

TOP-DOWN AND BOTTOM-UP REGULATION OF NEW ZEALAND ROCKY INTERTIDAL COMMUNITIES

BRUCE A. MENGE,¹ BRYON A. DALEY,² JANE LUBCHENCO, ERIC SANFORD, ELIZABETH DAHLHOFF,³
PATRICIA M. HALPIN, GREGORY HUDSON, AND JENNIFER L. BURNAFORD

*Department of Zoology, University of Canterbury, Christchurch, New Zealand,
and Department of Zoology, Oregon State University, Corvallis, Oregon 97331-2914 USA*

Abstract. Studies on the west coast of North America suggest that nearshore oceanographic conditions can have important effects on rocky intertidal community structure and dynamics. Specifically, upwelling-dependent processes in coastal waters can affect both top-down and bottom-up processes on adjacent rocky shores. As a first step in testing the prediction that similar linkages occur elsewhere, we investigated the effects and rates of predation, grazing, and recruitment on rocky intertidal community dynamics at upwelling and non-upwelling sites on the South Island of New Zealand. Comparative-experimental studies were done at each of two sites on both the east and west coasts of the South Island. We quantified benthic community structure, maximal wave force, nearshore sea-surface temperature, air temperature at low tide, nutrient concentrations, survival of mussels, rates and effects of predation, rates and effects of limpet grazing, recruitment of mussels and barnacles, and RNA:DNA ratios (a growth index) of mussels.

Overall, zonation patterns were similar on the upper shore on both coasts: barnacles (*Chamaesipho columna*) dominated the high zone, and mussels (*Mytilus galloprovincialis*) the middle zone. In the low zone, however, community structure differed markedly between coasts. East-coast low-zone communities were dominated by mussels with a moderate canopy of kelp, primarily *Durvillea* spp., while mussels were largely absent from west-coast low zones. Food webs were similar on the different coasts and included predaceous whelks, sea stars, oystercatchers, and herbivorous limpets. Field experiments showed that only sea stars and limpets had strong effects at west-coast sites, and only limpets had strong effects at east-coast sites. The sea star *Stichaster australis*, previously identified as a key-stone species on the west coast of the North Island, was common and important on the west coast of the South Island but was absent from the east coast.

Physical conditions (wave forces, low-tide air temperature) were comparable on the two coasts, suggesting that other factors caused the differences in low-zone community structure. Experiments and observations indicated that predation, grazing, prey recruitment, and mussel growth were greater on the west than on the east coast. While some between-coast contrasts in community dynamics could emanate from differences in species composition (e.g., the absence of *S. australis* from the east coast), the higher west-coast rates of most of the ecological processes studied suggest that between-coast differences may also depend on other factors. Among the alternatives, a difference in nearshore oceanographic conditions on the opposite coasts of the South Island seems most likely. Prior oceanographic research, and our onshore measurements of sea-surface temperature and nutrients indicate that summer upwelling may be relatively frequent on the west coast and rare on the east coast. While detailed oceanographic studies synchronized with benthic studies in nearshore coastal environments are needed to evaluate this hypothesis, present evidence is consistent with the view that rocky intertidal community structure and dynamics vary with large-scale oceanographic conditions in nearshore coastal environments around New Zealand.

Key words: barnacles; benthic–pelagic coupling; grazing impact; mussels; nearshore ecosystem dynamics; predation; recruitment; RNA:DNA; rocky intertidal community regulation; rocky intertidal oceanography; scale-dependent variability; sea stars.

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¹ E-mail: mengeb@bcc.orst.edu

² Present address: Section of Ecology and Systematics, Cornell University, Ithaca, New York 14850 USA.

³ Present address: Department of Biology, Santa Clara University, Santa Clara, California 95053 USA.

INTRODUCTION

Rocky intertidal communities have been productive systems for developing both empirical understanding and conceptual models of community patterns (e.g., Paine 1966, 1974, Dayton 1971, Connell 1975, Menge and Sutherland 1976, 1987, Bertness and Callaway 1994). These and many other studies provide insight into community dynamics that incorporate strong direct and indirect effects of biotic interactions and environmental stresses (Menge and Olson 1990). Despite these insights, comparisons among intertidal sites within a region usually reveal that much variation among communities remains unexplained by these factors, suggesting that additional processes need to be taken into account (e.g., Menge 1992). Among the possibilities are factors dependent on larger scale, oceanographically driven processes such as recruitment and productivity.

Most benthic marine organisms have planktonic stages, many with potentially long-range dispersal. As a result, successive generations of shore-based populations are often completely independent from one another (review in Caley et al. [1996]). Moreover, many marine species depend on oceanographic influences for food or nutrients and transport of propagules to appropriate adult habitat (e.g., Ebert and Russell 1988, Grosberg and Levitan 1992, Menge 1992). Oceanographic conditions vary over far larger scales than those usually studied by benthic marine ecologists, and are typically poorly known in nearshore waters (0–10 km from the shore). As a result, understanding the coupling between benthic and nearby pelagic environments has proceeded slowly.

As marine ecology and oceanography have matured, however, and with advances in technology and methodology, attention has focused more on nearshore coastal environments (e.g., Roughgarden et al. 1988, Menge 1992, Witman et al. 1993, Wing et al. 1995a, b, Robles et al. 1995, Menge et al. 1996, 1997a, b, Robles 1997, Connolly and Roughgarden 1998). For example, recent studies along the Oregon coast suggest that among-site variation in rocky intertidal community structure at intermediate, or “meso-scales” (i.e., 10’s to 100’s of kilometers) may be driven by consistent among-site differences in nearshore oceanographic processes (Menge 1992, Menge et al. 1994, 1996, 1997a, b). Inverse between-site differences in relative abundance of sessile invertebrates and macrophytes appear to vary with upwelling intensity, currents, and phytoplankton concentration. Specifically, high abundances of sessile invertebrates occurred on rocky shores adjacent to a region characterized by gyres and eddies that may both concentrate zooplankton and phytoplankton and transport them to shore during upwelling relaxations. High phytoplankton abundance supported increased growth of filter feeders, potentially reducing macrophyte abundance through competition

for space. High sessile invertebrate abundance also attracted high concentrations of predators, leading to high rates of predation. The oceanographic processes that appeared to drive these patterns were consistent in space, and were associated with features of coastal morphology and shelf bathymetry that influenced near-shore currents and circulation (Menge et al. 1997a).

Generality of benthic–pelagic links

The Oregon (USA) studies cited above suggest that pelagic and benthic ecosystems are coupled via the linkage: plankton-concentrating gyres → phytoplankton and invertebrate larvae → filter-feeding invertebrates → predators. Because these postulated connections between oceanographic conditions and intertidal community structure have implications for how near-shore ecosystems will respond to large-scale environmental perturbations, the issue of the generality of such linkages is important. Is the Oregon example unique, or are similar nearshore–onshore couplings seen on other coasts? To begin evaluating the generality of these results, we initiated a comparative-experimental study of rocky intertidal community dynamics in New Zealand. Our approach focused on comparisons and experiments aimed at quantifying processes that either directly or indirectly reflected certain “top-down,” “bottom-up,” and “larval transport” processes (see, e.g., Menge 1992, Robles et al. 1995, Menge et al. 1997a, b, Robles 1997). Studies were done at paired rocky shore sites on opposite coasts (east vs. west) of the South Island of New Zealand.

Here, “top-down” refers to effects of predation and grazing on invertebrates and algae. “Bottom-up” processes refer to factors that affect the abundance of plants and, through them, possibly higher trophic levels. Here we broaden this definition of “bottom-up” to accommodate the unique role of particle-feeding sessile invertebrates such as mussels and barnacles in rocky intertidal communities (e.g., Menge 1995). These organisms are heterotrophs (dependent on plankton or particulate material), but they are also “basal species” (like macrophytes, live attached to the rock surface and compete for space; Pimm 1982). Also like marine plants, sessile animals obtain their raw materials for growth and reproduction from seawater. Hence, factors such as phytoplankton and detritus that influence growth of filter feeders are “bottom-up” effects. For this reason we consider nutrients, plant-derived detritus, and primary production—whether of macrophytes or phytoplankton—to be “bottom-up” factors.

Recruitment of sessile organisms might also be considered a bottom-up process, because it positively affects macrophyte and filter-feeder abundance, and can thereby affect higher trophic levels (e.g., Menge et al. 1997a). However, this usage may confound specific processes (larval nutrition, larval transport) that may be distinct. Thus, until we have better insight into the relative influences of these processes, it seems appro-

priate to consider recruitment and larval transport separately from nutrients and productivity.

In this study, we quantified top-down effects directly, using experiments. Because the work was entirely shore based, and our access to appropriate laboratory facilities was limited, bottom-up and transport processes were quantified indirectly. Based on our Oregon work (e.g., Menge et al. 1994, 1997a, Dahlhoff and Menge 1996), we assumed that mussel growth was an indirect indication of the availability of particulate, water-borne food for filter feeders. While particulates include both living and dead phytoplankton and macrophyte detritus, studies in Oregon indicated that most such particulates were phytoplankton derived (B. Menge, *unpublished data*). Finally, our proxy for larval transport was the recruitment of mussels and barnacles to collectors placed in appropriate habitat onshore.

Rocky intertidal communities of the South Island of New Zealand

The southern-hemisphere latitudes spanned by the South Island of New Zealand (hereafter termed "the South Island": 42° to 44° S) are similar to those spanned by Oregon in the northern hemisphere (43° to 46° N). While the rocky intertidal flora and fauna differ almost completely at the generic level, higher level taxonomic compositions in these two biogeographic regions are quite similar (e.g., compare Morton and Miller [1968] and Morris et al. [1980]). Like most temperate rocky shores around the world (Stephenson and Stephenson 1972, Menge and Farrell 1989), rocky intertidal communities on wave-exposed hard substrata in both New Zealand and Oregon have generally similar zonation patterns. Barnacles dominate the high zones, mussels dominate the middle zones, and a mixture of algae, sessile invertebrates, and bare space dominate the low zones (e.g., Knox 1953, 1968, Paine 1971, Menge et al. 1994). On more wave-sheltered shores, mussel abundance decreases and seaweed abundance increases. Further, community processes operating on New Zealand shores, such as predation and competition, appear comparable to those elsewhere, such as Europe (Kitching et al. 1959, Connell 1961a, b, Hawkins and Hartnoll 1983), North America (Paine 1966, 1974, Connell 1970, Dayton 1971, Menge 1976, Lubchenco and Menge 1978), South America (Jara and Moreno 1984, Castilla and Duran 1985, Duran and Castilla 1989), and Australia (Underwood et al. 1983, Fairweather 1985, 1990).

On the North Island of New Zealand, experimental studies indicated that predation can determine the lower edge of distributional limits of dominant sessile animals. At Leigh on the east coast, for example, whelk predation prevented the establishment of persistent populations of barnacles *Chamaesipho brunnea* and *Epopella plicata* at lower shore levels (Luckens 1970, 1974, 1975a, b, 1976). At Anawhata on the west coast, Paine (1971) found that, like *Pisaster ochraceus* on the

west coast of North America, predation by the sea star *Stichaster australis* determined the lower distributional limit of mussels. Moreover, by selectively feeding on the mussel *Perna canaliculus*, *Stichaster* prevented this competitively dominant filter feeder from monopolizing the lower intertidal region, thereby allowing the coexistence of numerous, competitively inferior invertebrates and seaweeds. In other words, in this system *Stichaster* was a keystone species. On the South Island, apart from ongoing studies of grazer-macrophyte interactions at Kaikoura and other sites on the east coast (D. Schiel, *personal communication*), the determinants of rocky community structure are little studied.

Nearshore oceanographic conditions on the east and west coasts of the South Island, while poorly documented, seemed likely to offer contrasting environments. The South Island lies directly in the path of the eastward-flowing Tasman Current (Knox 1975, Stanton 1976, Vincent et al. 1991, Stanton and Moore 1992). On the central west coast, it splits into the northeasterly flowing Westland Current, and the Southland Current (Fig. 1). The latter wraps around the southern end of the South Island, guided by the subantarctic convergence and, continuing its parallel-to-the-coast flow pattern, flows northeasterly along the east coast of the South Island. On the west coast, the Westland Current flow is enhanced periodically by upwelling-favorable northeastward winds. The direction and strength of these winds are influenced by the orographic effect of the Southern Alps (Stanton and Moore 1992). Ekman transport in southern-hemisphere currents deflects to the left, creating conditions comparable to those for the larger Eastern Boundary Current ecosystems like the California Current and the Peru-Chile Current (e.g., Smith 1981, Bakun 1996). During strong northward winds, surface waters move westward offshore, drawing nutrient-rich water from depth to the surface along the coast, eventually leading to phytoplankton blooms along the west coast. Evidence obtained during the Tasman Boundary Experiment (TASBEX) studies (Stanton and Moore 1992) and from satellite (advanced very-high-resolution radiometer [AVHRR] imagery clearly indicates the occurrence of such upwelling along the northern half of the west coast (Vincent et al. 1991). Physical oceanographic measurements demonstrated that Ekman mass transports off the west coast were comparable in magnitude to those for the Oregon, Peru, and northwest Africa upwelling systems (Stanton and Moore 1992). An evident consequence of this west-coast upwelling is relatively high concentrations of chlorophyll *a* at shallow inshore depths (MacKenzie et al. 1988, Vincent et al. 1991), a pattern typical of other upwelling systems (e.g., Small and Menzies 1981, Bakun 1996). As in other upwelling ecosystems, conditions off the west coast of the South Island generally favor enhanced growth rates of the inshore plankton (Hall and Vincent 1990, Vincent et al. 1991).

Although the oceanographic patterns along the east

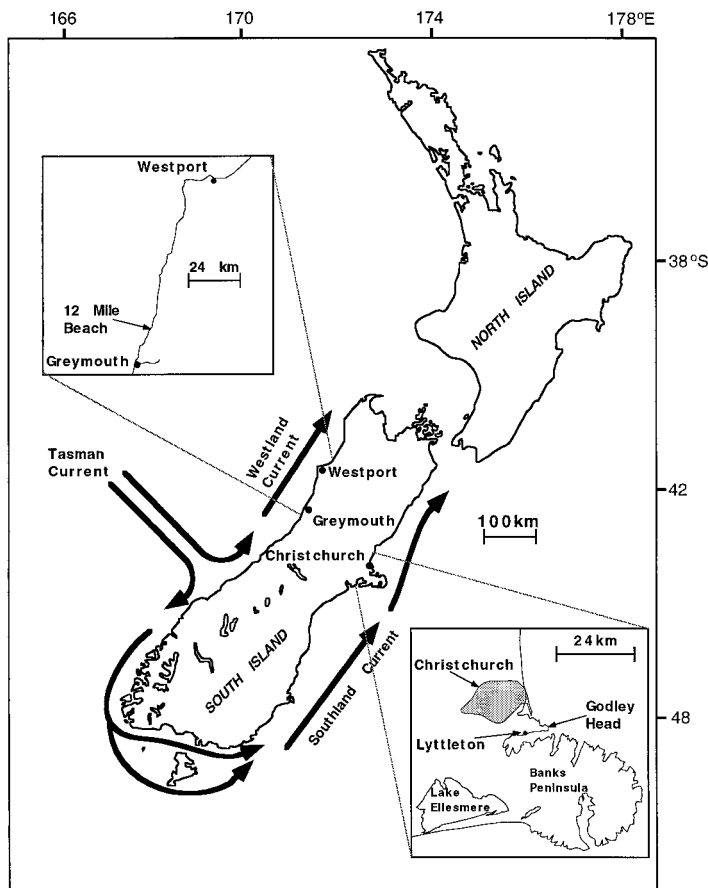


FIG. 1. Map of the South Island of New Zealand showing the locations of the study sites on the east coast (Godley Head near Christchurch where Boulder Bay and Box Thumb were located) and west coast (Twelve-Mile Beach near Greymouth where Twelve-Mile North and Twelve-Mile South were located).

coast of the South Island are less-well studied, wind, current, and sea-surface temperature patterns suggest that the prevailing conditions favor downwelling. Sea-surface temperatures taken in 1982 at Lyttelton (the port city for Christchurch), on the Banks Peninsula (Fig. 1), showed only two brief periods when water temperatures dropped sharply, a hallmark of upwelling conditions (Greig et al. 1988, McKendry et al. 1988). Ship-based sampling in May 1989 around the southern coast of the South Island found no evidence for upwelling (Butler et al. 1992). These observations, coupled with the tendency for onshore movement of surface water from the northward-flowing Southland Current via Ekman transport, are consistent with the interpretation of the east coast as a non-upwelling region, particularly the southern and central portions.

Satellite imagery (Vincent et al. 1991) of sea-surface temperatures on both coasts shows patterns consistent with these observations. Images from May 1989 clearly show the steep temperature gradient typical of upwelling on the west coast, with colder ($\sim 12\text{--}13^\circ\text{C}$) water nearshore and warmer ($16\text{--}17^\circ\text{C}$) water offshore (see Vincent et al. 1991: Fig. 6). On the east coast a thermal gradient is absent, and temperatures are consistently $\sim 13^\circ\text{C}$ from nearshore to well offshore, where cooler subantarctic water occurs (see Vincent et al.

1991: Fig. 13). Thus, although more detailed study of nearshore oceanographic conditions around the South Island is warranted, the emerging pattern is that the central and northern west coast is an upwelling region and the southern and east coasts are downwelling regions.

The relative proximity of east and west coasts (the central region of the South Island is only ~ 200 km wide) allowed simultaneous intensive field studies on both coasts. This research-favorable scenario, and the similarities to Oregon in zonation, higher-level taxa, and ecological roles of seastars and whelks, suggested that New Zealand offered an opportunity to examine the generality of the Oregon studies at larger geographic scales. Our general hypothesis was that contrasting, between-coast patterns in the sessile biota of rocky intertidal communities reflected contrasting regimes of biotic and physical processes. Based on studies in South Africa and Oregon suggesting that oceanographic conditions can drive variation in species interaction strengths (Bustamante et al. 1995a, b, Menge et al. 1997a), we predicted that key interaction web processes would be stronger on the west coast than on the east coast of the South Island. Moreover, we postulated that, relative to between-coast differences, within-coast variation would be less, and thus that we would doc-

ument few within-coast, among-site differences in community structure.

Predictions of oceanographic influences on intertidal communities

These contrasting west vs. east coast oceanographic scenarios off the South Island of New Zealand provide a useful comparison to the variation in upwelling conditions seen along the west coast of North America. Within Oregon, upwelling and current patterns vary consistently on scales of 10's to 100's of kilometers (Menge et al. 1997a, b). Based on consistent differences among sites with stronger and weaker upwelling in Oregon, we predicted that nearshore waters off rocky shores on the west and east coasts of New Zealand were likely to differ in both phytoplankton availability for benthic populations and in larval-transport patterns. South Island west-coast sites were expected to have high concentrations of phytoplankton-derived particulates for sessile filter-feeding invertebrates due to the effects of upwelling. East-coast sites were anticipated to have low particulate concentrations, because downwelling systems do not have the depth-derived nutrient pulses that fuel phytoplankton blooms. Although we were unable to sample phytoplankton directly, we quantified two indirect measures that can be associated with variation in productivity. We sampled nutrient concentrations in the water column and measured growth rates of intertidal mussels that were feeding on plankton.

