

SEASCAPE-DEPENDENT SUBTIDAL–INTERTIDAL TROPHIC LINKAGES

GIL RILOV¹ AND DAVID R. SCHIEL

Marine Ecology Research Group, School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand

Abstract. In this study, we test in southern New Zealand a conceptual model of food web linkage that is seascape dependent, which can explain some of the variability in rocky shore community structure among sites and coasts. Using a comparative-experimental approach at local and distant sites we demonstrate that mobile subtidal predators (fish and crabs) can exert strong predation pressure on small mussels in the low tidal zone, but only in sites where the seascape includes subtidal reefs. On intertidal benches with adjacent subtidal reefs (+SR), 60–100% of small (5–15 mm) transplanted mussels were removed within a day from experimental tiles on the low shore when unprotected from predation, compared to fully caged controls that had approximately 100% survival over several months. In partial cages that exclude fish but not crabs, survivorship was intermediate. In contrast, on benches without subtidal reefs (–SR) 40–100% of mussels survived for months, even if unprotected. This difference is expressed in lower cover (0–60%) of mussels on rocks at +SR benches compared to –SR benches (70–99%). The central to northern west coast of the South Island is composed mostly of –SR benches, and predation on small mussels there was low and similar to the –SR benches on the east coast, whereas the +SR benches on the east coast had much greater predation. This contrasts to other studies in New Zealand that examined only predation on larger mussels by seastars and concluded that predation is strong on the west coast and weak on the east coast. Excluding large predators from low-shore areas with new recruits for a year in one +SR site showed longer-term predation effects on their abundance and cover. Short-term sampling at the east coast sites showed that mussel settlement was greater in –SR compared to +SR sites, providing some evidence that seascapes may also affect settlement. Overall, predation depended on the local seascape and ultimately affected community structure via suppression of effective recruitment rates. This study emphasizes the importance of predation on early life stages of basal species and the influence of seascapes on top-down interactions between subtidal predators and their intertidal prey.

Key words: crabs; fish; intertidal bench; mussels; New Zealand; predation; rocky shore; settlement; subtidal reef.

INTRODUCTION

Understanding the variability in community structure at different scales has been a major focus of ecological studies for decades (Connell 1975, Underwood and Denley 1984, Menge and Olson 1990, Underwood et al. 2000, Robles and Desharnais 2002, Petraitis and Dudgeon 2004, Schiel 2004). In rocky intertidal communities, environmental-stress models (McQuaid and Branch 1985, Menge and Sutherland 1987, Menge and Olson 1990), alternative stable states (Petraitis and Dudgeon 2004), and variation in settlement (Caffey 1985, Gaines et al. 1985) are used to explain variability on a local scale (meters to kilometers), while biogeographical and dispersal limits can account for variability on a latitudinal, among-region, scale (100–1000 km; e.g., Connolly and Roughgarden 1998). Sites with

similar exposure to waves can support different communities along a single coast (Foster 1990, Bustamante and Branch 1996, Navarrete and Menge 1996, Connolly and Roughgarden 1998), and across coasts at similar latitudes (Menge et al. 1999, 2002, 2003). These differences are often associated with mesoscale, near-shore, oceanographic conditions that affect nutrient and larval supply (so-called “subsidies” or bottom-up control). Bottom-up effects can in turn enhance top-down control by increasing food availability to predators which, via positive feedback, increases predation pressure and reduces prey abundance. Such subsidy models are now prominent in the ecological literature (see Palumbi 2003).

Other models, however, may explain some of the local and mesoscale variability in intertidal community structure and species’ distributions (Underwood and Petraitis 1993). One such model could involve landscape dependent, or, in the case of marine systems, seascape dependent (sensu, Jones and Andrew 1993) interactions between reef-associated, mobile, subtidal predators and their intertidal prey. Food web linkages

Manuscript received 8 December 2004; revised 26 July 2005; accepted 8 September 2005. Corresponding Editor: W. J. Resetarits, Jr.

