks)	Mussels, limpets, chiton, crabs	2	In wave-exposed areas lobsters controlled mussel abundance, indirectly enhancing algal turfs. In wave-protected areas, lobsters, fish, and whelks jointly controlled mussel abundance, indirectly enhancing algal turfs.	(Robles and Robb, 1993)
20. Northeast Pacific, Vancouver I., BC, Canada	48°53'N, 125°20'W	<i>Pisaster</i> <i>ochraceus</i> (sea star)	Mussels, barnacles	1	Controlled abundance of mussels	(Robles et al., 1995)

2. Conceptual development

2.1. Stress-modified top-down community regulation

By the 1980s, researchers had documented strong top-down effects in rocky intertidal habitats around the world (e.g. Table 1). Many studies demonstrated that predators were capable of controlling prey communities on temperate and tropical rocky coasts and in many other marine habitats. Similar conclusions have been made for herbivores (Branch and Griffiths, 1988; Lubchenco and Gaines, 1981). However, early studies were typically single-site investigations that focused on determining whether patterns were determined by physical or biological processes. Answering such local-scale questions was an important step towards the development of a larger-scale perspective but offered limited insight into whether or not, and how, structuring processes might vary along major environmental gradients. In marine environments, early research had established that biota varied in consistent ways along key physical gradients that included wave force, moisture or humidity, light, desiccation, and salinity (e.g. Lewis, 1964; Stephenson and Stephenson, 1972).

A landmark study towards determining if food-chain dynamics varied systematically along gradients in wave exposure and thermal/desiccation stress was that of Dayton (1971, 1975). The rocky shores of Washington State exhibit classic patterns of zonation, distribution and abundance, with a high intertidal furoid/barnacle zone, a mid intertidal mussel zone, and a low intertidal algal zone. In more sheltered areas of the San Juan Islands, mussels are replaced as mid zone dominants by the large barnacle *Semibalanus cariosus* (Pallas, 1788). Abundant and/or common consumers in this community were sea stars (especially *Pisaster ochraceus* (Brandt, 1835)), whelks (primarily *Nucella* spp.) and limpets (*Lottia* spp., *Tectura scutum* (Rathke, 1833)). Establishing what has more recently been termed the ‘comparative-experimental’ method (McPeck, 1998; Menge, 1991a), Dayton (1971) performed identically-designed experiments to exclude predators and herbivores in the mid intertidal zone. Experiments were established at six sites varying in wave-exposure regime along the rocky shores of Washington State. Although details varied somewhat among sites, sessile invertebrate prey abundance was controlled at all sites by a combination of predation (by whelks and sea stars) and biological disturbance (limpet bulldozing of barnacle recruits). In this system, top-down effects appeared strong at all wave exposures.

Contrasting results emerged from a comparable study in New England (Menge, 1976; Menge and Sutherland, 1976). There a community composed of ecologically similar (though far fewer) species displayed patterns of zonation, distribution and abundance similar to those studied by Dayton (1971). Experiments conducted at six sites revealed that predation varied with wave exposure and zone (Menge, 1976). Predation was always weak in the high zone. At mid-zone sites with a high frequency of strong wave forces, whelk predation effects on sessile prey were also weak. At mid-zone sites with moderate wave forces, however, predation by whelks was strong. Additional field experimentation (Menge, 1978a,b) suggested that the mechanisms underlying variable predation among sites included inhibition of whelk foraging activity both by hydrodynamic forces and thermal/desiccation stress. A parallel series of studies suggested

similar trends of variation in effects of grazers on algal community structure, with similar underlying mechanisms (Lubchenco, 1983, 1986).

Thus, in New England, top-down forces varied along key environmental gradients of wave turbulence and thermal/desiccation stress. In general, top-down forces were strong in benign portions of the rocky intertidal environment. These were generally areas lower on the shore with moderate to weak wave forces and shorter periods of exposure to air. Under harsher conditions, such as wave-exposed headlands and/or high intertidal regions, top-down forces were weak or absent.

Such results led to the development of conceptual frameworks for the control of community structure that built on, but also modified, the HSS model. In a review Connell, (1975) noted that evidence available at the time suggested that the impact of top-down forces varied with physical environmental conditions. He proposed a model predicting that prey abundance and size structure in communities would vary along a gradient of physical harshness, due both to direct physical effects on survival and to indirect effects of physical factors on consumer–prey interaction strength. Independently, John Sutherland and I (Menge and Sutherland, 1976) also suggested that the relative importance of key species interactions varied predictably with environmental stress. Like Connell (1975), we predicted that predation should be strong in relatively benign environments and weak in harsh environments. We also suggested that the effects of predation varied inversely with competitive effects and trophic position. Species of high trophic status should be regulated primarily by competition while species of low trophic status should be regulated primarily by predation.

This model was later expanded (Menge and Sutherland, 1987) to incorporate direct effects of physical disturbance and variable recruitment density on community structure. The fundamental feature of these ‘stress-modified top-down’ or ‘environmental stress’ models remained, however, except when weakened by physical forces, top-down forces were a dominant ecological determinant of community structure. Hence, these models proposed that the HSS perspective was indeed too general. The environmental stress models argued that rather than having a fixed food chain length of three, communities can vary in food chain length. Further, this variation occurs as a consequence of gradients in environmental stress; and that as a result, biotic and physical forces vary in their relative determination of community dynamics.

2.2. Bottom-up community regulation

2.2.1. Theory

The alternative view of community regulation, or ‘bottom-up’ control, was the implicit partner of succession theory as developed by plant ecologists. This perspective held that since plant primary production fueled the animal biota, plants (along with nutrients and light) regulated communities from the bottom of the food chain upward to higher trophic levels (e.g. White, 1978). As implied in the previous section, this perspective was not widely embraced by all ecologists, perhaps because, in part, plant and animal ecologists interpreted the term ‘control’ differently, but also because examples could be cited that supported either perspective.

Fretwell (1977, 1987), however, put a new twist on the idea of bottom-up community

regulation. He combined the HSS food-chain perspective with the idea that food chains varied in length as a consequence of variable environmental gradients of nutrients and productivity. Fretwell proposed that, on landscape scales, gradients of primary production were the primary factor underlying communities of varying food chain length. In unproductive environments, food chains were just one link in length, consisting only of plants. Consumers might be present, but were not sufficiently abundant to have negative influences on plants. In environments of greater productivity, production eventually would reach levels capable of supporting an abundant herbivore level (adding a second-link to the food chain), with increasingly strong negative feedback on characteristics of plant assemblages. Following the same reasoning, increased productivity would first increase herbivore abundance, leading to increased herbivore pressure, and would eventually add a predator level (third-link), and then a secondary predator level (fourth-link). Ecological energetics dictated that, although five- or six-link food chains might be possible, the generally low efficiency of transfer of energy to higher trophic levels meant that most communities would fall in the range of one- to four-link food chains. In moving along a gradient of increasing productivity, the ‘food-chain dynamics’ hypothesis thus predicted that plants would be regulated by competition (one-link food chain), grazers (two links), competition (three links), and grazers (four links).

At least for three-link food chains, Fretwell (1977, 1987) thus envisioned an HSS-like scenario, with predation-controlled community structure, and alternation between control by competition–predation–competition at predator, herbivore, and plant trophic levels. His emphasis, however, was on the gradient in productivity as the prime determinant of food-chain dynamics. This perspective was later formalized in a mathematical model (Oksanen et al., 1981).

2.2.2. Evidence from non-marine ecosystems

Empirical evidence bearing on these different viewpoints was slow to accumulate and, as noted earlier, controversy regarding modes of control of communities persists to the present. It wasn’t until the 1980’s that observational evidence more or less consistent with HSS or Fretwell/Oksanen perspectives was offered from terrestrial (e.g. Oksanen, 1983, 1988) and freshwater environments (e.g. Carpenter et al., 1985). Experimental evidence for HSS-like dynamics has, however, only appeared relatively recently. By altering productivity levels in a food web in a northern California river, Wootton and Power (1993) observed results consistent with the Oksanen et al.’s (1981) prediction of alternating control by trophic level, and between food chains of length three and four links. Similarly, experiments in white oak forest demonstrated that birds indirectly enhanced plant growth by reducing insect herbivore abundance (Marquis and Whelan, 1994). In northern England, pesticide and turf transplant experiments at sites along a productivity gradient were consistent with the predictions of the Fretwell–Oksanen model (Fraser, 1998; Fraser and Grime, 1997). At low productivity sites, invertebrate herbivores had little effect on vegetation, and experimental assays of the effects of predators suggested that predation was weak. At successively more productive sites, the impact of grazers first increased (intermediate productivity) then decreased (high productivity) while the impact of predators steadily increased. Therefore, abundance of vegetation was most strongly affected by bottom-up factors at sites of low productivity

and by top-down factors at sites of high productivity. Finally, in Kentucky, adding detritus to a forest litter community increased the abundance of all trophic groups, including fungivores, omnivores, and predators (Chen and Wise, 1999). Hence, increasing the bottom-up resource base of the food web led to increases at all trophic levels.

2.2.3. *Marine evidence*

Long-term studies in a kelp bed in southern California have shown convincingly that community structure depends on the interdependence of small-scale, short-term ecological processes (including top-down effects such as grazing), and larger-scale, long-term processes that create variation in bottom-up effects (such as El Niño-related nutrient depletion; Dayton et al., 1984, 1992, 1999; Dayton and Tegner, 1984; Tegner and Dayton, 1987; Tegner et al., 1997). Beyond this important ongoing work, evidence for bottom-up influences on community dynamics in marine environments was limited until relatively recently. In part, this was due to the success of experimental research in shallow marine nearshore environments in repeatedly demonstrating strong top-down and competitive effects on local community structure (see above; Table 1). In addition, in rocky intertidal habitats at least, oceanographic variation was generally thought to occur at scales far greater than the variation documented by ecologists (e.g. Paine, 1986; Branch et al., 1987; Menge, 1992), so there was little impetus to study possible influences of bottom-up effects on benthic community structure.

By the late 1980's, this perspective had begun to shift. In South Africa, rocky intertidal communities on offshore islands were observed to have high algal abundances of algae, low abundances of grazing limpets, and dense colonies of seabirds. On mainland shores, birds and algae were scarce, and limpets were abundant. Researchers hypothesized that high algal abundance on islands resulted from two effects of birds: predation on the limpets and nutrient inputs from guano. Results of field experiments suggested joint strong influences of increased nutrients and bird predation on algal production and abundance on offshore islands harboring seabird nesting colonies (Bosman et al., 1986; Bosman and Hockey, 1986; Branch et al., 1987). That is, at least on a local scale, top-down and bottom-up effects evidently combined to regulate the structure of algal assemblages (Table 2).

In the Aleutian Islands of Alaska, extensive research had established that a food chain consisting of sea otters–sea urchins–kelps was a classic example of top-down control (Estes and Duggins, 1995; Estes and Palmisano, 1974; Estes et al., 1978). High abundance of kelp occurred on islands where sea otters evidently controlled sea urchin grazers, while low kelp abundance and high sea urchin biomass occurred on islands without sea otters. New insight into this scenario was gained by transplanting sessile filter-feeders (mussels and barnacles) to intertidal and subtidal habitats on kelp- or urchin-dominated islands, respectively (Duggins et al., 1989). Growth rates of both filter-feeders were faster on islands dominated by kelp and slower on islands dominated by sea urchins. Stable isotope analyses suggested that these differences resulted from large differences in the availability of kelp-derived detritus. Thus, benthic communities on islands dominated by sea otters and kelp appeared to be strongly influenced by both top-down and bottom-up influences.

