



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

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ABSTRACT

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

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1. Introduction

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

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

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

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

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

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

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

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

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

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

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

2. Methods

2.1. Study sites

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

2.2. Nutrient levels

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

glass-fiber filters with a pore size of 0.7 μm . The filtrate was transported to the laboratory on ice and frozen for later quantification of nitrate, nitrite, phosphate, and silicate on a Lachat autoanalyzer (Atlas et al. 1971). As with the sampling of recruitment rates of sessile invertebrates, BR and RR were treated as one site.

2.3. Community structure

We quantified the patterns of abundance of sessile organisms in the high zone at each site using the transect-quadrat method (Menge 1976). Thirty meter long transect lines were placed parallel to the water's edge through the middle of the high intertidal zone, and 0.25 m² square quadrats were placed at 3 m intervals to photographically sample 10 quadrats in each survey. Quadrats were divided into twenty-five subquadrats each 10 \times 10 cm in dimensions, representing 4% of the total area covered by the quadrat. Percent cover in each quadrat was estimated in the laboratory by visually subdividing each 10 \times 10 cm quadrat in each photograph into 1% increments, then tallying up the total percent covered by each taxon in each quadrat. In the high zone, algae were sparse, and those that were present were \leq 1 cm in height, so obscuring by canopy algae was not a problem.

At the beginning of the experiment (October 2003), ambient densities of limpets were surveyed at each site by counting all limpets in 12 to 30 randomly placed 175 cm² quadrats along a transect line parallel to the water's edge and through the middle of the experimental area. In March 2005 (17 months), a similar survey of 10 plots was conducted at each site.

Size structure of the limpet population was quantified twice at each site. In October 2004, we recorded the size of the first approximately 100 limpets encountered in a 10-cm wide belt-transect through the area around the experiment. We did not distinguish between species in this sample. In 2008, we quantified species-specific size structure of limpets and the chiton *Sypharochiton pelliserpentis* at a larger spatial scale by measuring all individuals encountered within several haphazardly chosen locations beyond the experimental area but still within each site (except Bird Rock). As in 2004, we aimed to measure 100 + individuals for each species, or all that could be found for sparser species, within a single low tide period.

2.4. Experimental design

Depending on the availability of appropriate habitat along the study walls, five (RR, BT, JH) or six (BR, WB) sets of experimental plots were established at each of the field sites. Each experimental replicate consisted of a limpet exclusion plot, a paint control-plot and a marked plot. All plots were circular, 15 cm in diameter and \sim 175 cm² in area. Plots were spaced relatively evenly at the same tidal height with about 20 cm between replicates. Treatments were assigned randomly to each plot in clusters of three to avoid having a run of adjacent plots with the same treatment. Because the tidal range differs between the two coasts (maximum ranges: east coast \sim 2.5 m, west coast \sim 3.5 m), and to match the ecological contexts between coasts, we placed the plots in the middle of the high zone at each site and not at a fixed height on the shore. Exclusion plots were created using a barrier of Z-spar marine epoxy (Seattle Marine, Seattle, Washington, USA) painted with copper-based *anti-fouling* paint to exclude limpets (and other "flat" molluscan herbivores such as chitons; Cubit 1984, Dye 1995, Freidenburg et al. 2007). Other herbivores, primarily including coiled molluscs at our sites (e.g., *Austrolittorina antipodes*, *A. cincta*, *Rissellopsis varia*) are not excluded by copper paint. We have found that using Z-spar as a base facilitates adherence of the copper paint, thereby reducing the frequency of paint repairs. Limpets were allowed access to the two control plots in each set of plots. Paint controls had a partial barrier of Z-spar coated with *anti-fouling* paint covering about half of the circumference of the plot to control for possible artifacts of paint while allowing grazers to enter. The marked plots had a similar partial barrier

of unpainted Z-spar, which allowed access across the entire perimeter of the plot. We did not use a Z-spar free treatment because prior experiments have shown that Z-spar alone has no influence on grazer activity or algal settlement and growth (e.g., Menge et al. 1999). At the start of the experiment, in October 2003, all algae and invertebrates were removed from the plots by scraping followed by application of lye-based oven cleaner (Cubit 1984, Menge et al. 1999). This method kills most remaining fleshy and calcified upright algae, but is less effective in removing crustose algae occurring in crevices (A. Guerry, B. Menge, personal observations). For this reason, we avoided placing plots on surfaces with such surface irregularities.

2.5. Experiment sampling protocol

The experiment was surveyed at each site after 5, 12, 14, 15, 17, and 20 months (from March 2004 to June 2005). Surveys used the established method of visually estimating the percent cover of all algae and sessile invertebrates in each plot (Meese and Tomich 1992, Dethier et al. 1993) and counting all mobile invertebrates. Direct visual estimation in the field was used instead of photographs to estimate cover to ensure that all taxa obscured by any canopies that formed were detected and quantified. Algae were identified to the lowest taxonomic resolution possible without destructive sampling. This resulted in an inhomogeneous taxonomic resolution of the "species richness" response variable with some units identified to species, and others to morphological groups (see Steneck and Dethier 1994). This approach has been widely used (e.g., Menge et al. 2005, Scrosati et al. 2011) and provides a conservative estimate of the diversity of the algal assemblage. Below, the diversity of algal taxonomic units is referred to as "algal taxon richness."

To examine the types of algae that colonized and persisted in the experiment, morphological groups based on the algal functional groups of Steneck and Dethier (1994) were used. Groups present in this experiment included microalgae (e.g., benthic diatoms, algal sporelings), and filamentous (e.g. *Cladophora* spp.), foliose (e.g. *Porphyra* spp., *Ulva* spp., *Enteromorpha* spp.), corticated (e.g. *Scytothamnus australis*, *Caulacanthus ustulatus*, *Stictosiphonia gracilis*, *Gelidium caulacanthum*), and encrusting forms (e.g. *Ralfsia verrucosa*, *Hildenbrandia* spp., coralline crusts).

Limpets were identified (if $>$ 5 mm) and counted in all plots, and then removed from any exclusion plots they had entered. With the exception of one sampling period at BT, few limpets invaded plots, and typically consisted of limpets that had recruited to the plot. After the final survey at 20 months (June 2005), all of the sessile organisms were scraped from each plot in order to calculate dry weights of each taxonomic unit. This involved some sub-sampling of encrusting forms that were difficult to remove from the rock-surface. Each sample was placed into a pre-weighed aluminum foil packet and dried to constant mass at 60 °C before weighing.

2.6. Grazing frequency

Grazer impacts integrate across grazer activity levels, grazer density and size, and species composition. We used a modified version of a technique developed by Thompson et al. (1997) to assess grazer activity at the various sites. Wax-filled disks (the bottom half of 14 mm diameter screw-end caps filled with melted dental wax) were embedded in the rock to detect grazing marks. To deploy them in the field (40/site, deployed evenly among the experimental plots), shallow depressions were drilled in the rock, filled partially with Z-spar, and wax-filled caps then were pressed into the soft Z-spar, ensuring that the disk surface was flush with the Z-spar and rock surface. The radulae of limpets and chitons leave distinctive marks on the wax as they graze (Thompson et al. 1997, Range et al. 2008), although not all species will graze on wax disks (Jenkins and Hartnoll 2001, Hutchinson and Williams 2003). Grazing pressure indices were estimated by scoring

the percent of each disk that was scraped by mollusks and by recording the proportion of scraped disks. To yield information about relative grazing intensity, disk deployments must be long enough to have some, but not all disks scraped. Although Thompson et al. (1997) found that the optimal period of deployment on the Isle of Man was 1–14 days, many disks at our sites remained untouched after 30 days. Some disks were still untouched after 76–90 days, but many had scrape marks so the disks were removed. The disks were examined in the laboratory using a dissecting microscope to score grazing activity.

