Inter-hemispheric comparison of bottom-up effects on community structure: Insights revealed using the comparative-experimental approach

Bruce A. Menge,* Eric Sanford,[†] Bryon A. Daley,[‡] Tess L. Freidenburg, Gregory Hudson and Jane Lubchenco

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

The comparative-experimental approach uses identically designed, replicated experiments at different sites along environmental gradients in order to gain insight into the changing dynamics of communities with changing environmental conditions. Such studies reveal how ecological processes vary in intensity and interact to produce community structure. Early emphases were on the community consequences of shifting top-down impacts, competition and disturbance with environmental stress. Recent advances include the more precise quantification of gradients and thus a better understanding of species responses to the environment, and the revelation that bottom-up forces can vary significantly on within-region scales, with major consequences for the impact of top-down forces and thus community dynamics. Here the use of the method to examine the role of geographic location (coastal ecosystems in different hemispheres) and oceanographic conditions (upwelling *vs* downwelling) on these bottom-up/top-down linkages is advanced. We show that a bottom-up factor (prey recruitment) and a top-down effect (predation rate) vary consistently with oceanographic conditions within each coastal ecosystem, and also between geographic locations (New Zealand, Oregon). In general, both recruitment and predation rates are higher in Oregon. It is postulated that these differences are common responses to oceanographic variation, and that between-hemisphere differences result from the stronger and more persistent upwelling in the California Current ecosystem.

Key words: bottom-up; predation; recruitment; top-down; upwelling.

INTRODUCTION

The 'comparative-experimental approach' has proven to be a powerful technique in the study of community and ecosystem dynamics (Dayton 1971; Menge & Sutherland 1976, 1987; Menge 1976, 1991a; McPeek 1998). In particular, this approach has been a central tool in efforts to investigate how community dynamics vary across large spatial scales (Dayton 1971; Menge 1976; Menge

et al. 1994, 1999). By performing identically designed, replicated experiments at different sites along environmental gradients, ecologists have evaluated how site-specific processes are modified by environmental conditions to generate large-scale patterns of structure and dynamics.

In marine intertidal habitats, early studies focused primarily on how species interactions were influenced by factors varying along wave exposure gradients (Kitching *et al.* 1959; Ebling *et al.* 1964; Dayton 1971; Menge 1976; Lubchenco & Menge 1978; Peterson 1979). In all of these studies, the focus was on top-down effects (predation, herbivory) and competition. Bottom-up effects (nutrients, productivity), although long assumed to be primary determinants of community structure and dynamics in many terrestrial, freshwater, and pelagic ocean communities (Fretwell 1977, 1987; White 1978; Carpenter *et al.* 1985, 2001), were until recently regarded as secondary to top-down

effects in benthic marine habitats (Menge 1992). The general assumption among benthic marine researchers was that oceanographic conditions were more or less homogeneous over scales of 100s to 1000s of kilometers and thus likely to have little influence in underlying variation in community structure and dynamics. Remote sensors, however, often revealed striking and consistent variation in oceanographic conditions (e.g. sea surface temperature, chlorophyll) associated with specific coastal areas, suggesting the alternative view that such variability may have important ecological consequences in coastal benthic environments. Indeed, recent studies in South Africa, Oregon, New Zealand and Chile have revealed strong bottom-up 'signals' in rocky intertidal communities (review in Menge 2000).

In this paper we examine the role of the comparative-experimental method in advancing our understanding of the functioning of nearshore ecosystems. We focus in particular on studies having as their central unit 'interaction webs' or that subset of strongly interacting species largely responsible for regulating communities (Menge & Sutherland 1987). Our ultimate goal is a search for general organizational principles as revealed by empirical studies. We first discuss the historical development of the approach, then summarize conceptual advances, and finish with a brief summary of recent insights regarding the role of bottom-up factors in determining community variation.

Origins of the approach

The widely cited classic studies by Dayton (Dayton 1971, 1975) on the shores of the outer coast and the San Juan Islands ('inner coast') of Washington appear to be the first influential example of the comparative-experimental approach. Dayton's research asked how species interactions and physical disturbance varied along an extended gradient of wave exposure and desiccation, and how this related to variation in community structure. Outer coast sites experienced heavier wave turbulence from oceanic swells and lower thermal and desiccation stress, while inner coast sites received moderate to little wave turbulence but more severe thermal and desiccation stress. Along this gradient, Dayton quantified shifts in species abundances

and composition, with mussels and kelps dominating mid and low zone space, respectively, at the outer coast sites. A large barnacle (*Semibalanus cariosus* (Pallas)), replaced mussels as the mid zone dominant at more exposed sites in the San Juan Islands, but at the most sheltered sites, all sessile animals were sparse. Canopy species dominated the low zone at all but the most sheltered site, where a sparse cover of 'fugitive' algal species was the primary spatial occupier.

Comparisons and experiments in the mid zone showed that predation by whelks and sea stars and inadvertent dislodgment by limpets prevented barnacles and ultimately mussels from dominating space in the lower mid zone at outer coast sites (Dayton 1971). Mussels (*Mytilus* spp.) were extremely sparse at inner coast sites, and in the absence of predation *S. cariosus* was the dominant space occupant in the mid zone. As suggested by hierarchical competition among the barnacle and mussel experiments in predator exclusion cages, each of these sessile organisms (*M. californianus* Conrad, *S. cariosus*) was the dominant competitor for space in the portion of the environmental gradient for which each was the main zone-forming species. Higher on the shore, disturbance from wave action and log abrasion prevented mussels (outer coast) or *S. cariosus* (inner coast) from occupying all the space.

In the low zone, competition for space was also hierarchical, and was the primary process underlying the dominance of different kelp species on different portions of the environmental gradient. Other experiments (Paine 1966, 1974; Paine & Vadas 1969) suggested that predation by sea stars prevented mussels from displacing low zone occupants, and that sea urchin herbivory could have localized affects on abundance and species composition of algae.

Insights gained from this pioneering comparative-experimental study were as follows. First, although competition for space was hierarchical, the outcome of competition varied along the environmental gradient. Species such as *M. californianus* or the kelp *Hedophyllum sessile* (C. Ag.) Setchell dominated under certain conditions (outer coast conditions for mussels, intermediate wave exposures for the kelp) but not others. The factors underlying the absence of mussels at inner coast sites were unclear; more recent studies suggest a

lack of recruitment is a major cause (B. A. Menge *et al.* unpublished data). Dayton suggested that physiological stress was the primary factor underlying the absence of *Hedophyllum* from the most wave-sheltered site. Second, although predation was not tested in the low zone, predation by sea stars and whelks on mussels and barnacles in the lower mid zone seemed strong along the entire environmental gradient, from wave-exposed to wave-sheltered sites. Third, physical disturbance was also an important space-clearing process along the entire gradient. Together, these two results seemed to explain the persistently high availability of free space, and suggested that competitive monopolies of space were thereby prevented by persistent and intense predation and disturbance.