¹ Present address: Department of Zoology, Cordley 3029, Oregon State University, Corvallis, Oregon 97331-2914 USA. E-mail: rilovg@science.oregonstate.edu

between adjacent habitats are common in nature, but are usually related to energy flow through the lower trophic levels (e.g., Wootton 1991, Polis et al. 1997, Wallace et al. 1997). Such linkages can also occur through movement of predators. In some terrestrial ecosystems, consumers move from their primary habitat to another nearby to forage (e.g., Donovan et al. 1997, Kollman and Buschor 2003). Linkages through the higher trophic levels (predators) have also been recognized in the last few decades across seascapes. For example, in temperate marine ecosystems, rocky reefs can influence benthic assemblages of the adjacent soft sediments (Lindquist et al. 1994, Barros et al. 2001), and “infaunal haloes” (e.g., Davis et al. 1982) are thought to be associated with foraging reef predators.

The intertidal zone has its own unique features of predation: it can be affected intermittently at low tide by large predators from the air (seabirds; Levings et al. 1986, Marsh 1986) or land (e.g., rodents; Navarrete and Casilla 1993, Stapp and Polis 2003) and at high tide by mobile subtidal predators such as crabs, lobsters and fish (Kitching and Ebling 1967, Menge et al. 1986a, b, Robles 1987, Burrows et al. 1999). The influence of mobile subtidal predators should depend at least partially, however, on the nature of the seascape. Where rocky shores include both intertidal and subtidal reefs, the potential for top-down effects from resident subtidal predators should be greater than in seascapes where intertidal benches are distant from subtidal reefs. Here, we test this seascape-dependent, food web linkage hypothesis by examining the effects of fish and crabs on intertidal mussels across sites in southern New Zealand.

New Zealand intertidal food webs

In recent studies in southern New Zealand, Menge et al. (1999, 2003) concluded that intermittent upwelling along the west coast enhances bottom-up processes and top-down predation effects in the intertidal zone, but on the east coast both effects are weak and macroinvertebrate predators (seastars and whelks) are rare. They measured predation effects using relatively large (30–50 mm) mussels. These were transplanted into the lower-midtidal zone and were rarely consumed on the east coast, probably because of the scarcity of seastars. Crabs and whelks were considered too scarce to have an effect and predation by fish was not considered (Menge et al. 1999, 2002, 2003). However, labrid fishes, especially *Notolabrus celidotus* and *N. fucicola*, are abundant on subtidal reefs around New Zealand and feed on invertebrate prey (Choat and Ayling 1987, Jones 1988, Hickford and Schiel 1995, Denny and Schiel 2001, Schiel and Hickford 2001). *N. celidotus* is a major consumer of recently seeded mussels on commercial mussel farms in New Zealand (Hayden 1995). During high tide, these fish readily feed on small mussels in the lower and middle parts of the intertidal zone (G. Rilov, unpublished data).

Not all rocky shores are contiguous with extensive subtidal reefs. Many are located along shallow sandy beaches or where the nearshore bathymetry is very shallow and lacks subtidal reefs (–SR). Our initial observations at sites near Christchurch suggested that mussel cover in general, and especially that of small mussels, is greater on benches located in –SR seascapes than on nearby benches adjacent to extensive subtidal reefs (+SR). We hypothesized that this pattern resulted from lower predation on small mussels in –SR sites or greater settlement/recruitment (“bottom-up” control) in such sites, or both. In this paper, the major top-down hypothesis is that seascape determines the strength and rate (intensity) of predation by subtidal predators. Different predation pressure may then be expressed in the differential structure of intertidal assemblages between seascapes with and without adjacent subtidal reefs. To test this hypothesis we used a comparative-experimental approach (e.g., Menge et al. 2002) at two spatial scales (Underwood and Petraitis 1993). First, we compare sites with different seascapes on a small scale on the east coast. Then, to test if our results can be generalized over a wider region, we compare more distant sites on the east and west coasts of southern New Zealand. Three null hypotheses were tested: (1) mussel population structure is similar in +SR and –SR seascapes; (2) predation rates and intensity on small mussels are similar in +SR and –SR seascapes; (3) mussels settlement is similar in +SR and –SR seascapes. We also tested the longer-term effects of predation in one east coast mussel population.