2.7. Recruitment of sessile invertebrates

Sessile invertebrate recruitment was quantified to provide part of the ecological context for the algal communities at each site. Barnacle recruitment was quantified by using polyvinylchloride (PVC) plates coated with a rubbery, textured surface (Saf-T-Walk; Farrell et al. 1991, Menge et al. 2003, Broitman et al. 2008). Identification and counts of cyprids and metamorphs were done in the laboratory using a dissecting microscope. Mussel recruitment was quantified by deploying plastic mesh collectors (“Tuffys”) that mimic the structure of benthic algae to which mussels recruit. In the laboratory, recruits were detached from the collectors by rinsing with a strong jet of water and then counted using a dissecting microscope (Menge et al. 1994, 1999, 2009, 2011). Recruitment collectors (5 plates, 5 tuffys) were replaced at each visit to the sites (month 5, 12, 14, 15, 17, and 20). Results are expressed as the number of recruits/day. Recruitment was sampled at all sites except BR where levels of recruitment were assumed to be similar to those at RR, only 200 m away. As has been noted previously (Menge et al. 2010), such deployments record the number of recruits surviving the deployment period, not total settlement. Further, although these deployments often were longer than the usual monthly replacement schedule used elsewhere, the resulting data are entirely consistent with monthly data obtained from these sites in previously published reports and with data taken since the current experiments were completed (Menge et al. 2003, Menge and Menge 2013).

2.8. Algal/sessile invertebrate interactions

Benthic algal communities are typically intermingled with assemblages of sessile invertebrates. To examine the potential importance of interactions of the algal assemblages with sessile invertebrates, when maximum percent cover of sessile invertebrates in any plot at each site in the last sampling period was >10%, percent cover of algae was correlated with that of invertebrates to suggest possible competition for space.

2.9. Data analysis

All data were transformed for analysis. We used the arc sine transformation for percent cover data and $\log(\ln[x + 1])$ transformations for count data. To first examine whether or not there were differences between the paint-control and the marked plots, separate non-parametric Kruskal-Wallis tests were used to compare algal species richness and percent cover of algae and sessile invertebrates in each set of plots at each site during each month. At Jackson Head, species richness (on four different occasions) and percent cover (on two occasions) in the two types of control plots differed (Kruskal-Wallis, $p < 0.05$). Therefore, in order to be conservative and consistent across all sites, paint-control plots rather than the marked plots were used for all comparisons with enclosures.

Nested analysis of variance (ANOVA) was employed to examine the effects of upwelling regime (upwelling or downwelling) on algal abundance (% cover and biomass) and diversity (species richness). For all nested ANOVAs the mean square value for the subgroups (sites) was used to test for significance of groups (upwelling regime) (Sokal and Rohlf 2012). For analyses of algal assemblages, the proportional

difference between the enclosure and the paint-control ((enclosure – paint-control) / enclosure) on the final sample date was used for each replicate as a metric of limpet effect size. Because some replicates had no sessile invertebrates in the enclosures, use of the same metric for limpet effects on invertebrates as we did for limpet effects on the algal assemblages was meaningless. Therefore, limpet effects on invertebrates were not expressed as a proportion of the value in the enclosure but simply as the difference in percent cover between enclosures and the paint-controls.

Nested ANOVA was also used to determine if the concentrations of nutrients in the water at each site varied as expected according to the described upwelling regimes. Finally, ANOVAs were used to examine differences between abundance, size-structure, and grazing-intensity of limpets at each site and to examine differences between sites with respect to the recruitment of sessile invertebrates.

3. Results

3.1. Nutrients

On average, west coast sites had nearly 4 times more N (nitrate + nitrite) and 1.5 times more P (phosphate) than east coast sites, but sites within coasts were not different from one another for either nutrient (Table 1, Fig. 1). Neither coasts nor sites differed with respect to Si (silicate) concentrations (Table 1, Fig. 1). Nutrient levels were consistent with those obtained in other SINZ studies (Menge et al. 1999, Guerry et al. 2009, Alestra and Schiel 2015).

3.2. Community structure: sessile organisms

The high zone at all sites had little cover of algae of any type (Table 2). Algal cover was highest at Jackson Head, occupying ~12% of the space. Mussels (*Xenostrobus pulex*) and barnacles (mostly *Chamaesipho columna*) together covered about 50% of the space, and 35% of the space was bare at this site. Algal cover at Raramai was next most abundant, occupying about 8% of the surface, with barnacles covering ~29%, and 67% of the space was bare. Both Box Thumb and Woodpecker Bay had very low covers of algae in the high zone (0–1% cover), with barnacles and mussels occupying 68% (Box Thumb) and 80% (Woodpecker Bay) of the space, and most remaining space being bare rock (30% at Box Thumb, 14% at Woodpecker Bay). Although these data provide only a snapshot of patterns at each site, observations made frequently since 1994 (Box Thumb) and 1999 (other sites) suggest these patterns have been persistent during those time periods.

3.3. Community structure: grazers

At the initiation of the experiment, limpets were approximately twice as dense at BT as they were at JH and RR and five times as dense as they were at WB and BR (Fig. 2A). Toward the end of the experiment, in March 2005, the same general pattern of relative abundance was apparent, except that densities at WB had increased to be comparable to those at JH and RR, sites of intermediate densities (Fig. 2B). A second measure of limpet density was obtained from counts of limpets in the paint-control and marked plots from each monitoring date. This integrated measure again indicates that limpet densities were greatest at BT and least at BR. Densities at the remaining sites were intermediate—limpets at JH and WB were less dense than at BT but more dense than at RR (Fig. 2C).

Although BR had the fewest limpets, on average, it had the largest limpets (Fig. 2D). BT, the site with the highest densities of limpets, had relatively small limpets (Fig. 2D). The sites with intermediate densities had intermediate sizes, except for WB, which had the smallest limpets (Fig. 2D). In the species-specific sample of grazer size structure, the *Cellana* species were generally the largest limpets, ranging in mean length from 12 to 28 mm, with similar median sizes, and with

Table 1
ANOVA results for nutrients, limpet effects, recruitment, and grazing intensity. All results are from nested ANOVAS except mussel recruitment which only tests 3 sites (see text). Values significant at $p = 0.05$ are in bold.

	Upwelling F-statistic (df numerator, denominator)	Upwelling p-value	Site (within upwelling) F-statistic (df numerator, denominator)	Site (within upwelling) p-value
Nutrients				
N + N	55.90 (1.2)	0.017	0.12 (2.12)	0.09
P	36.70 (1.2)	0.026	0.07 (2.12)	0.93
Si	1.11 (1.2)	0.400	0.63 (2.12)	0.55
Limpet effects				
Algal taxon richness	149.30 (1.3)	0.0001	0.22 (3.22)	0.88
Algal biomass	27.70 (1.3)	0.007	1.89 (3.22)	0.61
Algal % cover	3.48 (1.3)	0.160	18.45 (3.22)	<0.0001
Invertebrate % cover	0.012 (1.3)	0.920	4.00 (3.22)	0.02
Invertebrate biomass	0.57 (1.3)	0.510	3.37 (3.22)	0.04
Recruitment				
Barnacle	0.069 (1.2)	0.490	13.61 (2.22)	<0.0001
Mussel	—	—	11.17 (2.20)	0.001
Grazing intensity				
Wax disk marking	19.56 (1.3)	0.020	1.34 (3.20)	0.27

maximum sizes ranging from 21 to 38 mm (Table 3). The chiton *Sypharochiton pelliserpentis* was also large, with mean (and median) lengths ranging from 14 to 25 mm and maximum lengths ranging from 25 to 40 mm (Table 3). *Siphonaria australis*, *Patelloida corticata*, and *Notoacmea* spp. were progressively smaller, with mean shell lengths ranging from about 10–13, 9–11, and 6–7 mm, respectively (Table 3).