Comparative-experimental studies in New England and Panama

Inspired by both the results and the approach of Dayton, Menge and Lubchenco carried out similar studies along the coasts of New England and the Pacific Coast of Panama (Menge 1976; Lubchenco & Menge 1978; Lubchenco 1980, 1983, 1986; Menge & Lubchenco 1981; Lubchenco *et al.* 1984; Menge *et al.* 1986a,b). In temperate New England, rocky intertidal communities were generally similar in structure to those on the Washington coast, with the exception that in New England, rock surfaces in low intertidal zones were dominated by mussels, not free space. As in Washington, competition for space was hierarchical, and differences in community structure along a wave exposure gradient resulted in part from how species interactions were modified by environmental conditions. Although the effects of wave-related physical disturbance were generally greater at wave-exposed sites (Menge & Farrell 1989), infrequent catastrophic disturbance from the formation of sea ice has the potential to influence more sheltered sites as well (Wethey 1985). In contrast to Washington, however, predation and grazing intensity varied along the wave exposure gradient. Experiments suggested that low predation and grazing at more wave-exposed s ites was the result of inhibition of consumer activity by wave forces (Menge 1978a,b; Lubchenco 1986).

These insights led to the development of 'environmental stress' models of community regulation (Menge & Sutherland 1976, 1987; Menge & Olson 1990). These models predicted that community structure varied in predictable ways along gradients of both environmental stress and rates of recruitment of the habitat-forming species. Species interactions and their impact on community structure are contingent on the particular complement of physical conditions (wave forces, thermal conditions, salinity, light, etc.). Under the most severe environmental conditions, physical stresses prevent competitive exclusion and consumer activity and directly structure communities. Under moderate conditions, stress still inhibits consumers but does not prevent competitive exclusion, so competition is a dominant structuring agent. Under benign conditions, consumer activity is high and predation and grazing effects predominate in structuring communities. Low recruitment rates have the effect of lessening the role of competition for space, so that either environmental stress (severe environmental conditions) or predation (benign environmental conditions) are primary determinants of structure.

The studies in Panama were designed as a test of the environmental stress models. There, we learned that, as expected, predation and grazing were dominant forces in structuring these highly diverse rocky intertidal communities (Menge & Lubchenco 1981; Menge *et al.* 1983; Lubchenco *et al.* 1984; Menge *et al.* 1985, 1986a,b). We also discovered that rates of recruitment were extremely low in Panama (Menge 1991b), and thus as the models predicted, that competition was unimportant as a structuring agent. Although severe wave conditions do sometimes occur in Panama, physical disturbance was a minor factor because sessile organisms, the target of disturbance from waves and wave-borne objects, were extremely sparse, and therefore there was little to disturb.

Insights revealed by the New England and Panama studies thus focused attention on top-down forces, competition, and recruitment as key determinants of community structure. These results also suggested a conceptual framework, the environmental stress model, that helped to understand the among-site variation in each geographic location.

Unexplained variation, scale and ecosystem dynamics

Although the environmental stress models were successful at helping to understand certain aspects of community pattern, the causes of some variation were unexplained, or at least, remained untested. For example, in Dayton's studies the factors underlying changes in species composition along environmental gradients, such as the near-absence of mussels at inner coast sites, or of *Hedophyllum* from the most wave-sheltered sites, were not understood, and the generality of the role of predation in preventing mussels from displacing low zone macrophyte stands was untested.

Another example of unexplained variation was observed on the Oregon coast (Menge 1992). As was observed in Washington, most sites in Oregon exhibited the classic zonation pattern of a high intertidal barnacle/fucoid zone, a mid intertidal mussel zone, and a low intertidal macrophyte zone. However, closer observation revealed that at some sites, habitat-forming sessile invertebrates such as mussels and barnacles, normally mid-zone dominants, also occupied a substantial fraction of space in the low intertidal zone. In addition, rates of predation by sea stars were high at these sites. In contrast, at other sites, sessile invertebrates were nearly absent from the low zone, and sea star predation was low. Other observations suggested that, in fact, these differences might be attributable to differences in recruitment rates of sessile invertebrates and their predators, and/or to differences in secondary production or growth of sessile invertebrates. These observations led logically to the consideration of varying oceanographic conditions as a possible explanation of unexplained pattern. Simultaneous studies in South Africa (Bustamante *et al.* 1995a,b; Bustamante & Branch 1996a,b) pointed in a similar direction. That is, despite earlier assumptions that oceanographic variation occurred at scales too large to influence variation on the scale of local communities along the coast, new evidence was consistent with the hypothesis that bottom-up factors might contribute to the previously unexplained variation among sites, especially on scales of 10s to 100s of kilometers.

In Oregon, our initial focus was on two contrasting sites, Boiler Bay and Strawberry Hill, separated by 80 km. Dominant space occupiers in the wave-exposed low zone at Boiler Bay were macrophytes, including kelps, turfs, and surfgrass, whereas at Strawberry Hill, dominants were sessile invertebrates including mussels (*Mytilus* spp.) and barnacles (*Pollicipes polymerus* Sowerby, *Balanus* spp., *Semibalanus cariosus*) (Menge *et al.* 1994). Field studies indicated that both barnacles and mussels grew faster at Strawberry Hill, and water sampling confirmed our visual impression that the food of these filter-feeders, phytoplankton and detritus, was consistently more concentrated at this site (Menge 1992; Menge *et al.* 1994, 1997a,b). Subsequent investigations at eight sites ranging over ~250 km along the Oregon coast indicated that these two sites were representative of sectors of coastline, with some sectors having consistently lower concentrations of chlorophyll-a and particulates and others having higher concentrations (Menge *et al.* 1997a; Menge 2000, 2002). In addition, recruitment of mussels was correlated with chlorophyll-a concentration, suggesting a possible trophic effect of phytoplankton concentration on larval and recruit survival and growth (Menge 2002). Yet another potentially important bottom-up effect on invertebrates was suggested by correlation between recruitment rates and growth rates of both mussels and barnacles (Menge 2002; Sanford & Menge 2001). Adults of both mussels and barnacles are known to consume zooplankton (André *et al.* 1993; Navarrete & Wieters 2000), and one interpretation of a positive relationship between adult growth and recruitment rates is that growth is enhanced by predation on larvae.

Oceanographic evidence suggests that these bottom-up differences reflect variation in nearshore oceanography (Menge *et al.* 1997a). Along the Oregon coast, the path of the southward-flowing California Current is evidently influenced by the continental shelf margin. Satellite imagery and high frequency radar measurement of surface currents (Kosro *et al.* 1997; Menge *et al.* 1997a) indicate that during upwelling events, currents move faster and away from shore in the Boiler Bay sector, whereas both onshore and offshore movement of water is slower and more variable in the Strawberry Hill sector. Onshore water samples indicate that nutrients vary little between sites (Menge *et al.* 1997a). We have inferred from these patterns that transport of larvae and other

particulates in the Boiler Bay sector is primarily southward, offshore and rapid, leading to low concentrations of phytoplankton and larvae due to dilution. In the Strawberry Hill sector, currents are slower and often form an offshore eddy that we infer retains particulates and nutrients sufficiently long to generate phytoplankton blooms. Current reversals during upwelling relaxation tend to deliver surface water shoreward in a north-easterly direction, with the apparent consequence that water impacting the Boiler Bay sector has low chlorophyll-a and low larval concentration leading to low recruitment and low growth of sessile invertebrates. We infer further that water impacting the Strawberry Hill sector has high chlorophyll-a and high larval concentration, leading to high recruitment and high growth of sessile invertebrates. Thus, the dominance of seaweeds at Boiler Bay may depend on oceanographic conditions favoring macrophytes at the expense of invertebrates (high nutrients, low growth and recruitment of invertebrates). The dominance of invertebrates at Strawberry Hill may depend in part on conditions favoring invertebrates at the expense of algae despite high nutrients (high growth and recruitment of invertebrates, possibly leading to pre-emptive exclusion of macrophytes).