METHODS

Study sites

Surveys of benthic cover and predation experiments were done in different seascapes (+SR vs. –SR) at two spatial scales. Small-scale studies were done on four sites on Banks Peninsula near Christchurch (Fig. 1), all within an aerial distance of approximately 3 km. Black Rock (BR) and Box Thumb (BT) are +SR benches that extend underwater to create an extensive, rapidly sloping, subtidal reef to depths of 5–8 m. The reefs had lush subtidal brown algae and had bull kelp (*Durvillaea* spp.) at the intertidal-subtidal fringe. Underwater surveys during high tide showed that the labrids *N. celidotus* and *N. fucicola* are abundant at these sites and actively forage in the intertidal zone (G. Rilov, unpublished data). Cave Rock (CR) and Taylor’s Mistake (TM) are –SR rocky benches in which the substratum changes from rock to sand at the lower tide mark, and they are located at gently sloping sandy beaches with no nearby subtidal reefs. Underwater observations during high tide around these sites indicated that labrid fish are rare. The east coast sites were mostly composed of volcanic and hard metamorphic rocks. The maximum tidal range on the east coast is approximately 2.4 m. We define the low shore there as ex-

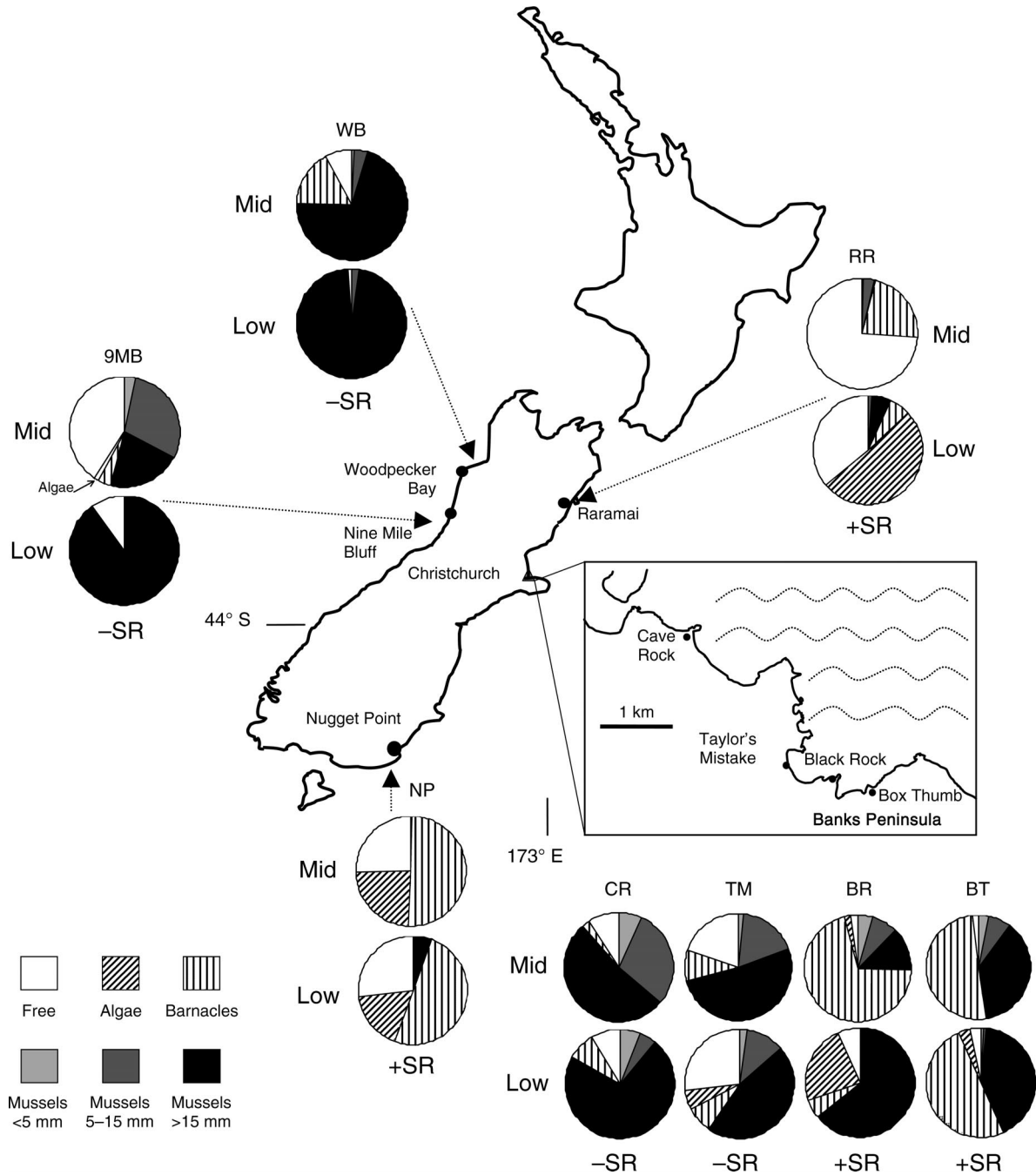


FIG. 1. Study sites and mean cover of major space occupiers (mussels divided into three size classes) in the low- and mid-shore levels (pie charts). The four sites near Christchurch are shown in the inset. +SR and -SR under pie charts designate the type of landscape (with subtidal reefs and without subtidal reefs, respectively). See *Methods: Study sites* for site abbreviations over pie charts.

tending from 0 to 0.8 m (lowest astronomical tide) and the mid shore from 0.8 to 1.6 m.

Surveys and experiments were conducted in additional sites for the large-scale study. Two sites, Raramai (RR) and Nugget Point (NP), located 180 km north and 400 km south of Banks Peninsula, respectively, were used as additional +SR sites (Fig. 1). As additional

-SR sites, we used two locations on the northern west coast separated by about 80 km: Nine Mile Bluff (9MB) and Woodpecker Bay (WB, Fig. 1). Benches at these -SR sites were composed of hard metamorphic rock covered by extensive mussel beds down to the middle low shore level where they were replaced by red algae and where seastars (*Stichaster australis*) are abundant.