Predictions regarding expected variation in recruitment patterns with changes in upwelling regimes are more complex. On the west coast of North America, larvae appear to be transported seaward during upwelling and onshore during relaxation; barnacle recruitment often coincides with relaxation events (Roughgarden et al. 1988, 1991, Farrell et al. 1991). Although upwelling occurs along most of the west coast of North America, it is more intense off California than Oregon, with significant variation occurring at a scale of 100's to 1000's of kilometers (Gaines and Roughgarden 1985, 1987, Roughgarden et al. 1988, Strub et al. 1990, Strub and James 1995). Currents are also more complex off California and, as a consequence, larvae appear to be transported further offshore than in Oregon (Roughgarden et al. 1988, Connolly and Roughgarden 1998). As a possible consequence of the latter phenomenon, in comparison to Oregon, barnacle recruitment in California tends to be much lower and is restricted to periods of upwelling relaxation (Roughgarden et al. 1988, Menge 1998, S. R. Connolly, B. A. Menge, and J. Roughgarden, *unpublished manuscript*).

On the South Island the west-coast upwelling region is small in extent, and current patterns suggested by satellite imagery seem more like those off Oregon than those off California (compare Vincent et al. [1991] to Strub and James [1995]). Because of this similarity to

Oregon, we expected to observe relatively high recruitment densities on the west coast of the South Island. On the east coast, based on first principles, the apparent downwelling might be expected to transport larvae to shore, and/or to keep near shore those released there by adults. However, three considerations suggest that recruitment should be low on the east coast. First, downwelling conditions might also tend to transport weakly swimming larvae (including barnacle and mussel larvae) to deeper depths, and, depending on the direction of bottom currents, perhaps eventually offshore. Second, downward transport is likely to remove larvae from the photic zone, and away from the areas of highest phytoplankton concentrations. Third, as noted above, the food of larvae, phytoplankton and detritus, is likely to be low in concentration even in the photic zone because the nutrient pulses that fuel phytoplankton blooms and rapid macrophyte growth are lacking in downwelling regions. These considerations led us to predict that recruitment of sessile invertebrates was likely to be low on the east coast.

If bottom-up factors and recruitment are higher on the west coast, top-down factors should also be stronger on the west coast. Higher recruitment and higher growth rates of sessile organisms—both of filter-feeding invertebrates due to high particulate concentrations and of algae due to high nutrients—should produce higher food concentrations that can support higher abundances of consumers. Thus, we predicted that both predation and grazing should be more intense on the west coast.

In this study, we quantified, on both east and west coasts of the South Island, (1) patterns of community structure, (2) sea and air temperatures at high and low tide, respectively, (3) nutrient concentration, (4) recruitment patterns of the dominant sessile animals (barnacles and mussels), (5) growth of competitively dominant space occupiers (mussels), and (6) strengths of biotic interactions, including predation and grazing. Logistical limitations prevented quantification of patterns of macrophyte growth and phytoplankton abundance and growth. Our results were largely as predicted: predation, grazing, prey recruitment, mussel growth, and nutrients were all greater on the west than on the east coast.

METHODS

Study sites

Four main study sites were selected, two on the east coast and two on the west coast of the South Island. All sites were wave exposed, and experienced moderate to high turbulence from waves, especially during storms. East-coast sites were located just south of Christchurch, on the north side of Banks Peninsula, at Godley Head near Taylor's Mistake (Fig. 1; 43°34' S, 172°48' E). The two sites were named "Boulder Bay" and "Box Thumb." Boulder Bay (hereafter "BB") was

a small reef ~20 m in diameter near the tip of Godley Head. The substratum was basaltic, with a complex topography consisting of outcrops, channels, and pools. Box Thumb (hereafter "BT") was a small peninsula ~2 km westward from BB along the north side of Godley Head, jutting towards the northeast. BT also had a basaltic substratum but had a much simpler topography with fewer outcrops and channels.

West-coast sites were ~20 km north of the town of Greymouth, on Twelve-Mile Beach at the settlement of Greigs (Fig. 1; 42°18' S, 171°19' E). The two sites were termed "Twelve-Mile North" and "Twelve-Mile South" ("TMN" and "TMS," respectively). These were similar sites located at opposite ends of an extensive rocky reef, ~0.3 km apart. The broad (~80 m), nearly horizontal shore had a highly complex topography, consisting largely of tabular, flat-topped outcrops separated by narrow channels, varying in depth to >2 m with increasing distance from the high intertidal gravel beach. The substratum was largely basaltic, but other rock types ran through the reef, including a seam of coal ~0.5 m in width. These sites had only low and middle zones; the portion of the shore that would have made the high zone was primarily a gravel beach, to landward of the rocky benches. Because of this, qualitative and some quantitative high-zone observations were made at sites ~1.5 and 3 km further north (Thirteen-Mile and Fourteen-Mile reefs). The landward end of the sites consisted of nearly vertical bluffs, rising about 6–8 m above the beach.

Tides were semidiurnal on both coasts. In New Zealand, the extreme lowest low tide is assigned a value of 0.0 m. At the east-coast sites, the tidal amplitude range was 2.4 m during spring tides to 1.3 m during neap tides (using Lyttelton [43°37' latitude, 172°43' longitude; ~6 km west southwest of BT] as the reference station; Lamont 1996). Approximate ranges of low, middle, and high zones are 0–0.8 m, 0.8–1.7 m, and 1.7–2.4 m, respectively. On the west coast, tidal amplitude was 3.7 m during spring tides and 1.4 m during neap tides (using Westport [41°44' latitude, 171°36' longitude; 70 km north of TMB] as the nearest recording station; Lamont 1996). Approximate ranges of low, middle, and high zones are 0–1.2 m, 1.2–2.5 m, and 2.5–3.7 m, respectively. Except for slightly wider zones, there were no evident consequences of the greater tidal amplitude on the west coast.

Our studies were done primarily from 29 September 1994 to 20 March 1995, with follow-up studies occurring from 9 January to 1 April 1997. Supplementary samples and observations (of recruitment and the sea star predation experiment) in May and September 1995 were provided by D. Schiel.

Quantification of physical conditions

Maximum wave force.—To characterize physical conditions at the site level, we quantified maximum wave force, air temperature (low tide), and sea-surface

temperature (high tide). Maximum wave force was estimated by deploying maximum-wave-force dynamometers (e.g., Bell and Denny 1994, Menge et al. 1996). Dynamometers quantify the magnitude of the largest wave during a sample period (measurements converted to newtons). Five replicate dynamometers were attached to the most wave-exposed mid-zone rocks at each site on each coast, with usual sampling periods of 24 h. Due to limited personnel, simultaneous dynamometer measurements at all sites were rarely done. Wave-force data therefore included uncontrolled variability resulting from between-day differences in wave conditions. Dynamometer readings were made most frequently at BT on the east coast and TMN and TMS on the west coast from 11 October 1994 to 4 March 1995.

Temperature.—Air and sea-surface temperatures were recorded using temperature-data loggers (Onset Computer Corporation, Pocasset, Massachusetts, USA). Loggers were fastened to the substratum in the lower mid-zone (about +1.0 m tide height) and set to record temperatures and time of day at hourly intervals. Air temperatures were estimated as the hourly temperature readings that occurred closest to the time of low tide at each site. Readings taken during neap low tides were not used since the highest low tide is about +1 m on both coasts (e.g., Lamont 1996), and recorded temperatures are therefore likely to be influenced by wave splash. Similarly, sea-surface temperatures were readings coinciding with high tides, again as determined from tide tables. Since loggers were at least 1 m below the sea surface, even during neap tides, all high-tide temperatures could be used.

Nutrient samples

Water samples were collected in December 1994 and January and February 1995 for quantification of chlorophyll *a* and nutrients. Unfortunately, due to equipment problems, the chlorophyll *a* data were unreliable. Water samples were collected at each main site. On the east coast, samples were also taken at a third site, Black Point (1 km northwest of Box Thumb). On the west coast, samples were also taken at two other sites, Thirteen-Mile Creek and Fourteen-Mile Creek (~1.5 and 3 km north of Twelve-Mile Beach, respectively). Samples were taken by filling acid-washed opaque plastic (high-density polyethylene) 250-mL bottles at the water's edge at low tide. Nutrient samples (50 mL) were filtered through 25-mm combusted Whatman glass-fiber filters with pore size of 0.7 μ m. The filtrate was transported to the laboratory on ice and frozen for later quantification of nitrate, nitrite, phosphate, and silicate in a Technicon autoanalyzer (Atlas et al. 1971).

Quantification of community structure

Zonation and spatial structure.—Percent cover of organisms was estimated using the transect-quadrat method (e.g., Lubchenco and Menge 1978). In most

cases, 30-m transect lines were placed parallel to the water's edge in high, middle, and low zones, and at regular (2-m or 3-m) intervals a quadrat (0.5×0.5 m) was placed on the line and photographed ($n = 15$ quadrats/transect). When plots fell over large crevices or in tide pools, the quadrat was moved to the next closest photographable mark on the transect line. This procedure probably introduced a bias in the sampling, since barnacles, mussels, and seaweeds tend to be less abundant in crevices, while chitons, gastropods, anemones, and colonial animals tend to be more abundant in crevices. Open, photographable (non-crevice) surfaces were the dominant spatial habitat, however, and our primary goal was to quantify spatial pattern on open surfaces, so we do not believe this sampling bias had much influence on our conclusions.

At 14-Mile Creek, the steep and highly complex topography did not permit haphazard placement of transect lines. Instead, quadrats were placed at selected sites in the approximate vertical center of each zone at horizontal intervals no less than 1 m apart. Site selection was determined in part by whether or not the quadrat would remain in place without slipping down the shore during photography.

Each 0.25-m^2 quadrat was subdivided with nylon cord into a grid of 25 subquadrats, each 10×10 cm in dimension. Subquadrats thus represented 4% of the total area encompassed by the quadrat. Since visual estimates appear at least as accurate as estimates obtained using clear random-dot plastic sheets (Meese and Tomich 1992, Dethier et al. 1993), percent cover was estimated visually from photographic prints. Per quadrat cover estimates for each space occupant were determined by summation across subquadrats. When little or no algal canopy is present, as at our sites, this method produces reasonably accurate estimates of the primary space occupants.

Limpet and predator density and size.—To provide a context for the predation and grazer manipulations, densities (no. individuals/ 0.25 m^2) of limpets, whelks, and sea stars were also estimated, either in the transects mentioned above (limpets and whelks) or in fixed plots (sea stars). Counts of limpets and whelks were made either directly in the field, or from photographs using a magnifying lens. Densities of *Stichaster* on the west coast were obtained by counting total numbers on isolated benches used as controls in the sea star predation experiments, and dividing these counts by the area (in square meters) of each bench.

Size of limpets and whelks was measured for individuals sampled in quadrats, usually supplemented with measurements of additional individuals in the vicinity of the transects. Size (grams wet mass) of *Stichaster* was estimated by weighing individuals directly in the field. In each case, all individuals encountered in the designated sampling area were measured.

Predator diets.—Feeding observations on whelks and sea stars were obtained in the field following stan-

dard methods (e.g., Connell 1961b, 1970, Paine 1966, Dayton 1971). Whelks and sea stars were turned over and prey being drilled or eaten were identified and measured. Oystercatchers (*Haematopus ostralegus*, *H. unicolor*), common on the Banks Peninsula, can leave a trail of empty limpet, chiton, and mussel shells as they forage through an area, and were the only birds observed to feed in this manner (B. Menge, B. Daley, J. Lubchenco, E. Sanford, P. Halpin, and J. Burnaford, *personal observations*). Such trails of freshly killed prey were discovered three times in the 6-mo study period in 1994–1995. All such prey that we could find were measured and identified, and attributed to Oystercatcher predation. While Oystercatchers also occurred on the west coast, we never found prey remains that could be clearly attributed to these birds. Diets of other birds occasionally observed roosting in the rocky intertidal, primarily red-billed and black-billed gulls (*Larus novaehollandiae* and *L. bulleri*, respectively), were not studied.

Quantification of ecological processes

Prey recruitment.—During austral summer 1994–1995, monthly recruitment of barnacles (*Chamaesipho columna*, *C. brunnea*, *Epopella plicata*, *Balanus* spp. were identifiable) and mussels (*Perna canaliculus*, *Mytilus galloprovincialis*, *Aulacomya ater maoriana* were identifiable) was quantified using techniques identical to those used in Oregon (e.g., Menge et al. 1994, Menge 2000, S. R. Connolly, B. A. Menge, and J. Roughgarden, *unpublished manuscript*). With exceptions noted below, collectors were placed at levels on the shore at each site that represented the upper and lower reaches of the vertical ranges of barnacles and mussels. Collectors were placed at the same fixed location at each site each month. Recruit collectors for barnacles were 10×10 cm, 5-mm-thick plexiglass plates coated with Safety-Walk, a rubbery substance with a uniformly textured surface (e.g., Farrell et al. 1991, Satchell and Farrell 1993). While abundances on plates are generally higher than on natural rock surface (B. Menge, *unpublished data*), comparisons among plates by zone, site, and coast are assumed to reflect natural variation in relative abundances in space and time. Plates (five per zone per site) were fastened with stainless-steel screws to rocks, and collected and replaced each month in high and middle zones at each east-coast site, and middle and low zones at each west-coast site. Low-zone samples were not taken at east-coast sites because adult barnacles were largely absent from these areas. High-zone samples were not taken at the west-coast sites because solid rock surfaces were absent at the main study sites. Counts and identifications of cyprids and metamorphs were made in the laboratory under a dissecting microscope.

Mussel-recruitment estimates were obtained using plastic-mesh ovoids ("Tuffys"; Menge et al. 1994). Ovoids (five per zone per site) were fastened with

screws to mid- and low-zone surfaces at each site on each coast and were collected and replaced monthly. In the laboratory, mussel recruits were detached from the plastic mesh by dissolving their byssal attachments in jars of bleach for 5 min, shaking the jar, and then pouring the contents of the jar through a 53- μ m sieve (method of B. Hayden, *personal communication*). After rinsing to remove the bleach, recruits were counted and identified under a dissecting microscope.

RNA:DNA ratios.—Mussels (*Perna*, *Mytilus*) are dominant space occupiers in the mid-zones and probable competitive dominants in the absence of predators and disturbance (e.g., Paine [1971] for *Perna*). Efforts to quantify growth using marked, transplanted mussels were thwarted by fouling of cages on the west coast, so relative growth of mussels in this study was determined by measuring RNA:DNA ratios of adductor muscle, gill, and mantle tissue. This biochemical indicator of protein-synthesis capacity was selected on the basis of previous field and laboratory studies by ourselves and others. RNA:DNA ratios have been demonstrated to be excellent indices of short-term organismal growth rate that respond rapidly to environmental variation in food availability and minimally to other environmental factors such as temperature (Buckley 1984, Wright and Hetzel 1985, Dahlhoff and Menge 1996).

Between-coast comparisons of mussel RNA:DNA ratios were made in January 1995. Mussels were collected from the mid-zone at each site, dissected in the field, and flash-frozen on dry ice. Samples were stored at -70°C in the laboratory in Christchurch, transported to Corvallis (Oregon, USA) on dry ice, and held at -70°C until RNA and DNA were quantified. RNA:DNA ratios were determined using ethidium bromide fluorescence following the method of Bentle et al. (1981) as modified by Dahlhoff and Menge (1996). Tissues were thawed on ice, weighed, and homogenized with a glass homogenizer in 2 mol/L NaCl. From each sample 50 μL was incubated in ethidium bromide and proteinase K at 37°C for 90 min, buffered, and fluorescence was recorded using a luminescence spectrofluorometer (Perkin-Elmer LS-5B luminescence spectrophotometer). RNA and DNA concentrations were estimated from a standard curve estimated from the fluorescence of known quantities of RNA (from calf liver) and DNA (from calf thymus).

Reciprocal transplant experiments tested whether differences in mussel-growth physiology were differentially influenced by the conditions on the east and west coasts. In early December 1994 similar-sized (4–5 cm long) individuals of *Perna* and *Mytilus* were placed ventral side down and covered with plastic mesh (Vexar, 1-mm mesh with 5-mm openings [Nor-Plex, Northwest Plastic Extrusion, Auburn, Washington, USA]) to allow them to reattach byssal threads to the rock (see below for further details of caging). For both species, transplants included within-coast treatments

(east to east, west to west) and between-coast treatments (west to east, east to west). Six cages containing 15 individuals of each species were established at TMN and BT (total number transplanted for each species = 90 mussels). Three cages were within-coast transplants and three were between-coast transplants. In early January and early February 1995, 8–10 mussels of each species were collected haphazardly from among the different cages and were dissected immediately. As in the comparative estimates of RNA:DNA ratios, samples of each tissue type were flash frozen in the field on dry ice, stored at -70°C , and shipped on dry ice to our laboratory in Corvallis for quantification of RNA:DNA ratios.

Mussel survival.—Mussels are often central components of rocky intertidal community organization, and in nearly all cases examined, their abundance and zonation patterns are intimately related to predation (e.g., Menge and Farrell 1989). On the South Island, mussel-abundance and zonation patterns were inversely related to predator abundance. On the east coast, the mussel *Mytilus galloprovincialis* was abundant and predators were scarce in both middle and low zones. On the west coast, in the mid-zone, mussels were abundant and predators were scarce, while in the low zone, mussels were scarce and predators abundant. This pattern suggested that contrasting low-zone patterns of mussel abundance and zonation between coasts were due to differential survival of mussels. We predicted that, due to predation, mussel survival would be higher in low-zone habitats on the east than on the west coast. To evaluate this possibility, mussel transplant experiments were established in the low zone at each of the two study sites on each coast. Methods were identical to those used in Oregon (Menge et al. 1994, Navarrete and Menge 1996). As in the RNA:DNA transplant experiments, similar-sized (4–5 cm long) mussels were held ventral side down against the rock substratum using plastic-mesh cages (20 \times 20 cm with 10-cm-wide flaps for attachment on each side; $n = 5$ cages per treatment, with 30 mussels per cage; see Menge et al. 1994: Fig. 5). Most mussels reattach firmly within 4–6 wk using this method.

Two general treatments used in this study were “–predators” (closed-mesh cages) and “+predators” (open or partial-mesh cages). In the latter, predator access to mussels was provided by opening the cages after mussels had reattached. On the east coast, where the most common intertidal predators were relatively small (whelks), openings were provided at the four corners of the cages by reattaching the cage sides so that 3–5 cm gaps were made between adjacent sides. Because working time in the low zone on the east coast was severely limited, we were unable to establish enough transplants to have both –predator and +predator treatments. Since low-zone predators (the sea star *Coscina nasterias calamaria*, the whelk *Thais orbita*) were scarce at these sites, and we rarely observed mussel

mortality from predation or any other factor in the low zone, we arbitrarily decided to forego the –predator treatment. In all previous such experiments (e.g., review in Menge and Farrell [1989]; see also Robles et al. 1995, Robles 1997) anywhere in the world, mussel survival in the absence of predators was high, usually >90%, so it seemed reasonable to assume the same would be true at our east-coast sites had we been able to establish these treatments. Nonetheless, since we lacked a low-zone check on mussel survival in the absence of predators on the east coast, we interpret our results with caution.