These bottom-up differences among sites were associated with differences in top-down effects (Menge 1992, 2002; Menge *et al.* 1994, 1996, 1997a; Navarrete & Menge 1996). Field experiments demonstrated consistently higher rates of predation by sea stars at Strawberry Hill, and revealed that these differences were consistent with the between-sector differences in bottom-up and oceanographic factors summarized above. We concluded that through trophic interactions, the bottom-up differences in growth and recruitment were the primary factors underlying the top-down differences in predation rate and impact.

Between-hemisphere comparison

These results suggested that sufficient variation in oceanographic conditions occurred on spatial scales of 10s to 100s of kilometers to underlie significant among site variations within an upwelling-influenced ecosystem, the Oregon coast. Many questions remained unanswered in these studies, but two that we focused on were (i) does

similar variation occur in independently evolved ecosystems; and (ii) do differences similar to those seen among sites within an upwelling region also occur between sites occurring in upwelling- versus downwelling-dominated regions? To address these questions, we carried out similar research on the South Island of New Zealand. We selected this location because of its climatic and biological similarities to Oregon, and because sites in contrasting oceanographic conditions on opposite sides of the island were only ~200 km apart, allowing simultaneous intensive field studies.

Study regions and sites

Although the biota of New Zealand and Oregon are independently evolved, sharing no species in common, they have broadly similar organismal composition and occur in comparable physical environments (Morton & Miller 1968; Morris *et al.* 1980). Barnacles dominate the high zone, mussels the mid zone, and a mix of macrophytes, sessile invertebrates and bare space occupy the low zone. Herbivores (limpets, littorines and other gastropods, chitons) and predators (whelks, sea stars) are common.

New Zealand is not one of the world's major upwelling regions, but oceanographic conditions do generate intermittent upwelling regions on the South Island (Stanton 1976; Vincent *et al.* 1991; Stanton & Moore 1992). The eastward-flowing Tasman Current separates on the west coast into the north-easterly flowing Westland Current and the Southland Current, which wraps around the southern end of the island, and then flows north-eastward parallel to the east coast. In the southern hemisphere, Ekman transport deflects to the left, creating upwelling conditions along the central and northern sectors of the west coast, and downwelling conditions inshore of the Southland Current (Menge *et al.* 1999).

In 1994–1995, studies identical in design to those carried out in Oregon were performed at two sites each on the central west and east coasts of the South Island of New Zealand (Menge *et al.* 1999). The west coast sites, Twelve-Mile Beach North and Twelve-Mile Beach South were in the intermittent upwelling region of the Westland Current and the east coast sites, Boulder Bay and Box Thumb, were in the downwelling region of the Southland

Current. The similarity in design allowed direct comparison of rates of recruitment of barnacles and mussels and of predation rates quantified in Oregon and New Zealand. We compared our New Zealand results to the earlier Oregon results obtained at Boiler Bay and Strawberry Hill, ~8 km apart on the central Oregon coast.

METHODS

Recruitment

In both Oregon and New Zealand, recruitment of barnacles was quantified using 10×10 cm plexiglass settlement plates coated with Safety Walk (3M, Minneapolis, MN, USA), a rubbery plastic with a uniformly textured surface (Menge *et al.* 1994). Recruitment of mussels was quantified using plastic-mesh balls (Tuffy pot scrubbers; The Clorox Company, Oakland, CA, USA) (Menge *et al.* 1994). Five replicate plates or tuffies were deployed monthly from October through March in the mid zone at each site. Cyprids and metamorphs were identified and counted in the laboratory under a dissecting microscope. Mussel recruits were counted by opening the tuffy, spreading it flat and scanning both sides under a dissecting microscope.

Densities of recruits are expressed as number per 100 cm^2 of plate or tuffy per month. We calculated annual average summer recruitment by totaling the number of recruits settling onto each replicate and dividing by the number of replicate-months. Replicates were sometimes missing, so site-by-tidal level averages were based only on the number of months for which data were available for each replicate. Recruitment in both New Zealand and Oregon tended to be low in winter and to reach a peak in late summer. Thus we compared only 'summer' data from each region (June–October for Oregon, November–March for New Zealand).

Predation

Predation rates also were quantified using an approach identical to that used in Oregon (Menge *et al.* 1999; Sanford 1999). Mussels (*M. californianus* or *M. trossulus* (Gould) in Oregon, *M. gallo-*

provincialis (Lamarck) and/or *Perna canaliculus* (Gmelin) in New Zealand) were translocated to the low zone foraging area of the sea stars (*Pisaster ochraceus* (Brandt) in Oregon, *Stichaster australis* (Verrill) in New Zealand). Clumps of 30–50 individuals, each ~4–6 cm in length, were placed under plastic mesh (Vexar; NorPlex, Auburn, WA, USA) and held in place with plastic washers and stainless steel screws inserted into plastic wall anchors in drilled holes. After 4–6 weeks, the mussels were firmly reattached, and cages were removed. Mussel clumps were located in replicate sections of shore with either sea stars present (+sea stars; the normal, 'reference' condition) or sea stars absent (–sea stars; the removal). Sea star removal was achieved manually, by dislodging and moving sea stars to adjacent areas at the site not involved in the experiment. Rates of predation were determined by periodically (weekly to monthly) quantifying the losses of mussels from each clump for three to five months. The –sea star treatments served as 'controls' for background mussel mortality due to causes other than sea stars. In the early Oregon experiments, loss in –sea star plots was sometimes unexpectedly high. Field observations indicated, however, that these losses were also due to sea star predation, imposed by individuals that had eluded our efforts to keep them away from the mussel clumps. More recent experiments using cages, fences or more effective manual removal techniques have shown that mussel mortality in 'controls' (–sea stars) is invariably slight ($< 5\%$), so we have based our estimates of mortality on $+$ sea star treatment data uncorrected by losses in –sea star treatments.

We present predation rates here as proportion of mussels in each clump lost per day (*per population* rates) or proportion of mussels lost per day per sea star (*per capita* rates). Per population mussel mortality rates were estimated as the slope of the mussel mortality curve for each mussel clump, averaged across the multiple clumps (five to 10) nested within each replicate plot (Navarrete & Menge 1996). Linear regression was used to estimate slopes. For regressions to accurately reflect actual loss rates, we did not include dates with zero mussels surviving beyond the first date with zero mussels. For this reason, the time period in days for regressions varied, with a minimum of 3 days required for each.

Per capita mortality rates were estimated as the proportion of mussels lost per day per sea star over the first 14 days of each experiment. Per capita comparisons were based on the second (1995) New Zealand experiment (Menge *et al.* 1999) and on an Oregon experiment carried out in 1997 (Sanford 1999). In this analysis, we wanted to compare predation rates under optimal conditions, so we used only data from high predation sites (Strawberry Hill in Oregon, Twelve-Mile Beach in New Zealand). These experiments were monitored at a higher frequency than were the earlier experiments, and sea star density was quantified on a per replicate transplant basis, allowing a more precise estimate of per capita predation rates (Sanford 1999). Since *Pisaster* have been shown to greatly reduce foraging activity during cold-water (upwelling) events, we used only data from the three non-upwelling periods (of five total sample periods) in the Oregon study (see Sanford 1999).