The central and northern west coast is characterized by rocky headlands and bluffs separated by sand and gravel beaches. A few large intertidal platforms and many boulders and pinnacles are found along this coast. The coast has a shallow bathymetry nearshore so that the intertidal benches end mostly in a gently sloping, subtidal sand or gravel bottom. Most accessible intertidal benches do not have extensive subtidal reefs adjacent to them, and thus can be defined as $-SR$ sites. The maximum tidal range in the west coast is ca. 3.7 m. The low and mid shore zones on this coast extend from 0–1.2 m and 1.2–2.4 m, respectively. Benches at both study sites were mostly at the lower tidal level (approximately 0.8–1.2 m). All our study sites are considered to be wave exposed (Morton and Miller 1968) and were at least superficially similar in their intertidal structure. They were composed of rocky intertidal benches with varying mussel cover and barnacles interspersed among and above them at the mid and low shore levels. BT, RR, and WB are sites used by Menge et al. (1999) and 9MB is a site located several kilometers south of Menge's 12 Mile Beach site.

Biotic characterization of the sites

To test the first null hypothesis (similar mussel population structure between seascapes) a survey was done in April 2004 at the eight study sites. We estimated the percentage cover of the main space occupiers on the rocks: different size classes of mussels (<5 mm, here defined as early recruits; 5–15 mm, juveniles/subadults; and >15 mm, adults), barnacles, algae (all types pooled), and "free" space (bare rock or thin crustacean coralline algae, hereafter "free space," see Menge et al. 1999) in the middle (east coast) to higher (west coast) parts of the low-shore and the middle mid-shore levels. This was done by using a 25 × 30 cm quadrat divided into 5 × 5 cm squares that was placed randomly along two 10-m transects laid parallel to the water edge at each shore level ($n = 10$ quadrats in each transect, i.e., $n = 20$ in each shore level).

Top-down effects

Seascape effect on predation by fish: small scale.—The second null hypothesis (similar effects of fish predation on small mussels between seascapes) was tested first on a small scale at the two $+SR$ sites (BR and BT) and the two $-SR$ sites (TM, CR) near Christchurch. The experimental units were mussels on 5 × 5 cm plastic tiles with 4 mm thick nylon carpet glued to one surface, which provided a heterogeneous substratum for mussel attachment. Juvenile/subadult mussels (5–15 mm shell length) were collected from low-shore rocks at a nearby site. These were a mixture of *Xenostrobus pulex* Lamarck and *Mytilus galloprovincialis* Lamarck because they were by far the most abundant small mussels in the area outside established beds. Twenty-five mussels were placed onto each tile, which were then wrapped with plastic mesh to secure the mus-