On the west coast, sea stars were the dominant intertidal predator. Since sea stars are on average much larger than whelks, a larger opening was needed for unimpeded predator access, so we removed opposite sides of the cages in the +predator cages. These +predator (partial) cages also served as “shade” controls for –predator (complete) cages, thereby ensuring that light, desiccation, and flow-alteration effects of the mesh were present in both +predator and –predator treatments. The presence of mesh in both treatments, however, probably also reduced bird predation, so this factor was not evaluated by these experiments. We never saw birds foraging intertidally on mussels at TMB however, so it seems unlikely that bird predation was important. Survival of mussels was determined by counting the number of survivors per cage.

In the last two months of the study we removed two opposite sides of the cages at east-coast sites as we had done from the start on the west coast. This was done to determine if the different methods of providing predator access led to a bias in mussel survival. No alteration of results attributable to this change was observed.

Predation intensity.—Predators, mostly the sea star *Stichaster australis*, were abundant on the west coast. Two methods were used to evaluate the rate of predation and its effects on mussels. In the first set of experiments, mussels were transplanted to isolated benches with either normal, unmanipulated populations of sea stars or to benches from which sea stars had been manually removed (e.g., Menge et al. 1994, Navarrete and Menge 1996). This method avoids the complication induced by natural asynchrony in the recruitment of prey to benches in sea star experiments by starting with known, similar numbers and sizes of adult mussels translocated to the low intertidal zone, within the normal foraging range of sea stars.

Two chronologically overlapping experimental trials were conducted. Mussels were transplanted and protected from predation by a cage until they had reattached firmly to the rock. The experiment was initiated when the cage was removed and the mussels were susceptible to predation by sea stars. The dates of mussel transplant, cage removal (=onset of experiment) and termination of experiment were as follows: Trial 1—mid-October 1994, 5 November 1994 to 20 March

1995; Trial 2—early January 1995, 1 February to 15 May 1995. The experiment was repeated to evaluate the influence of position of the transplant on the bench with respect to *Stichaster* foraging patterns and shore topography. In Trial 1, transplants were scattered across the bench tops without controlling for their proximity to the bench edge. However, as the tide recedes, feeding sea stars generally retreat to channel walls around each pedestal-like bench. When submerged, seastars crawled up the walls and onto the bench tops, where the first transplants they encountered and attacked were those closest to the bench edge. Sea stars located transplants in the middle of bench tops more slowly, so that average predation rates had high variance. After we had observed this pattern, Trial 2 included a treatment (edge vs. center) designed to control for these differences in prey accessibility. Half of the transplants were positioned at the bench edge and half were positioned in the middle of the bench top.

In each trial, 5 or 10 cages with 50 mussels each were transplanted to each of two +*Stichaster* and two (or one in experiment two) –*Stichaster* benches. In Trial 1, (five cages) all mussels were *Mytilus*, while in the second experiment (Trial 2) five edge and five center cages included equal numbers of *Perna* and *Mytilus*. Both mussel species were included to evaluate if sea star predation was selective. Counts of mussels and removals of sea stars were done at 2-wk intervals throughout the study except for Trial 2 where the last count was made 2 mo after the penultimate count.

The second method of determining the effect of *Stichaster* employed manual removal experiments (e.g., Paine 1966, 1971) using the same benches as in the above experiments. In addition to the transplants, after the removals were begun in November 1994, we quantified the response of natural prey abundance (percent cover) in January and March 1995. To estimate percent cover of mussels at increasing distances from the edge of the established bench-top mussel beds, we sampled benches on the top, at the edge, and on the channel walls below the edge. Increases in mussel cover observed were entirely from recruitment and subsequent growth of these recruits occurring during austral summer (approximately October–March) 1994–1995. The position of previously established, “adult” mussels, identifiable through a striking border with larger, older mussels to shoreward and smaller, younger mussels to seaward on each bench, did not change during the experiment.

Grazing intensity.—To determine variation in intensity of limpet grazing (mainly *Cellana ornata* and *C. radians*), we performed enclosure experiments in the lower mid-zone. These were located above low-zone, turf-covered surfaces but either below the middle mussel zone on the west coast or in gaps in the lower mussel bed on the east coast. Our design also evaluated how grazing varied across spatial scales ranging from within a site, to between-sites but within coasts, to between

coasts. On the west coast, little surface was available at TMS in the lower mid-zone, so grazer-exclosure experiments were done at a site located between TMN and TMS (called "Twelve-Mile Central," or TMC). Grazer-exclosure experiments employed methods identical to those done in Oregon (Menge et al. 1997a, B. Menge, *unpublished data*). Areas of rock substratum $\sim 20 \times 30$ cm in area were scraped clear of all organisms. Then, to remove more of the algal crusts still adhering to the rock, plots were sprayed with oven cleaner (NaOH, which degrades to NaCl and water when in contact with seawater; Cubit 1984). Limpet exclusion was achieved using barriers of copper-based anti-fouling paint ("Unepoxy," Kop-Coat Inc., Patit Paint Division, Rockaway, New Jersey, USA; e.g., Cubit 1984, Olson 1992, Paine 1992; see Benedetti-Cecchi and Cinelli [1997] for a critique of this method). Five replicates, each consisting of three treatments (+grazer, -paint; +grazer, +paint; -grazer, +paint) were established in each substratum/sub-habitat combination. Marked plots (the +grazer, -paint treatment) were marked at four corners with Z-spar marine epoxy (Kop-Coat, Inc., Pittsburgh, Pennsylvania, USA), to delineate a rectangle of $\sim 20 \times 30$ cm. Paint controls (the +grazer, +paint treatment) were partially surrounded with a discontinuous strip of paint. Paint was applied across the top and at both sides of the 20×30 cm rectangle, but not across the bottom or corners. By allowing grazers access to the plot through these gaps, this treatment controlled for potential paint effects vs. grazer exclusion. The enclosure (the -grazer, +paint treatment) excluded grazers with a complete barrier of paint surrounding the plot. When the substratum could be dried, the paint was applied directly to the rock. When seepage from surrounding habitat kept the rock moist, we first applied a strip of Z-spar and then painted directly on the curing epoxy. Z-spar was smoothed flat on all substrata to avoid both alteration of flow and creation of small tidepools. Since Z-spar is inert when it has cured, and both limpet grazing and algal settlement and growth occur on this compound in the absence of paint (B. Menge, B. Daley, J. Lubchenco, E. Sanford, P. Halpin, and J. Burnaford, *personal observation*), the alternative methods of applying paint are unlikely to influence our results.

All limpet-exclosure experiments were begun in December 1994 and were monitored monthly until early March, both photographically and by making visual estimates of cover of algae and sessile invertebrates in each plot. Limpet densities in all plots were counted monthly. Limpets entering exclosures were removed every 2 wk.

Data analysis

Because the positions of replicates on the rock were the same for each sample period, repeated-measures ANOVA was used to analyze maximum wave-force data, recruitment data, and experiments on mussel sur-

vival, mussel growth (RNA:DNA) reciprocal transplants, sea star predation rate, and exclosure of grazers. When site was included in the analysis, the ANOVAs were nested, with site nested within coast. Three-way ANOVA was used to analyze the comparative RNA:DNA ratio data and sea star removal experiments. Among the independent variables, coast, zone, and experimental treatments (e.g., +predators, -predators, +grazers, -grazers; see above) were analyzed as fixed, and site was regarded as random.

Data were analyzed with SYSTAT (version 7.0; Wilkinson 1996), JMP (SAS Institute 1995) and SAS (SAS Institute 1989). In those cases where we analyzed the same data set with different software packages, results were identical. The multivariate assumption of compound symmetry (Tabachnick and Fidell 1989) was evaluated by comparing *P* values to those adjusted with the Huynh-Feldt statistic (Wilkinson 1996). In univariate analyses, assumptions of normality and independence of error terms were evaluated by visual examination of probability plots of residuals and plots of residuals vs. estimated values, respectively. In most cases, transformation of the data was necessary to satisfy these assumptions. Count data were log transformed ($\ln[y + 1]$) and percent cover or proportional data were arcsine square-root transformed (e.g., Sokal and Rohlf 1995). Homogeneity of variances was checked by Cochran's test (Winer et al. 1991). When variances were heteroscedastic, we performed parametric analyses with transformed data. In such cases, conclusions were conservative, and based on the significance of the *P* values and sample size (e.g., Underwood 1981, 1997). Only when $P \ll 0.05$ and $n \geq 6$ did we conclude that an effect was probably ecologically significant.

Where possible and appropriate, variance components were calculated following Sokal and Rohlf (1995) and Underwood (1997) to estimate the percentage of variation due to different factors. Variance components are sensitive to experimental design, and are difficult to interpret if magnitudes of interactions are similar to main effects (Underwood 1997), so comparisons are made only within experiments and are interpreted conservatively.

The analysis of wave-force data was constrained by several factors. The samples were never taken simultaneously between coasts, replication was sometimes reduced due to loss of "wiffle-ball" drogues, and there were tide series when no data were available on the east coast. We thus confined the statistical analysis to the six time periods when samples were taken within 4-6 d on both east and west coasts during which weather patterns had not changed significantly. Other analyses were straightforward; additional details are in relevant table headings or figure captions.

RESULTS

Community structure

Zonation and spatial structure.—In general, wave-exposed east-coast sites had high zones dominated by

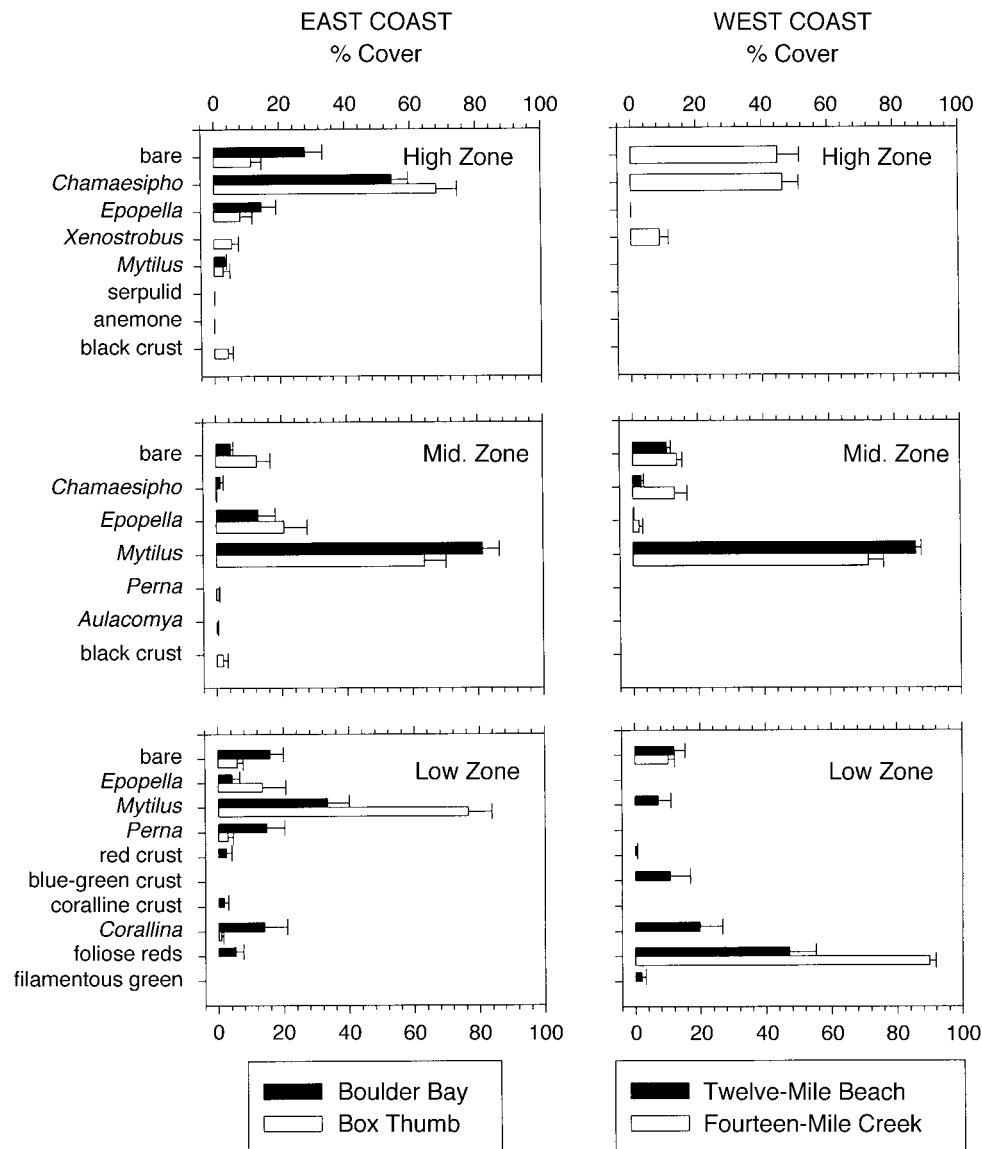


FIG. 2. Community structure on South Island, New Zealand: primary space occupancy at Boulder Bay and Box Thumb (high, middle, and low zones) on the east coast and at Twelve-Mile Beach North (middle and low zones) and Fourteen-Mile Creek (high, middle, and low zones) on the west coast ($N = 15$ quadrats \times three zones \times two sites \times two coasts = 180). Error bars for this and all subsequent figures are 1 SE. Complete scientific names for identified species are *Chamaesipho columna*, *Epopella plicata* (barnacles), *Xenostrobus pulex*, *Mytilus galloprovincialis*, *Perna canaliculus*, *Aulacomya ater maoriana* (mussels); and *Corallina officinalis* (coralline alga). Foliose reds include *Gigartina decipiens* and *G. clavifera*.

barnacles, and middle and low zones dominated by mussels (Fig. 2). Zonation of west-coast sites was similar, with the exception that barnacle abundance in the high zone was somewhat lower than on the east coast, and low zones were dominated by turf-forming algae (Fig. 2; B. Menge, B. Daley, J. Lubchenco, E. Sanford, P. Halpin, and J. Burnaford, *personal observations*). On the east coast, canopy-forming algae were essentially absent from high and middle zones, and not particularly abundant in the low zone at any site, although the large kelps (*Durvillea willana* and *D. antarctica*) were abundant at the lowest low-tide mark (0.0 m datum; B.

Menge, B. Daley, J. Lubchenco, E. Sanford, P. Halpin, and J. Burnaford, *personal observations*). The dominant high-zone space occupier on both coasts (Fig. 2) was the barnacle *Chamaesipho columna*. Subdominants included the barnacle *Epopella plicata* and the mussels *Mytilus galloprovincialis* and *Xenostrobus pulex*. In the mid-zone, *M. galloprovincialis* was the spatial dominant on both coasts, with *E. plicata* as a subdominant on the east coast and *C. columna* as a subdominant on the west coast.

Low-zone spatial patterns on both coasts were more complex (Fig. 2). On the east coast, *M. galloprovin-*

TABLE 1. Densities and sizes of limpets and predators at the two east-coast sites of South Island, New Zealand.

Species	Zone†	Year	Box Thumb	Boulder Bay
Density (no. individuals/0.25 m ²)				
<i>Cellana ornata</i>	High	1995	16.9 ± 5.2	...
	High	1997	3.9 ± 2.0	6.9 ± 1.4
	Mid	1995	4.5 ± 2.2	...
	Mid I	1997	5.9 ± 1.3	3.4 ± 1.7
	Mid II	1997	26.3 ± 6.4	...
<i>C. radians</i>	Mid	1997	2.1 ± 0.7	0.06 ± 0.06
	Low	1997	...	0.7 ± 0.7
<i>Lepsiella scobina</i>	High	1995	2.3 ± 1.1	...
	High	1997	2.3 ± 1.6	2.1 ± 1.2
	Mid	1995	2.5 ± 3.1	...
	Mid I	1997	3.5 ± 1.3	0 ± 0
	Mid II	1997	1.7 ± 0.9	...
<i>Thais orbita</i>	Mid	1995	0.3 ± 0.3	0 ± 0
	Low	1997	0 ± 0	0.07 ± 0.07
Shell length (mm)‡				
<i>Cellana ornata</i>	High	1997	11.2 ± 0.4 (50)	12.4 ± 0.6 (56)
	Mid	1997	8.7 ± 0.3 (51)	11.3 ± 0.7 (49)
<i>C. radians</i>	Mid	1997	20.4 ± 0.7 (92)	12.2 ± 0.6 (100)
<i>Lepsiella scobina</i>	High	1997	14.3 ± 0.3 (50)	11.1 ± 0.3 (50)
	Mid	1997	13.9 ± 0.3 (50)	12.2 ± 0.3 (56)
<i>Thais orbita</i>	Mid	1997	25.9 ± 0.7 (50)	19.9 ± 0.8 (46)
	Low	1997	29.1 ± 0.5 (50)	27.1 ± 0.6 (51)

Notes: Densities are mean ± 1 SE of the mean, $n = 15$ quadrats per zone per site. *Cellana ornata* and *C. radians* are limpets; *Lepsiella scobina* and *Thais orbita* are whelks.

† Mid = middle zone; Mid I = lower mid-zone; Mid II = upper mid-zone.

‡ Sample sizes are in parentheses.

cialis was the spatial dominant, with the mussel *Perna canaliculus*, *E. plicata*, and the red coralline alga *Corallina officinalis* as subdominants. On the west coast, mussels were scarce in the low zone, and primary space was dominated by bare rock/crustose algae (upper low zone) and foliose red algae (lower low zone; mostly *Gigartina decipiens* and *G. clavifera*). The upper low zone (not evident in Fig. 2) had no parallel on the east coast, where bare space was largely in gaps in the mussel bed, presumably caused by disturbance from winter storms.

Limpet and predator densities and sizes.—On the east coast, density of *Cellana ornata* was temporally and spatially variable in high and middle zones. This limpet was largely absent from the low zone (Table 1). Between east-coast sites, *C. ornata* were similar in size within zones but tended to be larger in the high zone. A larger limpet, *C. radians*, was essential absent from the high zone (B. Menge, B. Daley, J. Lubchenco, E. Sanford, P. Halpin, and J. Burnaford, *personal observations*). When present in middle and low zones, *C. radians* occurred at relatively low densities (Table 1). *C. radians* was larger than *C. ornata* at Boulder Bay (BB), but at Box Thumb (BT) the two species were more similar in size.

On the east coast, *Lepsiella scobina* was the most common whelk, and occurred only in middle and high zones (Table 1, B. Menge, B. Daley, J. Lubchenco, E.

Sanford, P. Halpin, and J. Burnaford, *personal observations*). Densities and sizes of these whelks varied little between zones or sites. The larger *Thais orbita*, although present in middle and low zones, was scarce (Table 1). Another whelk, *Haustrum haustrum*, was rare on wave-exposed shores. Although the effect of *Thais* may not be accurately reflected by its abundance in the intertidal (Fairweather 1988), the scarcity of whelks at the Godley Head sites suggests that these consumers are likely to have small effects on prey. Sea stars (*Coscinasterias calamaria*, *Patiriella regularis*) occurred at east-coast sites (B. Menge, B. Daley, J. Lubchenco, E. Sanford, P. Halpin, and J. Burnaford, *personal observations*), but <10 of each were seen in 6 mo. Based on scarcity and lack of evidence for sea star feeding in the intertidal, neither was considered a significant member of the east-coast intertidal food web.