The New Zealand studies were conducted in 1994–1995. The Oregon recruitment studies were begun in 1989 and have been conducted continuously since then. Predation experiments in Oregon were done in 1990, 1991, 1993, 1997, 1999 and 2000. Here we focused primarily on data from 1989 to 1991, as the results have remained consistent through time, and data from this period were sufficient for our comparisons. We also included recruitment data from 1995 as this allowed comparison between regions within the same year.

Data analysis

Data were analyzed using the general linear model module of SYSTAT, version 10 (SPSS, Chicago, IL, USA). To compare Oregon recruitment results directly with both the Oregon predation data and the New Zealand predation and recruitment data, we have presented recruitment data from Oregon from 1989 to 1991 and 1995. Recruitment data from 1995 only were used in the analysis to remove possible temporal confounding of the comparisons. Oregon predation rate data were not available from 1995, so we compared the 1990, 1991 and 1997 Oregon results to the 1994–1995 and 1995 experiments in New Zealand. For recruitment and per population predation rate analyses, we categorized the data by geographic location (Oregon, New Zealand) and by 'oceanographic conditions.' In Oregon, the contrasting oceanographic conditions were the differences between Boiler Bay and Strawberry Hill in upwelling intensity, phytoplankton productivity and larval transport (Menge *et al.* 1997a,b; Menge 2002). In New Zealand, the contrasting oceanographic conditions were the between-coast differences in upwelling versus downwelling conditions, which also corresponded to a difference in productivity and larval transport (Menge *et al.* 1999). For the per capita predation rate analysis, as we used only data from the highest predation sites, we categorized the data by geographic location only (Oregon, New Zealand).

Visual inspection of untransformed studentized residuals indicated the data were neither normal nor independent so the data were transformed for analysis (ln [$x + 1$] for recruitment, ln [$x \times 100$] for predation rates). Cochran's c-test (Winer *et al.* 1991) indicated that variances for the recruitment analysis were homoscedastic, but that even after transformation, variances for the predation rate analysis were heteroscedastic. Differences in this latter analysis were highly significant, however, suggesting that these results were likely to be robust (Underwood 1981, 1997).
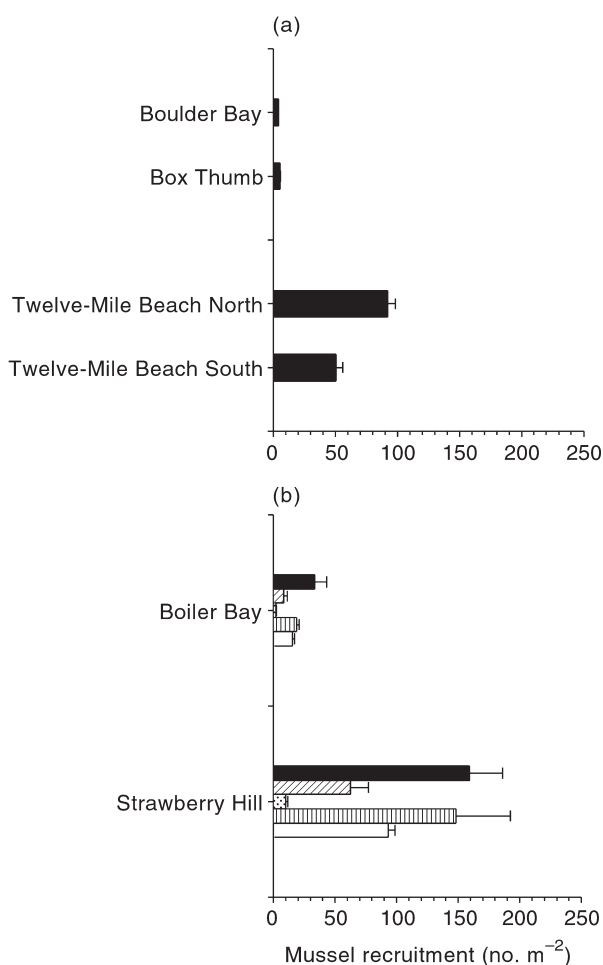
RESULTS

Recruitment of mussels differed both between geographic locations (higher in Oregon than in New Zealand) and between sites in contrasting oceanographic conditions (higher at Strawberry Hill in Oregon and on the west coast in New Zealand) (Table 1). Judging from the magnitude of the mean squares, oceanographic conditions accounted for the majority of the variation among sites in mussel recruitment. Recruitment density of mussels was consistently higher at the more productive sites (Strawberry Hill in Oregon, Twelve-Mile Beach in New Zealand; Fig. 1, Table 1, the interaction between location and conditions was not significant). In Oregon, mussel recruitment at Strawberry Hill was about five- to eight-fold greater than at Boiler Bay, while in New Zealand, west coast mussel recruitment was about nine- to 23-fold greater than the east coast (Fig. 1).

Recruitment of barnacles was context dependent, with high rates at both Oregon sites but with

Table 1 Analysis of variance test of the effect of geographic location (Oregon, New Zealand) and oceanographic conditions (upwelling, downwelling) on mussel recruitment.

Source of variation	d.f.	MS	F	P	R^2
Geographic location	1	5.6328	66.7	<<0.000001*	
Oceanographic conditions	1	34.4867	408.1	<<0.000001*	
Location × conditions	1	0.2638	3.13	0.09	0.955
Error	26	0.0845			

MS, mean square; d.f., degrees of freedom. *Significant effects.

Fig. 1. Average monthly recruitment of mussels during 'summer'. (a) New Zealand (*M. galloprovincialis, Perna canaliculus, Aulocomya maiorana* Iredale combined). (■) 1994–1995. (b) Oregon (*M. trossulus, M. californianus* combined). (■) 1989; (▨) 1990; (▒) 1991; (▥) 1995; (□) Total.

in the upwelling-influenced areas (New Zealand west coast, both Oregon sites) regardless of geographic location. Judging from the magnitude of the mean squares, however, more variance was attributable to geographic location than to oceanographic conditions. In Oregon, barnacle recruitment showed no consistent between-site trends, being higher at one site in some years, and higher at the other site in other years (Fig. 2). In New Zealand, in contrast, barnacle recruitment density at west coast sites was approximately 18- to 20-fold greater than at east coast sites (Fig. 2). In 1995, barnacle recruitment in Oregon ranged from approximately 3.5- to 65-fold greater than in New Zealand.

Per population predation rates displayed differences similar to those of recruitment between geographic locations and oceanographic conditions. In Oregon, predation was greater at Strawberry Hill than at Boiler Bay, and in New Zealand, predation was greater on the west coast than on the east coast (Fig. 3, Table 3). The magnitude of the mean squares suggested that as with barnacle recruitment, more of the variation in predation rates was attributable to geographic location than to oceanographic conditions in each region. Predation was evidently more intense in Oregon than in New Zealand (Fig. 3, Table 3) with Oregon rates six- to 10-fold greater than New Zealand rates. Predation rates within Oregon varied by 1.8- to 3.8-fold, while within New Zealand, predation rates varied by 6.1- to 23-fold, suggesting a larger relative impact of downwelling (*vs* upwelling) conditions on predation (i.e. in New Zealand) than of variation within an upwelling ecosystem (i.e. in Oregon).