sels until they were attached firmly. In each site, five plots were randomly established on the low shore (within 20 cm of vertical height) along approximately 25 m of shoreline, with one partial cage (to exclude fish) and one no-cage control (open plots) within each plot. Partial cages were designed to exclude fish and birds, but allow access to benthic invertebrates such as crabs, whelks, and seastars. No other type of cages was used in this experiment, because no artifact was detected in extensive small-scale experiments (G. Rilov, unpublished data). There were no observed effects of the cages on water flow, and predation effects occurred rapidly (see *Results*). The frame of the fish exclusion cages was 10 × 10 × 10 cm and made from 6-mm steel rods. A rigid plastic mesh with holes of 16 × 16 mm was wrapped around each cage. This mesh prevented access to large predatory fish and minimized cage effects (such as reduction in light or water motion). A gap of 3 cm was left between the mesh and the rock surface to allow access to benthic predators.

On 21 January 2003, mussels were settled for attachment on 40 tiles as described above and all tiles were placed in the same site, BR, to reduce potential effects of site on attachment and survival prior to the initiation of the experiment. The experiment began on 19 February after the tiles were distributed to all sites and treatments. The number of live mussels on tiles was monitored at low tide for 27 days in the $+SR$ site (after which almost all mussels were gone) and for 203 day in the $-SR$ sites. To test if mussels are more accessible to predators on experimental tiles than on bare rock we also transplanted mussels directly on the rock in the low shore at one site (BR). Five clumps of 25 uncaged small mussels were placed on the rock surface and held until attached under a soft plastic mesh with steel nails and wall anchors inserted in six holes drilled around the mussels. This mesh was removed after mussels were firmly attached to the reef.

Seascape effect on predation by fish and macro-invertebrates: large scale.—For this experiment, we used sites that were more remotely dispersed: two $+SR$ sites (BR and RR on the east coast) and two $-SR$ sites (9MB and WB on the west coast). A full-factorial design that included "coast" as main effect (with $+SR$ and $-SR$ sites on both the west and east coasts) was impossible because there are no accessible intertidal benches with contiguous reefs along the central and northern west coast. From our previous experiment, it was clear that another predator was eating mussels besides fish at $+SR$ sites. The most likely candidates were crabs that may have reached through the 3-cm gap between the mesh and rock in partial-cage treatments. In this experiment, therefore, full cages were added as a treatment to exclude both fish and large invertebrate predators such as crabs and seastars. The full cage had a similar shape as the partial cage and used the same plastic mesh with 16 × 16 mm holes that in this case extended all the way to the rock surface (full cage).

Mussels were settled on tiles in mid April 2003 and the experiment initiated between 13 May and 15 May 2003. Treatments were arranged in five plots along approximately 25 m of shoreline in each site. Monitoring of survival was done on days 1–3, and then at 2–6 wk intervals for up to 6 mo (except for BR, where we had to terminate the experiment at day 74 because many of the cages were damaged by the following monitoring date). On the west coast sites, seastars were abundant, and they were counted within a 2 m radius around each plot on 12 June 2003.

Long-term predation effects on early recruits.—On +SR intertidal benches of the east coast, small recruits (1–5 mm) were rare outside mussel patches (see *Results*) and they mostly occurred within barnacle patches. Although barnacles can facilitate mussel recruitment (e.g., Lively and Raimondi 1987) in areas of high predation, small mussels could be vulnerable to large predators (fish, crabs) once they grow above the height of barnacle tests. To test the long-term effects of predators on mussel recruits within barnacle patches, Full cages were set over areas covered by barnacles and early mussel recruits (<5 mm) at BR. Nearby marked 10 × 10 cm open areas with similar barnacle cover (>80%) were used as controls. The experiment began near the end of the major settlement season (April 2003) and lasted for 12 mo. The number of mussels and percentage of cover were monitored every few weeks and the presence of macrograzers and whelks was noted. Mussel shell lengths were measured using calipers.