Table 2

Top-down and bottom-up control in rocky intertidal communities, in all cases, evidence was obtained using a combination of quantitative observation, comparison among sites, and experimentation

Region; community (scale range in km)	Environmental gradient	Trophic composition	Bottom-up effects	Top-down effects	Citations
South Africa (islands with seabird colonies vs. mainland with no seabird colonies) (10's)	Islands vs. mainland: nutrients are high on islands (from bird guano); low on mainland	Oystercatchers; wading birds; limpets; Polychaetes; Amphipods; macroalgae	<i>Greater on islands:</i> Benthic algal productivity; supports increased growth, size, and reproductive output of limpets; increased abundance of algal-dwelling invertebrates; increased abundance of wading birds	<i>Greater on islands:</i> Predation by oystercatchers on limpets; results in low density of limpets	(Bosman et al., 1986; Bosman and Hockey, 1986; Branch et al., 1987)
South Africa (wave-exposed vs. wave-protected areas; multiple sites in upwelling gradients along mainland coast) (1's to 1000's)	Upwelling/productivity gradient: high in west to low in east. Affecting nutrients; productivity of phytoplankton and benthic macroalgae; algal detritus	Limpets; filter-feeding invertebrates; macroalgae	<i>Greater on exposed shores than in bays:</i> Filter-feeder biomass (10–50×). <i>Greater at areas of high upwelling:</i> Nutrients; phytoplankton and benthic algae productivity; biomass of foliose algae, filter-feeders and grazers. <i>Lesser at areas of high upwelling:</i> coralline algae, red algal turfs	<i>Greater at areas of high upwelling:</i> Grazing by limpets maintains low biomass of in situ benthic algae; restricts algal association to coralline crusts and small foliose reds	(Branch and Griffiths, 1988; Bustamante and Branch, 1996; Bustamante et al., 1995a,b; Eekhout et al., 1992; McQuaid and Branch, 1985)

Oregon, USA (wave-exposed areas 80 km apart varying in upwelling intensity)	Upwelling intensity; Phytoplankton productivity, detritus concentration	Sea stars, whelks, shorebirds; limpets, chitons, snails; Filter-feeding invertebrates; macroalgae, surfgrass	<i>Greater at the more productive area:</i> Phytoplankton concentration and productivity; detritus concentration; mussel recruitment; filter-feeder growth rates and mussel recruitment	<i>Greater at the more productive area:</i> Predation rates by sea stars on mussels and grazing by limpets	(Menge, 1992; Menge et al., 1994, 1996, 1997a,b)
Oregon and northern California, USA (multiple wave- exposed areas along 400 km of coast)	Upwelling intensity; phytoplankton productivity; nutrient concentration	Sea stars, whelks; limpets; chitons, snails; filter-feeding invertebrates; macroalgae, surfgrass	<i>Greater at sites of higher phytoplankton productivity:</i> Growth rates and recruitment of filter-feeders; <i>Greater at sites of consistently higher nutrients:</i> Algal growth, biomass	<i>Greater at sites of higher phytoplankton productivity and recruitment of prey:</i> Predation by sea stars on mussels	(Freidenburg et al., unpublished data; Menge et al., unpublished data)
New England, USA (rocky intertidal sites 10's of km apart in the Damariscotta River Estuary, Maine)	Flow rate; particle delivery; microalgal biomass accumulation; Recruitment; nutrients	Crabs, whelks; littorine snails; barnacles and mussels; fucoid algae	<i>Greater at high flow sites:</i> Recruitment of barnacles, mussels, snails; growth of barnacles and whelks; higher rates of particle delivery. <i>Lesser at high flow sites:</i> Crab predatory activity.	<i>Greater at low flow sites:</i> Predation by crabs on whelks, littorines, mussels, and barnacles	(Leonard et al., 1999; Leonard et al., 1998)
New Zealand (rocky intertidal sites 200 km apart on South Island)	Upwelling vs. downwelling oceanographic regimes	Sea stars, whelks; limpets, chitons; barnacles and mussels; microalgae	<i>Greater at upwelling sites:</i> Nutrients; recruitment of barnacles, mussels; growth of mussels	<i>Greater at upwelling sites:</i> Predation rates on mussels, predation effect on community	(Menge et al., 1999)

In rocky intertidal habitats on Tatoosh Island, Washington state, USA, Wootton et al. (1996) manipulated nutrients and molluscan grazers in an effort to determine the relative influence of each factor on biomass of algae and on density of micrograzers, in this case larval chironomids. Experiments were done during an El Niño year and two non-El Niño years. Results suggested that addition of nutrients (fertilizer inside porous clay pots) had no effect on algal biomass, but led to increased abundance of micrograzers. In contrast, exclusion of molluscan grazers led to large increases of algal biomass and abundance of micrograzers. This experiment thus suggested that grazing (on algae) and competition (molluscan grazers vs. micrograzers) had strong effects. Although addition of nutrients seemed to have little effect, Wootton et al. (1996) did not test if nutrients actually were increased by their method or if nutrients were naturally limiting to algal growth, so firm conclusions regarding bottom-up influences in this system await further study.

Recruitment of species at the basal level of food webs can be considered a bottom-up effect when it increases the abundance of prey organisms (e.g. Menge et al., 1999). Most early analyses of rocky intertidal community dynamics were conducted in regions having high rates of recruitment of sessile invertebrates. However, studies focused on recruitment demonstrated that recruitment densities could vary dramatically on local to geographic scales (Denley and Underwood, 1979; Underwood et al., 1983; Caffey, 1985; Gaines and Roughgarden, 1985; Raimondi, 1990; Menge, 1991b). Such variation can significantly influence population and community structure, both directly and indirectly (Underwood et al., 1983; Fairweather, 1988; Sutherland, 1990; Menge, 1991b; Caley et al., 1996; Minchinton and Scheibling, 1991, 1993; Robles et al., 1995). For example, in Nova Scotia, barnacle recruit abundance was a major determinant of barnacle density on the upper shore (Minchinton and Scheibling, 1993). Lower on the shore, a post-recruitment factor, predation, controlled barnacle density.

Collectively, these studies suggested that, in contrast to conventional wisdom, bottom-up factors can have a strong influence on population and community structure and dynamics in marine benthic communities. Bottom-up effects vary on larger spatial scales and over longer temporal scales, so further progress in understanding the regulation of marine communities depends on expanding the scope of research to a greater range of scales and to a larger suite of ecological processes (Dayton and Tegner, 1984; Levin, 1992; Menge et al., 1996; Menge and Olson, 1990; Wiens, 1989).

During the past decade, several workers have initiated studies to explicitly integrate top-down and bottom-up effects in analyses of community and/or ecosystem dynamics. Below, I summarize these studies. Although few, these studies illustrate the general approach and suggest that, despite the diverse geographic regions investigated, some important general principles are emerging. In particular, all suggest that physical oceanographic variation occurring even on scales as small as 10's of km can underlie striking variation in community structure and dynamics.

2.3. Top-down/bottom-up regulation

2.3.1. Theory

The nutrient/productivity model (hereafter N/PM; Oksanen et al., 1981) and the environmental stress model (hereafter ESM; Menge and Olson, 1990; Menge and

Sutherland, 1987) contrast in predicting where in the food chain predation and competition are most important. As noted earlier, the N/PM predicts that control by these factors alternates with trophic level and that length of food chains increases with increases in productivity. The ESM predicts that, rather than alternating, predation increases in importance and competition decreases in importance from high to low trophic levels. In addition, food chain length decreases with increases in environmental stress.

Why the different predictions? The applicability of these models may vary among habitats and environmental conditions, depending on whether nutrients and productivity, or environmental stress are the ‘dominant’ environmental gradients (Menge and Olson, 1990). Additionally, the ESM assumes that omnivory (feeding on more than one trophic level) can be ecologically important, while the N/PM assumes that omnivory is ecologically insignificant. Mounting evidence suggests that omnivory can be a powerful structuring force (Persson et al., 1988; Diehl, 1992, 1993; Lawler and Morin, 1993; Menge et al., 1986a; Morin and Lawler, 1996; Persson, 1999; Polis, 1999). In addition, within- and between-trophic level heterogeneity, size-structured interactions, and behaviorally-mediated interactions can all lead to departures from the alternating-control expectations of the N/PM (e.g. Osenberg and Mittelbach, 1996; Persson, 1999; Strong, 1992).

Based on such evidence, alternative conceptual models have been proposed (e.g. Menge et al., 1996; Osenberg and Mittelbach, 1996; Persson, 1999; Polis, 1999). One of these incorporates omnivory with bottom-up influences (Fig. 1). As in the models of Oksanen et al. (1981) and Fretwell (1987), web structure complexity increases with increased nutrients and productivity (N/P). In addition, the model assumes that omnivory increases in importance with increased N/P. As suggested in Fig. 1, this feature eliminates the alternating-control feature of the N/PM. Instead, predation, in the general sense, controls lower trophic levels when food chain lengths are longer and the strength of this control increases with increased N/P. As in the ESM, limitation by food and competition are primary controlling factors at high trophic levels.

The strongest evidence that top-down and bottom-up processes interact to produce community structure has accumulated in freshwater environments but evidence from both terrestrial and marine ecosystems is also increasing (e.g. Persson, 1999). Below, I review the studies in marine rocky intertidal environments that have evaluated how top-down and bottom-up forces interact to influence pattern in a community and ecosystem context.

2.4. Empirical evidence

2.4.1. South Africa

Research in South Africa provided the first, and in some respects most complete, evidence that rocky intertidal community structure was strongly influenced by both bottom-up and top-down factors. Results cited earlier suggested that variation in nutrient input (e.g. seabird guano) could affect algal growth and biomass and propagate to higher trophic levels (Bosman et al., 1986; Bosman and Hockey, 1986; Branch et al., 1987; Table 2). In another study on the South Africa mainland, biomass of filter feeders and

NUTRIENT/PRODUCTIVITY MODEL WITH OMNIVORY

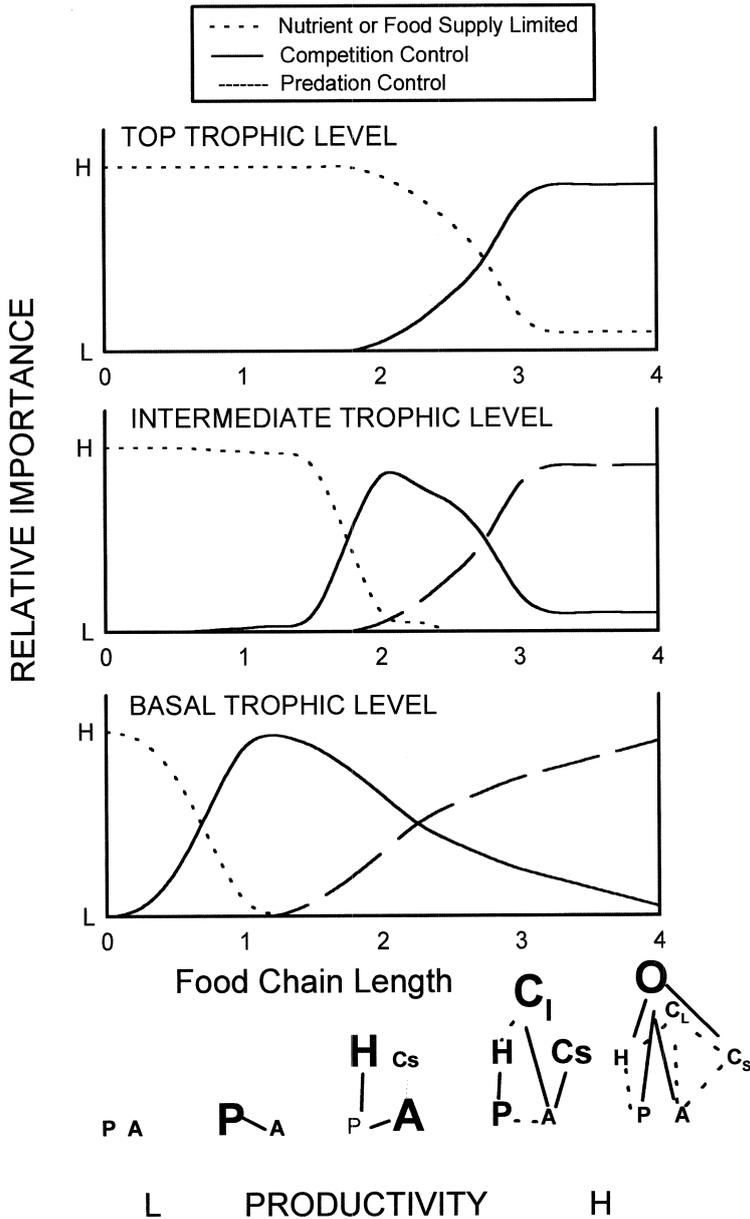


Fig. 1. Predictions of a N/PM incorporating omnivory. Web diagrams at bottom suggest the relative abundances (large letter = high abundance, small letter = low abundance) and interaction strengths (solid link = strong effect, dotted link = weak effect) between benthic plants (P), sessile animals (A), mobile herbivores (H), small carnivores (C_s), large carnivores (C_l) and omnivores (O). From Menge et al. (1996).