These between-oceanographic conditions differences in per population predation rates, however, are confounded by differences in predator density.
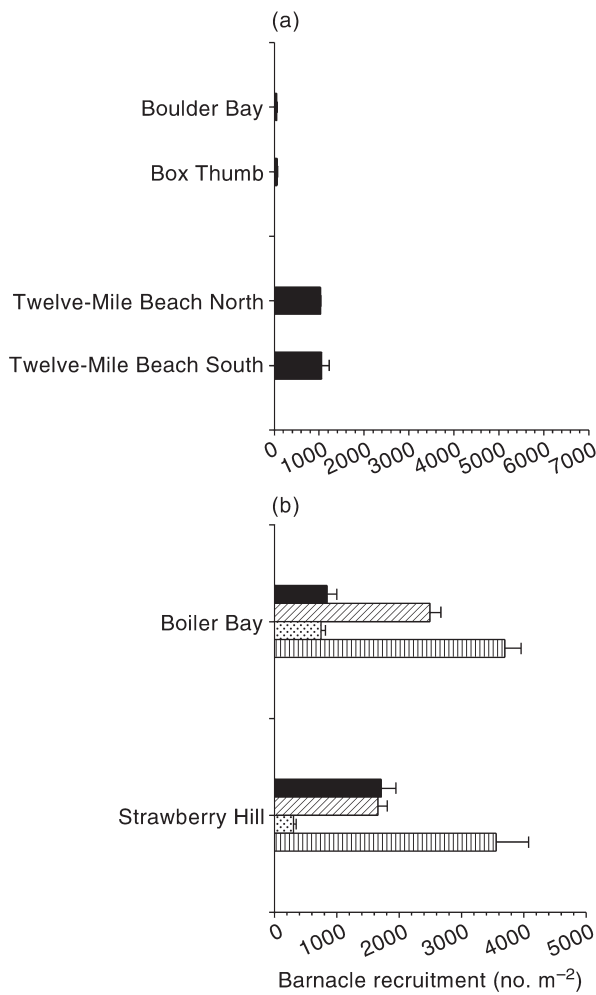
higher rates at west coast than east coast sites in New Zealand (Fig. 2, Table 2). The significant location–condition interaction (Table 2) suggested that for barnacles, recruitment was generally high

Fig. 2. Average monthly recruitment of barnacles during 'summer'. (a) New Zealand (*Chamaesipho columna* (Spengler), *C. brunnea* Moore, *Epopella plicata* (Gray) combined). (■) 1994–1995. (b) Oregon (*Chthamalus dalli* Pilsbry, *Balanus glandula* Darwin combined). (■) 1989; (▨) 1990; (▨) 1991; (▥) 1995.

At wave-exposed sites in Oregon, sea stars were more abundant at Strawberry Hill ($\sim$2–5/m^2) than at Boiler Bay ($\sim$0–0.7/m^2; Menge *et al.* 1994; Navarrete & Menge 1996). Similarly, at wave-exposed sites in New Zealand, sea stars were more abundant at Twelve-Mile Beach ($\sim$1.2–2.3/m^2) than at Box Thumb and Boulder Bay (0–0.01/m^2; Menge *et al.* 1999; B. A. Menge *et al.* unpublished data). Thus, the differences
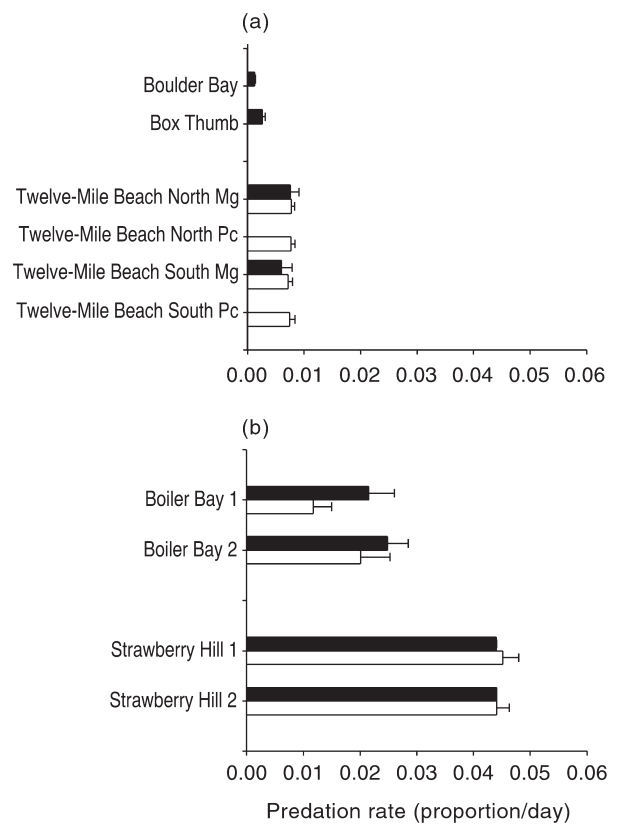
Fig. 3. Rate of predation on mussels (proportion of translocated mussels/day) by sea stars. (a) New Zealand (*Stichaster australis*). (■) 1994–1995, Expt 1; (□) 1995, Expt 2. (b) Oregon (*Pisaster ochraceus*). (■) 1990; (□) 1991.

Table 2 Analysis of variance test of the effect of geographic location (Oregon, New Zealand) and oceanographic conditions (upwelling, downwelling) on barnacle recruitment.

Source of variation	d.f.	MS	F	P	R^2
Geographic location	1	49.4547	497.8	<<0.000001*	
Oceanographic conditions	1	13.9161	140.1	<<0.000001*	
Location × conditions	1	15.1650	152.6	<<0.000001*	0.973
Error	26	0.0994			

MS, mean square; d.f., degrees of freedom. *Significant effects.

Table 3 Analysis of variance test of effect of geographic location (Oregon, New Zealand) and oceanographic conditions (upwelling, downwelling) on per population predation rates.

Source of variation	d.f.	MS	F	P	R²
Geographic location	1	14.8058	274.2	<<0.000001*	
Oceanographic conditions	1	4.3283	80.2	0.000001*	
Location × conditions	1	0.2477	4.6	0.053	0.962
Error	12	0.0540			