Mussel settlement

To test our third null hypothesis (similar settlement between seascapes) settlement was measured in the summer months during the peak of the settlement season, the austral summer (Menge et al. 1999), at the two –SR and two +SR at Banks Peninsula. Collectors made of plastic-mesh, ovoid, pot scrubbers (“Tuffies,” see Menge et al. 1994, 1999) were used. Five collectors were fastened to the reef on the low shore level and collected after a month. Collectors were stored in –20°C freezers until analysis. Recently settled mussels were extracted from the collectors by placing each collector into a jar with 10% bleach solution for 4 min to dissolve the byssal threads. The jar was shaken and the contents sieved through three mesh sizes. Recruits were distinguished to species under a dissecting microscope and counted. For the purpose of this paper all size classes were pooled.

Data analysis

Where percentage of cover and survival were the variables analyzed, data were arcsine-square-root transformed (Sokal and Rohlf 1995). In the analysis of percentage of cover of different size classes of mussels on rocks and of settlement of different mussel species in collectors, a nested (sites nested in seascape) MAN-

OVA was done using Wilk’s test for multivariate effects (sizes or species); univariate ANOVA was then used on the different dependent variables (STATISTICA 7, StatSoft, Tulsa, Oklahoma, USA). Seascape, shore height, or month were fixed factors and sites were random. In the predation experiments, a nested ANOVA was used with seascape (+SR/–SR) and treatment (no cage, partial cage, full cage) as fixed factors, and site (nested in seascape) and plot (nested within sites) as random factors. Where “plot” (i.e., blocks of treatments within sites) was nonsignificant and $P > 0.25$ it was pooled into the error term for final analyses. Homogeneity of variances was checked by Cochran’s test. When variances were heteroscedastic we still used parametric analyses because significance levels were usually very high (allowing an assumption that the probability of Type I errors was likely to be low), but conclusions were conservative and were based on the significance of P values and degrees of freedom (e.g., Underwood 1997).

RESULTS

Biotic characterization of the sites

The dominant mussel species in the New Zealand intertidal zone are the greenshell mussel *Perna canaliculus* (maximum shell length 160 mm), the blue mussel *Mytilus galloprovincialis* (120 mm), the ribbed mussel *Aulacomya ater maoriana* Iredale (80 mm), and the black mussel *Xenostrobus pulex* (30 mm). In this paper, we are primarily concerned with mussels as a filter-feeding assemblage and, consequently, do not analyze the separate species here. Furthermore, small mussels (<10 mm) can be difficult to distinguish to species level without the aid of a dissecting microscope.

The average total cover of mussels at –SR sites was approximately three times higher than at +SR sites in both the low-shore (81.5 ± 6.1 and 26.5 ± 7.1 [mean \pm SE], respectively; range, 68–98% and 5–49%) and mid-shore (73.3 ± 5.2 and 20.0 ± 5.6 ; range, 54–89% and 3–46%, respectively) levels (Fig. 1). The multivariate analysis showed a highly significant effect of seascape, site, shore height, and their interactions (seascape × shore height, site(seascape) × shore height) on mussel cover ($P < 0.0003$ for all factors and their interactions; see MANOVA table in Appendix A). Examining the effects separately on the different size classes showed that there was an effect of seascape on the cover of large mussels ($F_{1,6} = 13.27$, $P = 0.011$) and juveniles/subadults (5–15 mm; $F_{1,6} = 9.05$, $P = 0.024$) but not on early recruits (<5 mm; $F_{1,6} = 0.73$, $P = 0.42$, Fig. 1, and see ANOVA table in Appendix A). Shore height affected juveniles/subadults ($F_{1,6} = 8.41$, $P = 0.027$) and there was a strong site × shore height effect on all size classes ($P < 0.0001$). This interaction was caused mostly by the great difference in mussel cover between the two Banks Peninsula sites (which