The composition of limpet assemblages varied among sites, with no apparent differences with respect to coast (east vs. west; Fig. 3). BR was the least diverse, with only 3 limpet species occurring in the plots throughout the course of the experiment. RR was the most diverse, with 6 limpet species and one chiton species (*Sypharochiton pelliserpentis*). *Cellana ornata* was by far the most common limpet at BR. *Siphonaria australis* was the most common limpet at JH and RR, though *C. radians*, *C. ornata*, *Notoacmea* sp., and *C. denticulata* (RR) or *C. strigilis* (JH) were also fairly common. The small limpet *Notoacmea* spp. was the most common at WB and BT. WB also had relatively large numbers of *C. radians*; at BT *C. radians*, *C. ornata*, and *S. australis* were also common.

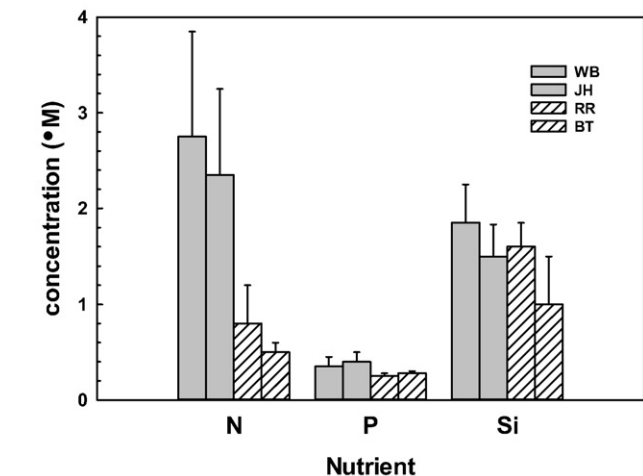


Fig. 1. Average nutrient concentrations at 4 sites during October 2003–January 2004 (4 sampling events/site). Values are mean + 1 SE. Intermittently upwelled west coast sites (WB and JH) are shown in gray fill; downwelling-dominated east coast sites (RR and BT) are hatched.

3.4. Experimental results: grazer effects on algal assemblages

In general, limpets had a greater effect on algal communities at the downwelling-dominated east coast sites than at the intermittently-upwelled west coast sites. At the east coast sites, benthic algae were more abundant and more diverse in limpet-exclusion plots on all sampling dates (Table 1, Figs. 4C–E, 5C–E). At the west coast sites, algal abundance differed between plots with and without limpets on the first 1–2 sampling dates (month 5 and/or month 12), but these differences did not persist. At JH, limpet-exclusion plots were more diverse than in controls until the 15th month, but algal taxon richness never differed at WB between plots with and without limpets (Figs. 4A, B, 5A, B). At BT after 5 months limpets had heavily recruited to all plots such that limpet densities in exclosures and controls were similar. Removal of limpets from exclosures took the entire available sampling time, so data from the month 5 survey are missing for BT (Figs. 4E, 5E). Thereafter, limpet densities in the exclosures at BT were more consistent with the experimental design.

At the end of the experiment, limpet effects (the proportional difference between treatments with and without limpets ((exclosure – paint-control) / exclosure), or (E – P / E) as described above) on algal taxon richness and biomass varied by upwelling regime but not by site within upwelling regime (Table 1, Fig. 6A, B). In contrast, limpet effects on algal percent cover differed by site but not by upwelling regime (Table 1, Fig. 6C). Limpet effects on algal taxon richness were, on average, six times larger at east coast than at west coast sites (Fig. 6A,

Table 2
High intertidal community structure. Abundances of major taxa or functional groups at four study sites. Data are mean % cover ± 1SE averaged over 10 quadrats sampled per site. No data were available for Bird Rock, but patterns were similar to those at Raramai. Sessile organism abundances were sampled in October 2007.

Taxon or group	Raramai	Box thumb	Woodpecker bay	Jackson head
<i>Sessile organisms</i>				
Bare rock	66.8 ± 8.2	30.3 ± 6.9	14.2 ± 3.2	34.8 ± 7.1
<i>Xenostrobus pulex</i>	0 + 0	18.7 ± 8.1	56.5 ± 5.5	8.1 ± 2.0
<i>Chamaesipho columna</i>	14.8 ± 7.3	48.9 ± 8.0	23.5 ± 2.8	40.9 ± 7.8
<i>Chamaesipho brunnea</i>	13.9 ± 4.2	0 + 0	0 + 0	0 + 0
<i>Epopella plicata</i>	0.01 ± 0.01	2.1 ± 1.8	4.8 ± 1.1	0.4 ± 0.2
Total barnacles	28.6 ± 7.5	51.0 ± 7.6	28.3 ± 3.4	42.3 ± 11.6
Total red algal cover	1.8 ± 1.0	0 + 0	0.1 ± 0.1	11.6 ± 3.8
Total brown algal cover	5.9 ± 3.5	0 + 0	0 + 0	0 + 0
Total green algal cover	0 + 0	0 + 0	0 + 0	0 + 0
Total coralline crust cover	0 + 0	0 + 0	0.9 ± 0.6	1.2 ± 0.7

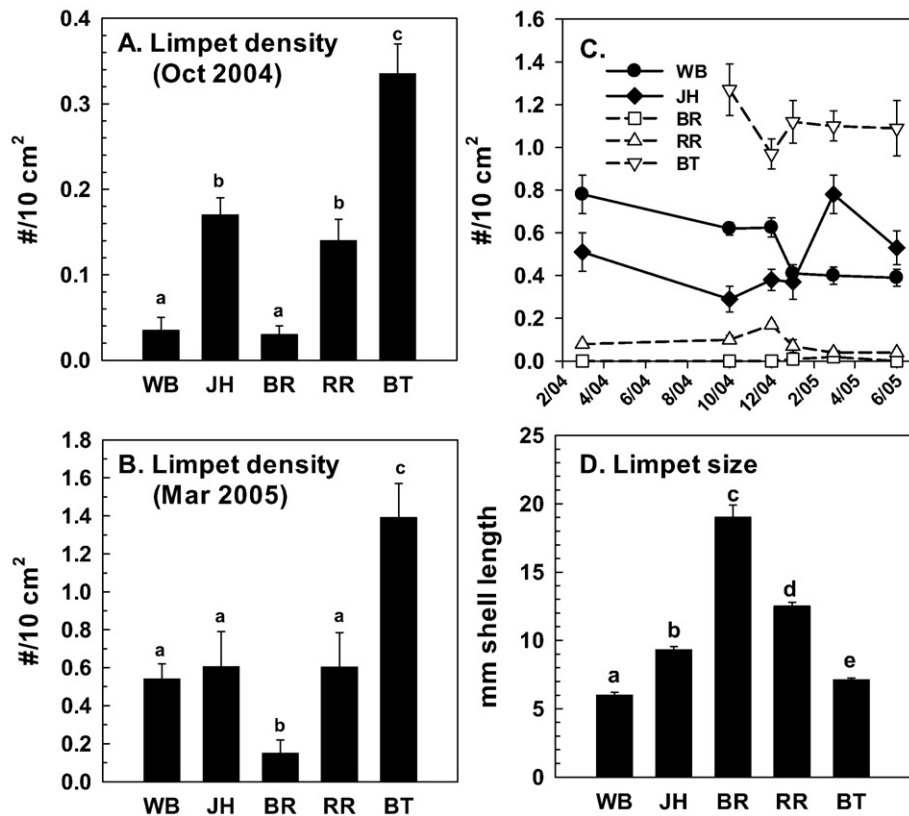


Fig. 2. Limpet densities, and sizes at the 5 sites. Bars with different letters are different (post-hoc tests using Tukey's HSD) at $p \leq 0.05$. A. Mean limpet densities (± 1 SE) at the beginning of the experiment, October 2003 (one-way ANOVA, site effect $F_{4,106} = 28.94$, $p < 0.001$). B. Densities in March 2005 (one-way ANOVA, site effect $F_{4,47} = 16.89$, $p < 0.001$). C. Densities in the paint-control and marked plots throughout the experiment. Values are means ± 1 SE. Analysis of the long-term averages of each site throughout the experiment with post-hoc Tukey's HSD yields site ranking of $BT > JH = WB > RR > BR$ (one-way ANOVA, site effect $F_{4,49} = 99.9$, $p < 0.001$). D. Mean ± 1 SE limpet sizes at each site (one-way ANOVA, site effect $F_{4,543} = 59.8$, $p < 0.001$).