MS, mean square; d.f., degrees of freedom. *Significant effects.
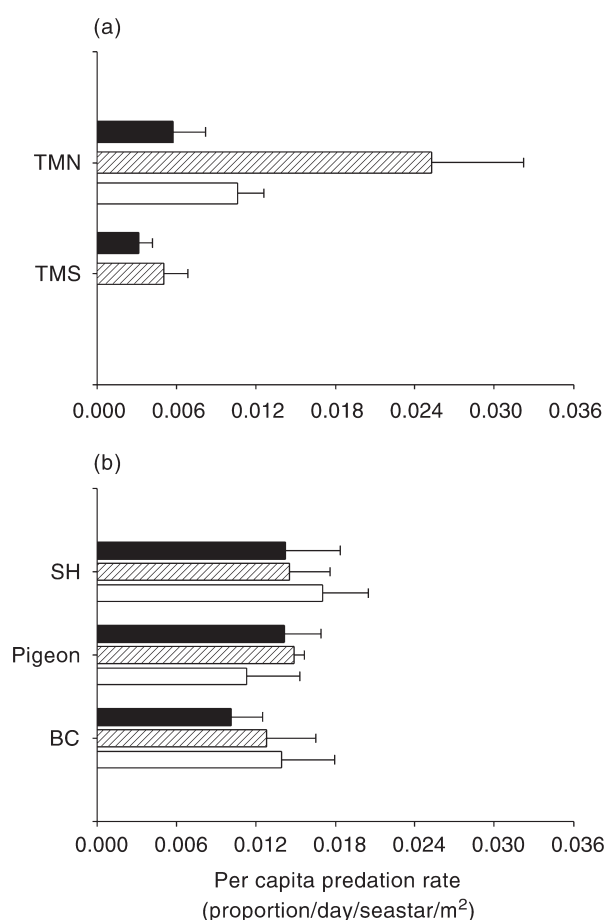
Fig. 4. Per capita rate of predation on mussels (proportion of transplanted mussels per day, divided by local sea star density) during 14-day trials. (a) New Zealand, 1995. (■) Center; (▨) Edge; (□) Edge plot after three outlier replicate values are removed. In New Zealand, predation was quantified both on the edge and the center of two experiment benches (Menge *et al.* 1999). (b) Oregon, 1997. (■) Period 1; (▨) Period 2; (□) Period 3. In Oregon, predation was quantified on three experimental benches, during three separate non-upwelling periods (Sanford 1999).

between sites in difference oceanographic conditions and even between geographic locations may be attributable to differences in predator abundance.

Per capita rates, however, suggest that there may be fundamental differences in sea star predation between geographic locations (Fig. 4). With the exception of one site ('edge' of bench at Twelve Mile Beach North; Fig. 4), per capita predation rates at Strawberry Hill were about threefold greater than per capita predation rates at Twelve-Mile Beach. Analysis of variance suggested that three of the five replicates for the Twelve Mile Beach North edge site were outliers; with the outliers included, Oregon rates tended to be greater than New Zealand rates but the difference was not significant ($P = 0.08$; 1, 54 d.f.). Omission of the outliers from the analysis yielded a large between-geographic location difference ($F = 29.2$; p = 0.000002; 1, 51 d.f.), but this site still had the highest rate of predation observed in the New Zealand experiments. As has been noted elsewhere (Menge *et al.* 1999), the New Zealand results suggested a potentially important effect of topography on sea star predation.

DISCUSSION

Bottom-up and top-down influences

The comparison between New Zealand and Oregon suggests that both bottom-up influences (in this case, prey recruitment) and top-down processes (predation) are both more strongly affected by downwelling conditions than by more localized variation within an upwelling ecosystem such as that off Oregon. Predation rates and mussel

recruitment (but not barnacle recruitment) were greater under oceanographic conditions favoring higher transport rates (and greater productivity) in both geographic locations, but the relative differences were greater in New Zealand than in Oregon. Barnacle recruitment did not differ between sites in Oregon, but was substantially greater at the upwelling-influenced sites in New Zealand than the downwelling-influenced sites.

In general, these rates were all greater in Oregon than in New Zealand, although for mussel recruitment the greatest differences were due to the more local influences of oceanographic conditions. This comparison thus suggests that the strength of bottom-up/top-down linkages varies in response to oceanographic conditions, and that such responses can be general among geographic locations. Thus, despite their totally different evolutionary histories, the coastal ecosystems of Oregon and New Zealand show strikingly similar responses to oceanographic conditions. The interhemispheric differences in magnitudes of these rates, particularly of predation, are associated with differences in upwelling regime between these two locations. The California Current ecosystem is well known as one of the world's three or four most productive upwelling ecosystems (Gross 1990; Bakun 1996). The New Zealand coast, while relatively productive in some areas, is far less extensive, with upwelling zones occurring along the northern west coast of the South Island, and certain other locations (Vincent *et al.* 1991; Stanton & Moore 1992). In particular, however, the upwelling patterns on the west coast of the South Island are more intermittent, and less predictable from year to year than are those along the Oregon coast. Temperature data from both locations (1993–2001 in Oregon, 1994–1995 and 1999–2001 in New Zealand) indicate that upwelling events in New Zealand are briefer, occur for a shorter duration of the year and, in some years, do not occur at all (B. A. Menge *et al.* unpublished data).

Oceanographic mechanisms

The mechanisms underlying these differences remain only sketchily understood. In Oregon and California, recruitment events of barnacles are associated with upwelling relaxations (Roughgarden *et al.* 1988, 1991; Farrell *et al.* 1991), but the transport mechanisms delivering mussels to the shore are still unknown. Thus, barnacle recruitment occurs during temporary reversals from upwelling to downwelling conditions. In New Zealand, recruitment was dramatically higher in the intermittent-upwelling zone of the northern west coast than on the east coast (Menge *et al.* 1999). That is, recruitment here may also be associated with reversals between upwelling and downwelling conditions. More recent data confirm this difference; recruitment is high at sites inshore of the intermittent upwelling regime of the Westland Current. Further, the low recruitment observed at our sites on the Banks Peninsula seems generally characteristic of sites experiencing persistent downwelling inshore of the Southland Current and (B. A. Menge *et al.* unpublished data).

Why do such areas have such low recruitment? Evidently surface waters do not entrain larvae, but since at least some rocky shores in downwelling regions harbor populations of sessile invertebrates, the fate of the propagules of these invertebrates is unclear. We suggest that the answer lies in the difference between persistent versus intermittent downwelling. In persistent downwelling systems, released larvae may be transported downwards offshore to depths below those favoring phytoplankton blooms (i.e. below the photic zone) in nutrient-poor water, and most may thus starve before they can reach waters favoring growth of phytoplankton. In intermittent systems, released larvae are presumably transported offshore by the Ekman surface layer that forms during upwelling in waters that are nutrient-rich and more likely to develop phytoplankton blooms. Under these conditions, shoreward movement of surface waters during upwelling relaxations is more likely to transport larvae in sufficient numbers to recolonize the appropriate adult habitat. However, whether this or alternative scenarios explain the differences seen in New Zealand remains an open question.

Factors affecting predation rate

The differences in predation, both within geographic locations and between hemispheres, are strongly associated with bottom-up influences. Prey supply as influenced by different recruitment rates (Figs 1,2) seems to be a major influence. Secondary production, or prey growth, may also be a

factor. In both Oregon and New Zealand, evidence suggests that rates of phytoplankton and/or benthic macrophyte production, and growth rates of sessile filter-feeding invertebrates, covary with rates of recruitment and predation documented here (Menge 1992, 2000, 2002; Menge *et al.* 1994, 1997a,b, 1999). The extent to which larval condition and survival is affected by differences in phytoplankton, and the consequences with respect to recruitment, are unclear. Previous published reports are mixed (Olson 1989; Basch & Pearse 1996), but recent evidence (R. Emlet, personal communication) suggests that on the Oregon coast, barnacle larvae raised under high food conditions have higher survival in field outplants than do larvae raised under low food conditions.