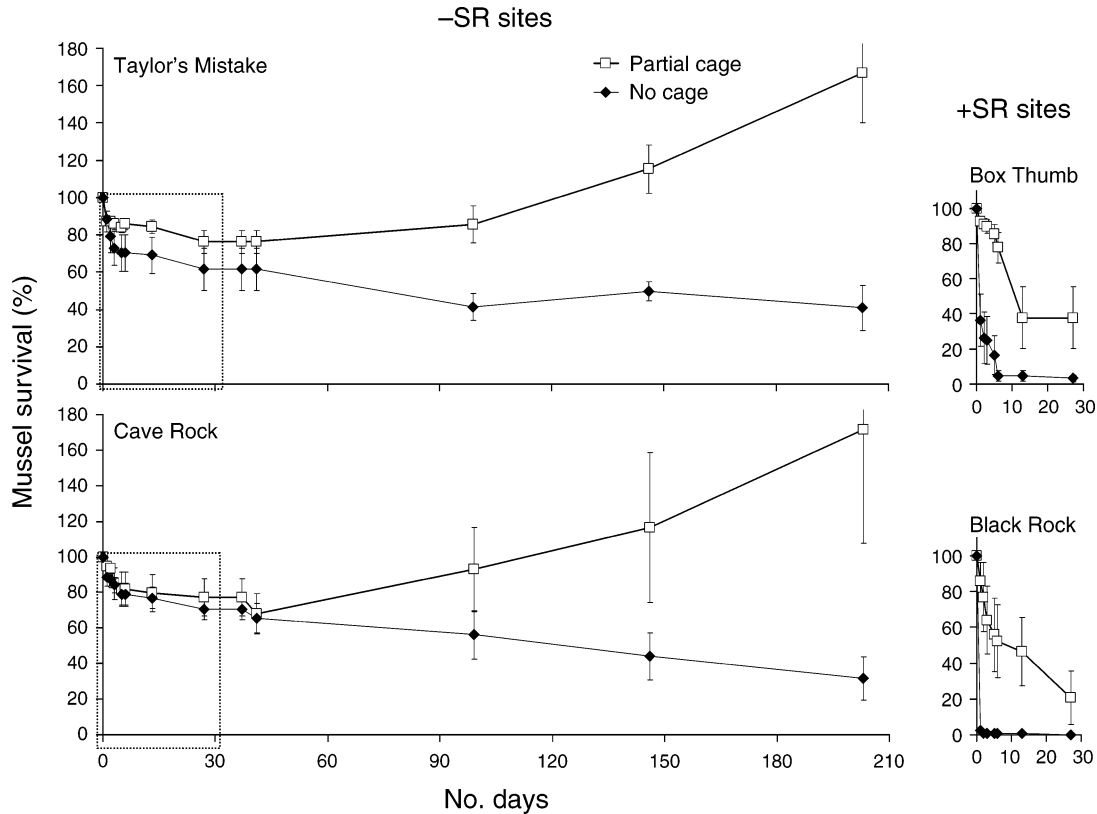


FIG. 2. Small-scale predation experiment done at sites near Christchurch on the New Zealand east coast, February–October 2003. Survival (mean \pm SE) of small mussels (5–15 mm) with (no cage) and without (partial cage) the effect of fish at sites with subtidal reefs (+SR; Box Thumb and Black Rock) and without subtidal reefs (–SR; Taylor's Mistake and Cave Rock). The dotted rectangle in the –SR sites indicates the same time frame shown for the +SR sites.

had relatively high cover of mussels) and the two sites north and south of it (very low cover, Fig. 1). On the low shore, distinct patches of juvenile and sub-adult mussels (5–15 mm) occurred outside mature beds of large mussels in most –SR sites, but rarely in +SR sites. On the mid shore, however, such patches were present to some degree in both +SR and –SR sites. Mussels in that size range were also seen within patches of large mussels as an “understory.” Early recruits (<5 mm) were found in +SR mainly within barnacle patches, whereas in –SR habitat, they were also found directly on rock surfaces.

Top-down effects

Seascape effect on predation by fish: local scale.— At the two +SR sites, mussels exposed to predators (no-cage treatment) were quickly removed (Fig. 2). At one site (BR) only a few mussels survived as long as 24 h. At this site, there also was a no-cage treatment in which mussels were attached directly to the rock. All of these mussels also disappeared within 24 h, indicating that the use of tiles does not affect predation rate. In contrast, mussel survival in the no-cage treatment at –SR sites was very high (>70%) until day 27 and reduced to around 40% after 200 d (Fig. 2). In the