Table 1). Similarly, limpet effects on algal biomass were greater on east coast than on west coast sites (Fig. 6B, Table 1). Notably, although limpet effects on percent cover were negative at most sites (cover in P treatment was less than in E treatment, yielding a positive number in Fig. 6C), limpets at JH had positive (cover in P was more than in E, yielding a negative number in Fig. 6C), not negative effects on algal cover (Table 1).

Limpet effects at the coast scale were detected not only from differences in the cover of algae in enclosures, but also through differences in the relative abundance of algae in paint-control plots. The large differences between enclosures and paint controls on the east coast were driven by the high percent cover of algae in the plots without limpets and the negligible cover of algae in the paint controls (which were similar to the marked plots; Figs. 4 & 7). West coast enclosures generally had lower covers of algae than east coast enclosures, but in contrast to very low covers in east coast paint controls, algal cover in west coast paint controls was moderate. Most algae persisting in paint controls were encrusting forms, though microalgae and corticated algae also occurred (Fig. 7B, C). Finally, grazing intensity, as measured by radular-scrapings on the wax disks, was greater at east coast than at west coast sites (Figs. 8A, B).

3.5. Experimental results: grazer effects on sessile invertebrates

Grazer effects on sessile invertebrate cover differed by site but not by upwelling regime (Fig. 6D, Table 1). Upwelling-influenced WB (west coast) and downwelling-influenced BT (east coast) had more abundant sessile invertebrates (primarily mussels at WB and barnacles at BT) in all treatments than did other sites. Sessile invertebrates were more abundant in paint-controls than in enclosures, with mean differences

(enclosure – paint controls) between the two of -23.9% (± 7.4) and -26.9% (± 8.3) at WB and BT respectively. At the other three sites, cover of sessile invertebrates was very low in general, with differences ranging from -1.0% to $+1.8\%$ cover.

Grazer effects on sessile invertebrate biomass were similar to those for % cover (Table 1), with differences at the site scale but not at the coast scale. As with cover, sessile invertebrate biomass was high at WB and BT and low at the other three sites.

3.6. Invertebrate recruitment

Barnacle and mussel recruitment differed by site but not by upwelling regime (Table 1). Barnacle recruitment was greatest at WB and lowest at JH and RR (Fig. 9). Although barnacle recruitment tended to be higher at BT than at JH or RR, recruitment did not differ among these sites. Mussel recruitment at WB was approximately two orders of magnitude greater than at JH, RR, or BT (Fig. 9). Among the 3 sites with similarly low recruitment in comparison to WB, mussel recruitment varied by site (Table 1), with RR experiencing lower recruitment than JH and BT (Fig. 9).

3.7. Algal/sessile invertebrate interactions

At 20 months, sessile invertebrates were abundant at WB and BT (maximal covers of 95% and 80.5% respectively), but sparse at BR, RR, and JH (maximal covers of 1%, 5%, and 10% respectively). At both WB and BT, the abundance of sessile invertebrates was inversely correlated to the abundance of algae (WB: $r = -0.71$, $p = 0.001$; BT: $r = -0.68$, $p = 0.005$).

Table 3
Mean shell or body length for the major grazing species at four sites in New Zealand. Data collected in October 2008. N = sample size.

Species	Site	Mean body length ± 1SE (mm)	Range	Median	n
<i>Cellana ornata</i>	Raramai	14.9 ± 0.22	6–24	15	148
	Box Thumb	12.2 ± 0.42	4–24	12	102
	Woodpecker Bay	18.1 ± 0.45	6–26	19	115
	Jackson Head	18.8 ± 0.34	9–32	19	156
<i>Cellana radians</i>	Raramai	19.6 ± 0.32	6–29	19	168
	Box Thumb	11.7 ± 0.37	4–22	12	102
	Woodpecker Bay	11.5 ± 0.61	4–21	11.5	48
	Jackson Head	22.4 ± 1.70	7–33	25	28
<i>Cellana denticulata</i>	Raramai	28.2 ± 0.35	18–38	29	115
	Box Thumb	Absent	–	–	–
	Woodpecker Bay	Absent	–	–	–
	Jackson Head	Absent	–	–	–
<i>Siphonaria australis</i>	Raramai	12.3 ± 0.39	6–18	12	57
	Box Thumb	11.1 ± 0.15	7–16	11	102
	Woodpecker Bay	12.8 ± 0.78	9–20	13	13
	Jackson Head	9.8 ± 0.31	5–20	9	72
<i>Patelloida corticata</i>	Raramai	10.7 ± 0.22	6–18	10	105
	Box Thumb	9.3 ± 0.22	5–16	9	103
	Woodpecker Bay	10.1 ± 0.21	5–15	10	101
	Jackson Head	8.7 ± 0.20	5–13	9	107
<i>Notoacmea</i> spp.	Raramai	7.4 ± 0.21	5–13	7	86
	Box Thumb	6.6 ± 0.23	4–14	6	105
	Woodpecker Bay	6.1 ± 0.16	4–10	6	53
	Jackson Head	6.7 ± 0.37	4–12	7	48
<i>Sypharochiton pelliserpentis</i>	Raramai	21.1 ± 1.36	11–28	23	14
	Box Thumb	14.5 ± 0.40	6–25	14	99
	Woodpecker Bay	18.5 ± 0.83	7–34	18	77
	Jackson Head	25.2 ± 0.74	8–40	25.5	100

4. Discussion

4.1. Key findings

The effect of grazers, primarily limpets, on algal taxon richness and biomass in benthic communities in the high intertidal zone of the SINZ appeared linked to nearshore oceanographic conditions. In the experiment, grazers had a greater effect on algal species richness and biomass at downwelling-dominated east coast sites than at intermittently-upwelled west coast sites. At east coast sites, grazers decreased species richness and biomass, whereas at west coast sites, grazers had little effect. This finding is consistent with the predictions of the grazer-reversal hypothesis (Proulx and Mazumder 1998). That is, grazing decreased algal taxon richness when nutrient inputs were relatively low and increased or had no effect on algal taxon richness when nutrient inputs were relatively high. In contrast to these results, however, other algal community characteristics seemed driven by local-scale, not oceanic processes. For example, site effects were evidently stronger than coast (upwelling) effects for barnacle and mussel recruitment and grazer effects on sessile invertebrate percent cover and biomass. These latter results are consistent with those in previous studies (Menge et al. 2003).