their carnivores was greater on wave exposed shores than on sheltered bays. Energetic estimates suggested the difference in biomass depended on different rates of input of algal detritus from adjacent subtidal habitats (McQuaid and Branch, 1985; Table 2). Similar results were observed in a large-scale survey (5000 km), where biomass of filter-feeders on exposed shores was 10–50 \times that in bays (Bustamante and Branch, 1996). Although differences in predation often underlies such differences, field evidence and energetic modelling suggested that greater concentration of detritus and the rate of turnover of detritus at exposed sites were the primary cause. Estimates indicated that exposed shores could sustain a mussel biomass of 478 g (dry flesh mass) m^{-2} ; whereas sheltered shores only 23 g m^{-2} . Predicted values were similar to field estimates, suggesting that differences in food supply were sufficient to explain the contrast in filter-feeder biomass.

What was the source of the particulate food? Estimates revealed that in situ productivity was insufficient to support the high biomass of filter-feeders on wave-beaten shores, suggesting dependence on external subsidies (Bustamante and Branch, 1996). Isotope analyses showed that indeed, 60–85% of the food of filter-feeders came from particulate subtidal kelp (Bustamante and Branch, 1996). Effects of predation and recruitment could also differ between wave-exposures, but food supply, a bottom-up factor, was clearly important.

Building on these results, Bustamante and colleagues (Bustamante et al., 1995a,b) documented striking large-scale gradients of nutrients and primary productivity of benthic and planktonic algae around the South Africa coast, all changing from high in the upwelling-dominated west to low in the east over a distance of \sim 2500 km. Along these gradients, average biomass (g ash-free dry mass m^{-2}) of both grazers and filter-feeders and maximum shell length of a dominant grazer, the limpet *Patella granularis*, were greater with higher intertidal primary productivity.

As with the filter-feeders, calculations for the two most abundant limpets (*Patella argenvillei* and *P. granatina*) showed that in situ productivity was incapable of meeting their energetic needs. Field experiments testing the hypothesis that both are subsidized by subtidal kelp (drift, in the case of *P. granatina*, and live kelp fronds for *P. argenvillei*) showed that in the absence of kelp, limpet survival and body mass declined sharply in comparison to limpets with normal supplies of kelp. The limpet biomass sustained by this kelp input was the highest ever recorded anywhere for intertidal grazers—up to 771 g wet flesh m^{-2} . Bottom-up effects in this system clearly had an important effect on community structure and dynamics. Since earlier studies (Branch and Griffiths, 1988; Eekhout et al., 1992) had shown negative effects of limpet grazing on benthic algae, these bottom-up subsidies of grazers evidently resulted in top-down control of the in situ algae by the grazers.

2.4.2. Oregon

Studies on the coast of Oregon contemporary with those in South Africa also suggest that benthic–pelagic links can have a strong effect on rocky intertidal community structure (Menge, 1992; Menge et al., 1994; Menge et al., 1996, 1997a,b; Table 2). Patterns in the low intertidal zone suggested the hypothesis that community structure depended on smaller-scale processes such as species interactions, wave forces, and

thermal/desiccation gradients and on larger-scale oceanographic processes such as nutrients, phytoplankton productivity, detritus, and larval transport. Surveys revealed differences in the abundance of two dominant space-occupying groups (sessile invertebrates vs. macrophytes) in the low intertidal zone at two sites (Menge, 1992; Menge et al., 1997b). At wave-exposed sites at Boiler Bay, abundance of macroalgae was high and abundance of filter-feeders (barnacles and mussels), limpets, and invertebrate predators was low. In contrast, at wave-exposed sites at Strawberry Hill, ~80 km to the south, abundance of macroalgae was low and abundance of filter-feeders, limpets and invertebrate predators was high. Periodic surveys indicated that these between-site differences have persisted since the early 1980's.

2.4.3. Top-down effects

What factors underlie these differences? Since top-down factors are commonly invoked to explain such variation, studies focused first on predation and grazing. Two approaches were taken to test predator effects. The impact of predation was tested by investigating colonization patterns in the presence and absence of predators (e.g. Dayton, 1971; Fairweather and Underwood, 1991; Menge, 1976; Paine, 1974). The rate of predation was determined by quantifying survival of mussels transplanted from mid to low zone areas with and without sea stars (normal densities and manual removals, respectively; Menge et al., 1994). The former method documents the community impact of predation while the latter method provides insight into both rates and potential predation without the confounding effects of differential rates of colonization and growth of prey in the early stages of recolonization in predation impact experiments.

Predation-impact results suggested that at wave-exposed sites, as in Washington State (Paine, 1966, 1974, 1984), the mid zone-occupying mussel *Mytilus californianus* (Conrad, 1837) spread from the mid into the low zone in the absence but not in the presence of the sea star *Pisaster ochraceus* (Menge et al., 1994). Similar changes in the position of the lower limit of mussels occurred at both Boiler Bay and Strawberry Hill. However, colonization of small (20 × 20 cm) plots kept free of predators suggested predation effects at Strawberry Hill were much stronger than at Boiler Bay. Predation-rate experiments were consistent with this result; predation intensity was far greater at Strawberry Hill (Menge et al., 1994, 1996; Navarrete and Menge, 1996; Fig. 2).

The effects of grazers on microalgae were tested by manipulating limpet and chiton density using barriers of antifouling paint (e.g. Cubit, 1984; Paine, 1984; Paine, 1992; see Benedetti-Cecchi and Cinelli (1997) for a critique; Fig. 3). The response variable was percent cover of microalgae, consisting mostly of early colonists including filamentous greens, reds, and benthic diatoms (Cubit, 1984). The short-term impact of grazing by limpets and chitons, as estimated by the difference between algal cover in – grazer and + grazer treatments, was consistently greater at Strawberry Hill, both in space and time (Fig. 3, Table 3). In 1994, plant–grazer interactions proceeded at different rates on local scales (Table 3; within-subjects, time × block interaction) and the impact of grazers at each site changed over time (Table 3; within subjects, time × site × treatment interaction). In 1995, neither of these effects occurred but outcomes varied through time at each site (Table 3; time × site interaction). Although some data violated

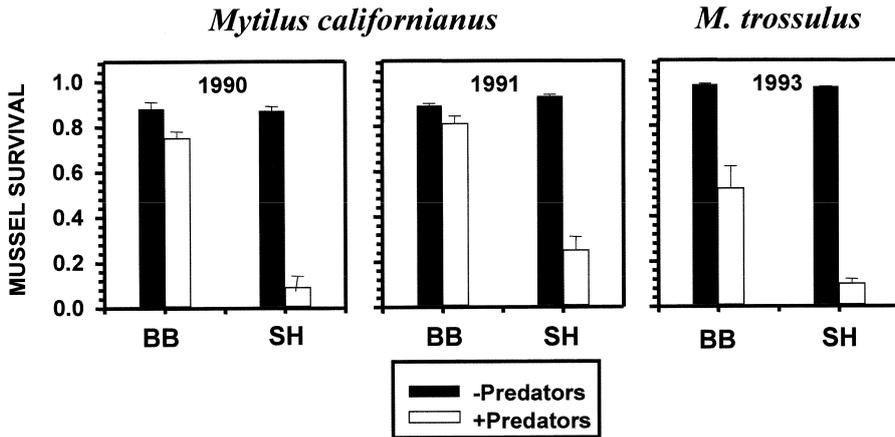


Fig. 2. Results of experiments testing the effects of invertebrate predation on survival of transplanted prey (mussels; *Mytilus californianus* in 1990, 1991, *M. trossulus* in 1993). Survival estimates are from the end of each experiment, generally in early autumn. Data from Menge et al. (1994) and Navarrete and Menge (1996).

statistical assumptions, the large magnitude of the effects suggested that these results were robust (e.g. Underwood, 1981, 1997).

These results suggested that grazing and predation both were greater at Strawberry Hill. Note, however, that only the grazer result is consistent with the hypothesis that top-down factors underlie the between-site differences in community structure. Grazing was greater where macrophyte abundance was lower. In contrast, predation was stronger, not weaker, where abundance of mussels and barnacles was greater.

2.4.4. Bottom-up effects

Why was predation stronger at the site with larger prey populations? An alternative to top-down determination of between-site differences in abundance of prey (filter-feeders) is a bottom-up explanation. Filter-feeders might be more abundant at Strawberry Hill because particulate food concentrations were greater there, fueling higher survival of larvae and/or recruits and faster growth of benthic individuals (i.e. rates of secondary production were higher; see Duggins et al., 1989; Witman et al., 1993). In addition (or alternatively), recruitment rates of the larvae of filter-feeders might be greater at Strawberry Hill.

Differences in growth of filter feeders (Menge, 1992; Menge et al., 1994, 1997a; Fig. 4) strongly suggested that the sites differed in food concentration. Since food for filter feeders can include both phytoplankton and detritus, a water sampling program was initiated to determine if the concentration and productivity of phytoplankton and concentration of detritus in nearshore waters differed between Boiler Bay and Strawberry Hill. Results showed that phytoplankton and detritus availability for filter-feeders was consistently higher, sometimes by orders of magnitude, at Strawberry Hill than at Boiler Bay (Menge et al., 1997b; Fig. 5). These differences are persistent in time and space, occurring to the present (2000) from 1993, during upwelling and upwelling