Yet, these factors (food supply, prey growth) may not be the only ones influencing predation rate. Both per population and per capita predation rates appear greater in Oregon than in New Zealand (Figs 3,4). An enduring question is why predation rates differ so greatly between hemispheres. The two dominant predators, the sea stars *Pisaster ochraceus* in Oregon and *Stichaster australis* in New Zealand are roughly similar in size and both are generalist predators that feed preferentially on mussels (Paine 1966, 1969, 1971, 1974, 1994; Menge *et al.* 1999). Summer sea water temperatures in New Zealand tend to be several degrees warmer than in Oregon (11–19°C *vs* 8–13°C), which through Q_{10} effects, if anything, might be expected to favor faster feeding by *Stichaster*. Both are robust sea stars, and occur abundantly at the more wave-exposed portions of their rocky reef habitats (where their favorite prey, mussels, tend to be most abundant). Although we have not quantified attachment strength of the mussels, field collections strongly suggest that *Pisaster* prey are more strongly attached to the shore than are *Stichaster* prey, from which we infer that, if anything, *Pisaster* should feed more slowly. So why aren't the predation rates of the two species more nearly equal?

The per capita rate differences suggest that one possibility is simply that predation rates are at least partly an effect of specific sea star characteristics. Field observations indicate that *Stichaster* clings less firmly to the rocks and to prey than does *Pisaster*. Although they are similar in size, *Stichaster* has more arms (10–12) than does *Pisaster* (usually five), and this may affect the power with which they attach. Why this, or other features of a difference in arm number might affect predation rates, however, are unclear.

An alternative, and perhaps more likely, possibility is that this difference in predation rate may result from the different tidal regimes in the two regions. New Zealand has a semidiurnal tidal cycle, with two high and two low tides of approximately equal elevation each day, whereas Oregon (and the US West Coast) experiences a mixed semidiurnal tidal cycle, with low and high tides reaching unequal elevations (NOS 2001a,c). Thus, during spring tides, Oregon has essentially one low tide per day rather than the two occurring in New Zealand. From the perspective of a sea star, which can forage only when covered by water, this means that in New Zealand foraging is interrupted twice per day for up to a total of 12 h and in Oregon only once per day for up to 6 h, and hence that feeding periods are of longer duration (~18 h) in Oregon than in New Zealand (~6 h).

Longer periods of aerial exposure may also increase potential desiccation in New Zealand, which may in turn drive important behavioral differences between *Stichaster* and *Pisaster*. Although *Pisaster* sometimes migrates up and down the shore with rising and falling tides, this sea star also frequently suspends vertical migrations and remains hunched over patches of prey for days at a time (Robles *et al.* 1995; E. Sanford and B. A. Menge, personal observation). In contrast, foraging *Stichaster* generally migrate upshore with the incoming tide, where they remove prey before retreating to the low shore before each low tide. This foraging strategy likely minimizes exposure to thermal stress, but more frequent vertical migrations by *Stichaster* may also contribute to lower per capita predation rates relative to *Pisaster*. It is noteworthy that *Stichaster* predation in New Zealand may be more intense at the edge of reefs, where mussels are easily removed during brief foraging bouts at high tide (Fig. 4; see Menge *et al.* 1999). We thus hypothesize that this difference in feeding period and the related difference in potential desiccation leads to the higher mussel mortality rates observed in Oregon.

As tidal regimes are not amenable to manipulation, direct field tests are probably impossible, but laboratory studies could be employed to address

these hypotheses. Comparative field experiments could be employed in regions with tidal regimes comparable to those of New Zealand and Oregon to determine if similar patterns in feeding rate occur in independent ecosystems. For example, the New England coast has a semidiurnal tidal regime (NOS 2001b), and thus if our hypothesis is correct, sea star predation rates should be lower than on the US west coast and comparable to that in New Zealand. Although studies of predation have been carried out in New England (Menge 1976, 1983; Lubchenco & Menge 1978), experiments of comparable design to those presented here are unavailable for comparison.

In our experiments on predation rate, we have assumed that sea stars accounted for all mussel mortality. In both ecosystems, however, there exist other predators of mussels, including primarily whelks and crabs. In Oregon, whelks contribute a small but significant portion of predation on the smaller mussel *M. trossulus* (Navarrete & Menge 1996), but almost never feed on the California mussel (E. Sanford and B. A. Menge, personal observations, unpublished data). Crabs (*Cancer productus*) eat mussels but are scarce on wave-exposed areas and probably have little impact on mussel populations (Menge *et al.* 1994). Similarly, in New Zealand, although whelks, at least, will eat mussels, whelks and crabs are both scarce at our wave-exposed sites and thus are also unlikely to have much impact. We conclude that at both geographic locations, sea star predation is the primary source of predation-induced mortality of mussels.

Progress in understanding coastal ecosystems and the comparative-experimental approach

The results presented here suggest that the comparative-experimental approach is widely applicable in ecological systems, and can provide powerful insights into the dynamics of communities. A major advance made by the comparison between New Zealand and Oregon is the suggestion that the intensity of species interactions can be directly compared, and that predation at least is greater in Oregon. The patterns of recruitment of their primary prey (Figs 1,2; Menge *et al.* 1999), of productivity (Menge 2000, 2002), and possibly of tidal regimes suggest that differences in oceanographic

conditions may be a key determinant of top-down differences. These results also raise the possibility that a conceptual framework can be developed that will permit the generation of testable predictions on important elements of community dynamics at local to geographic scales. Research is currently underway to address this possibility.

ACKNOWLEDGMENTS

REFERENCES

ANDRÉ C., JONSSON P. R. & LINDEGARTH M. (1993) Predation on settling bivalve larvae by benthic suspension feeders: The role of hydrodynamics and larval behavior. *Marine Ecology Progress Series* 97: 183–192.

BAKUN A. (1996) *Patterns in the Ocean*. California Sea Grant/Centro de Investigaciones Biologicas del Noroeste, La Paz, Baja.

BASCH L. V. & PEARSE J. S. (1996) Consequences of larval feeding environment for settlement and metamorphosis of a temperate echinoderm. *Oceanologica Acta* 19: 273–285.

BUSTAMANTE R. H. & BRANCH G. M. (1996a) The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. *Journal of Experimental Marine Biology and Ecology* 196: 1–28.

BUSTAMANTE R. H. & BRANCH G. M. (1996b) Large scale patterns and trophic structure of southern African rocky shores: The roles of geographic variation and wave exposure. *Journal of Biogeography* **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.

CARPENTER S. R., COLE J. J., HODGSON J. R., KITCHELL J. F., PACE M. L., BADE D., COTTINGHAM K. L., ESSINGTON T. E., HOUSER J. N. & SCHINDLER D. E. (2001) Trophic cascades, nutrients, and lake productivity: Whole-lake experiments. *Ecological Monographs* **71**: 163–186.

CARPENTER S. R., KITCHELL J. F. & HODGSON J. R. (1985) Cascading trophic interactions and lake productivity. *Bioscience* **35**: 634–639.

DAYTON P. K. (1971) Competition, disturbance, and community organization: The provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**: 351–389.

DAYTON P. K. (1975) Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecological Monographs* **45**: 137–159.

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. *Journal of Animal Ecology* **33**: 73–82.

FARRELL T. M., BRACHER D. & ROUGHGARDEN J. (1991) Cross-shelf transport causes recruitment to intertidal populations in central California. *Limnology and Oceanography* **36**: 279–288.

FRETWELL S. D. (1977) The regulation of plant communities by food chains exploiting them. *Perspectives in Biology and Medicine* **20**: 169–185.

FRETWELL S. D. (1987) Food chain dynamics: The central theory of ecology? *Oikos* **50**: 291–301.