The most parsimonious explanation for grazer effects on algal taxon richness is through effects on plant biomass and abundance (Proulx and Mazumder 1998, Hall et al. 2000). Examination of grazer effects on algal biomass (Fig. 6B) suggests this mechanism was operating here. At east coast sites, algal biomass in the paint-control plots was negligible. With negligible biomass, it is not surprising that few species occurred. At west coast sites, grazer effects on algal biomass were not distinguishable from zero, and algal biomass in the plots with and without grazers was similar (Fig. 6B). This parity was also reflected in algal taxon richness data (Fig. 6A). However, examination of grazer effects on algal percent cover was less clear (Fig. 6C). Although east coast patterns were the same as for biomass, patterns differed on the west coast. At WB, grazer effects on algal percent cover were similar to those on the east coast,

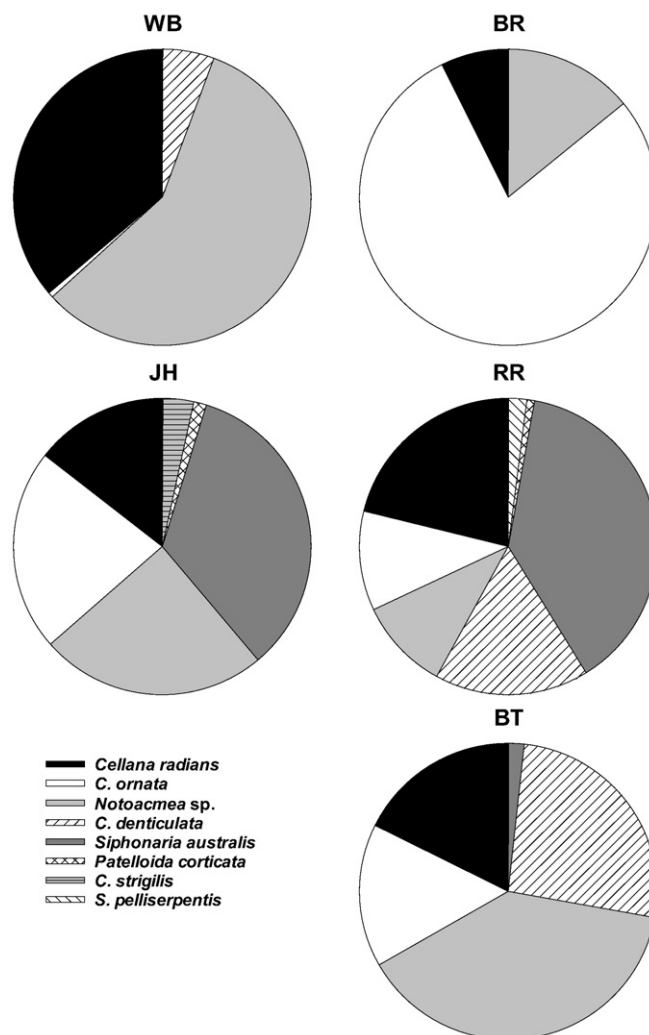


Fig. 3. Limpet species composition (with chitons) at the 5 sites. WB and JH are on the west coast; BR, RR, and BT are on the east coast. Values are the percent of the total number of limpets (>5 mm) observed in all plots at each site throughout the duration of the experiment.

with higher algal abundance in the enclosures than in paint-controls. In contrast, at JH grazers appeared to have a positive, not negative effect on algal abundance, with higher algal coverage in the paint-controls than in the enclosures (Figs. 5, 6C). This positive effect was most likely due to facilitation of crustose algae by herbivores (e.g., Paine and Vadas 1969, Estes and Palmisano 1978, Lubchenco and Cubit 1980, Littler et al. 1983, Vinuela et al. 2014) (Fig. 7). Neither pattern was reflected in algal taxon richness (Fig. 4B, 6A).

A potential explanation for between-coast differences in grazer effects on algal taxon richness and biomass is the apparent difference in grazing intensity between upwelling regimes. Intermittently-upwelled west coast sites had lower grazing intensity, as measured by radula marks on the wax disks, than did downwelling-dominated east coast sites (Fig. 8A, B). This difference in grazing intensity cannot be explained by differences in limpet abundance, size-structure or species composition because these measures were not related to upwelling regime (Figs. 2A–D, 3, Table 3).

One possible interpretation of this pattern is based on foraging behavior. Most limpets and chitons feed by crawling over the rock, scraping microalgae (and in some cases, macroalgae) off the substratum with their radula (e.g., Nicotri 1977, Underwood 1980, Hawkins and Hartnoll 1983, Hawkins et al. 1992, Hodgson 1999, Jenkins and Hartnoll 2001, Jenkins et al. 2001, Hutchinson and Williams 2003). Microalgae can

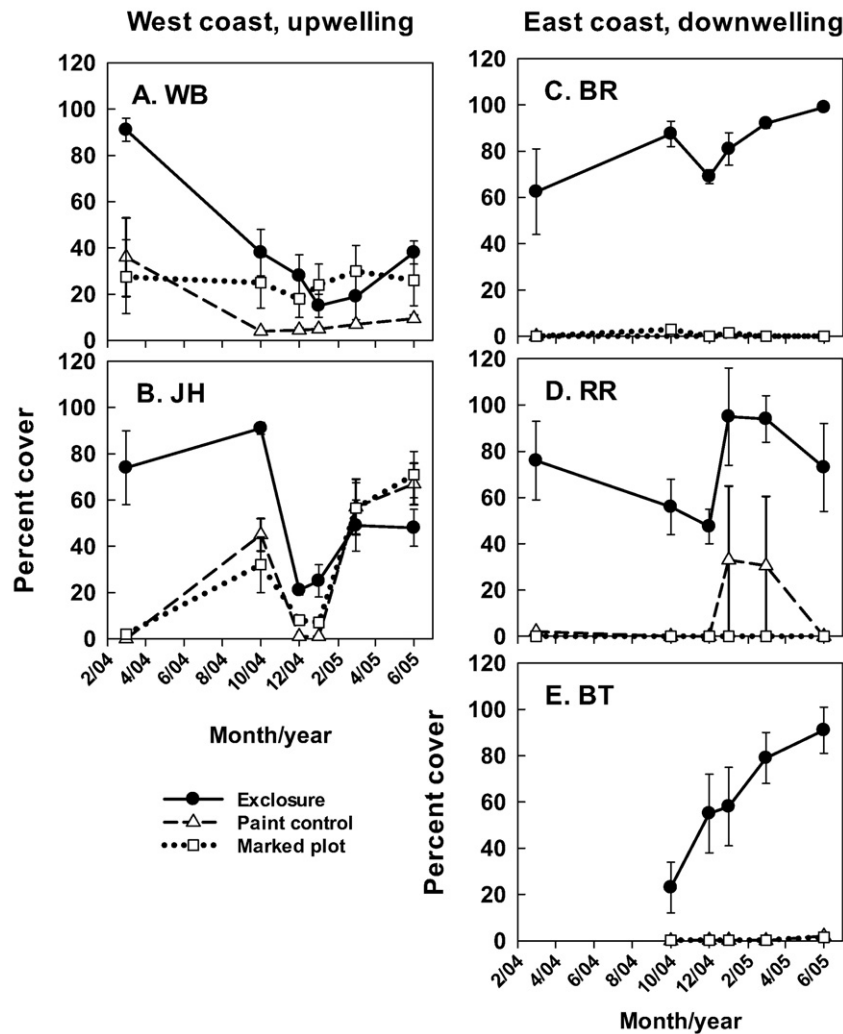


Fig. 4. Algal percent cover in the three treatments at each site over the 20-month duration of the experiment. Values represent means (± 1 SE).

include benthic diatoms as well as the spores and sporelings of benthic macroalgae (Lodge 1948, Dayton 1971, Castenholz 1973, Dayton 1975, Nicotri 1977). At higher-nutrient west coast sites, the production and/or turnover of benthic microalgae may be greater, such that grazers can achieve the same level of intake by grazing over a smaller surface area. Although we did not measure grazer activity directly, grazing intensity, as measured by the wax disks, suggests activity was greater at the lower-nutrient east coast sites (Fig. 8A, B).