On the west coast, data on whelk density and size are more limited. With the exception of total limpet density estimates obtained in the limpet-exclusion experiments (see *Community dynamics: Growing intensity*, below), no limpet data were available. Qualitative observations indicated that *Lepsiella* and *Thais* were both rare at our west-coast sites but similar in size to east-coast animals (B. Menge, B. Daley, J. Lubchenco, E. Sanford, P. Halpin, and J. Burnaford, *personal observations*); neither is regarded as an important pred-

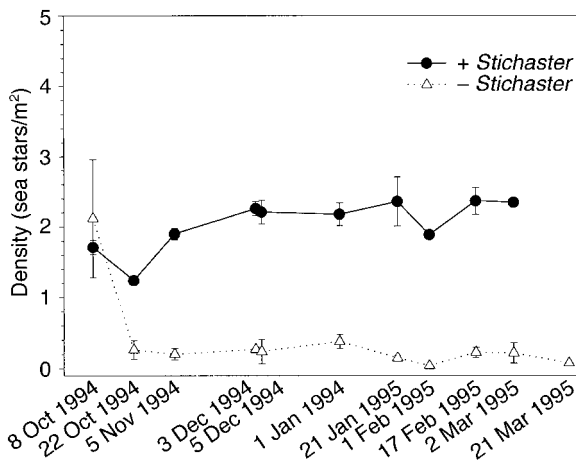


FIG. 3. Density of *Stichaster australis* on control (+*Stichaster*) and sea star removal (–*Stichaster*) reefs from 8 October 1994 to 21 March 1995 on the experimental benches at Twelve-Mile Beach (west coast of South Island, New Zealand). Density estimates were obtained by counting the number of sea stars on each bench ($N = 2$ benches \times 2 treatments = 4 benches) during each visit, divided by the area of each bench included in the foraging range of the sea stars, judged to be the entire area below the lower limit of large mussels.

ator during our studies at Twelve-Mile Beach (TMB). *Thais* was large and abundant at another site 35 km to the north of TMB (Woodpecker Bay; B. Menge and E. Sanford, *personal observations*), however, and further study will be needed to evaluate its general community role.

In contrast, the sea star *Stichaster australis* was abundant at the west-coast sites (Fig. 3). Sea star sizes (wet mass) at TMB ranged from 36 g to 202 g (mean \pm 1 SE = 100.5 ± 2.7 g; $n = 177$ individuals). At Woodpecker Bay, *Stichaster* ranged to larger sizes, from 39 g to 760 g (mean \pm 1 SE = 185.6 ± 14.4 g; $n = 76$ individuals). Associated with this difference in size structure of *Stichaster* was the unquantified observation that *Perna* were much more abundant at Woodpecker Bay than at TMB (B. Menge and E. Sanford, *personal observations*). *Perna* is one of the favored prey of the sea star (Paine 1971). Studies on the west coast of North America (Menge et al. 1994, Robles et al. 1995) suggest that dense concentrations of mussels may concentrate their predators and support faster growth and larger sizes of predators.

Predator diets.—On the east coast, whelks and oystercatchers were top predators. *Lepsiella* fed exclusively on barnacles and mussels. Out of 107 prey consumed, 64.5% were *Chamaesipho*, 32.7% were *M. galloprovincialis*, and 2.8% were *Epopella*. Only 6.4% of 1661 animals sampled were feeding. On the North Island, Luckens (1975a) observed *Lepsiella* to have a broader diet, feeding on 13 species including barnacles, mussels, oysters, limpets, snails, and tubeworms. The scarcity of *Thais orbita* limits inferences about its diet, although we observed individuals feeding on mussels.

Elsewhere *T. orbita* is reported to have a broad diet. On Rottnest Island off western Australia, *T. orbita* (formerly *Dicathais aegrota*) ate primarily whelks, limpets, snails, mussels, chitons, and crabs (Phillips 1969, Black 1979). Eastern Australian *T. orbita* appear to feed primarily on barnacles (Fairweather 1988). Oystercatchers ate *M. galloprovincialis* (36% of 25 items eaten), *Perna* (28%), *Aulacomya* (16%), *Cellana radians* (16%), and *C. ornata* (4%).

On the west coast, the diet of *Stichaster* was very similar to that observed by Paine (1971) on the west coast of the North Island. Though this sea star was a generalized predator—consuming mussels, barnacles, whelks, and other gastropods—most of its diet was *M. galloprovincialis* (82% of 1536 prey items eaten by 176 sea stars). Although *Perna* were very rare in the sea star's diet at TMN and TMS (0.1%), *Stichaster* readily consumed *Perna* when available (Paine 1971, B. Menge, B. Daley, J. Lubchenco, E. Sanford, P. Halpin, and J. Burnaford, *personal observation*; see *Community dynamics; Predation effects: rates of Stichaster predation* below). The near-absence of *Perna* from the diet of the TMB populations was undoubtedly due to the scarcity of this mussel at these sites (Fig. 2). *Stichaster* ate mostly the small, newly recruited mussels (modal size = 6 mm, $n = 1265$ total eaten) on channel walls and bench edges, at least during summer 1994–1995. This predominance of small mussels in the sea star's diet most likely reflects availability as opposed to any preference for small prey. As noted previously, in January–March 1995 when these observations were made, foraging sea stars at TMB first encountered and fed upon a solid band of recent recruits located below the higher band of larger adult mussels.

Environmental conditions

Maximum wave forces.—Wave forces did not differ between coasts but differed between sites within coasts (Table 2). The between-site difference was mostly attributable to lower maximum wave-force estimates at BB (Fig. 4A), a likely artifact resulting from an interaction of the dynamometer with topography (full extension of the dynamometer in flow is prevented on steep surfaces; M. Denny, *personal communication*). Because of this effect, patterns at BT where dynamometers were attached on more gently sloping surfaces probably better represent east-coast conditions in east-west comparisons.

Wave forces varied over time but differently on each coast (Table 2, coast \times time interaction), suggesting that wave regimes differed between coasts. On average, patterns on the east coast tended to fluctuate inversely from those on the west coast (Fig. 4B), but wave forces tended to covary between sites within coasts (Fig. 4A).

Low-tide air temperatures.—Air-temperature regimes in the intertidal zone at low tide were generally similar but patterns of daily fluctuations differed between coasts. Both within- and between-coasts, the

TABLE 2. Results of nested repeated-measures ANOVA (sites nested within coasts) on maximum wave-force estimates at six time periods for which estimates were available at both sites on each coast.

Source of variation	Univariate analysis					Multivariate analysis			
	SS	df	MS	F	P	Wilks' λ	df	F	P
Between subjects									
Coast	0.1525	1	0.1525	0.09	>0.75				
Site(Coast)	3.3280	2	1.6640	6.95	0.0099				
Error	2.8751	12	0.2396						
Within subjects									
Time	1.9111	5	0.3822	10.74	≤ 0.0001	0.1501	5, 8	9.06	0.0038
Time \times Coast	2.0270	5	0.4054	6.50	<0.01	0.1041	5, 8	13.77	0.0009
Time \times Site(Coast)	0.6244	10	0.0624	1.75	0.089	0.2699	10, 16	1.48	0.23
Error	2.1363	60	0.0356						

Notes: Error terms: coast was tested over site(coast), and time \times coast was tested over time \times site(coast). Variances were homogeneous, Cochran's C (transformed data) = 0.2094; $C_{0.95}(20, 3) = 0.2205$. Probabilities significant to five or more decimal places are shown as $P \leq 0.0001$.

maximum temperatures recorded ($\sim 26^\circ\text{C}$) and temperature ranges recorded were nearly identical (Fig. 5). On each coast, twice-daily low-tide temperatures oscillated between large and small changes as low tides changed from night/day (large differences) to early morning/late afternoon (small differences). The magnitudes of the recordings oscillated differently between

coasts, however, reflecting the difference in times of lows on the two coasts (Lamont 1996). East-coast low tides coincide with west-coast high tides (and vice versa), so that when east-coast low tides occur at midday and midnight, west coast low tides occur in early morning and late afternoon. Such differences might suggest that, in the short term, intertidal shores on opposite

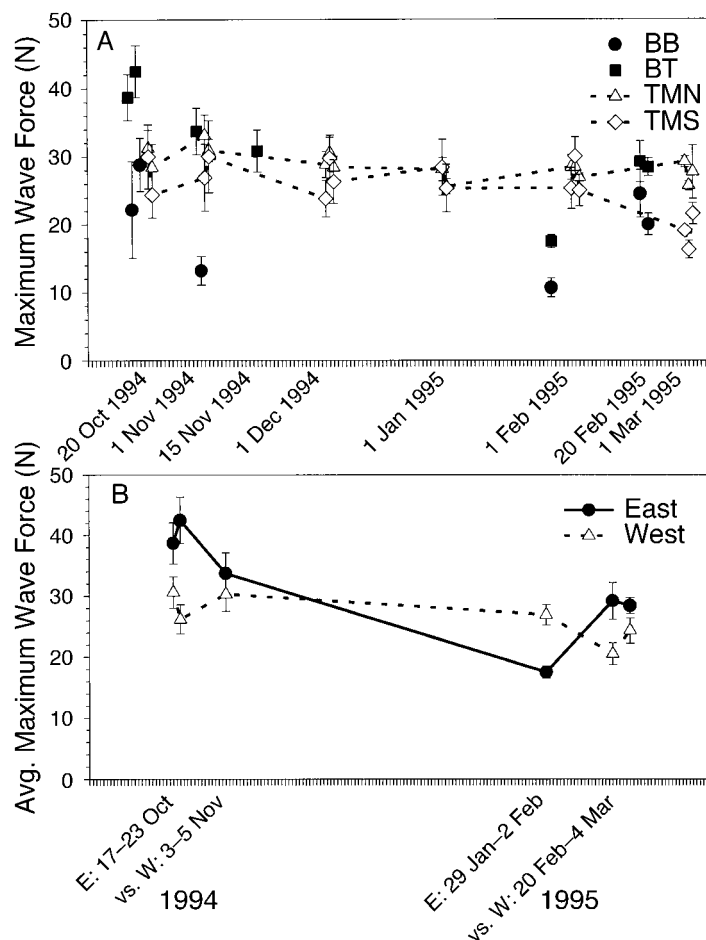


FIG. 4. Maximum wave forces on South Island (New Zealand), 1994–1995. (A) Separate estimates at each site on each coast, by sample date. East coast: BB (Boulder Bay) and BT (Box Thumb). West coast: TMN (Twelve-Mile Beach North) and TMS (Twelve-Mile Beach South). (B) Average wave forces for each coast, based on combining data from each of the two sites on each coast ("E: 17–23 Oct vs. W: 3–5 Nov" means east-coast samples taken on 17–23 October are compared to west-coast samples taken on 3–5 November). $N = 5$ dynamometers $\times 2$ sites $\times 2$ coasts = 20 dynamometers. See *Methods: Quantification of physical conditions: Maximum waveforce* for further explanation.

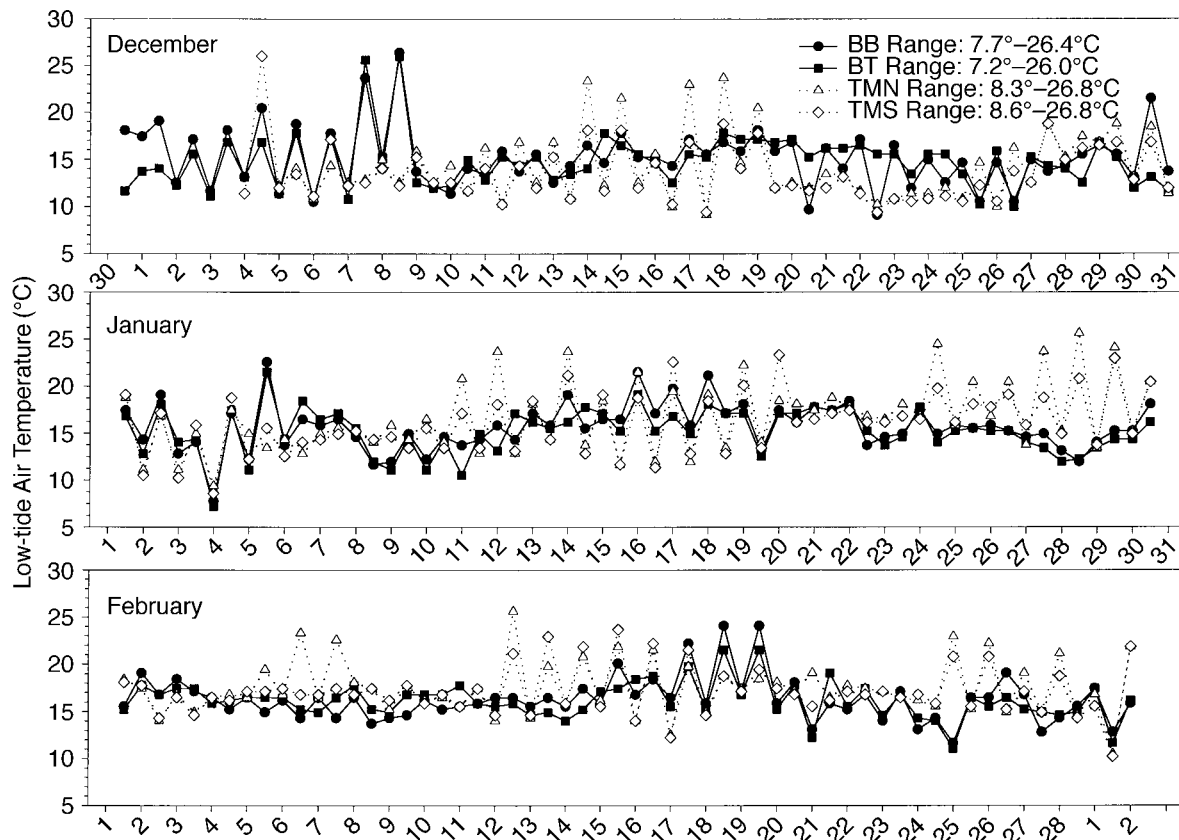


FIG. 5. Low-tide air temperatures at BB (Boulder Bay) and BT (Box Thumb) on the east coast and TMN and TMS (Thirteen-Mile Beach North and South, respectively) on the west coast of South Island, New Zealand, from 30 November 1994 to 2 March 1995. Values presented are the temperatures recorded nearest the time of low tide. One data logger was placed at about +1.0 m at each site on both coasts, for a total of four data loggers. See *Methods: Quantification of physical conditions: Temperature* for further explanation.

coasts may be differentially affected by environmental stress. However, despite the contrasting patterns of temperature oscillation, air temperatures were always moderate, never falling below 7°C or above 27°C. We conclude that, although short-term (daily, weekly) differences in thermal environment are likely between coasts, low-tide thermal regimes are similar between coasts over the long term.

High-tide seawater temperatures.—High-tide temperature data documented patterns consistent with the characterization of the west coast as an upwelling system and the east coast as a non-upwelling system (Fig. 6). On the west coast, rapid within-day transitions of 2–3°C between periods of relative stasis lasting several days to a week were regularly recorded. Such patterns are a hallmark of upwelling systems, with the sharp temperature drops signaling the arrival at the surface of deep, cold upwelled water (Bakun 1996). Six such periods were recorded between early December 1994 and early March 1995. These patterns parallel those seen further offshore on the west coast during ship-based oceanographic studies in the late 1980s (e.g., Stanton 1976, Stanton and Moore 1992).

In contrast, on the east coast the temperature fluctuations were less in magnitude and of shorter duration (Fig. 6). Only one and perhaps two periods of sustained, sharply decreased sea-surface temperatures were observed, both in early January 1995, but even these were brief relative to those on the west coast. Generally, temperature fluctuations were far less on the east than on the west coast, and the coldest temperatures recorded were almost never below 14°C, which is well above the 10–13°C range seen commonly on the west coast.

Nutrient concentrations.—Nutrient (nitrate, phosphate, and silicate) concentrations were similar on both coasts in December 1994 and February 1995 but strikingly greater on the west coast in January 1995 (Fig. 7, Table 3). Nitrate varied among sites (Table 3; within subjects, Time \times Site(Coast) interaction was significant, $P = 0.01$) but most variance was associated with differences between coasts and sample times. Phosphate also varied among sites (Table 3; between subjects, Site(Coast) was significant, $P = 0.008$) but, again, the majority of variance was associated with temporal and coast differences. Silicate varied the most

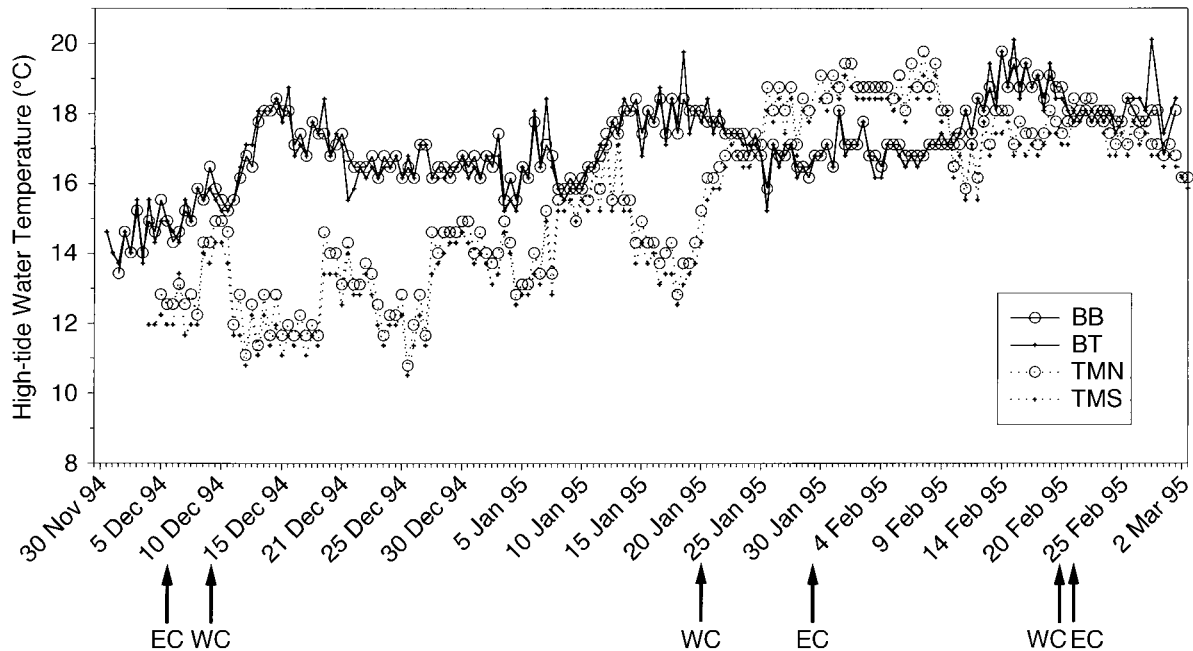


FIG. 6. High-tide sea water temperatures at BB and BT on the east coast and TMN and TMS on the west coast of South Island, New Zealand, from 30 November 1994 to 2 March 1995. Values presented are the temperatures recorded nearest the time of high tide. See Fig. 5 legend for further explanation. Arrows at bottom indicate dates of nutrient samples for east (EC) and west (WC) coasts.

among sites (Table 3; within subjects, $\text{Time} \times \text{Site}(\text{Coast})$ interaction was significant, $P = 0.0005$), but here too a substantial proportion of variance was associated with coast and time. We conclude that in January at least, nutrient concentrations, particularly of nitrate, were substantially greater on the west than on the east coast.