Grazer Exclusion Experiment

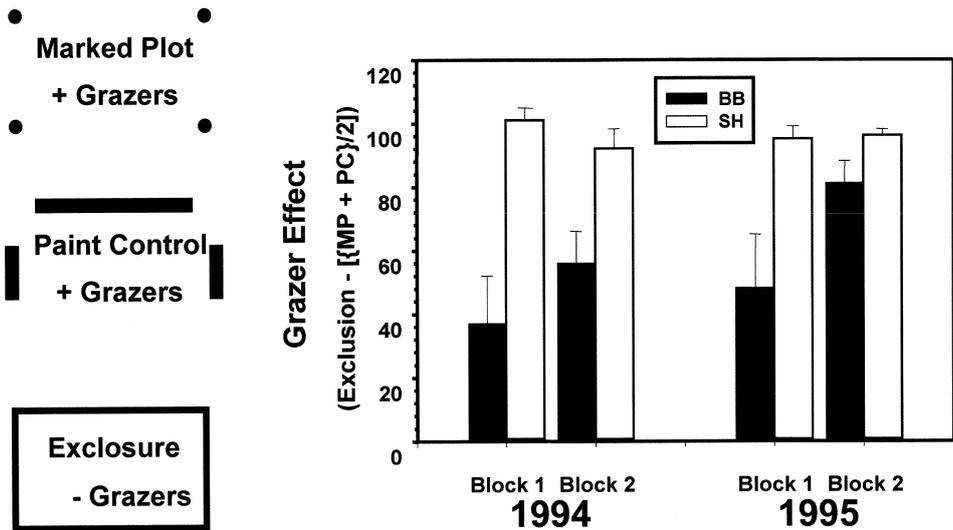


Fig. 3. Results of grazer exclusion experiments at Boiler Bay and Strawberry Hill in 1994 and 1995. Grazer effect was quantified as the percent cover of microalgae (algal sporelings, filamentous species such as *Bangia* spp., *Ulothrix* spp., and *Urospora* spp.) in exclusions minus the average cover in marked plots and paint controls, both of which had grazers present. A diagrammatic indication of the appearance of the three treatments is shown to the left of the histogram. A complete (–grazer) or partial barrier (+ grazer) is formed by first applying marine epoxy ('Z-spar') around the plot and then painting the setting epoxy. The effect of the paint is tested by also establishing plots without paint (+ grazer). Plots were first scraped clear of macroalgae and sessile animals and sprayed with lye oven cleaner to remove lingering microalgae and thin, non-calcareous encrusting algae. Some crustose algae persisted but did not appear to influence between-treatment differences. Two blocks of five replicates each were established in 1994 and 1995 at sites of intermediate wave exposure at Boiler Bay and Strawberry Hill.

relaxations events, in all seasons, and in all years (Menge et al., unpublished data). Recruitment of mussels (but intriguingly, not barnacles) has also differed consistently, sometimes by orders of magnitude between sites (Menge et al., 1994, 1997a; Menge, unpublished data).

What causes this remarkable consistency in food environment and mussel recruitment rate? Evidence to date suggests that these differences may be associated with an oceanographic discontinuity induced by variation in the width of the continental shelf along the central Oregon coast. During upwelling, sea surface satellite imagery shows the development of a gyre over the Stonewall/Heceta Banks, a widening of the continental shelf lying offshore of Strawberry Hill. No such sea surface structure has ever been observed offshore of Boiler Bay, where the continental shelf is narrow. Further, the width of the nearshore zone of cold water during upwelling is narrow at Boiler Bay and wide at Strawberry Hill. My coworkers and I thus hypothesized that current and eddy structure during upwelling dilute plankton off Boiler Bay and

Table 3

Repeated measures analysis of variance on short-term (two month) results of herbivore enclosure experiments conducted at Boiler Bay and Strawberry Hill in 1994 (begun early June) and 1995 (begun mid May), results from two consecutive monitoring dates were analyzed from each summer (July 8 and July 26 in 1994, June 26 and July 11 in 1995), visual examination indicated that residuals were normal and error terms were independent for all dates except 26 July 1994, data were arcsin/square root-transformed for analysis; nonetheless, variances were heteroscedastic in all cases^{a,b}

Source	d.f.	MS	F	P
<i>Between subjects – 1994</i>				
Site	1	0.0631	0.56	0.46
Block	1	0.2454	2.18	0.15
Treatment	1	26.860	238.8	≪ 0.00001
Site × treatment	1	1.1043	9.82	0.003
Error	49	0.1125		
<i>Within subjects – 1994</i>				
Time	1	0.0492	0.82	0.37
Time × site	1	0.0899	1.49	0.23
Time × block	1	0.3177	5.27	0.03
Time × site × treatment	1	0.6074	10.08	0.003
Error	49	0.0603		
<i>Between subjects – 1995</i>				
Site	1	0.7977	7.86	0.007
Block	1	0.1560	1.54	0.22
Treatment	1	30.699	302.5	≪ 0.00001
Site × treatment	1	1.8340	18.1	0.00008
Error	55	0.1015		
<i>Within subjects – 1995</i>				
Time	1	0.0675	2.18	0.15
Time × site	1	0.5023	16.2	0.0002
Time × block	1	0.1077	3.48	0.07
Time × treatment	1	0.1053	3.40	0.07
Time × site × treatment	1	0.0155	0.50	0.48
Error	55	0.0309		

^a Results from marked plot and paint control treatments were lumped after preliminary analyses indicated that they were not different ($P > 0.05$ in all cases).

^b Significance level was $P = 0.05$; P -values < 0.05 are indicated in boldface.

concentrates it off Strawberry Hill (Menge et al., 1997a). During relaxation, onshore winds from the southwest push surface waters towards the coast, delivering either high (Strawberry Hill region) or low (Boiler Bay region) concentrations of phytoplankton and zooplankton to intertidal habitats. Recent quantification of sea-surface currents with coastal radar (HF radar) and drifters (Barth et al., 1998; Kosro et al., 1997) verifies these interpretations of sea surface currents. These measurements also show that currents off Boiler Bay are faster and consistently southward, whereas off Strawberry Hill, currents inshore of the main jet of the California Current are slower and often entrained in a counterclockwise gyre.

The observed nearshore physical oceanographic patterns, with the studies of com-

Filter Feeders: Growth Rates

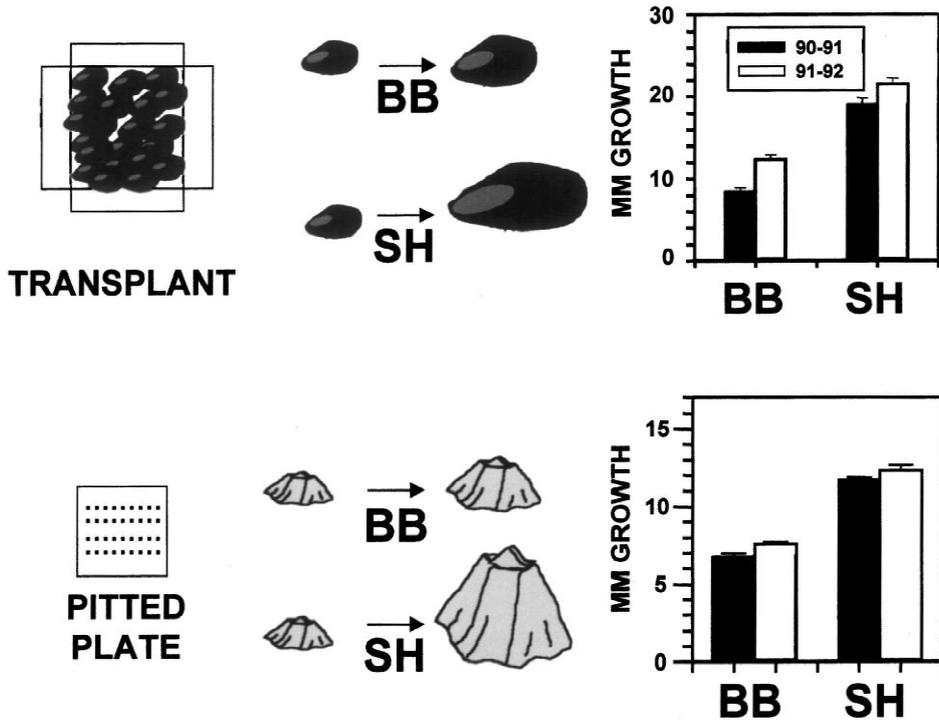


Fig. 4. Diagrams of methods used to quantify growth rates of mussels (top half) and barnacles (bottom half) and summaries of results at Boiler Bay and Strawberry Hill. Mussel growth was estimated as the shell increment added over 12 months to marked transplanted mussels. Barnacle growth was estimated as the increase in basal diameter of individuals growing uncrowded on pitted settlement plates. Barnacles will only settle in the pits of smooth plastic plates, and spacing the pits wider than their maximum basal diameter prevents crowding from influencing growth. The central diagrams suggest the general magnitude of growth differences between the two sites.

munity dynamics onshore, suggest that rocky intertidal community structure and dynamics vary with nearshore oceanographic conditions through the links of phytoplankton and larvae. This study is but a single case (and thus a ‘pseudoreplicate’), however, and the generality of these patterns, their postulated cause, and many details of actual mechanisms await the results of further study.

2.4.5. New England

Recent studies in New England provide the first evidence from this well-studied community that bottom-up processes can interact with top-down forces to have a major effect on among-site variation in community structure (Leonard et al., 1998; Table 2). In the Damariscotta River estuary in Maine, community structure at rocky intertidal sites

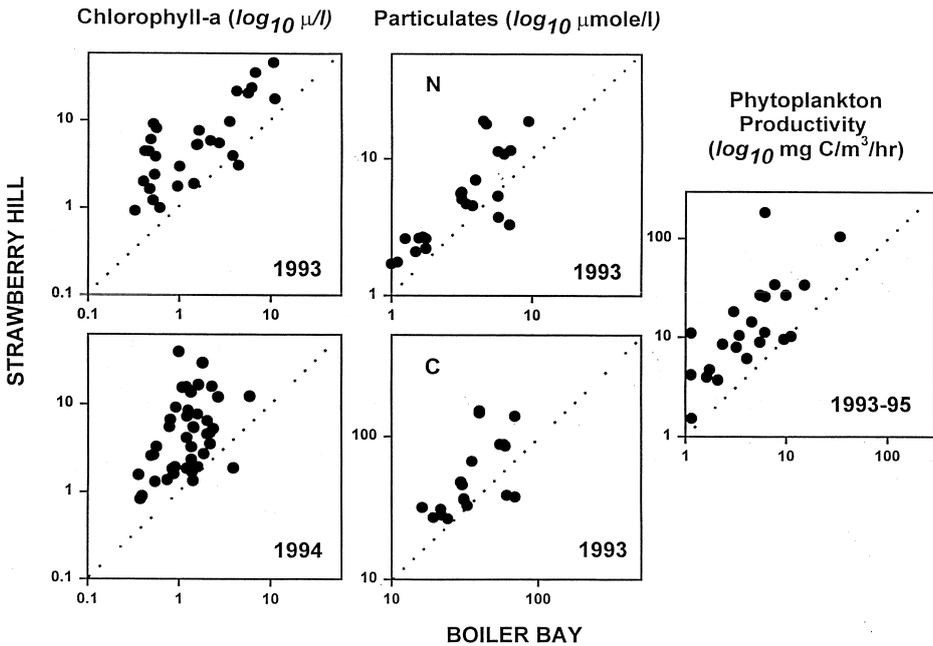


Fig. 5. Concentrations of chlorophyll-a (Summers 1993, 1994), organic particulates (nitrogen in top panel, carbon in bottom panel, both from 1993), and phytoplankton productivity (1993–1995 combined) at Strawberry Hill in relation to concentrations sampled at Boiler Bay. Each data point represents samples taken on a single day. The dotted diagonal lines represent equal concentrations at each site.

varied with flow-related processes, and flow-dependent factors influenced top-down effects both directly and indirectly. At fast-flow areas, sessile invertebrates (barnacles and mussels), herbivorous littorine snails, whelks, and crabs were abundant and the fucoid alga *Ascophyllum nodosum* (L.) Le Jol was sparse. At slow-flow communities, sessile invertebrates, littorines, whelks and crabs were sparse and *Ascophyllum* was abundant.

Bottom-up forces were broadly defined to include recruitment as well as nutrient concentration, rates of particle delivery, and microalgal biomass accumulation. Combining flow rates with estimates of phytoplankton concentration (as estimated by chlorophyll-a), Leonard et al. (1998) showed that particle delivery rates were substantially greater at high flow sites. In addition, they quantified recruitment of mussels, barnacles, and littorines using a combination of collectors (mussels), settlement in marked plots (barnacles) and settlement in dead barnacle tests (littorines). The impact of particle delivery on growth rates of sessile animals was estimated by quantifying growth rates of mussels and barnacles. Growth rates of whelks and littorines were estimated by measuring growth of the shell lip in marked individuals. Microalgal production was estimated by measuring biomass accumulation on ceramic plates in the presence and absence of grazers. Top-down forces were quantified by estimating rates of predation by

crabs on whelks, littorines, and mussels, and by determining the effect of grazers on microalgal biomass accumulation.