Grazer species composition varied among sites (Fig. 3), and this could underlie variation in grazing impact. However, all sites had moderate to high abundances of the patellid genus *Cellana* (i.e., *C. ornata*, *C. radians*, *C. denticulata*, *C. strigilis*; Fig. 3), which tend to be relatively large (e.g., Table 3), and are known to have strong effects on algal abundance (e.g., Underwood 1980, Underwood and Jernakoff 1984, Dunmore and Schiel 2003). Other species in this grazing guild may be less important in exerting grazing effects on algae. For example, siphonariid limpets vary greatly in whether or not they graze on microalgae vs. macroalgae (Hodgson 1999). Given the sparsity of macroalgae at our sites (Table 2), however, it seems like that *Siphonaria australis* feeds on both. *Notoacmea* spp. were small (mean and median lengths of 6–7 mm; Table 3), so may have contributed less to overall grazing impacts than the larger *Cellana* species. *Patelloida corticata* is most common lower on the shore and in association with encrusting coralline algae, which usually coats its shell (A. Guerry, B. Menge, personal observations), and was likely a minimal contributor to grazing effects. Though relatively large, the chiton *S. pelleris* was sparse around our experiments

(Fig. 3), perhaps due to the center of their abundance occurring lower on the shore and to our avoidance of areas with crevices, where most chitons are found during low tide. *C. ornata* and *C. radians* were generally the most abundant large limpets at all sites (Fig. 3), so it seems likely that the grazing impacts we documented were due primarily to these species.

After 20 months, algal types occurring in the experiment did not differ systematically between the two upwelling regimes (Fig. 7). This is contrary to the experimental and observational patterns reported by Nielsen and Navarrete (2004) and Broitman et al. (2001), where corticated algae were more abundant at sites of high upwelling intensity and ephemeral algae were more abundant at sites of low upwelling intensity. Examination of morphological groups (Fig. 7) did show that, while algae were scarce in the plots to which limpets were allowed access on the east coast, when they did occur, they were almost always the more herbivore-resistant encrusting forms (e.g., Littler et al. 1983, Steneck and Dethier 1994). On the west coast, + grazer plots were often dominated by encrusting algae, but microalgae and corticated and foliose macroalgae also occurred (Fig. 7).

4.2. Nutrient inputs

In general, measurements of nutrient concentrations (N and P but not Si) matched the a priori assignment of sites to upwelling regimes and were thus consistent with the oceanic context of these sites described previously (Menge et al. 1999, 2003). Nitrogen is often the

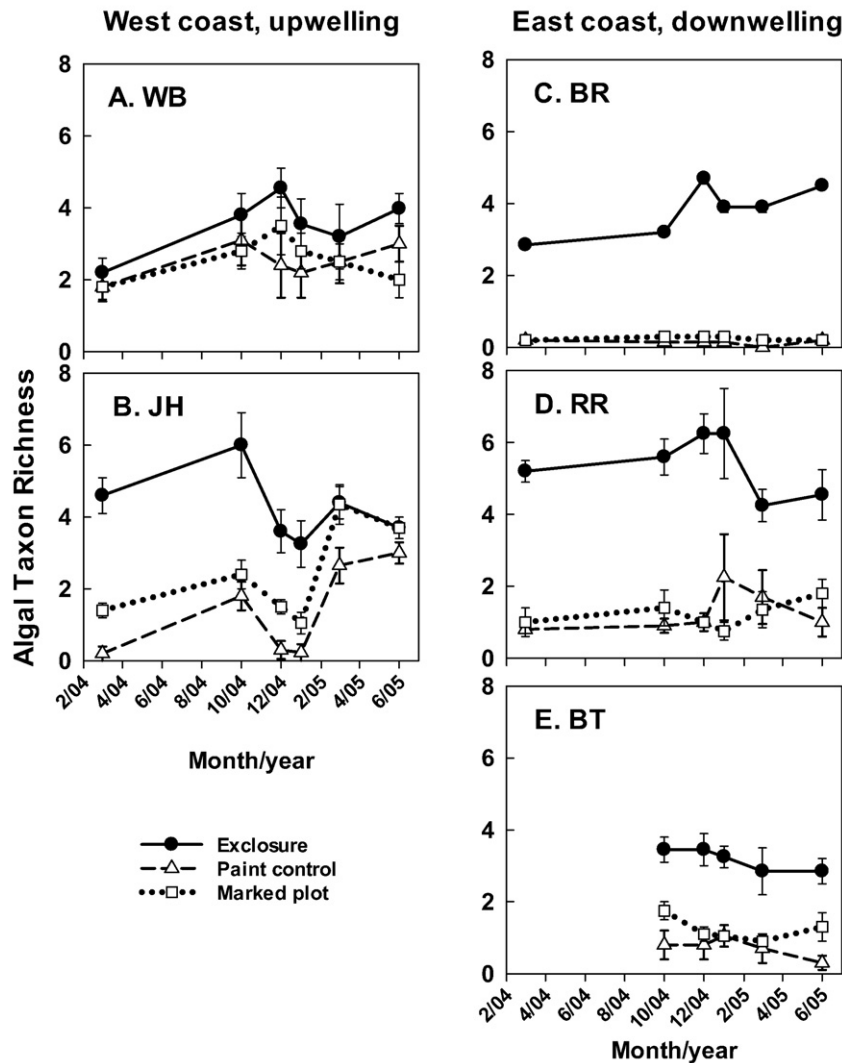


Fig. 5. Algal taxon richness in the 3 treatments at each site over the 20-month duration of the experiment. Values represent means (± 1 SE).

limiting macronutrient in marine systems (Ryther and Dunstan 1971). Nearshore waters along New Zealand's coastlines are among the most N-poor temperate systems globally (Vincent et al. 1991, Chang et al. 1995), and intertidally-measured levels of nutrients in other studies echo this pattern (Guerry et al. 2009, Alestra and Schiel 2015). For comparison with the west coast average of $2.5 \mu\text{M}$ and east coast average of $<1 \mu\text{M}$ in this study, summertime concentrations in Oregon, USA (a relatively nutrient-rich temperate system; Dickson and Wheeler 1995, Hill and Wheeler 2002) can be $>20 \mu\text{M}$ (Barth et al. 2007). In the New Zealand high intertidal, despite low nitrate + nitrite levels, the difference between east and west coasts was evidently sufficient to produce differences in algal cover and/or biomass, and thereby underlie varying top-down herbivore impacts.

4.3. Sessile invertebrates and interactions with limpets and algae

Sessile invertebrates were an important component of the benthic community at only two sites, WB (west coast) and BT (east coast). This pattern is partially explained by the differences in recruitment among the sites. Mussel and barnacle recruitment were up to two orders of magnitude higher at WB than at other sites. Although mean barnacle recruitment over the course of the experiment at BT was not higher than it was at RR, BR, or JH, earlier results (Menge et al. 2003) detected higher recruitment at BT than at other low recruitment sites.

Also, a pulse of barnacle recruitment at BT during February and March of 2005 yielded densities of recruits similar to those at WB (A. Guerry, personal observations). In general, these patterns of recruitment match those seen previously (Menge et al. 2003).