GROSS M. G. (1990) *Oceanography: a View of the Earth*. Prentice Hall, Englewood Cliffs, NJ.

KITCHING J. A., SLOANE J. F. & EBLING F. J. (1959) The ecology of Lough Ine VIII. Mussels

and their predators. *Journal of Animal Ecology* **28**: 331–341.

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.

LUBCHENCO J. (1980) Algal zonation in a New England rocky intertidal community: An experimental analysis. *Ecology* **61**: 333–344.

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: *Community Ecology* (eds J. M. Diamond & T. Case) pp. 537–555. Harper & Row, New York.

LUBCHENCO J. & MENGE B. A. (1978) Community development and persistence in a low rocky intertidal zone. *Ecological Monographs* **48**: 67–94.

LUBCHENCO J., MENGE B. A., GARRITY S. D., LUBCHENCO P. J., ASHKENAS L. R., GAINES S. D., EMLET R., LUCAS J. & STRAUSS S. (1984) Structure, persistence, and role of consumers in a tropical rocky intertidal community (Taboguilla Island, Bay of Panama). *Journal of Experimental Marine Biology and Ecology* **78**: 23–73.

McPEEK M. A. (1998) The consequences of changing the top predator in a food web: A comparative experimental approach. *Ecological Monographs* **68**: 1–23.

MENGE B. A. (1976) Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecological Monographs* **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 (Berlin)* **34**: 17–35.

MENGE B. A. (1978b) Predation intensity in a rocky intertidal community. Relation between predator foraging activity and environmental harshness. *Oecologia (Berlin)* **34**: 1–16.

MENGE B. A. (1983) Components of predation intensity in the low zone of the New England rocky intertidal region. *Oecologia* **58**: 141–155.

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. *Journal of Experimental Marine Biology and Ecology* **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) Top-down and bottom-up community regulation in marine rocky intertidal habitats. *Journal of Experimental Marine Biology and Ecology* **250**: 257–289.

MENGE B. A. (2002) Bottom-up: top-down determination of rocky intertidal shorescape dynamics. In: *Food Webs at the Landscape Level* (eds G. A. Polis, M. E. Power & G. Huxel). (In press.)

MENGE B. A., ASHKENAS L. R. & MATSON A. (1983) Use of artificial holes in studying community development in cryptic marine habitats in a tropical rocky intertidal region. *Marine Biology* **77**: 129–142.

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. *Ecological Monographs* **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. *Ecological Monographs* **69**: 297–330.

MENGE B. A., DALEY B. A. & WHEELER P. A. (1996) Control of interaction strength in marine benthic communities. In: *Food Webs: Integration of Pattern and Dynamics* (eds G. A. Polis & K. O. Winemiller) pp. 258–274. Chapman & Hall, New York.

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? *Proceedings of the National Academy of Sciences, 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. *Limnology and Oceanography* **42**: 57–66.

MENGE B. A. & FARRELL T. M. (1989) Community structure and interaction webs in shallow marine hard-bottom communities: Tests of an environmental stress model. *Advances in Ecological Research* **19**: 189–262.

MENGE B. A. & LUBCHENCO J. (1981) Community organization in temperate and tropical rocky intertidal habitats: Prey refuges in relation to consumer pressure gradients. *Ecological Monographs* **51**: 429–450.

MENGE B. A., LUBCHENCO J. & ASHKENAS L. R. (1985) Diversity, heterogeneity and consumer pressure in a tropical rocky intertidal community. *Oecologia (Berlin)* **65**: 394–405.

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. *Journal of Experimental Marine Biology and Ecology* **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 (Berlin)* **71**: 75–89.

MENGE B. A. & OLSON A. M. (1990) Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution* **5**: 52–57.

MENGE B. A. & SUTHERLAND J. P. (1976) Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* **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. *American Naturalist* **130**: 730–757.

MORRIS R. H., ABBOTT D. P. & HADERLIE E. C. (1980) *Intertidal Invertebrates of California*. Stanford University Press, Stanford, CA.

MORTON J. E. & MILLER M. C. (1968) *The New Zealand Sea Shore*. Collins, London.

NAVARRETE S. A. & MENGE B. A. (1996) Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecological Monographs* **66**: 409–429.

NAVARRETE S. A. & WIETERS E. A. (2000) Variation in barnacle recruitment over small scales: Larval predation by adults and maintenance of community pattern. *Journal of Experimental Marine Biology and Ecology* **253**: 131–148.

NOS (2001a) *Tide tables 2001: Central and Western Pacific Ocean and Indian Ocean*. National Oceanic and Atmospheric Administration, Riverdale, MD.

NOS (2001b) *Tide tables 2001: East coast, North and South America*. National Oceanic and Atmospheric Administration, Riverdale, MD.

NOS (2001c) *Tide tables 2001: West coast, North and South America*. National Oceanic and Atmospheric Administration, Riverdale, MD.

OLSON R. R. (1989) Food limitation of planktotrophic marine invertebrate larvae: Does it

control recruitment success? *Annual Review of Ecology and Systematics* **20**: 225–247.

PAINE R. T. (1966) Food web complexity and species diversity. *American Naturalist* **100**: 65–75.

PAINE R. T. (1969) The *Pisaster–Tegula* interaction: Prey patches, predator food preference, and intertidal community structure. *Ecology* **50**: 950–961.

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 (Berlin)* **15**: 93–120.

PAINE R. T. (1994) *Marine Rocky Shores and Community Ecology: An Experimentalist's Perspective*. Ecology Institute, Oldendorf/Luhe.

PAINE R. T. & VADAS R. L. (1969) The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnology and Oceanography* **14**: 710–719.

PETERSON C. H. (1979) The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. *Oecologia (Berlin)* **39**: 1–24.

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.

ROUGHGARDEN J., GAINES S. D. & POSSINGHAM H. (1988) Recruitment dynamics in complex life cycles. *Science* **241**: 1460–1466.

ROUGHGARDEN J., PENNINGTON J. T., STONER D., ALEXANDER S. & MILLER K. (1991) Collisions of upwelling fronts with the intertidal zone: the cause of recruitment pulses in barnacle populations of central California. *Acta Oecologica* **12**: 35–51.

SANFORD E. (1999) Regulation of keystone predation by small changes in ocean temperature. *Science* **283**: 2095–2097.

SANFORD E. & MENGE B. A. (2001) Spatial and temporal variation in barnacle growth in a coastal upwelling system. *Marine Ecology Progress Series* **209**: 143–157.

STANTON B. R. (1976) Circulation and hydrology off the west coast of the South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **10**: 445–467.

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 Journal of Marine and Freshwater Research* **26**: 339–358.

UNDERWOOD A. J. (1981) Techniques of analysis of variance in experimental marine biology and ecology. *Annual Reviews of Oceanography and Marine Biology* **19**: 513–605.

UNDERWOOD A. J. (1997) *Experiments in Ecology*. Cambridge University Press, Cambridge.

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 Journal of Marine and Freshwater Research* **25**: 21–42.

WETHEY D. S. (1985) Catastrophe, extinction, and species diversity: A rocky intertidal example. *Ecology* **66**: 445–456.

WHITE T. R. C. (1978) The importance of relative shortage of food in animal ecology. *Oecologia* **33**: 233–242.

WINER B. J., BROWN D. R. & MICHELS K. M. (1991) *Statistical Principles in Experimental Design*. McGraw Hill, New York.