Community dynamics

Prey recruitment: barnacles.—Recruitment of barnacles to collectors was far greater on the west coast than on the east coast (Fig. 8C–F). On the east coast, recruitment in high zones was sparse, with maximum densities ~ 5 barnacles/100 cm², while mid-zone maxima ranged between 100–200 barnacles/100 cm². Most settlement on the east coast occurred in February and March (Fig. 8A–D) and, in concert with their dominance of primary substratum space, *Chamaesipho columna* and *Epopella plicata* were the most common recruits. On the west coast, mid-zone recruitment was far greater, ranging into the thousands per 100 cm². In addition to *C. columna* and *E. plicata*, the barnacles *C. brunnea* and an unidentified *Balanus* species also settled in modest numbers. No high zone existed at TMB so no between-coast comparisons are possible for this zone. In the west-coast low zone, recruitment densities were similar to, or greater than those in the mid-zone at both sites (Fig. 8E–H).

In the mid-zone, *C. columna* recruitment densities varied most strongly between coasts, accounting for $>90\%$ of the variance (Table 4A: between-subjects

analysis). Settlement patterns of *C. columna* also varied over time and between sites (Table 4A: within-subjects analysis; $\text{Month} \times \text{Site}(\text{Coast})$ interaction was significant). On the east coast, recruitment was greater in middle than in high zones, and Zone accounted for most variation in *C. columna* and *E. plicata* ($\sim 45\%$ and 75% , respectively) (Table 4B: East coast; within-subjects analyses). Recruitment patterns of both species also varied asynchronously through time between sites and between zones (Table 4B: Within-subjects analysis; $\text{Month} \times \text{Site}$ and $\text{Month} \times \text{Zone}$ interactions were significant for both species). Results of both the univariate and the more conservative multivariate analyses were consistent, suggesting the analyses are robust.

On the west coast, similar recruitment trends were observed for *C. columna* (Table 4). Between-zone differences were lower in magnitude than on the east coast, however, because west-coast recruitment densities in middle and low zones both tended to be high (Fig. 8E–H). Densities varied sharply through time (Fig. 8E–H, Table 4C: Within-subjects analysis, $\text{Month } P \ll 0.0001$), and temporal variation accounted for the majority of the variance ($\sim 64\%$). Although *Epopella* recruitment also varied with site and zone over months (Table 4), the low densities of these recruits and the low densities of adults on the west coast suggest these patterns were of minor importance to community variation.

Prey recruitment: mussels.—Mussel recruitment was also much denser on the west coast than on the east coast, but temporal variation and within- and be-

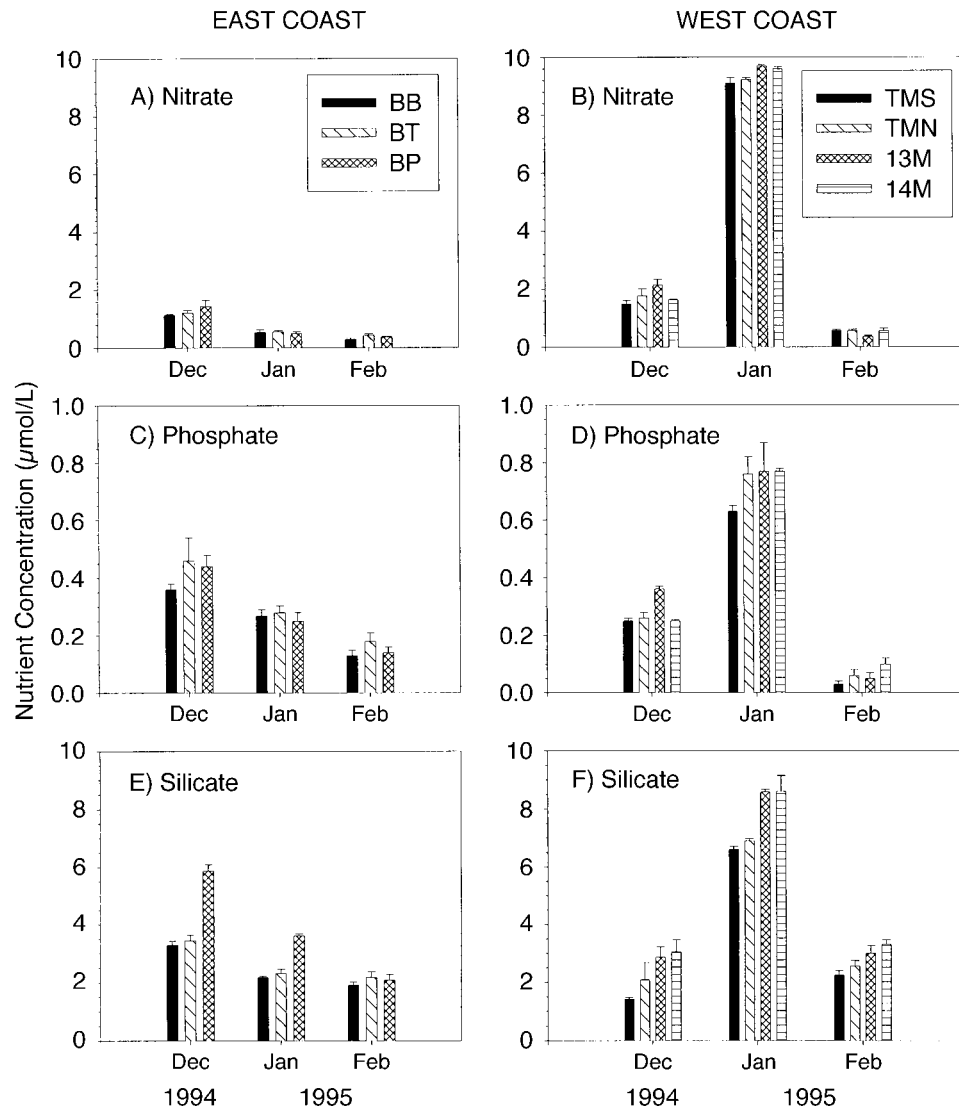


FIG. 7. Nutrient concentrations (mean and 1 SE; nitrate, phosphate, and silicate) on the east and west coasts of South Island, New Zealand, in December 1994, and January and February 1995. East-coast sites included Black Point (BP; ~1 km northwest of BT) as well as BB and BT. West-coast sites included Thirteen-Mile Creek (13M) and Fourteen-Mile Creek (14M), sites ~1.5 and 3 km north of TMB, respectively. $N = 6$ samples \times 3 (east) or 4 (west) sites \times 3 dates \times 2 coasts, or a total of 252 water samples. See Fig. 5 legend for other code explanations.

tween-zone heterogeneity resulted in complex patterns (Fig. 9, Table 5). Overall, recruitment-density variation depended on Site, Coast, and Zones (Table 5: Between subjects; the interaction between Zone \times Site(Coast) was significant). In other words, density of mussel recruits was contingent on the specific combinations of each of the factors. Temporal changes were striking, but only on the west coast, and were less at TMS than TMN (Fig. 9; Table 5: Within subjects; Month \times Zone \times Site(Coast) was significant). Coast accounted for most of the variance (~59%), however, even though the main effect of coast in the between-subjects analysis was not significant due to high variation and low degrees of freedom.

On the east coast, mid- and low-zone recruit densities were similar on both benches (Fig. 9A–D). In both zones at both sites, *Mytilus galloprovincialis* was the more numerous of the three species identifiable in these samples. *M. galloprovincialis* was found throughout the middle and low zones, but adults were more dominant in the mid-zone (Fig. 2). Mussel recruitment occurred throughout our study period, but on the east coast was heaviest in January and February 1995.

On the west coast, mussel-recruit densities were much higher, occurred throughout the study period, and with the exception of TMS low zone, were highest in December and April (Fig. 9E–H). Recruitment densities at TMS low were less than both the TMS mid-zone

TABLE 3. Results of repeated-measures ANOVA testing the effects of coast and site on nutrient concentrations (nitrate, phosphate, silicate) on east and west coasts of the South Island of New Zealand.

Source of variation	Univariate analysis					Multivariate analysis			
	df	MS	F	P	Variation explained (%)	Wilks' λ	df	F	P
Nitrate									
Between subjects									
Coast	1	16.8691	1406.9	$\ll 0.0001$	51.3				
Site(Coast)	5	0.0120	1.52	0.21	0.05				
Error	35	0.0079			...				
Within subjects									
Time	2	10.6651	894.0	$\ll 0.0001$	21.6	0.0121	2, 34	1390.3	$\ll 0.0001$
Time \times Coast	2	10.8014	369.4	$\ll 0.0001$	21.8	0.0153	2, 34	1097.2	$\ll 0.0001$
Time \times Site(Coast)	10	0.0292	2.45	0.01	0.2	0.5395	10, 68	2.46	0.01
Error	64	0.5490			...				
Phosphate									
Between subjects									
Coast	1	0.0531	5.97	0.06	2.8				
Site(Coast)	5	0.0089	3.79	0.008	2.2				
Error	32	0.0023			...				
Within subjects									
Time	2	0.8467	213.0	$\ll 0.0001$	37.2	0.0627	2, 31	231.9	$\ll 0.0001$
Time \times Coast	2	0.5210	131.9	$\ll 0.0001$	22.8	0.0967	2, 31	144.8	$\ll 0.0001$
Time \times Site(Coast)	10	0.0040	0.99	0.46	0.0	0.7684	10, 62	0.87	0.56
Error	64	0.0040			...				
Silicate									
Between subjects									
Coast	1	1.2819	2.78	0.18	10.0				
Site(Coast)	5	0.4608	14.29	$\ll 0.0001$	17.3				
Error	35	0.0322							
Within subjects									
Time	2	2.7350	168.0	$\ll 0.0001$	14.7	0.0628	2, 34	253.7	$\ll 0.0001$
Time \times Coast	2	4.4684	73.59	$\ll 0.001$	23.8	0.0624	2, 34	255.2	$\ll 0.0001$
Time \times Site(Coast)	10	0.0607	3.73	0.0005	1.2	0.4361	10, 68	3.50	0.0009
Error	70	0.0163							

Notes: East-coast sites were BT, BB, and Black Point; west-coast sites were TMS, TMN, Thirteen-Mile Creek, and Fourteen-Mile Creek. Sample dates were 6 (east) and 9 (west) December 1994, 29 (east) and 21 (west) January 1995, and 22 (east) and 20 (west) February 1995. Coast was tested over Site(Coast), and Time \times Coast was tested over Time \times Site(Coast). $N = 6$ samples per site per month. Variances for nitrate were homoscedastic; Cochran's $C = 0.1633 < C_{0.95}(21, 5) = 0.1735$. Variances for phosphate and silicate were heteroscedastic; phosphate Cochran's $C = 0.2244$, and silicate Cochran's $C = 0.2601$, both $> C_{0.95}(21, 5) = 0.1735$. For additional explanation of site codes see Fig. 5 legend.

and TMN. This difference was most likely responsible for the significant Zone \times Site(Coast) interaction (Table 5). As on the east coast, *M. galloprovincialis* was the most abundant recruit in both middle and low zones.

Mussel growth.—Growth, as reflected by higher RNA:DNA ratios of both *M. galloprovincialis* and *Perna canaliculus* was strikingly greater on the west than on the east coast (Fig. 10, Table 6). All three factors—tissue, species, and coast—contributed significantly to the differences seen among the ratios (Table 6; three-way interaction was significant). Examination of the data suggests that with the exception of *Perna* adductor ratios, which were similar on both coasts, all ratios were higher on the west coast (unplanned comparisons; Fisher's least significant difference, $P \ll 0.0001$). Moreover, ratios for *Perna* were greater than for *Mytilus* (Fisher's LSD, $P \ll 0.0001$), and gill ratios were lower than adductor or mantle (Fisher's LSD, adductor = mantle $>$ gill, $P \ll 0.0001$). Evidently, the primary cause of the significant interaction was the relatively high ratio for east coast *Perna* adductor tissue. Al-

though the significant interaction is the interpretable effect, as summarized above, coast explains the largest fraction of total variance (Table 6).

The translocation experiments suggest that, as with *Mytilus californianus* in Oregon (Dahlhoff and Menge 1996), growth of adductor tissue for both *Perna* and *Mytilus* tended to respond quickly to changes in oceanographic conditions (Fig. 11; Table 7). For *Perna*, RNA:DNA ratios were higher in January and February in control (west to west, east to east) transplants on the west coast than the east coast. West- to east-coast transplants converged with east to east control transplants by January, and east- to west-coast transplants converged with west to west control transplants by February (Fig. 11). Similar trends were observed in *Mytilus* with the exceptions that ratios were different in December before transplantation, and that east to east controls inexplicably increased sharply between January and February to levels similar to those of both west to west controls and east to west transplants. We do not know the causes of the unexpected increase in RNA:

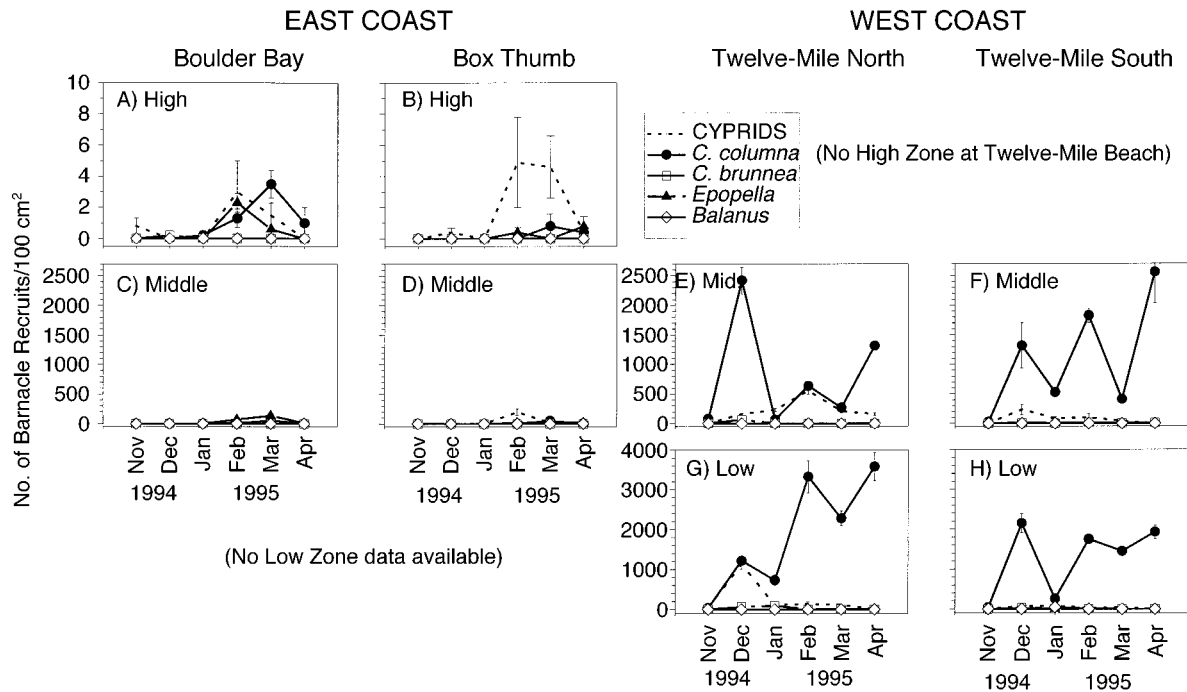


FIG. 8. Recruitment densities of barnacles at BB and BT on the east coast, and TMN and TMS on the west coast of South Island, New Zealand. Estimates are from counts of metamorphs and cyprids observed on collectors placed in the middle and high zones on the east coast and middle and low zones on the west coast. *Chamaesipho columnna* recruits were distinguished by their bluish-gray coloration, *C. brunnea* by their brownish color, *Epopella* by the bristles around the operculum and its whitish color, and *Balanus* by its white color. Note the different scales for the ordinates in high, middle, and low zones. $N = 5$ collectors per zone per site per coast, or a total of 40 collectors/mo.

DNA ratios in *Mytilus* east to east controls, nor for weak and variable responses of gill or mantle tissue in the transplant experiments (data not shown).

Thus, both the comparative results (Fig. 10) and the transplant-experiment results suggest that environmental conditions on the west coast encourage higher RNA:DNA ratios, and that these ratios can change rapidly, within 1–2 mo, when conditions are altered. We conclude that growth physiologies of both mussel species differ between coasts, in concert with apparent differences in oceanographic conditions.

Predation effects: mussel survival.—As expected, in the presence of predators in the low zone, transplanted *Mytilus* survived better on the east than on the west coast (Table 8A, within-subjects analysis; Time \times Coast interaction was significant, Fig. 12). On both coasts, patterns of survival were similar between sites (Table 8). Although survival appeared lower at BT than at BB, no significant effect of site was detected in the analysis (Table 8). Similar results were obtained in the more conservative multivariate analysis (Table 8B). These results suggest that predation rates on mussels in the low zone varied at the largest, geographic scale, but not at the intermediate, site-within-coast scale. As discussed in the next section, however, local scale (among-replicate) variability in west-coast results (here termed “Experiment 1” to distinguish it from Exper-

iment 2 in the next section), as suggested by large standard error bars, was high (Fig. 12).

Predation effects: rates of *Stichaster* predation.—Since predators other than sea stars (e.g., whelks) were relatively scarce and small at Twelve-Mile Beach, the results reported in the previous section, with the addition of results from sea star exclusion treatments, provide estimates of rates of predation by sea stars. In contrast to the nearly 100% survival on $-Stichaster$ benches (Fig. 12), mussel survival on $+Stichaster$ benches dropped sharply between 4 December and 1 January (Fig. 12, Table 8). Thereafter, mussel mortality steadily increased through the end of the experiment in March 1995. As noted in the *Methods* section, field observations during the experiment indicated the likelihood of a “position” effect as the basis of the failure of the *Stichaster* to completely eliminate the transplanted mussels, thus causing the large within-site variances noted in the previous section. Mussels in clumps transplanted to the middle of the experimental benches had high survival, while those on the edges of the benches, most likely to be the first encountered by sea stars crawling up the bench walls, were completely eliminated by 1 January.

This potential effect of foraging behavior provided one rationale for the modified design of the second experiment (Experiment 2). In addition, we wished to

TABLE 4. Results of nested repeated-measures analysis of variance (RM-ANOVA) of recruitment of barnacles to collectors, South Island, New Zealand. (A) RM-ANOVA testing the effect of coast (east vs. west) and site nested within coast (BB and BT on the east coast and TMN and TMS on the west coast) on mid-zone recruitment of *Chamaesipho columna* from November 1994 to April 1995. (B) Within-east-coast RM-ANOVA on the effects of site and zone (high vs. middle) on recruitment of *C. columna* from November 1994 to April 1995 and recruitment of *Epopella plicata* in February, March, and April 1995. (C) Within-west-coast RM-ANOVA on the effects of site and zone (middle vs. low) on recruitment of *C. columna* from November 1994 to April 1995 and recruitment of *E. plicata* in December 1994, and February, March, and April 1995.