Bottom-up effects (recruitment of barnacles, mussels and herbivorous snails, and growth of barnacles and whelks) were generally greater at high-flow sites and top-down effects (predation by crabs on whelks, littorines, mussels and barnacles) were generally greater at low-flow sites (Leonard et al., 1998, 1999). The bottom-up differences were attributed to higher rates of delivery at high-flow sites of planktonic larvae (direct effect: recruitment differences, indirect effect: higher growth of whelks) and particulate food (direct effect: barnacle growth). Top-down differences were attributed to inhibition by currents of foraging activity by crabs. Thus, community structure differences depended largely on contrasting flow regimes. In this case, variation in community structure evidently resulted from a combination of processes invoked by both environmental stress and nutrient/productivity models.

2.4.6. New Zealand

The rocky shores of the South Island of New Zealand harbor intertidal communities that are similar in many respects to those on other temperate rocky coasts (Stephenson and Stephenson, 1972). As at many other locations, zones dominated by barnacles, mussels and macrophytes generally occur at wave-exposed high, mid and low shore levels. Nonetheless, as in other biogeographic regions, community structure can vary on larger spatial scales, even at sites of roughly comparable wave exposure. Rocky shores on the east coast of the South Island have nearly solid covers of barnacles (*Chamaesipho columna* Spengler and *Epopella plicata* (Gray)) in the high zone and mussels (*Mytilus galloprovincialis* Lamarck and *Perna canaliculus* (Gmelin)) in the mid and low zones (Knox, 1953; Menge et al., 1999). Very low on the shore a canopy of brown algae (*Durvillea willana* Lindauer, *D. antarctica* (Chamisso) Hariot) is dominant. As on the east coast, rocky shores on the west coast of the South Island have dense populations of barnacles in the high zone and dense populations of mussels in the mid zone. In the low zone, however, algal turfs, crustose algae and bare space replace mussels as primary space occupants. These differences are comparable to those observed on wave-exposed and wave-protected shores in New England (Menge, 1976; Lubchenco and Menge, 1978), but occur on a much larger scale and at sites with similar wave forces.

What processes are responsible for these differences in the low zone communities on opposite sides of the South Island? In addition to the differences listed above, nearshore marine ecosystems on the east and west coasts of the South Island vary in two important ways (Table 2, Menge et al., 1999). First, although similar biota occur on both sides, the sea star *Stichaster australis* Verrill is far more abundant on the west coast. Second, the northwest coast experiences intermittent upwelling (Stanton and Moore, 1992; Vincent et al., 1991; Menge et al., 1999) whereas the east coast experiences little or no upwelling (Grieg et al., 1988; McKendry et al., 1988; Menge et al., 1999). Thus, rocky intertidal communities on opposite coasts are likely to be subject to different regimes of top-down and bottom-up effects (Menge et al., 1999). Alternatively, the community differences may simply have resulted from unknown historical chance events or dispersal bottlenecks that led to the between-coast difference in sea star abundance.

To evaluate the top-down/bottom-up hypothesis, studies of processes likely to reflect

direct and indirect oceanographic influences were conducted at two sites on each coast (Menge et al., 1999). Bottom-up processes (recruitment, mussel growth, nutrients and chlorophyll-a concentration) and top-down processes (predation, grazing) were quantified at all sites. Evaluation of the alternative ‘low dispersal rate of *Stichaster* to the east coast’ hypothesis was stymied by practical and ethical considerations. The most direct test would be to manually boost east coast *Stichaster* densities to levels observed on the west coast and study the consequences. If translocated sea stars persisted and interacted strongly with mussels at east coast site, we could infer that the community differences were due to recruitment-limitation of the sea star. Other approaches for testing this possibility have not yet been attempted.

Both top-down and bottom-up effects were greater on the west coast (Fig. 6). Predator-impact and predation-intensity experiments suggested that predation was strong on the west coast and weak on the east coast (Fig. 6A; Menge et al., 1999). Sea star manipulations suggested that, as in an earlier study on the North Island (Paine, 1971),

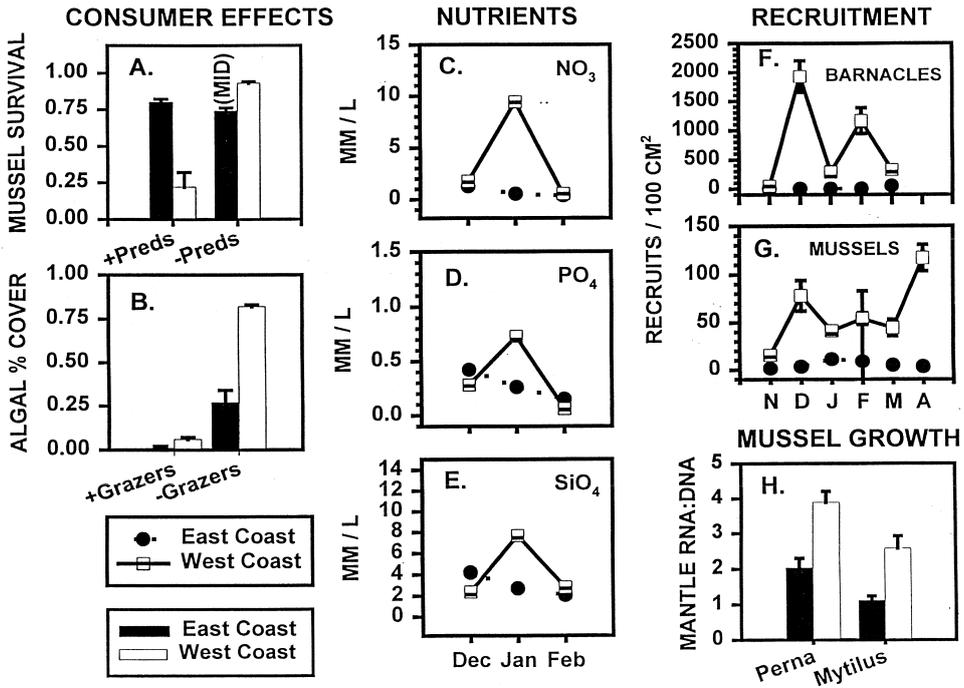


Fig. 6. Summary of results of studies of top-down and bottom-up effects in on opposite coasts of the South Island of New Zealand (see Menge et al., 1999 for details of results and methods). A. Survival of transplanted mussels (*M. galloprovincialis*) in the presence and absence of predators. East coast results are from mid zone experiments; west coast results are from the upper low zone. B. Effects of grazers on east and west coasts, quantified as the difference between treatments with and without grazers (see Fig. 3). C, D, E. Concentrations of nitrate, phosphate, and silicate, respectively, in December 1994, and January and February 1995. F. Recruitment densities of barnacles on settlement plates, November 1994 to April 1995. G. Recruitment densities of mussels in plastic mesh collectors, November 1994 to April 1995. H. Protein synthesis capacity, a molecular index of growth estimated by RNA:DNA ratio, in *Perna canaliculus* and *M. galloprovincialis*.

most of the effect documented in the predation experiments was due to *Stichaster*. Grazing was significant on both coasts, but based on differences between + grazer and – grazer treatments (Fig. 6B), also appeared stronger on the west coast. These results are confounded by parallel differences in algal productivity (Menge et al., unpublished data), however, further study on this top-down/bottom-up link is needed.

Bottom-up factors also appeared stronger on the west coast. During a summer upwelling event, nutrient concentrations were higher on the west than on the east coast (Fig. 6C–E). Recruitment of both barnacles and mussels was consistently higher on the west coast (Fig. 6F and G), often by orders of magnitude. Finally, mussel growth, as reflected by RNA:DNA ratios (an index of cellular protein synthesis), was higher on the west coast for both *Perna* and *Mytilus* (Fig. 6H). Thus, both top-down and bottom-up effects appear to be greater on the west coast, characterized by upwelling conditions, than on the east coast, with non-upwelling conditions.

3. Discussion

The studies summarized above (see also Table 2) are consistent with the hypothesis that bottom-up and top-down effects are linked in rocky intertidal communities in ways that offer insight into previously unexplained variability among communities. The present collection of published works is limited in number and scope, however, and issues of generality, mechanisms, and linkage magnitude, among other things, are still quite open. Below I consider the broad issue of how these results advance more general principles of marine ecosystem dynamics, discuss several unresolved problems, and suggest some future directions.

3.1. Variation in characteristic scale of bottom-up effects

The evidence from these cases is consistent with the hypothesis that oceanographic factors can contribute significantly to rocky intertidal community variation. The characteristic scales of the specific oceanographic processes seeming to underlie the variation in community structure are diverse. Differences in South Africa and New Zealand depended on a contrast *between* upwelling vs. non-upwelling regimes ranging to 1000's of km, for example, while differences in Oregon represented variation *within* an upwelling regime on a scale of 10's to 100's of km. The alternative community structures investigated in New England were dependent on yet another process, contrasting flow regimes, occurring on a scale of 10's of km. In this case flow differences were related to variation associated with tidal change, not upwelling. Flow can vary on large scales, however, since, for example tidal amplitude and resulting currents can vary dramatically on regional and global, as well as local scales. In all cases the pelagic sources of variation occurred at substantially larger scales than the 10's of m scales upon which the benthic processes operated.

Yet another potentially important source of oceanographic variation, not explicitly addressed in the above examples, is the temporal, longer-term variation associated with shifts between El Niño and La Niña conditions (e.g. Dayton et al., 1992, 1999). Here

again, the oceanographic and benthic processes operate at radically different scales and frequencies, but clearly interact to produce variation in community structure.

Do these examples suggest a predictive framework? With the exception of the South African island–mainland comparison, the common thread in all cases appears to be among-site differences in particle (phytoplankton, detritus, larvae) concentration. The significance of this lies in its effect on recruitment and/or growth of filter-feeding invertebrates, and the consequences of this greater concentration of resources to processes higher in the food chain that respond to these bottom-up inputs in ecologically meaningful ways. Predator (sea stars, whelks) or herbivore densities can be elevated, or sizes can be larger, where bottom-up inputs are greater.

Based on these dynamics, we can predict that when oceanographic processes favor the delivery of higher concentrations of phytoplankton, detritus, and/or larvae, invertebrates are more likely to dominate the structure and dynamics of rocky intertidal communities. As the examples cited suggest, the oceanographic processes underlying differential particle delivery can vary. Perhaps the clearest contrasts are between upwelling and downwelling regimes, such as that in New Zealand, or on west vs. east coasts of South Africa and between different flow regimes, as in New England. As suggested by the studies in Oregon, however, oceanographic variation with ecologically significant consequences can also occur within upwelling regimes. The processes involved are complex, however, and we still do not have a firm mechanistic understanding of the specific factors causing the consistent among-site differences documented in Oregon and California. For example, although chlorophyll-*a*, mussel recruitment, and growth of mussels and barnacles all tend to covary among sites, some sites are ‘outliers’ (Menge, unpublished data). At some sites, chlorophyll-*a* is low but mussel recruitment is high. As summarized in the next section, this is but one of several unresolved issues.

3.2. Unresolved issues

As with most new research directions, the study of top-down/bottom-up dynamics in rocky intertidal areas has generated more questions than answers. Among the more immediate problems are questions relating to the role of nutrients, the relative importance of food concentration vs. larval transport, the mechanisms of dispersal, and the mechanisms that underlie the community effects summarized above. Success in addressing these problems will rely increasingly on interdisciplinary research.