At the sites with significant sessile invertebrate components of the benthic community, WB and BT, sessile invertebrates were more abundant and achieved a higher biomass in paint-control plots (limpets present) than they did in enclosures (limpets absent) (Fig. 6D), indicating a positive interaction between sessile invertebrates and limpets. Although limpets can have negative effects on sessile invertebrates through bulldozing while grazing (Dayton 1971, Branch 1981, Hawkins 1983, Underwood 1985, Menge et al. 2010), and densities of the two are often negatively correlated (Underwood et al. 1983), limpets can also have positive effects on sessile invertebrates by decreasing space competition with benthic algae (e.g., Branch 1976, Choat 1977, Creese 1982, Dungan 1986).

The negative correlation between algal abundance and sessile invertebrate abundance at WB and BT suggests that, in this system, where abundant, barnacles and mussels compete with algae for space on the rock. Although this pattern has been seen previously (e.g., Dungan 1986), in other systems barnacles were observed to have no effect on algal recruitment (Jernakoff 1983), or on facilitation of algal colonization (Farrell 1991). Because the two sites in this experiment at which sessile invertebrates were important community components were on

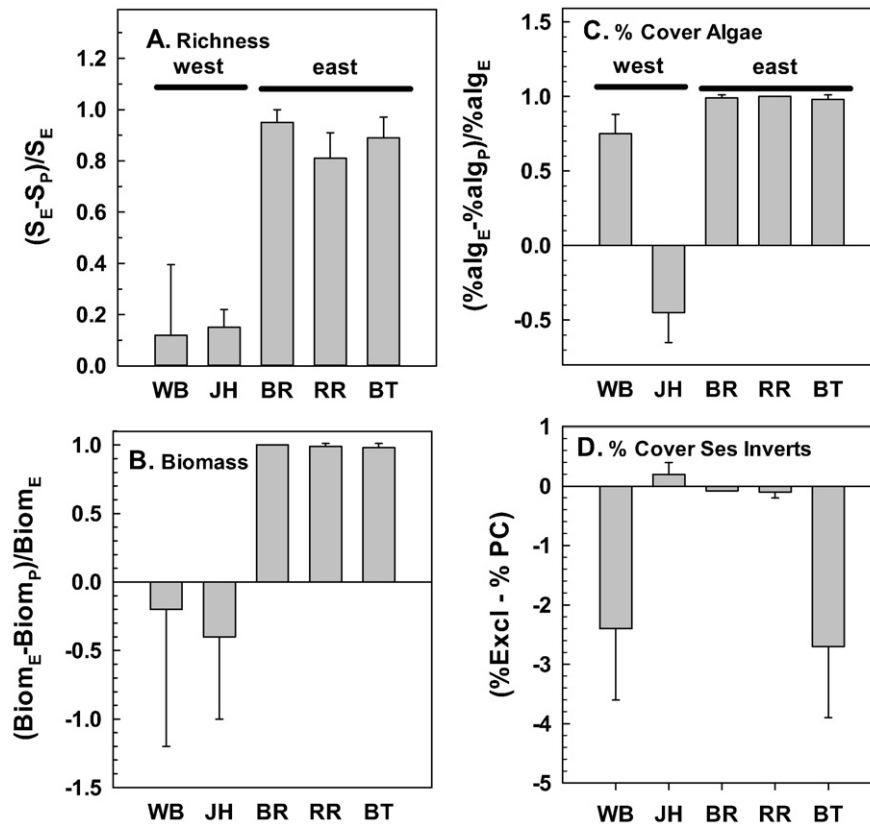


Fig. 6. Limpet effects on A. algal taxon richness (S), B. algal biomass, C. algal abundance (% cover), and D. sessile invertebrate abundance (% cover). Ordinate labels show the index used for each effect. Values are means \pm 1 SE.

different coasts, interactions with sessile invertebrates do not explain the observed differences in grazer effects on algal communities.

4.4. Comparison with other large-scale nutrient-grazer studies

Low intertidal results in a similar grazer-exclusion experiment at east and west coast sites on the SINZ apparently contrast with this study (Menge et al. 1999). After 4 months the total impact of grazers was similar and strong at both intermittently-upwelled and downwelling-dominated sites. These authors suggested, however, that when the total amount of space available for limpet grazers is considered, grazing pressure was probably stronger on the west coast. Two primary differences in the experiments may explain this contrast. First, the present experiment was conducted in the high zone, and second, lasted longer, 20 vs. 4 months. In fact, our short-term (12-month) results do indicate that grazing was similar and strong on both coasts (see Figs. 4, 5). However, as succession proceeded, the initial growth of microalgae was succeeded by more complex macroalgal assemblages. Further, higher on the shore, lower recruitment and slower growth are expected, likely due to the generally more stressful conditions (Bertness et al. 1999, Menge 2000b). It is not surprising that the complex interplay of top-down and bottom-up forces may change throughout time and in different environmental contexts.

In a similar experiment in Chile, Nielsen and Navarrete (2004) found that herbivores were less dense with lower biomass at more strongly upwelled sites but had greater per capita effects than at more weakly upwelled sites. An interesting similarity between the Chilean study and ours is that at weakly upwelled sites, algal biomass differed at the end of the experiment (1 year) between plots with and without herbivores, but did not at the strongly upwelled sites. Similarly, in Australia, nutrient addition had little impact on top down effects in relatively nutrient-rich Eastern Australia sites, but in nutrient-poor South Australia

sites, nutrient enrichment in intertidal, but not subtidal habitats, led to increased macroalgal cover in the absence of grazers (Bulleri et al. 2012).

In South Africa, herbivore (mostly limpets) biomass was positively correlated with nutrients and algal productivity across a large biogeographic scale from west to south to east coasts (Bustamante et al. 1995). Experiments on the west coast suggested that nutrient-supported kelp productivity underlaid the high biomass, survival and condition of the enormous limpets that dominate these shores. Dye (1995) tested the effects of limpet grazing on algal abundance in eastern South Africa, showing a large effect, but we are unaware of experiments testing limpet effects on the more productive west coast of South Africa. Although these results are intriguing, the number of investigations of the relationship between nutrient inputs and top down responses across large spatial scales are still limited. Further research aimed at understanding interactions between nutrient inputs and algal productivity in coastal habitats and the effects of grazers on the structure and dynamics of intertidal communities is necessary to determine the mechanisms underlying these results.

4.5. The importance of local processes

Although our study is consistent with a large-scale oceanic influence on grazer effects on algal taxon richness and biomass, other community characteristics appeared independent of upwelling regime. Local, site-specific processes were likely important drivers of the recruitment of barnacles and mussels and of the effects of grazers on algal and invertebrate percent cover and invertebrate biomass (Table 1). This suggests that local factors such as the composition of the local algal assemblage (a key determinant of the species pool in short-dispersing groups such as algae [Kinlan and Gaines 2003]) can outweigh the importance of the oceanic context. For example, the prevalence of relatively