Source of variation	Univariate analysis					Multivariate analysis			
	df	MS	F	P	Variation explained (%)	Wilks' λ	df	F	P
A) Between-coast comparison									
Between subjects									
Coast	1	560.3895	736.9	$\ll 0.0001$	92.4				
Site(Coast)	2	0.7605	4.13	0.04	0.3				
Error	13	0.1842			1.2				
Within subjects									
Month	5	16.0188	64.15	$\ll 0.0001$	2.2	0.0392	5, 9	44.02	$\ll 0.0001$
Month \times Coast	5	15.3686	9.79	< 0.005	1.9	0.0134	5, 9	133.03	$\ll 0.0001$
Month \times Site(Coast)	10	1.5700	6.29	$\ll 0.0001$	0.3	0.1098	10, 18	3.63	0.008
Error	65	0.24969			...				
B) Within-coast comparisons									
East coast: <i>Chamaesipho columna</i>									
Between subjects									
Site	1	0.5661	2.82	0.12	0.9				
Zone	1	18.6065	92.6	$\ll 0.0001$	45.3				
Site \times Zone	1	1.6480	8.20	0.014	3.9				
Error	12	0.2009			9.9				
Within subjects									
Month	5	10.4040	39.4	$\ll 0.0001$	20.8	0.0255	5, 8	61.1	$\ll 0.0001$
Month \times Site	5	0.9423	3.57	0.007	1.4	0.2919	5, 8	3.88	0.04
Month \times Zone	5	2.9277	11.1	$\ll 0.0001$	5.5	0.0937	5, 8	15.5	0.006
Month \times Site \times Zone	5	0.1385	0.52	0.76	0.0	0.7376	5, 8	0.57	0.72
Error	60	0.2642			...				
East Coast: <i>Epopella plicata</i>									
Between subjects									
Site	1	5.7917	10.9	0.006	4.8				
Zone	1	82.4738	155.3	$\ll 0.0001$	74.6				
Site \times Zone	1	0.5323	1.00	0.34	0.0				
Error	13	0.5311			...				
Within subjects									
Month	2	4.1453	13.3	0.0001	2.3	0.3581	2, 12	10.8	0.002
Month \times Site	2	3.4386	11.1	0.0003	1.9	0.4102	2, 12	8.62	0.005
Month \times Zone	2	2.1236	6.83	0.004	1.1	0.3215	2, 12	12.7	0.001
Month \times Site \times Zone	2	0.2275	0.73	0.46	0.0	0.8050	2, 12	1.45	0.27
Error	26	0.3111			...				
West coast: <i>Chamaesipho columna</i>									
Between subjects									
Site	1	0.0085	0.17	0.69	0.0				
Zone	1	7.5545	151.8	$\ll 0.0001$	21.8				
Site \times Zone	1	1.8343	36.8	0.0002	5.2				
Error	13	0.0498			...				
Within subjects									
Month	5	26.6474	241.0	$\ll 0.0001$	64.2	0.0036	5, 5	274.7	$\ll 0.0001$
Month \times Site	5	0.2441	2.21	0.07	0.3	0.4259	5, 5	1.35	0.38
Month \times Zone	5	1.3471	12.2	$\ll 0.0001$	3.0	0.0860	5, 5	10.6	0.01
Month \times Site \times Zone	5	2.4734	22.3	$\ll 0.0001$	5.7	0.1045	5, 5	8.57	0.02
Error	45	0.1107			...				
West coast: <i>Epopella plicata</i>									
Between subjects									
Site	1	2.3821	9.78	0.008	7.5				
Zone	1	0.0085	0.03	0.85	0.0				
Site \times Zone	1	7.2188	29.6	0.0001	24.6				
Error	13	0.2435			...				

TABLE 4. Continued.

Source of variation	Univariate analysis					Multivariate analysis			
	df	MS	F	P	Variation explained (%)	Wilks' λ	df	F	P
Within subjects									
Month	3	2.8366	8.90	0.0001	6.7	0.2829	3, 11	9.29	0.002
Month \times Site	3	3.9569	12.4	≤ 0.0001	9.6	0.2717	3, 11	9.83	0.002
Month \times Zone	3	4.3409	13.6	≤ 0.0001	10.6	0.2431	3, 11	11.4	0.001
Month \times Site \times Zone	3	0.8346	2.62	0.06	1.4	0.5270	3, 11	3.29	0.06
Error	39	0.3187			...				

Notes: In (A), Variances (ln-transformed data) were homogeneous; Cochran's $C = 0.16$, $C_{0.95}(24, 4) = 0.1921$. Coast was tested over Site(Coast) and Time \times Coast was tested over Time \times Site(Coast). In (B), Variances (transformed data) were homogeneous; Cochran's $C = 0.1714$, $C_{0.95}(24, 4) = 0.1921$. In (C), Variances were not homoscedastic; Cochran's $C = 0.2434$, $C_{0.95}(24, 3) = 0.2205$. In all cases, unadjusted P values and adjusted P values (with Huynh-Feldt epsilon, $= 1.0$ in all cases) were identical, indicating that the assumption of compound symmetry was met. P values significant to >4 decimal places are shown as ≤ 0.0001 . For calculations of percentage of variance explained, the models were considered fixed. Estimates were calculated after Underwood (1997), and proportions were calculated using the sum of variance components totalled over both between- and within-subjects factors as the denominator (e.g., Lively et al. 1993). Residual error accounts for the percentage of variance remaining after that explained by each factor is totalled for each model.

determine if sea star foraging was affected by the presence of the other common mussel, *Perna*. Specifically, our experiment was designed to determine if preferential predation might explain the low abundance of *Perna* relative to that of *Mytilus* at Twelve-Mile Beach. To test this, equal numbers ($n = 25$ animals per species) of *Perna* and *Mytilus* were included in each cage. Results of Experiment 2, which incorporated a position treatment (edge vs. middle of bench) in addition to the sea star treatment (+*Stichaster* vs. -*Stichaster*), were consistent with those of Experiment 1 in revealing a strong effect of sea star predation on mussel survival (Fig. 13, Table 9). As expected, position on the reef was an important determinant of the rates of loss of transplanted mussels (Table 9, Experiment 2, Between subjects; Position \times *Stichaster* interaction was significant). Mussels transplanted to the center of the bench survived better than those on the edge (Fig. 13). *Stichaster* did not appear to discriminate between mussel species. Predation rates on *Perna* and *Mytilus* were indistinguishable (Fig. 13, survival of *Perna* and *Mytilus* did not differ; RM-ANOVA, between-subjects, $F = 0.21$, $P = 0.65$, $df = 1, 58$).

The ecological effect of these high rates of predation was to control the lower limit of mussels, mostly *Mytilus* (Fig. 14). In January 1995, mussel cover in the presence and absence of sea stars did not differ ($P = 0.71$, $df = 1, 72$), but by March 1995 a clear effect of sea star removal was evident. On -*Stichaster* benches, mussel cover on the bench edge and wall were 2 \times and 4 \times , respectively, that on bench edge and wall in +*Stichaster* treatments (Fig. 14). Change in mussel cover was contingent on the combination of all three factors (Table 10; the three-way interaction was significant), but position on the benches accounted for over half the variance (53%), indicating that the increases at the lower bench levels in -*Stichaster* treatments were the most important change.

Grazing intensity.—The total impact of grazers, defined as the difference between +grazer and -grazer treatments at the end of the experiment was similar on both coasts (Fig. 15). However, contrasting rates of change in algal cover suggest that limpet grazing intensity may be greater on the west than on the east coast. Results in +grazer treatments (marked plots and paint controls) indicated that limpets kept rock surfaces nearly free of microalgae (algal sporelings and diatoms, species not identified) at both sites on each coast (Fig. 15). Algal cover in marked plots did not differ significantly from that in paint controls (Table 11; $P \geq 0.56$). Thus, throughout the experiment, cover of algae in +grazer treatments was always $<10\%$ at both east and west coast sites. In striking contrast to +grazer treatments, algae reached high covers in all -grazer treatments (Fig. 15). The rates of these changes differed between coasts, however. Increases in algal cover were generally fast on the west coast, reaching their peak after only 1 mo, and slower on the east coast, reaching similar peak covers but taking 3 mo (Fig. 15). This temporal difference between coasts is indicated by the contrasting between-subjects and within subjects results for the Coast \times Grazers effect (Table 11). The overall (between-subjects) effect of grazers did not vary with coast ($P = 0.42$), but when time is considered (months; within subjects), the Month \times Coast \times Grazers interaction was highly significant ($P = \leq 0.0001$). This presumably reflects the contrasting patterns of algal cover in January (both east sites lower than west sites) and March (both east sites higher than west sites). These qualitative differences imply that grazing rates and/or algal growth rates are higher on the west coast. The larger short-term differences between -grazer and +grazer treatments on the west coast, with the similar limpet densities among BT, TMN, and TMC, suggests that grazing by west-coast limpets may have been faster, and thus that top-down effects were greater. Simi-

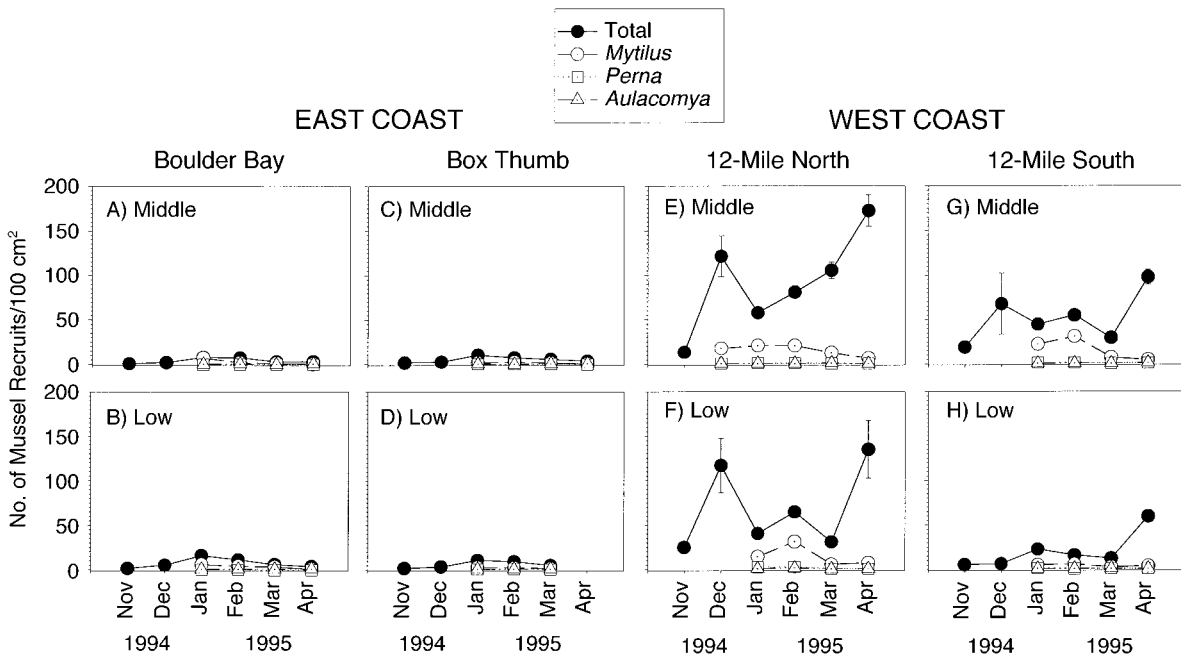


FIG. 9. Recruitment densities of mussels at BB and BT on the east coast, and TMN and TMS on the west coast of South Island, New Zealand, as estimated from counts of metamorphs observed on collectors placed in the middle and low zones. Total counts include mussel recruits too small to be identifiable to species plus the counts of the identifiable species. Most of these are likely to be *Mytilus galloprovincialis*. *Perna canaliculus* is distinguishable by the bright-green bands on its shell; *Aulacomya ater maoriana* by its more prominent shell ridges, and *Mytilus* by its brown to black, smooth shell. $N = 5$ collectors per zone per site per coast, or a total of 40 collectors/mo.

TABLE 5. Results of nested repeated-measures ANOVA testing the effect of coast (east vs. west), site within coast (BB and BT on the east coast and TMN and TMS on the west coast), and zone (middle vs. low) on total mussel recruitment (*Mytilus galloprovincialis*, *Perna canaliculus*, *Aulacomya ater maoriana*) from November 1994 to April 1995 on South Island, New Zealand.

Source of variation	Univariate analysis					Multivariate analysis			
	df	MS	F	P	Variation explained (%)	Wilks' λ	df	F	P
Between subjects									
Coast	1	141.3691	12.04	0.08	59.1				
Zone	1	2.3772	26.32	0.0003	1.0				
Coast \times Zone	1	11.8832	4.56	0.2	5.4				
Site(Coast)	2	11.7430	80.64	≤ 0.0001	15.9				
Zone \times Site(Coast)	2	2.6037	27.88	≤ 0.0001	3.4				
Error	31	0.1456			...				
Within subjects									
Month	4	11.0234	65.23	≤ 0.0001	7.9	0.0552	4, 28	119.85	≤ 0.0001
Month \times Coast	4	1.2440	1.06	> 0.25	0.05	0.3946	4, 28	10.74	≤ 0.0001
Month \times Zone	4	0.2169	1.28	0.28	0.03	0.7387	4, 28	2.48	0.07
Month \times Coast \times Zone	4	0.4381	2.59	> 0.50	0.0	0.7577	4, 28	2.24	0.09
Month \times Site(Coast)	6	1.1783	6.97	0.0001	1.1	0.4178	8, 56	3.83	0.001
Month \times Zone \times Site(Coast)	8	0.5269	3.12	0.008	0.5	0.5030	8, 56	2.87	0.01
Error	124	0.1690							

Notes: Coast was tested over site(coast), coast \times zone over zone \times site(coast), month \times coast over month \times site(coast), and month \times coast \times zone over month \times zone \times site(coast). Variances (transformed data) were homogeneous, Cochran's $C = 0.1452$, $C_{0.95}(20, 4) = 0.1921$. Huynh-Feldt Epsilon for within-subjects analysis for Month = 0.73873, so corrected P values were used. P values significant to nine (between subjects) or five (within subjects) decimal places were rounded to $P \leq 0.0001$.

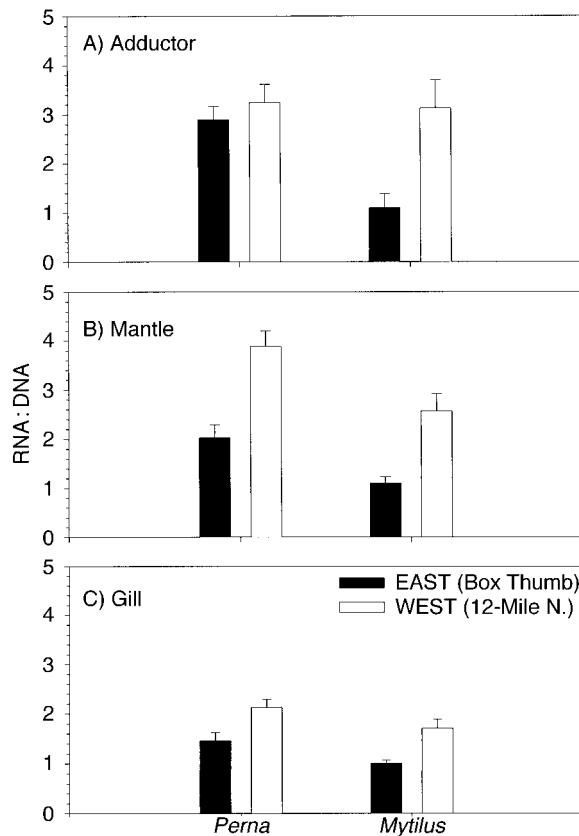


FIG. 10. RNA:DNA ratios (mean and 1 SE) for adductor, mantle, and gill of *Perna canaliculus* and *Mytilus galloprovincialis* at Box Thumb on the east coast and Thirteen-Mile Beach North on the west coast of South Island, New Zealand. $N = 10$ mussels \times 2 species \times 2 coasts = 40 total mussels.

larly, the faster algal growth rates in $-$ grazer treatments may indicate that bottom-up effects were stronger on the west coast as well. Alternatively, growth rates could have been similar but algal recruitment rates could have been higher on the west coast. In either case, the consistency of within-coast patterns and the clear between-coast differences suggest that the mechanisms under-

lying limpet–microalgal interactions vary both quantitatively and qualitatively with coast.

When considered in more detail, these experiments also revealed among-site, within-coast variation (Fig. 15, Table 11; Grazers \times Site(Coast) interactions in both between subjects and within subjects were significant, and Table 12; final covers of algae, barnacles, and mussels varied with site nested within coast). These differences presumably reflect two within-coast sources of variation. On the east coast, algal cover at BB increased more quickly in $-$ grazer treatments than at BT (Fig. 15C, G). On the west coast, algal cover at TMN decreased sharply in March, evidently in part because of major increases in abundance of barnacles and mussels at this site (Fig. 15I–K). At TMC, a somewhat less wave-exposed location, recruitment of these sessile invertebrates was less and the decline in algal cover was more modest.

Limpet abundances in $-$ grazer treatments were consistently low, suggesting that our method of exclusion was effective (Fig. 15D, H, L, P). Limpet abundances in $+$ grazer plots varied among sites (RM-ANOVA, between subjects; Site(Coast), $F = 18.28$, $df = 2, 36$, $P < 0.0001$), but not consistently between coasts (RM-ANOVA, between subjects; Coast, $F = 0.41$, $df = 1, 2$, $P > 0.50$). The low limpet abundance at BB was probably due in part to the fact that there was even less suitable limpet habitat (bare space) at this site than at BT (B. Menge, B. Daley, J. Lubchenco, E. Sanford, P. Halpin, and J. Burnaford; *personal observation*). Although there was some variation in limpet abundance in marked plots vs. paint controls as well as among sites (BB was low relative to the other three sites), these differences seemed unimportant at least with respect to algal cover in $+$ grazer treatments. This conclusion is supported in reanalyses, by coast, that include limpet numbers as a covariate. Limpet number per plot contributed little to variation in algal cover either overall, or in relation to temporal change on either the east or the west coasts (RM-ANOVA, analysis not shown; $P > 0.21$ in all cases).

TABLE 6. Results of three-way ANOVA of RNA:DNA ratios of mussels collected in December 1994 (South Island, New Zealand).

Source of variation	df	MS	F	P	Variation explained (%)
Coast	1	4.3368	72.64	≤ 0.0001	40.4
Species	1	2.5750	43.13	≤ 0.0001	23.8
Tissue	2	0.8574	14.36	≤ 0.0001	15.1
Coast \times Species	1	0.3661	6.13	0.015	2.9
Coast \times Tissue	2	0.1334	2.23	0.11	1.4
Species \times Tissue	2	0.1171	1.96	0.15	1.1
Coast \times Species \times Tissue	2	0.2797	4.69	0.01	4.2
Error	108	0.0597			...