3.2.1. Nutrients

Does spatial or temporal variation in nutrient flux also play a role in rocky intertidal communities? Although Dayton and colleagues (e.g. Dayton et al., 1999) have clearly demonstrated major effects of nutrient depletion on subtidal kelps, until recently, there was little evidence to suggest that variation in nutrient concentrations in rocky intertidal habitats might have ecologically significant consequences. During an El Niño summer, for example, local-scale nutrient addition experiments on Tatoosh Island, Washington State (USA) increased the abundance of micrograzing crustaceans but not macroalgae (Wootton et al., 1996). No effect of nutrient addition was observed during non-El Niño conditions. In Oregon, recent evidence implicates large-scale differences in nutrient

regimes, also during an El Niño, as a potentially important source of variation in algal assemblages (Freidenburg et al., unpublished data). Algal responses varied by species, by algal division (brown algae responded to the 1997–1998 El Niño but reds evidently did not), and through time. In another study using experimental tidepools in Oregon, nutrient addition increased algal productivity and abundance, but had no bottom-up effect on herbivore abundance (Nielsen, unpublished data).

In southern California, growth of the intertidal kelp *Egregia menziesii* (Turn.) Aresch, 1876 varied predictably in regions of consistently different nutrient regimes (Blanchette et al., unpublished manuscript). North of Point Conception, persistent upwelling generates consistently high nutrient concentrations while south of Point Conception, there is little upwelling and nutrients are consistently low. Measurements showed that *Egregia* growth is dramatically greater where nutrient concentrations are higher. Further, reciprocal transplant experiments suggest that growth of plants slows when translocated to low nutrient regimes and speeds up when translocated to high nutrient regimes.

What is the role of iron in relation to other nutrients in determining rocky intertidal community structure? Recent evidence suggests that iron concentrations may vary with the width of the continental shelf, and in relation to river inputs along nearshore coastal regions (Hutchins and Bruland, 1998; Hutchins et al., 1998, 1999). Since iron is a catalyst for the use of nitrogen by phytoplankton (Martin and Fitzwater, 1988; Sunda and Huntsman, 1997; Takeda, 1998), its availability may underlie the spatial pattern and magnitude of blooms along the coast and therefore be potentially important in explaining patterns of variation in this bottom-up process.

While these observations and speculations are intriguing, further research at small- to large-scales, over long time periods, and in the laboratory and field will be necessary to determine the general nature and importance of the effects of nutrients in rocky intertidal communities.

3.2.2. Food concentration vs. larval transport

What is the nature and importance of the link(s) between nutrient regimes, phytoplankton, zooplankton and benthic populations and communities? In particular, exactly what ‘particles’ are responsible for the higher growth rates at some sites? In Oregon, some evidence suggests that phytoplankton and phytoplankton-derived detritus underlie variation in mussel and barnacle growth. For example, growth of mussels and barnacles is usually faster at sites of greater phytoplankton concentration. However, rapid growth of barnacles (*Balanus glandula*, Darwin, *Chthamalus dalli*) and mussels (*Mytilus trossulus* Gould, *M. californianus* Conrad) persists through fall and winter months at such sites even though phytoplankton blooms cease during this period. All these species settle mostly in late summer or fall, and by winter (December or January) individuals have grown from recruit-size (≤ 1 mm) to as much as 10 mm (barnacle basal diameter) or 20 mm (*M. trossulus* shell length; Menge, 2000; Sanford and Menge, 2000; Menge, personal observations). By the end of winter, barnacles at Strawberry Hill can be $2 \times$ larger than at Boiler Bay (Sanford and Menge, 2000). Moreover, growth can be decoupled from phytoplankton concentration. Although chlorophyll-a concentration accounted for 60% of the variance in mussel growth rates (1997–1998 data), high growth rates of filter-feeders occurred at some sites with low phytoplankton productivity,

and relatively low growth rates occurred at some sites with high productivity (Menge et al., 2000).

The underlying explanation for these departures from expectation remains unknown. Sanford and Menge (2000) speculate that predation on zooplankton by filter-feeding barnacles and mussels may account for some of the unexplained variation in growth rates. Although barnacles and mussels have been observed with zooplankton in their guts (Barnes, 1959), this alternative needs further investigation. Other possible factors yet to be explored include (at least) the possibilities that growth variation is dependent on specific phytoplankton (or zooplankton) species whose relative abundances vary among sites, that growth is affected by dissolved organic matter, or that growth reflects an interaction between site-specific food regime variation and thermal regimes.

Are bottom-up effects on food web dynamics relatively more dependent on transport of propagules or on nutrient and/or phytoplankton effects? The greater abundance of sessile prey, particularly mussels, at Strawberry Hill, for example, could result entirely from higher rates of larval transport and recruitment. Greater phytoplankton concentrations at these and similar sites could have little influence on community dynamics. Alternatively, denser recruitment of mussels could depend not on higher rates of transport of larvae to Strawberry Hill but on greater concentrations of phytoplankton food for settlers. Larvae could be delivered at similar rates to both sites but survive better at Strawberry Hill. A third alternative is that the differences are a synergistic consequence of both processes. Present knowledge does not permit an assessment of these alternatives, and testing them will be difficult. Rigorous tests must at least include nearshore studies of larval transport, phytoplankton community composition and dynamics (e.g. Pineda, 1999), both field and laboratory investigations of larval condition, and the effect of particulates on recruit survival.

3.2.3. Mechanisms of top-down/bottom-up dynamics

To what extent, and under what conditions do predation and grazing depend on bottom-up processes? Does omnivory vary with the magnitude of bottom-up effects? Are predator–prey and herbivore–plant food chains decoupled and does the degree of coupling vary with which oceanographic process is most variable? Nutrients, phytoplankton and larvae, for instance can all vary independently, and may thus have independent effects on community processes. Although each of these questions is under active investigation, I can offer little insight into most of these questions at the moment with the exception that current evidence from Oregon and New Zealand suggests that herbivore–plant food chains can sometimes be decoupled from predator–prey food chains.

3.2.4. Dispersal dynamics

What are the determinants of larval dispersal and transport dynamics? At present, we have little knowledge of whether larval ecology is characterized by sources and sinks, or sites that disproportionately produce and receive larvae, respectively (Morgan, 1995; Palumbi, 1995). Traditionally, marine ecologists have assumed that, in general, meroplankton are broadcast into nearshore regions where they join a planktonic community that is relatively uniformly dispersed along the coast. While most workers

perceived that this assumption was unlikely to be realistic, only recently have studies been carried out on scales sufficiently large to begin evaluating this alternative. Another widely acknowledged assumption is that larvae disperse great distances from their natal habitats, suggesting that little opportunity exists for genetic differentiation among coastal populations. Recent studies have begun to suggest that for some larvae, at least, there may be a high degree of local-scale retention (Palumbi, 1995; Shanks, 1995). Expansion of research on this question is therefore eagerly anticipated. Potentially powerful approaches include both field and laboratory studies of larval ecology, physiology and genetics. With the advent of more sensitive genetic markers, the methods of molecular genetics should also prove to be a powerful tool in addressing this question (Palumbi, 1995).

3.2.5. The necessity of interdisciplinary approaches

Although limited in extent, the several investigations of benthic–pelagic coupling and top-down/bottom-up community dynamics in rocky intertidal communities have opened an exciting and highly challenging new direction of interdisciplinary research in nearshore marine environments. Such research simultaneously imposes several new demands. Because the key processes involved operate at vastly different scales, ecologists must extend their efforts to dramatically larger spatial scales, including a higher density of study sites, and longer temporal scales. These scales and the greater expertise needed to address problems that span them will require a strongly interdisciplinary approach, including at least physical oceanographers, biological oceanographers, larval biologists, and ecologists. Insight into the physiological, biochemical, molecular, behavioral and genetic mechanisms underlying variation in larval condition, recruit survival, and larval transport will depend on the expertise of scientists in these areas. Modelling and simulations can help address issues that are impractical or impossible to study directly in the field, and can also general novel questions, so involvement of theoreticians is also needed. Finally, the insights and even greater scales revealed by remote sensors such as satellite imagery (sea-surface temperature, chlorophyll, sea level), coastal (HF) radar (quantification of highly resolved surface currents), Acoustic Doppler Current Profilers (ADCPs), field-deployable fluorometers (fluorescence as an index of chlorophyll concentration) and similar equipment have greatly expanded our understanding of open ocean environments. Application of this technology to very nearshore environments has begun to open new vistas and dramatically increases our ability to study the dynamics of these regions.

4. Conclusion

Recent research in nearshore marine environments has begun to close the gap between knowledge of bottom-up effects in these habitats compared to the more advanced understanding in terrestrial and particularly freshwater environments. It is not surprising that findings suggest that bottom-up effects are in fact tightly linked to top-down processes and thereby can have significant, and sometimes dramatic effects on community structure. Although considerable progress has been made, the present body

of knowledge is limited and needs to be expanded to other regions and to be made in much greater depth in areas already under study.

Acknowledgements

I thank Tony Underwood for the invitation to write this review for the *Journal of Experimental Marine Biology and Ecology*. I have benefitted from the advice, criticism, and assistance of a legion of friends, colleagues, postdoctoral fellows, graduate students, undergraduate students and offspring. Although too numerous to list here, I am deeply grateful to all of you. A heartfelt thanks to my partner, colleague and co-PI Jane Lubchenco, for her career-long support, companionship, and critiques. My studies of rocky intertidal oceanography have been supported by grants from the National Science Foundation, the Andrew W. Mellon Foundation (J. Lubchenco co-PI), the Wayne and Gladys Valley Foundation, Robert Lundeen (to J. Lubchenco), and the David and Lucile Packard Foundation (J. Lubchenco co-PI). This is contribution number 16 from PISCO, the Partnership for Interdisciplinary Studies of Coastal Oceans, A Long-Term Ecological Consortium supported by a grant from the David and Lucile Packard Foundation. [AU]

References

- Barnes, H., 1959. Stomach contents and microfeeding of some common cirripedes. *Can. J. Zool.* 37, 231–236.
- Barth, J.A., Bogucki, D., Pierce, S.D., Kosro, P.M., 1998. Secondary circulation associated with a shelfbreak front. *Geophys. Res. Lett.* 25 (15), 2761–2764.
- Benedetti-Cecchi, L., Cinelli, F., 1997. Confounding in field experiments: direct and indirect effects of artifacts due to the manipulation of limpets and macroalgae. *J. Exp. Mar. Biol. Ecol.* 209, 191–194.
- Bosman, A.L., DuToit, J.T., Hockey, P.A.R., Branch, G.M., 1986. A field experiment demonstrating the influence of seabird guano on intertidal primary production. *Est. Coastal Shelf Sci.* 23, 283–294.
- Bosman, A.L., Hockey, P.A.R., 1986. Seabird guano as a determinant of rocky intertidal community structure. *Mar. Ecol. Prog. Ser.* 32, 247–257.
- Branch, G.M., Barkai, A., Hockey, P.A.R., Hutchings, L., 1987. Biological interactions: causes or effects of variability in the Benguela ecosystem? *S. Afr. J. Mar. Sci.* 5, 425–445.
- Branch, G.M., Griffiths, C.L., 1988. The Benguela ecosystem. Part V. The coastal zone. *Oceanogr. Mar. Biol. Ann. Rev.* 26, 395–486.
- Bustamante, R.H., Branch, G.M., 1996. Large scale patterns and trophic structure of southern African rocky shores: the roles of geographic variation and wave exposure. *J. Biogeogr.* 23, 339–351.
- Bustamante, R.H., Branch, G.M., Eekhout, S., 1995a. Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. *Ecology* 76, 2314–2329.
- Bustamante, R.H., Branch, G.M., Eekhout, S., Robertson, B., Zoutendyk, P., Schleyer, M., Dye, A., Hanekom, N., Keats, D., Jurd, M., McQuaid, C., 1995b. Gradients of intertidal primary productivity around the coast of South Africa and their relationships with consumer biomass. *Oecologia* 102, 189–201.
- Caffey, H.M., 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecol. Monogr.* 55, 313–332.
- Caley, M.J., Carr, M.H., Hixon, M.A., Hughes, T.P., Jones, G.P., Menge, B.A., 1996. Recruitment and the local dynamics of open marine populations. *Ann. Rev. Ecol. Syst.* 27, 477–500.
- Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., 1985. Cascading trophic interactions and lake productivity. *BioScience* 35, 634–639.