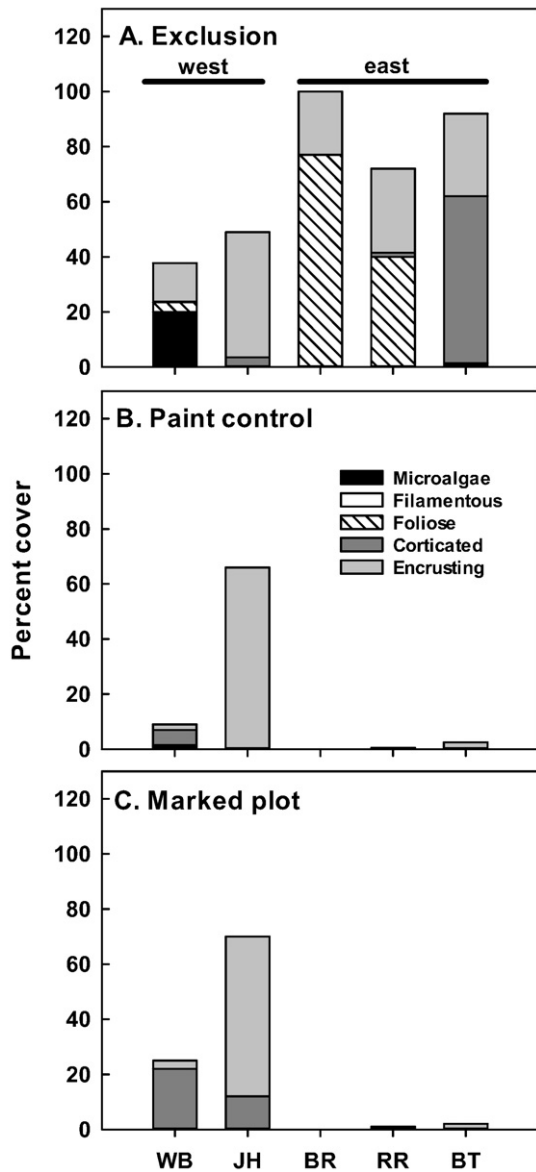


Fig. 7. Mean abundance of morphological groups of algae at the end of the experiment (month 20) in A. exclosures, B. paint-control plots, and C. marked plots.

herbivore-resistant encrusting algae at JH (Fig. 7) may explain the difference between limpet effects on algal percent cover at JH compared to all other sites (Fig. 6C).

Factors underlying small-scale variation in recruitment include variation in wave action, internal waves, environmental stress, availability of substratum, larval abundance, kelp-associated predation on larvae, retention mechanisms, and shore topography among others (Gaines et al. 1985, Gaines and Roughgarden 1987, Pineda 2000, Shanks and Brink 2005, Rilov and Schiel 2006, Rilov et al. 2008, Shanks 2009, Shanks et al. 2010). We do not know why recruitment density varied as it did in our study, but an earlier hypothesis (Menge et al. 2003) suggested that local current patterns were likely important. JH, for example, is near the southern end of the west coast of the South Island and thus where the open-sea Tasman Current is deflected northward to become the Westland Current. Hence, upcurrent sources of larvae might be limited. BT is located on the northern side of the Banks Peninsula, and is bathed by the waters of a gyre formed in the lee (north side) of the peninsula as the Southland Current flows northward. Although larval production along the east coast of the South Island seems likely to be low (due to generally low abundances of reproducing adults), the gyre likely

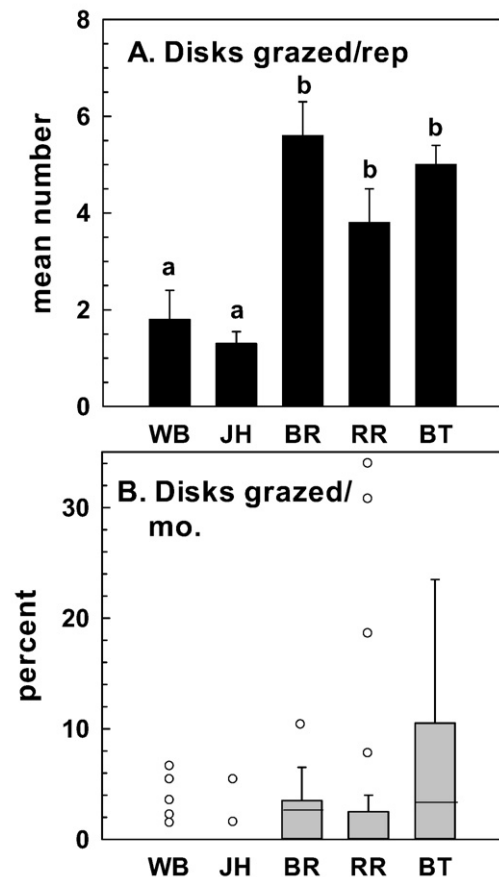


Fig. 8. A. Grazing intensity as measured by the number of wax disks grazed per replicate at each site ($n = 8$ disks/replicate, 40/site). B. Box plot of grazing intensity measured by the percent of the surface of all disks grazed at each site. The center line of each box represents the median, boxes represent 50% of the data, and whiskers show the range of the data that fall within $1.5 \times$ the inner-quartile range. Circles represent outliers.

provides a retention and accumulation mechanism that may have resulted in the somewhat higher recruitment seen at BT compared to the other east coast sites. Thus, hypothetically, these local-scale sources of variation could lead to low (relative to other west coast sites) recruitment at JH, and higher (relative to other east coast sites) recruitment at BT, placing them into a category of intermediate recruitment.

4.6. Conclusions

The results from this experiment were consistent with the grazer-reversal hypothesis. That is, the sites with lower nutrient inputs had the strongest top-down effect of limpets on algal abundance and diversity. Contrary to the expected pattern of tight linkages between bottom-up and top-down effects (Menge 2000a), these results suggest that in the high zone, and over a relatively long time period, stronger bottom up effects (increased nutrients) don't necessarily yield stronger top-down effects, at least for limpets and chitons grazing on algae. Clearly, further research aimed at understanding the contexts in which the strengths of bottom-up and top-down forces are likely to be tightly linked—and in which they are likely to act in concert or inversely—will provide critical information about the ways in which ecological communities are structured. More broadly, these results demonstrate the crucial role of scale in driving community structure. In this case, we found evidence for a strong influence of larger-scale oceanic conditions on some aspects of the grazer-herbivore component of New Zealand rocky shores, and an effect of more local-scale ocean-related variability on other aspects. This work adds depth to the growing body of evidence that suggests

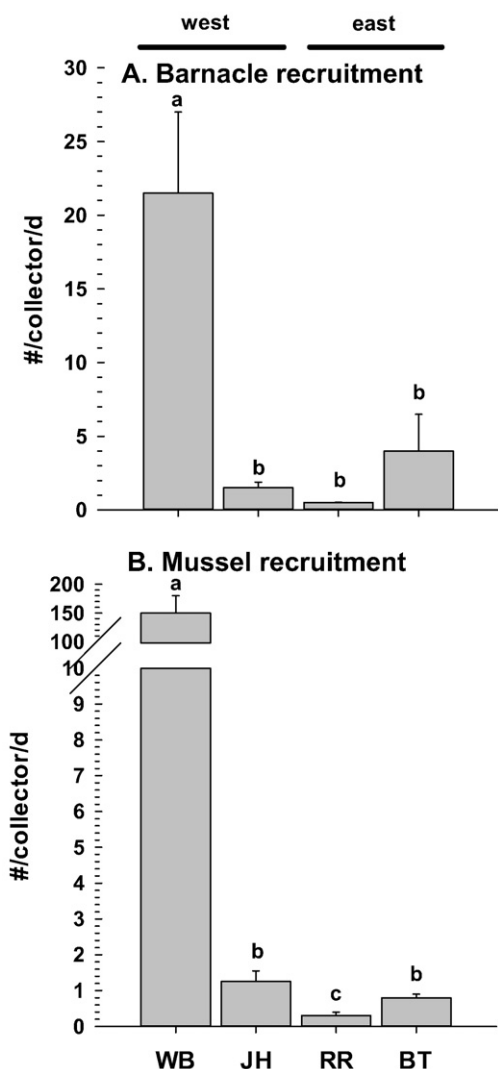


Fig. 9. Barnacle (A) and mussel (B) recruitment over the course of the experiment. Values are means \pm 1 SE across all sampling periods. Letters represent significant differences or lack thereof (Tukey's HSD). In panel B, one-way ANOVA and Tukey's HSD compared JH, RR, and BT only.

that subsidies from adjacent systems can have profound effects on the structure and functioning of ecological systems.

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