Notes: Factors evaluated, all fixed, were coast (east vs. west), species (*Mytilus galloprovincialis* and *Perna canaliculus*), and tissue (adductor muscle, mantle, and gill). Variances (transformed data) were homogeneous; Cochran's $C = 0.1127$, $C_{0.95}(15, 9) = 0.1736$. Very significant P values were rounded to 0.0001.

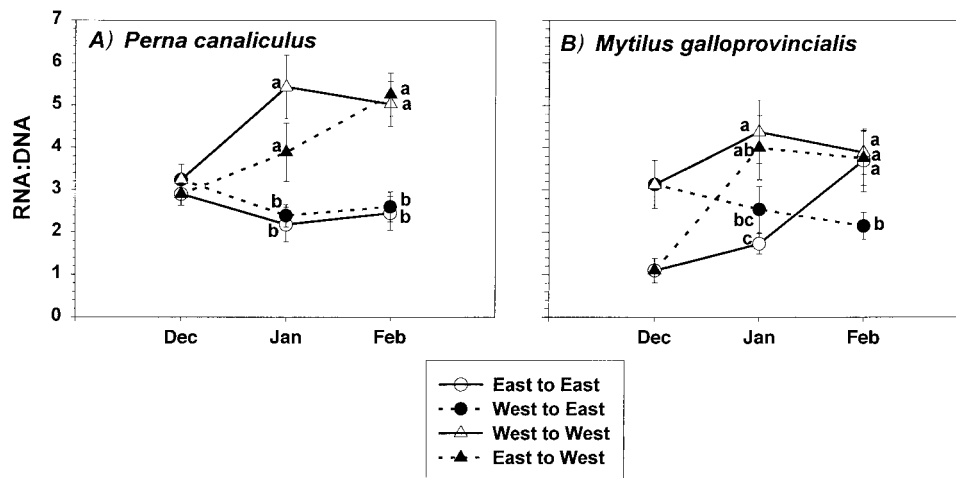


FIG. 11. RNA:DNA ratios for adductor muscle of *Perna canaliculus* and *Mytilus galloprovincialis* in transplant experiments on the east and west coasts of South Island, New Zealand. Symbols with the same lowercase letter were not significantly different; those with different letters were significantly different (Fisher's LSD test; significant $P = 0.05$). $N = 8$ or 9 mussels per species sampled per coast. Changes in gill and mantle tissue showed no consistent pattern, so the data are not shown.

Finally, note that at BB the limpet densities were similar in +grazer and -grazer treatments (Fig. 15D). This suggests that limpet exclusion was ineffective at BB, yet algal cover differed greatly between +grazer and -grazer treatments. This apparent discrepancy is probably a simple consequence of two factors—handling differences between treatments and high mobility of limpets. In all plots, limpets were counted at each monitoring visit, but then were removed only from -grazer plots. Although limpets clearly reinvaded at BB, returning to densities similar to those in surrounding habitat, the period of limpet absence was evidently sufficient to release microalgae from grazer control. Further, limpets in +grazer treatments were free to move in and out of plots, and counts within plots at low tide did not necessarily reflect grazing activity, which takes place mostly when plots are under water.

We conclude that although the longer term impact of limpet grazing is similar between coasts, in the short term at least, grazing appears more intense on the west than on the east coast. Similarly, in the absence of grazers, either algal growth or algal recruitment is also higher on the west than on the east coast. In addition, substantial differences among sites within a coast can occur. This local-scale variation may depend on several factors, including differences in the abundance of potential competitors for space with limpets (e.g., barnacles, mussels), and small-scale differences in algal recruitment rates or conditions for algal growth.

DISCUSSION

East vs. west coasts

The primary difference in community structure between east- and west-coast rocky intertidal sites (on South Island, New Zealand) occurred in the low zone. East-coast sites had high covers of mussels, and west-

coast sites low covers of mussels. Although intertidal food-web composition was similar, with sea stars, whelks, and limpets present on both coasts, east-coast sites had relatively low predator abundances. Sea star patterns differed in both abundance and species composition, with compositional differences confounding abundance differences. *Stichaster australis* occurred only on the west coast and was very abundant. The sea star *Coscinasterias calamaria*, also a predator of mussels and barnacles, was present but rare in the intertidal of both coasts.

Whelks were scarce in the low zones on both coasts, and were presumed unlikely to have much effect on sessile prey at either location, although other observations in New Zealand and elsewhere suggest this conclusion may bear reexamination. As mentioned earlier, *Thais orbita* were large and abundant at another west coast site, Woodpecker Bay. This observation, the larger size of *Stichaster*, and the higher abundance of *Perna* at this site (see *Methods: Quantification of community structure: Limpet and predator density and size*, above) are intriguing and will be a focus of future studies. In Australia, *T. orbita* are highly mobile, and can forage intertidally from subtidal resting sites (Fairweather 1988). This suggests the possibility that, at our sites, low numbers in the intertidal might be misleading as to the possible impact of these whelks. However, the subtidal off TMB (Twelve-Mile Beach) appeared to be primarily sandy, suggesting a suboptimal whelk habitat. East-coast subtidal areas appeared rocky, but we saw no sign of unexplained predation in the intertidal that could result from whelks refuting in the subtidal. Apart from oystercatchers, no other predators, including crabs, were observed at our wave-exposed sites.

Limpets, primarily *Cellana radians* and *C. ornata*

TABLE 7. Results of repeated-measures ANOVA on changes in RNA : DNA ratios in transplant experiments between coasts on South Island, New Zealand, for *Perna canaliculus* and *Mytilus galloprovincialis*.

Source of variation	Univariate analysis				Multivariate analysis			
	df	MS	F	P	Wilks' λ	df	F	P
<i>Perna canaliculus</i>								
Between subjects								
Treatment	3	26.9138	10.35	$\ll 0.0001$				
Error	32	2.6000						
Within subjects								
Time	2	5.3282	3.28	0.05	0.7568	2, 31	4.98	0.013
Time \times Treatment	6	7.4792	4.61	0.001	0.4420	6, 62	0.0002	
Error	64	1.6227						
<i>Mytilus galloprovincialis</i>								
Between subjects								
Treatment	3	12.5863	4.26	0.012				
Error	31	2.9513						
Within subjects								
Time	2	12.5813	4.55	0.014	0.7642	2, 30	4.63	0.018
Time \times Treatment	6	9.5169	3.44	0.005	0.5611	6, 60	3.35	0.007
Error	62	2.7636						

Notes: Factors were time and transplant treatment, where treatments were east to east, west to east, east to west, and west to west. To be conservative in the analysis for *Perna*, the *P* value for time was adjusted with the Geisser-Greenhouse epsilon ($\epsilon = 0.8841$) because both normal and Huynh-Feldt *P* values were 0.044, making the significance level uncertain (H-F $\epsilon = 1.0$).

were common at all sites but BB (Boulder Bay). Although several other limpet species were present at our sites, and some were common (e.g., *Notoacmea parviconoidea*, found mostly on mussel shells), *C. radians* and *C. ornata* were by far the two most abundant species occupying bare rock and crustose-alga-covered surfaces. Chitons, primarily *Sypharochiton pelliserpentis*, were also common in middle and low zones at all sites, but are thought to consume primarily mac-

roalgae (e.g., Otway 1994, P. Fairweather, *personal communication*).

These contrasting patterns of structure of the rocky intertidal communities at east- and west-coast wave-exposed sites of the South Island of New Zealand appeared to have contrasting underlying dynamics. Our studies indicated that recruitment, growth of mussels, predation, and grazing were all higher or more intense on the west than on the east coast.

TABLE 8. Comparison of survival of mussels transplanted to the low zone at east-coast sites (BB and BT) and west-coast sites (TMN and TMS). Nested repeated-measures ANOVA compared data from December 1994, and January, February, and March 1995.

A) Univariate repeated-measures ANOVA					
Source of variation	df	MS	F	P	Variation explained (%)
Between subjects					
Coast	1	3.7329	11.97	0.065	16.0
Site(Coast)	2	0.3118	0.88	0.43	0.0
Error	16	0.3549			...
Within subjects					
Time	3	1.6911	33.04	0.00001	5.8
Time \times Coast	3	0.6776	51.33	0.0001	2.2
Time \times Site(Coast)	6	0.0132	0.26	0.86	0.0
Error	48	0.0512			...
B) Multivariate repeated-measures ANOVA					
Source of variation	df	Wilks' λ	F	P	
Time	3, 14	0.1973	18.98	0.00003	
Time \times Coast	3, 14	0.4893	4.87	0.016	
Time \times Site(Coast)	6, 28	0.7355	0.77	0.60	

Notes: Huynh-Feldt epsilon was substantially < 1.0 ($\epsilon = 0.4951$) so Huynh-Feldt-adjusted *P* values were used in within-subjects analysis. Error terms in the nested RM-ANOVA analysis: for Coast, Site(Coast) mean square; for Time \times Coast, Time \times Site(Coast) mean square. Variances (transformed data) were homogeneous; Cochran's $C = 0.2075 < C_{0.95}(15, 4) = 0.2419$.

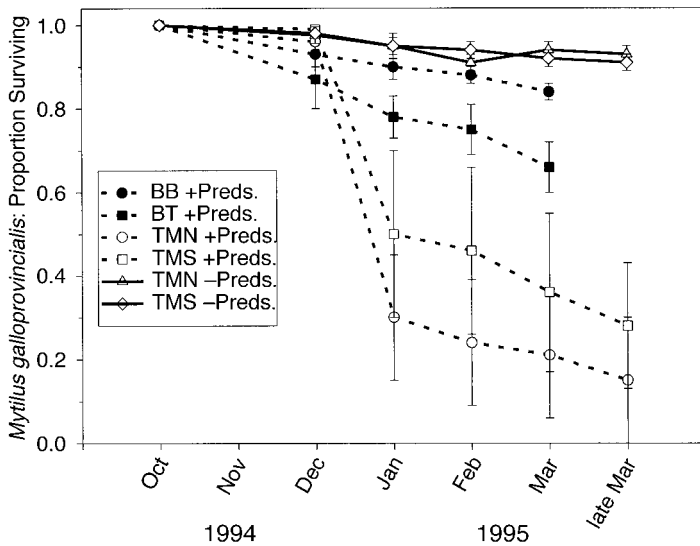


FIG. 12. Survival of *Mytilus galloprovincialis* in transplant experiments in the low zone at east- and west-coast sites of South Island, New Zealand. Because predators were scarce on the east coast and little mussel mortality was anticipated, there were no -predator transplants at BB or BT. $N = 5$ transplants (30 mussels per transplant) \times 2 sites \times 1 (east) or 2 (west) treatments, or 10 (east) and 20 (west) total transplants. For site codes, see Fig. 5 legend; +Preds. = predators present, -Preds. = predators absent.

Recruitment

Although within-coast, between-zone differences in barnacle recruitment were expected, and documented (at least on the east coast), the most interesting difference observed was in the mid-zone, where recruitment of barnacles was strikingly greater on the west coast (Figs. 8–11, Tables 3–6). Similarly, mussel-recruitment densities on west coast low- and mid-zone surfaces were consistently greater than on the east coast.

In theory, high rates of recruitment may reflect at least two distinct nearshore processes. High food abundance (detritus, particulate organic material, phytoplankton) may enhance growth, survival, or both for filter-feeding recruits of sessile invertebrates (e.g., Duggins et al. 1989, Bustamante et al. 1995a, b, Menge et al. 1996, 1997a; R. E. Emlet, unpublished data). An alternative but not mutually exclusive possibility is that high rates of recruitment may result from high rates of

larval transport to settlement habitat (Gaines and Roughgarden 1987, Roughgarden et al. 1988, Menge et al. 1997a, Connolly and Roughgarden 1998). Although we cannot distinguish these on the basis of present information, either in New Zealand or elsewhere, both may be important. For example, studies in Oregon (USA) of the response of barnacle (*Balanus glandula*) larvae to differing levels of phytoplankton food abundance suggest that, with higher food concentrations, the sizes and survival of resulting outplanted recruits are larger and higher, respectively (R. Emlet, unpublished data). Although further work is needed, both in Oregon and New Zealand, these results are consistent with the hypothesis that recruitment of sessile invertebrates is influenced by food concentrations for larvae.

The studies of Gaines et al. (1985, 1987), Shanks (1995), Piñeda (1991) and others clearly indicate that transport of larvae can have an important influence on

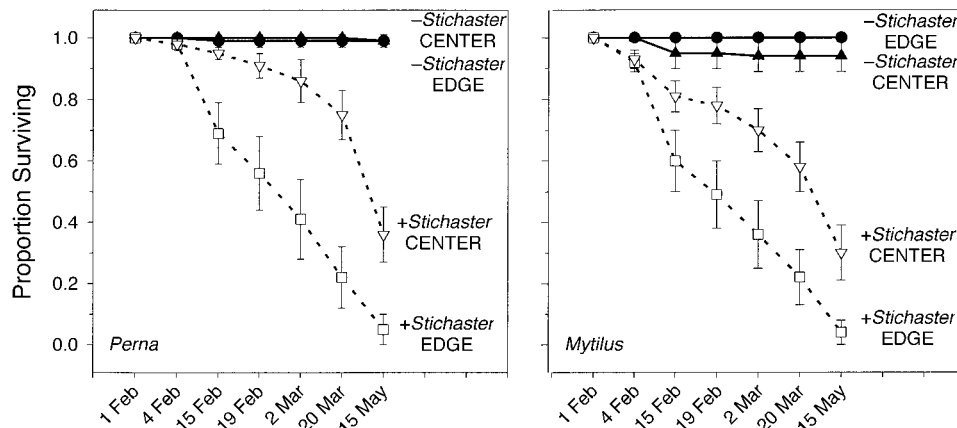


FIG. 13. Survival of *Perna canaliculus* and *Mytilus galloprovincialis* at Twelve-Mile Beach on the west coast of South Island, New Zealand, with and without predatory sea stars. $N = 5$ transplants \times 1 control and 2 experimental benches \times 2 positions (center or edge) \times 2 sea star treatments (present [+]) or absent [-] = 60 total transplants.

TABLE 9. Repeated-measures ANOVA testing the effect of *Stichaster australis* predation on mussel survival in two separate experiments at Twelve-Mile Beach, New Zealand.

Source of variation	Univariate analysis					Multivariate analysis			
	df	MS	F	P	Variation explained (%)	Wilks' λ	df	F	P
Experiment 1									
Between subjects									
Site	1	0.8141	0.27	0.61	0.0				
<i>Stichaster</i>	1	36.867	12.15	0.003	31.8				
Site \times <i>Stichaster</i>	1	0.7134	0.24	0.63	0.0				
Error	16	3.0345			...				
Within subjects									
Time	4	6.9811	12.72	0.0005	4.8	0.28929	4, 13	7.98	0.0018
Time \times Site	4	0.1749	0.32	0.66	0.0	0.83545	4, 13	0.64	0.64
Time \times <i>Stichaster</i>	4	6.2727	11.43	0.00089	1.1	0.44536	4, 13	4.05	0.024
Time \times Site \times <i>Stichaster</i>	4	0.1677	0.30	0.67	0.0	0.86337	4, 13	0.51	0.73
Error	64	0.5490			...				
Experiment 2									
<i>Perna canaliculus</i> survival									
Between subjects									
Reef position	1	0.6073	8.70	0.007	6.2				
<i>Stichaster</i>	1	5.6105	80.34	≤ 0.0001	63.3				
Position \times <i>Stichaster</i>	1	0.5818	8.33	0.008	6.7				
Error	26	0.0698			...				
Within subjects									
Time	1	0.2700	12.39	0.002	1.4				
Time \times Position	1	0.0409	1.88	0.18	0.1				
Time \times <i>Stichaster</i>	1	0.2543	11.68	0.002	1.3				
Time \times Position \times <i>Stichaster</i>	1	0.0350	1.61	0.22	0.07				
Error	26	0.0218			...				
<i>Mytilus galloprovincialis</i> survival									
Between subjects									
Reef position	1	0.2188	2.89	0.10	1.7				
<i>Stichaster</i>	1	6.2649	82.73	≤ 0.0001	71.8				
Position \times <i>Stichaster</i>	1	0.4576	6.04	0.02	4.4				
Error	26	0.0758							
Within subjects									
Time	1	0.1751	15.64	0.0005	1.0				
Time \times Position	1	0.0099	0.88	0.36	0.0				
Time \times <i>Stichaster</i>	1	0.1751	15.64	0.0005	0.9				
Time \times Position \times <i>Stichaster</i>	1	0.0099	0.88	0.36	0.0				
Error	26	0.0112							

Notes: In Experiment 1 the sample dates analyzed were December 1994, and January, February, early March, and late March 1995 (see Fig. 12); variances were homoscedastic; Cochran's $C = 0.1999 < C_{0.95}(15, 4) = 0.2419$. In Experiment 2, the analysis was based only on the last two sample dates (20 March, 15 May) due to heteroscedastic variances of earlier sample dates. Variances were homoscedastic; Cochran's $C = 0.1255 < C_{0.95}(20, 4) = 0.1921$.

abundance of sessile invertebrates in rocky intertidal communities. While some key studies of larval transport have taken place off New Zealand (e.g., Zeldis and Jillett 1982, Jillett and Zeldis 1985, Kingsford and Choat 1986), the problem of coupling between rocky intertidal community dynamics and larval transport remains unstudied in New Zealand. Nonetheless, the similarity between oceanographic conditions along the west coasts of North America and New Zealand summarized in the *Introduction* suggests that transport processes also may be comparable. This possibility is discussed in more detail below.