- Castilla, J.C., Duran, L.R., 1985. Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos* 45, 391–399.
- Chen, B., Wise, D.H., 1999. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology* 80, 761–772.
- Connell, J.H., 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* 31, 61–104.
- Connell, J.H., 1970. A predator–prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecol. Monogr.* 40, 49–78.
- Connell, J.H., 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. In: Cody, M.L., Diamond, J.M. (Eds.), *Ecology and Evolution of Communities*. Belknap Press, Cambridge, Massachusetts, pp. 460–490.
- Cook, R.E., 1977. Raymond Lindeman and the trophic-dynamic concept in ecology. *Science* 198, 22–26.
- Cubit, J., 1984. Herbivory and the seasonal abundance of algae on a high intertidal rocky shore. *Ecology* 65, 1904–1917.
- Darwin, C.R., 1859. *The Origin of Species By Means of Natural Selection*. John Murray, London, UK.
- Dayton, P.K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41, 351–389.
- Dayton, P.K., 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* 45, 137–159.
- Dayton, P.K., Currie, V., Gerrodette, T., Keller, B.D., Rosenthal, R., Ven Tresca, D., 1984. Patch dynamics and stability of some California kelp communities. *Ecol. Monogr.* 54, 253–289.
- Dayton, P.K., Tegner, M.J., 1984. Catastrophic storms, El Niño, and patch stability in a southern California kelp forest community. *Science* 224, 283–285.
- Dayton, P.K., Tegner, M.J., Edwards, P.B., Riser, K.L., 1999. Temporal and spatial scales of kelp demography: the role of oceanographic climate. *Ecol. Monogr.* 69, 219–250.
- Dayton, P.K., Tegner, M.J., Parnell, P.E., Edwards, P.B., 1992. Temporal and spatial patterns of disturbance and recovery in a kelp forest community. *Ecol. Monogr.* 62, 421–445.
- Diehl, S., 1992. Fish predation and benthic community structure: the role of omnivory and habitat complexity. *Ecology* 73, 1646–1661.
- Diehl, S., 1993. Relative consumer sizes and the strengths of direct and indirect interactions in omnivorous feeding relationships. *Oikos* 68, 151–157.
- Duggins, D.O., Simenstad, C.A., Estes, J.A., 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245, 170–173.
- Dungan, M.L., 1986. Three-way interactions: barnacles, limpets, and algae in a Sonoran Desert rocky intertidal zone. *Am. Natur.* 127, 292–316.
- Dungan, M.L., 1987. Indirect mutualism: complementary effects of grazing and predation in a rocky intertidal community. In: Kerfoot, W.C., Sih, A. (Eds.), *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England, Hanover, New Hampshire, pp. 188–200.
- Duran, L.R., Castilla, J.C., 1989. Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. *Mar. Biol.* 103, 555–562.
- Ebling, F.J., Kitching, J.A., Muntz, L., Taylor, C.M., 1964. The ecology of Lough Ine XIII. Experimental observations of the destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. *J. Anim. Ecol.* 33, 73–82.
- Eekhout, S., Raubenheimer, C.M., Branch, G.M., Bosman, A.L., Bergh, M.O., 1992. A holistic approach to the exploitation of intertidal stocks: limpets as a case study. *S. Afr. J. Mar. Sci.* 12, 1017–1029.
- Ehrlich, P., Birch, L.C., 1967. The ‘balance of nature’ and ‘population control’. *Am. Natur.* 101, 97–107.
- Elton, C.S., 1927. *Animal Ecology*. Sidgwick & Jackson, Ltd, London.
- Estes, J.A., Duggins, D.O., 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecol. Monogr.* 65, 75–100.
- Estes, J.A., Palmisano, J.F., 1974. Sea otters: their role in structuring nearshore communities. *Science* 185, 1058–1060.
- Estes, J.A., Smith, N.S., Palmisano, J.F., 1978. Sea otter predation and community organization in the western Aleutian Islands. *Alaska. Ecol.* 59, 822–833.
- Fairweather, P.G., 1985. Differential predation on alternative prey, and the survival of rocky intertidal organisms in New South Wales. *J. Exp. Mar. Biol. Ecol.* 89, 135–156.

- Fairweather, P.G., 1988. Consequences of supply-side ecology: manipulating the recruitment of intertidal barnacles affects the intensity of predation upon them. *Biol. Bull.* 175, 349–354.
- Fairweather, P.G., Underwood, A.J., 1991. Experimental removals of a rocky intertidal predator: variations within two habitats in the effects of the prey. *J. Exp. Mar. Biol. Ecol.* 154, 29–75.
- Fairweather, P.G., Underwood, A.J., Moran, M.J., 1984. Preliminary investigations of predation by the whelk *Morula marginalba*. *Mar. Ecol. Prog. Ser.* 17, 143–156.
- Fawcett, M.H., 1984. Local and latitudinal variation in predation on an herbivorous marine snail. *Ecology* 65, 1214–1230.
- Fraser, L.H., 1998. Top-down vs. bottom-up control influenced by productivity in a North Derbyshire, UK, dale. *Oikos* 81, 99–108.
- Fraser, L.H., Grime, J.P., 1997. Primary productivity and trophic dynamics investigated in a North Derbyshire, UK, dale. *Oikos* 80, 499–508.
- Fretwell, S.D., 1977. The regulation of plant communities by food chains exploiting them. *Persp. Biol. Med.* 20, 169–185.
- Fretwell, S.D., 1987. Food chain dynamics: the central theory of ecology? *Oikos* 50, 291–301.
- Gaines, S.D., Roughgarden, J., 1985. Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proc. Natl. Acad. Sci. USA* 82, 3707–3711.
- Garrity, S.D., Levings, S.C., 1981. A predator–prey interaction between two physically and biologically constrained tropical rocky shore gastropods: direct, indirect, and community effects. *Ecol. Monogr.* 51, 267–286.
- Grieg, M.J., Ridgway, N.M., Shakespeare, B.S., 1988. Sea surface temperature variations at coastal sites around New Zealand. *New Zealand J. Mar. Freshw. Res.* 22, 391–400.
- Hairton, N.G., Smith, F.E., Slobodkin, L.B., 1960. Community structure, population control, and competition. *Am. Natur.* 94, 421–425.
- Hairton, N.G.J., Hairton, N.G.S., 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *Am. Natur.* 142, 379–411.
- Hairton, N.G.J., Hairton, N.G.S., 1997. Does food web complexity eliminate trophic-level dynamics? *Am. Natur.* 149, 1001–1007.
- Hunter, M.D., Price, P.W., 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73, 724–732.
- Hutchins, D.A., Bruland, K.W., 1998. Iron-limited diatom growth and Si:N uptake ratios in a coastal upwelling regime. *Nature* 393, 561–564.
- Hutchins, D.A., DiTullio, G.R., Zhang, Y., Bruland, K.W., 1998. An iron limitation mosaic in the California upwelling regime. *Limnol. Oceanogr.* 43, 1037–1054.
- Hutchins, D.A., Franck, V.M., Brzezinski, M.A., Bruland, K.W., 1999. Inducing phytoplankton iron limitation in iron-replete coastal waters with a strong chelating ligand. *Limnol. Oceanogr.* 44, 1009–1018.
- Kingsland, S.E., 1985. *Modeling Nature*. Chicago University Press, Chicago, IL.
- Kitching, J.A., Sloane, J.F., Ebling, F.J., 1959. The ecology of Lough Ine VIII. Mussels and their predators. *J. Anim. Ecol.* 28, 331–341.
- Knox, G.A., 1953. The intertidal ecology of Taylor's Mistake. Banks Peninsula. *Trans. Roy. Soc. New Zealand* 81, 189–220.
- Kosro, P.M., Barth, J.A., Strub, P.T., 1997. The coastal jet: observations of surface currents along the Oregon continental shelf from HF radar. *Oceanography* 10, 53–56.
- Lawler, S.P., Morin, P.J., 1993. Food web architecture and population dynamics in laboratory microcosms of protists. *Am. Natur.* 141, 675–686.
- Leonard, G.H., Levine, J.M., Schmidt, P.R., Bertness, M.D., 1998. Flow-driven variation in intertidal community structure in a Maine estuary. *Ecology* 79, 1395–1411.
- Leonard, G.H., Ewanchuk, P.J., Bertness, M.D., 1999. How recruitment, intraspecific interactions and predation control species borders in a tidal estuary. *Oecologia* 118, 492–502.
- Levin, S.A., 1992. The problem of pattern and scale in ecology. *Ecology* 73, 1943–1967.
- Lewis, J.R., 1964. *The Ecology of Rocky Shores*. The English Universities Press Ltd, London, UK.
- Lively, C.M., Raimondi, P.T., 1987. Desiccation, predation, and mussel–barnacle interactions in the northern Gulf of California. *Oecologia (Berl.)* 74, 304–309.

- Lubchenco, J., 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. *Ecology* 64, 1116–1123.
- Lubchenco, J., 1986. Relative importance of competition and predation: early colonization by seaweeds in New England. In: Diamond, J.M., Case, T. (Eds.), *Community Ecology*. Harper and Row, New York, pp. 537–555.
- Lubchenco, J., Gaines, S.D., 1981. A unified approach to marine plant–herbivore interactions. I. Populations and communities. *Ann. Rev. Ecol. Syst.* 12, 405–437.
- Lubchenco, J., Menge, B.A., 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.* 48, 67–94.
- Lubchenco, J., Menge, B.A., Garrity, S.D., Lubchenco, P.J., Ashkenas, L.R., Gaines, S.D., Emler, R., Lucas, J., Strauss, S., 1984. Structure, persistence, and role of consumers in a tropical rocky intertidal community (Taboguilla Island, Bay of Panama). *J. Exp. Mar. Biol. Ecol.* 78, 23–73.
- Luckens, P.A., 1970. Breeding, settlement and survival of barnacles at artificially modified shore levels at Leigh, New Zealand. *New Zealand J. Mar. Freshw. Res.* 4, 497–514.
- Luckens, P.A., 1975. Predation and intertidal zonation of barnacles at Leigh, New Zealand. *New Zealand J. Mar. Freshw. Res.* 9, 355–378.
- Marquis, R.J., Whelan, C.J., 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75, 2007–2014.
- Martin, J.H., Fitzwater, S.E., 1988. Iron deficiency limits phytoplankton growth in the north-east Pacific subarctic. *Nature* 331, 341–343.
- McIntosh, R.P., 1985. *The Background of Ecology: Concept and Theory*. Cambridge University Press, Cambridge, England.
- McKendry, I.G., Sturman, A.P., Owens, I.F., 1988. Interactions between local winds and coastal sea surface temperatures near the Canterbury coast. *New Zealand J. Mar. Freshw. Res.* 22, 91–100.
- McPeck, M.A., 1998. The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecol. Monogr.* 68, 1–23.
- McQuaid, C.D., Branch, G.M., 1985. Trophic structure of rocky intertidal communities: response to wave action and implications for energy flow. *Mar. Ecol. Prog. Ser.* 22, 153–161.
- Menge, B.A., 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecol. Monogr.* 46, 355–393.
- Menge, B.A., 1978a. Predation intensity in a rocky intertidal community. Effect of an algal canopy, wave action and desiccation on predator feeding rates. *Oecologia (Berl.)* 34, 17–35.
- Menge, B.A., 1978b. Predation intensity in a rocky intertidal community. Relation between predator foraging activity and environmental harshness. *Oecologia (Berl.)* 34, 1–16.
- Menge, B.A., 1991a. Generalizing from experiments: is predation strong or weak in the New England rocky intertidal? *Oecologia* 88, 1–8.
- Menge, B.A., 1991b. Relative importance of recruitment and other causes of variation on rocky intertidal community structure. *J. Exp. Mar. Biol. Ecol.* 146, 69–100.
- Menge, B.A., 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? *Ecology* 73, 755–765.
- Menge, B.A., 2000. Recruitment vs. post-recruitment processes as determinants of barnacle population abundance on Oregon rocky shores. *Ecol. Monogr.* 70, 265–288.
- Menge, B.A., Berlow, E.L., Blanchette, C.A., Navarrete, S.A., Yamada, S.B., 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecol. Monogr.* 64, 249–286.
- Menge, B.A., Daley, B.A., Lubchenco, J., Sanford, E., Dahlhoff, E., Halpin, P.M., Hudson, G., Burnaford, J.L., 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecol. Monogr.* 69, 297–330.
- Menge, B.A., Daley, B.A., Wheeler, P.A., 1996. Control of interaction strength in marine benthic communities. In: Polis, G.A., Winemiller, K.O. (Eds.), *Food Webs: Integration of Pattern and Dynamics*. Chapman and Hall, New York, NY, pp. 258–274.
- Menge, B.A., Daley, B.A., Wheeler, P.A., Dahlhoff, E., Sanford, E., Strub, P.T., 1997a. Benthic–pelagic links and rocky intertidal communities: bottom-up effects on top-down control? *Proc. Natl. Acad. Sci. USA* 94, 14530–14535.