Bottom-up effects

Factors affecting growth and abundance of organisms lower in the food web appeared greater in mag-

nitude on west than on east coasts. Our indications of between-coast differences in the magnitude of bottom-up effects are based on two indirect indicators of such factors: mussel growth physiology and nutrient concentrations. As noted earlier, rates of growth of mussels are considered a bottom-up factor, because growth reflects, in part, the rate of food intake (e.g., Menge et al. 1994, 1997a, Dahllhoff and Menge 1996). The rate of food intake, in turn, can in some cases reflect differences in rates of primary productivity. For example, along the Oregon coast, mussel and barnacle growth rates were highest where phytoplankton abundance and productivity were highest (Menge et al. 1994, 1996, 1997a, b). In the present study, two methods of estimation of growth rates were attempted—for short-term growth, RNA:DNA ratios, and for long-term growth,

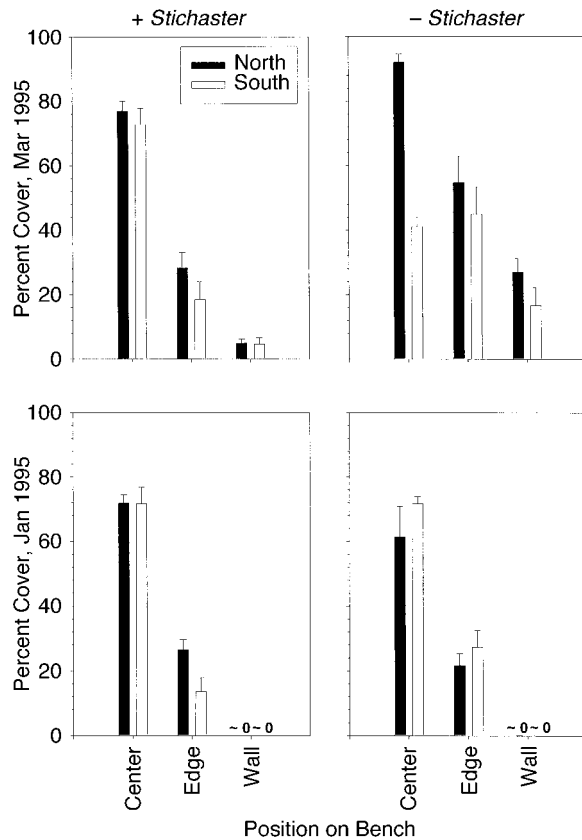


FIG. 14. Changes in cover (means and 1 SE) of *Mytilus galloprovincialis* at TMN ("North") and TMS ("South") on the west coast of South Island, New Zealand. Bench walls were not sampled in January, but we observed no mussel cover at this level. $N = 10$ quadrats sampled \times 2 benches \times 2 sea star treatments (+ or -) \times 2 or 3 bench positions (center, edge, or wall), = 80 (January) and 120 (March) quadrats.

shell accretion by marked mussels—but only the RNA:DNA estimates provided useful information. Marked, transplanted mussels in west-coast cages suffered repeatedly from the cages being filled by plant litter (itself a suggestion of higher rates of delivery of detritus), so grew minimally. Mussels sampled for between-coast comparisons (Fig. 10) were naturally occurring, un-

caged animals, however, so they were not subject to this potential artifact. Transplanted mussels used in quantifying RNA:DNA ratios were caged, but these were not filled with detritus to the same extent as those with marked mussels, perhaps because they were higher on the shore (i.e., mid-zone vs. low zone).

The higher RNA:DNA ratios in west coast *Mytilus galloprovincialis* (Fig. 10) are consistent with the hypothesis that bottom-up effects are greater on the west coast. Further, the rapid convergence of RNA:DNA ratios of transplanted mussels towards those of mussels in the transplanted environment and away from those of mussels in the original environment suggests that growth physiology is highly sensitive to differences in food environments (Fig. 11). These patterns are nearly identical to those seen in the California (USA) mussel, *M. californianus*, along the Oregon coast (Dahlhoff and Menge 1996). We suggest here that they have a common underlying basis: particulate food concentration is higher in nearshore ecosystems due to higher phytoplankton productivity. This pattern has been clearly documented for the Oregon coast (Menge et al. 1996, 1997a, b, Dahlhoff and Menge 1996).

Onshore water samples taken during austral summer months suggest that nutrient concentrations are sometimes considerably greater on the west than the east coast (Fig. 7). This difference is consistent with the suggestion that nearshore environments on the west coast are upwelling ecosystems. Comparison between the nutrient concentrations we recorded in our samples with the high-tide water-temperature records obtained simultaneously support this interpretation. Samples taken on both coasts in December 1994 and February 1995 coincided with non-upwelling periods on both coasts, and nutrient concentrations were similar on both coasts (Fig. 6). Samples taken in January 1995, however, coincided with the end of a period of low temperatures on the west coast and a period of stable, higher temperatures on the east coast (Fig. 6). Assuming that these differences in temperature regime reflect upwelling (west) and non-upwelling (east) conditions, the high concentrations of nutrients on the west coast and lower concentrations on the east coast are consistent

TABLE 10. Results of three-way ANOVA testing effect of site (TMN, TMS), position (bench top, bench edge, and bench wall), and *Stichaster* (present vs. absent) on cover of mussels.

Source of variation	df	MS	F	P	Variance explained (%)
Site	1	1.1619	25.88	≤ 0.0001	5.7
<i>Stichaster</i>	1	1.0063	22.42	≤ 0.0001	4.9
Position	2	5.2149	116.17	≤ 0.0001	53.1
Site \times <i>Stichaster</i>	1	0.3762	8.38	0.005	1.7
Site \times Position	2	0.1558	3.47	0.03	1.1
<i>Stichaster</i> \times Position	2	0.4179	9.31	0.0002	3.8
Site \times <i>Stichaster</i> \times Position	2	0.2362	5.26	0.007	2.0
Error	108	0.0449			...

Notes: $N = 10$ quadrat samples per site \times sea star treatment \times position. Variances were heteroscedastic; Cochran's $C = 0.1689 > C_{0.95}(20, 9) = 0.1357$.

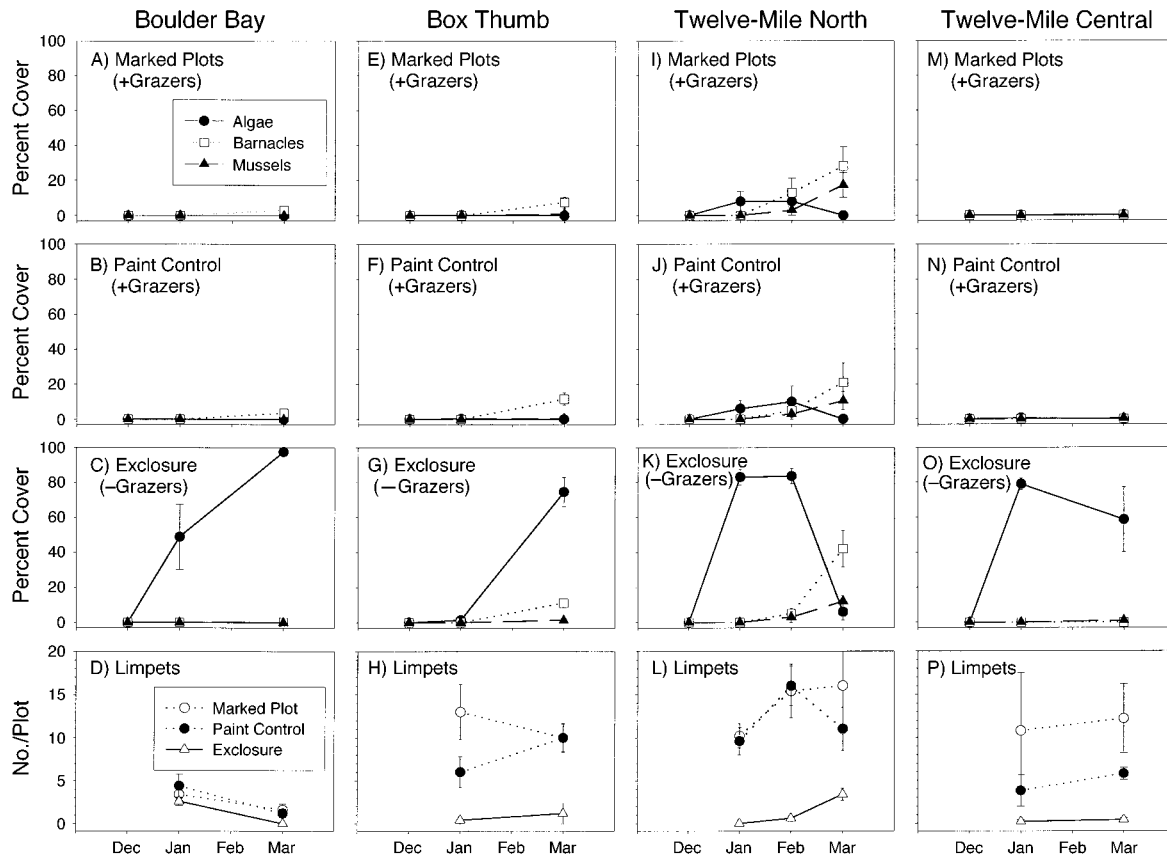


FIG. 15. Changes in cover of algae, barnacles, and mussels in grazer-exclosure experiments at BB (A–C) and BT (E–G) on the east coast and at TMN (I–K) and TMC (M–O) on the west coast of South Island, New Zealand, December 1994 to March 1995. Limpet numbers (primarily *Cellana* spp.) in each treatment are also shown (D, H, L, and P). $N = 5$ plots \times 3 grazer treatments \times 2 sites \times 2 coasts = 60 total plots. Error bars are ± 1 SE.

with expectations. Unfortunately, as noted earlier, efforts to quantify rates of growth and production of macrophytes and phytoplankton were unsuccessful for technical reasons. Such estimates are quite feasible, however, and remain a focus for future research. We postulate that a pattern consistent with upwelling/non-upwelling ecosystem contrasts will emerge when quantitative studies are made on the west and east coasts of New Zealand.

In contrast to these differences in nutrient concentration between coasts, consistent among-site nutrient variation was not observed along the Oregon coast (Menge et al. 1997a, b). We believe that these between-system differences reflect two scales of variation. Our New Zealand studies contrasted upwelling to downwelling ecosystems, while our Oregon studies dealt with within-upwelling ecosystem variation. Further study is necessary to determine if within-upwelling ecosystem variation similar to that in Oregon occurs on the west coast of New Zealand.

Top-down effects

The near-absence of mussels from the low zone on the west coast seems clearly due to the presence there

of abundant populations of sea stars. In clear contrast, as suggested by the pattern of high mussel abundance in the low zone (Fig. 2), high mussel survival in transplants (Fig. 12), and the lack of any other evidence that predation effects were strong in middle and high zones, east-coast communities seemed little affected by predation. The fact that our west-coast results were similar to those obtained by Paine (1971), even though different species of mussels dominated on North and South Islands, suggests that the controlling effects on low intertidal community structure of *Stichaster* are persistent in time and general in space.

The large difference in the survival of transplanted mussels on the two coasts (Fig. 12) suggests the tentative conclusion that predation effects were stronger on the west than the east coast of the South Island. However, the total absence of *Stichaster* from the east coast confounds an interpretation of top-down differences based on oceanographic differences (see *Introduction*), and suggests the alternative (and untestable) hypotheses that between-coast differences in community structure depend ultimately on historical events or dispersal barriers. The whelk *Thais orbita* occurs on both coasts, however, and field experiments on feeding

TABLE 11. Results of repeated-measures ANOVA testing the effect of coast (east vs. west), site within coast (Boulder Bay and Box Thumb on the east coast and Twelve-Mile Beach North and South on the west coast of South Island, New Zealand) and grazers (+grazers and -grazers) on algal cover in January and March 1995.

Source of variation	df	MS	F	P	Variance explained (%)
Full model					
Between subjects					
Coast	1	0.0033	0.006	0.99	0.0
Grazers	1	17.0897	421.62	≤0.0001	60.5
Coast × Grazers	1	0.0268	0.67	0.42	0.0
Site(Coast)	2	0.5540	0.75	0.60	0.0
Grazers × Site(Coast)	2	0.7397	18.25	≤0.0001	5.1
Error	52	0.0405			...
Within subjects					
Month	1	0.0213	0.72	0.40	0.0
Month × Coast	1	3.9433	3.56	0.23	6.5
Month × Grazers	1	0.1545	5.19	0.027	0.2
Month × Coast × Grazers	1	3.1960	10.00	≤0.0001	5.8
Month × Site(Coast)	2	0.3821	2.02	0.37	0.7
Month × Grazers × Site(Coast)	2	0.1889	6.34	0.003	0.6
Error	52	0.0298			...
+Grazer treatments only					
Between subjects					
Coast	1	0.0367	1.48	0.39	1.3
Site(Coast)	2	0.0242	3.23	0.05	2.5
Error	36	0.0075			
Within Subjects					
Month × Coast	1	0.0294	0.93	0.47	0.0
Month × Site(Coast)	2	0.0315	4.14	0.024	1.9
Error	36	0.0076			
-Grazer treatment only					
Between subjects					
Coast	1	0.0042	0.004	0.99	0.0
Site(Coast)	2	0.9581	8.34	0.0033	8.8
Error	16	0.0796			
Within subjects					
Month	1	0.1090	1.37	0.26	0.2
Month × Coast	1	5.3398	12.95	0.078	24.5
Month × Site(Coast)	2	0.4125	5.18	0.018	3.3
Error	16	0.0796			

Notes: Data from both +grazer treatments (marked plots and paint controls) were combined after a preliminary test indicated that algal cover in these treatments did not differ (in all analyses, including repeated measures between subjects and within subjects, and multivariate tests, the treatment effect was not significant, either as a main effect or in interaction terms; $P > 0.56$). The error terms for Coast and Month × Coast were the mean squares for Site(Coast) and Month × Site(Coast); the error terms for Site(Coast) and Month × Site(Coast) were the mean squares for Grazers × Site(Coast) and Month × Grazers × Site(Coast). Variances (transformed data) for the full model were heteroscedastic; Cochran's $C = 0.3565 > C_{0.95}(20, 4) = 0.1921$.

rates with this species would be a valuable step towards determining if predation rates by the same species were qualitatively different between coasts. Preliminary experiments with this whelk revealed a trend towards higher rates of predation on the west coast (B. Menge, B. Daley, J. Lubchenco, E. Sanford, P. Halpin, and J. Burnaford, *unpublished data*), but were limited in temporal scope and replication. Resolution of the issue of whether or not between-coast differences exist in predation related to nearshore oceanographic conditions will require further experimentation.

In the middle and low zones, limpets (*Cellana* spp.) were the most abundant grazers of microalgae on both coasts. Because of their relatively large sizes and mode

of grazing, limpets are probably more effective grazers on areas of bare rock than on areas covered by barnacles and mussels, or by algal turfs. Bare-space availability was relatively low at all tidal levels on the east coast (~10% cover; Fig. 2, B. Menge, B. Daley, J. Lubchenco, E. Sanford, P. Halpin, and J. Burnaford, *personal observations*). On the west coast, bare space in the upper low zone was nearly 3 times more available than on the east coast (e.g., $27.7 \pm 5.8\%$ cover [$n = 15$ quadrats] at Fourteen-Mile Creek; similar or higher availability occurred at TMN; B. Menge, B. Daley, J. Lubchenco, E. Sanford, P. Halpin, and J. Burnaford, *personal observations*), suggesting availability of habitat for these grazers was higher on the west coast.

TABLE 12. Multivariate analysis of variance testing effects of grazing by limpets on abundance (percent cover) of algae, barnacles, and mussels at the end of the grazer-exclusion experiment.

Source of variation	Dependent variables (% cover)	Univariate analysis				Multivariate analysis			
		df	MS	F	P	Wilks' λ	df	F	P
Coast	Algae	1, 52	1.8603	55.41	$\ll 0.0001$	0.409	3, 50	24.08	$\ll 0.0001$
	Barnacle	1, 52	0.138	4.97	0.03				
	Mussel	1, 52	0.3683	31.68	$\ll 0.0001$				
Grazers	Algae	1, 52	10.2398	305	$\ll 0.0001$	0.1414	3, 50	101.22	$\ll 0.0001$
	Barnacle	1, 52	0.0212	0.76	0.39				
	Mussel	1, 52	0.00048	0.04	0.84				
Grazers \times Coast	Algae	1, 52	1.9024	56.66	$\ll 0.0001$	0.4496	3, 50	20.4	$\ll 0.0001$
	Barnacle	1, 52	0.0709	2.55	0.12				
	Mussel	1, 52	0.0012	0.1	0.75				
Site(Coast)	Algae	2, 52	0.599	16.65	$\ll 0.0001$	0.2788	6, 100	14.9	$\ll 0.0001$
	Barnacle	2, 52	1.3129	47.29	$\ll 0.0001$				
	Mussel	2, 52	0.3039	26.13	$\ll 0.0001$				
Grazers \times Site(Coast)	Algae	2, 52	0.5356	15.95	$\ll 0.0001$	0.5742	6, 100	5.33	<0.0001
	Barnacle	2, 52	0.0686	2.47	0.09				
	Mussel	2, 52	0.0009	0.08	0.93				

Notes: "Grazer-present" treatments (marked plot and paint control) were combined after a preliminary MANOVA showed that these treatments did not differ, either as main effects or in interaction terms (df = 1, 32 in main effects and Treatment \times Coast interaction; df = 2, 32 in Treatment \times Site(Coast) interaction; $P > 0.20$ for all univariate and multivariate tests). Error mean squares: for algal cover, 0.0336; for barnacle cover, 0.0277; for mussel cover, 0.0116. Variances were heteroscedastic; Cochran's $C = 0.3512 > C_{0.95}(20, 4) = 0.1921$. Bonferroni-adjusted P value for univariate tests = 0.0167 (0.05/3 tests); significant P values in the univariate analysis, using this significance level, are shown in boldface type.

Thus, even though the total impact of grazers was similar between coasts, on an areal basis, grazing probably had a greater influence on overall community structure on the west coast. Moreover, the short-term rates of grazing suggested by our experiments were greater on the west than the east coast. Based on these considerations, we tentatively conclude that grazer effects are stronger on the west than the east coast.

Conclusions

These results suggest that recruitment rates are higher, and that top-down and bottom-up forces are stronger, on the west coast of New Zealand's South Island than on the east coast. Because these contrasting patterns of community structure and dynamics are parallel to those occurring between regions of contrasting nearshore productivity and transport along the Oregon coast, we postulate that they have a similar cause. That is, we suggest that phytoplankton productivity and particulate abundance along the west coast of New Zealand tend to be greater than along the east coast because the nearshore oceanographic conditions of these two ecosystems are different. Specifically, the northern west coast is dominated by upwelling while the east coast is dominated by downwelling. The contrasting water-temperature patterns and nutrient-concentration patterns are consistent with this suggestion. More-intensive investigation is necessary, however, before firm conclusions regarding the postulated patterns of benthic-pelagic coupling along the east and west coasts of New Zealand are possible. Judging from our results in Oregon, we predict that on the west coast of South Island, phytoplankton concentrations will be consis-

tently higher, and that nearshore conditions will favor higher rates of larval transport to the rocky intertidal shores than occur on the east coast. Efforts to test these predictions are being planned.

If further study proves consistent with our predictions, this research has some intriguing implications. First, the similarity between our earlier Oregon results and the New Zealand results suggests that coastal benthic hard-bottom biota can be tightly linked to oceanographic processes in the very near shore (0–10 km offshore). While this statement seems logical, such effects have drawn little attention from either marine ecologists or biological oceanographers, primarily because logistical problems and funding availability kept their attention focused onshore and offshore, respectively (e.g., Menge 1992). Under current predictions of potentially severe and far-reaching environmental perturbations, including both short-term (e.g., El Niño-Southern Oscillation) and long-term changes (e.g., global climate change), however, it is important to investigate the dynamics of nearshore ecosystems as a whole and particularly to understand the nature and importance of couplings of these adjacent environments. The high commercial value of coastal environments heightens the importance of the need to understand how the nearshore "black box" ecosystem works.

For these reasons, we believe that our results represent an important step towards an integrated understanding of the dynamics of nearshore ecosystems. Ultimately we need studies that examine these systems on multiple scales in space and time, at multiple levels of biotic organization, and that integrate physical and biotic factors into a synthesis of the functioning of

adjacent benthic and pelagic systems along the coastlines of the world. Such knowledge is essential if we are to anticipate the consequences of, and respond to, impending disruptions to these essential ecosystems. We believe such a research program is both feasible and urgently needed.

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