- Menge, B.A., Daley, B.A., Wheeler, P.A., Strub, P.T., 1997b. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. *Limnol. Oceanogr.* 42, 57–66.
- Menge, B.A., Freidenburg, T.L., Allison, G.A., Daley, B.A., Hudson, G., Lubchenco, J., Wheeler, P.A., Strub, P.T., 2000. Rocky intertidal oceanography: quantifying bottom-up effects in relation to rocky intertidal community structure. Unpublished manuscript.
- Menge, B.A., Lubchenco, J., 1981. Community organization in temperate and tropical rocky intertidal habitats: prey refuges in relation to consumer pressure gradients. *Ecol. Monogr.* 51, 429–450.
- Menge, B.A., Lubchenco, J., Ashkenas, L.R., Ramsey, F., 1986a. Experimental separation of effects of consumers on sessile prey in the low zone of a rocky shore in the Bay of Panama: direct and indirect consequences of food web complexity. *J. Exp. Mar. Biol. Ecol.* 100, 225–269.
- Menge, B.A., Lubchenco, J., Gaines, S.D., Ashkenas, L.R., 1986b. A test of the Menge–Sutherland model of community organization in a tropical rocky intertidal food web. *Oecologia (Berl.)* 71, 75–89.
- Menge, B.A., Olson, A.M., 1990. Role of scale and environmental factors in regulation of community structure. *Trends Ecol. Evol.* 5, 52–57.
- Menge, B.A., Sutherland, J.P., 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *Am. Natur.* 110, 351–369.
- Menge, B.A., Sutherland, J.P., 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *Am. Natur.* 130, 730–757.
- Minchinton, T.E., Scheibling, R.E., 1991. The influence of larval supply and settlement on the population structure of barnacles. *Ecology* 72, 1867–1879.
- Minchinton, T.E., Scheibling, R.E., 1993. Free space availability and larval substratum selection as determinants of barnacle population structure in a developing rocky intertidal community. *Mar. Ecol. Prog. Ser.* 95, 233–244.
- Morgan, S.G., 1995. Life and death in the plankton: larval mortality and adaptation. In: McEdward, L. (Ed.), *Ecology of Marine Invertebrate Larvae*. CRC Press, Boca Raton, FL, pp. 279–321.
- Morin, P.J., Lawler, S.P., 1996. Effects of food chain length and omnivory on population dynamics in experimental food webs. In: Polis, G.A., Winemiller, K.O. (Eds.), *Food Webs: Integration of Patterns and Dynamics*. Chapman & Hall, New York, NY, pp. 218–230.
- Murdoch, W.W., 1966. ‘Community structure, population control, and competition’ – A critique. *Am. Natur.* 100, 219–226.
- Navarrete, S.A., Menge, B.A., 1996. Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecol. Monogr.* 66, 409–429.
- Nielsen, K.J., 2000. Bottom-up and top-down forces in tidepools: test of a food chain model in a rocky intertidal community. *Ecology* (unpublished manuscript).
- Oksanen, L., 1983. Trophic exploitation and arctic phytoplankton biomass patterns. *Am. Natur.* 122, 42–52.
- Oksanen, L., 1988. Ecosystem organization: mutualism and cybernetics or plain Darwinian struggle for existence? *Am. Natur.* 131, 424–444.
- Oksanen, L., Fretwell, S.D., Arruda, J., Niemela, P., 1981. Exploitation ecosystems in gradients of primary productivity. *Am. Natur.* 118, 240–261.
- Osenberg, C.W., Mittelbach, G.G., 1996. The relative importance of resource limitation and predator limitation in food chains. In: Polis, G.A., Winemiller, K.O. (Eds.), *Food Webs: Integration of Patterns and Dynamics*. Chapman & Hall, New York, NY, pp. 134–148.
- Paine, R.T., 1966. Food web complexity and species diversity. *Am. Natur.* 100, 65–75.
- Paine, R.T., 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. *Ecology* 52, 1096–1106.
- Paine, R.T., 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia (Berl.)* 15, 93–120.
- Paine, R.T., 1984. Ecological determinism in the competition for space. *Ecology* 65, 1339–1348.
- Paine, R.T., 1986. Benthic community–water column coupling during the 1982–1983 El Niño. Are community changes at high latitudes attributable to cause or coincidence? *Limnol. Oceanogr.* 31, 351–360.
- Paine, R.T., 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* 355, 73–75.
- Palumbi, S.R., 1995. Using genetics as an indirect estimator of larval dispersal. In: McEdward, L. (Ed.), *Ecology of Marine Invertebrate Larvae*. CRC Press, Boca Raton, FL, pp. 369–387.
- Persson, L., 1999. Trophic cascades: abiding heterogeneity and the trophic level concept at the end of the road. *Oikos* 85, 385–397.

- Persson, L., Andersson, G., Hamrin, S.F., Johansson, L., 1988. Predator regulation and primary production along the productivity gradient of temperate lake ecosystems. In: Carpenter, S.R. (Ed.), *Complex Interactions in Lake Communities*. Springer-Verlag, New York, NY, pp. 45–68.
- Peterson, C.H., 1979. The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. *Oecologia (Berl.)* 39, 1–24.
- Pimm, S.L., 1991. *The Balance of Nature?*. University of Chicago Press, Chicago, Illinois.
- Pineda, J., 1999. Circulation and larval distribution in internal tidal bore warm fronts. *Limnol. Oceanogr.* 44, 1400–1414.
- Polis, G.A., 1999. Why are parts of the world green? Multiple factors control productivity and the distribution of biomass. *Oikos* 86, 3–15.
- Polis, G.A., Strong, D., 1996. Food web complexity and community dynamics. *Am. Natur.* 147, 813–846.
- Raimondi, P.T., 1990. Patterns, mechanisms, and consequences of variability in settlement and recruitment of an intertidal barnacle. *Ecol. Monogr.* 60, 283–309.
- Robles, C., Robb, J., 1993. Varied carnivore effects and the prevalence of intertidal algal turfs. *J. Exp. Mar. Biol. Ecol.* 166, 65–91.
- Robles, C.D., Sherwood-Stephens, R., Alvarado, M., 1995. Responses of a key intertidal predator to varying recruitment of its prey. *Ecology* 76, 565–579.
- Sanford, E., Menge, B.A., 2000. Spatial and temporal variation in barnacle growth in a coastal upwelling system. *Mar. Ecol. Prog. Ser.* (in press).
- Shanks, A.L., 1995. Mechanisms of cross-shelf dispersal of larval invertebrates and fish. In: McEdward, L. (Ed.), *Ecology of Marine Invertebrate Larvae*. CRC Press, Boca Raton, FL, pp. 323–367.
- Sih, A., Crowley, P., McPeck, M., Petranka, J., Strohmeier, K., 1985. Predation, competition and prey communities: a review of field experiments. *Ann. Rev. Ecol. Syst.* 16, 269–311.
- Stanton, B.R., Moore, M.I., 1992. Hydrographic observations during the Tasman boundary experiment of the west coast of South Island, New Zealand. *New Zealand J. Mar. Freshw. Res.* 26, 339–358.
- Stephenson, T.A., Stephenson, A., 1972. *Life Between Tidemarks On Rocky Shores*. Freeman, San Francisco, CA.
- Strong, D.R., 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73, 747–754.
- Sunda, W.G., Huntsman, S.A., 1997. Interrelated influence of iron, light and cell size on marine phytoplankton growth. *Nature* 390, 389–392.
- Sutherland, J.P., 1990. Recruitment regulates demographic variation in a tropical intertidal barnacle. *Ecology* 71, 955–972.
- Takeda, S., 1998. Influence of iron availability on nutrient consumption ratio of diatoms in oceanic waters. *Nature* 393, 774–777.
- Tegner, M.J., Dayton, P.K., 1987. El Niño effects on Southern California kelp forest communities. *Adv. Ecol. Res.* 17, 243–279.
- Tegner, M.J., Dayton, P.K., Edwards, P.B., Riser, K.L., 1997. Large-scale, low-frequency oceanographic effects on kelp forest succession: a tale of two cohorts. *Mar. Ecol. Prog. Ser.* 146, 117–134.
- Underwood, A.J., 1981. Techniques of analysis of variance in experimental marine biology and ecology. *Ann. Rev. Oceanogr. Mar. Biol.* 19, 513–605.
- Underwood, A.J., 1997. *Experiments in Ecology*. Cambridge University Press, Cambridge, UK.
- Underwood, A.J., Denley, E.J., Moran, M.J., 1983. Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia (Berl.)* 56, 202–219.
- Vincent, W.F., Howard-Williams, C., Tildesley, P., Butler, E., 1991. Distribution and biological properties of oceanic water masses around the south Island, New Zealand. *New Zealand J. Mar. Freshw. Res.* 25, 21–42.
- White, T.R.C., 1978. The importance of relative shortage of food in animal ecology. *Oecologia* 33, 233–242.
- Wiens, J.A., 1989. Spatial scaling in ecology. *Funct. Ecol.* 3, 385–397.
- Witman, J.D., Leichter, J.J., Genovese, S.J., Brooks, D.A., 1993. Pulsed phytoplankton supply to the rocky subtidal zone: influence of internal waves. *Proc. Natl. Acad. Sci. USA* 90, 1686–1690.
- Wootton, J.T., Power, M.E., 1993. Productivity, consumers, and the structure of a river food chain. *Proc. Natl. Acad. Sci. USA* 90, 1384–1387.
- Wootton, J.T., Power, M.E., Paine, R.T., Pfister, C.A., 1996. Effects of productivity, consumers, competitors, and El Niño events on food chain patterns in a rocky intertidal community. *Proc. Natl. Acad. Sci. USA* 93, 13855–13858.