fish-exclusion (partial) cages, mussel survival declined slowly over 27 d at the +SR sites, while, at the –SR sites, it remained very high and eventually increased to >100% due to the survival of new recruits on the tiles (Fig. 2). There was no detectable plot effect ($P > 0.25$) in the initial analysis and it was pooled into the error term for the final analysis. Variability among cages was high in the +SR sites. In the first few days, there was a strong treatment effect ($F_{1,2} = 309.7$, $P = 0.003$ for day 3) but, more importantly, a seascape \times treatment interaction ($F_{1,2} = 203.6$, $P = 0.005$; Appendix B ANOVA table). This interaction was because of the high survival rates in cages at both seascapes, but low survival in the no-cage treatment at +SR and high survival at –SR site. The site effect was also significant, mainly because survival was declining slightly faster at BR than at BT. By day 27, the interaction disappeared but the single factors of seascape and treatment affected survival ($F_{1,2} = 53.6$, $P = 0.018$ and $F_{1,2} = 48.1$, $P = 0.02$, respectively; Appendix B). Differences between the open and caged treatments were apparent in the +SR sites after one day, but were evident much later in the –SR sites: 99 d in TM and 146 d in CR (Fig. 2).

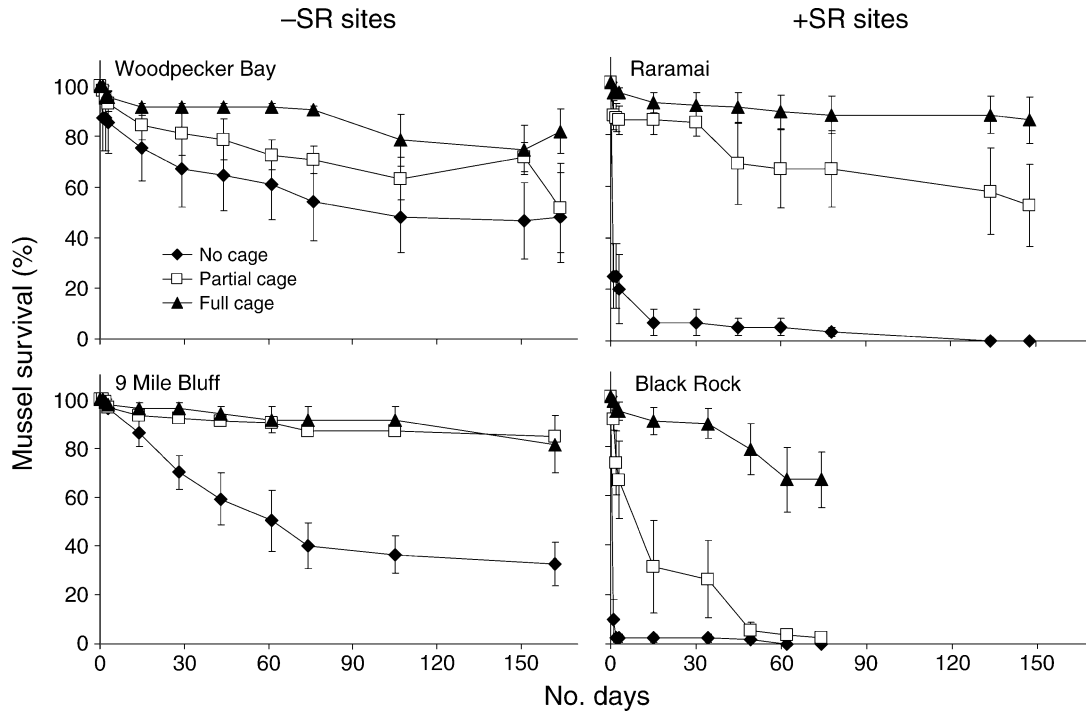


FIG. 3. Large-scale predation experiment. Survival (mean \pm SE) of small mussels (5–15 mm) exposed to all predators (no cage), with fish excluded (partial cage) and with all large predators excluded (full cage) at sites with (+SR; Black Rock and Raramai) and without subtidal reefs (-SR; Woodpecker Bay and 9 Mile Bluff) in May–October 2003.

Seascape effect on predation by fish and macro-invertebrates: large scale.—The second experiment, done at +SR and -SR sites separated by hundreds of kilometers, had similar results to those from the small-scale experiment (Fig. 3, Appendix C for ANOVA table). Over the first 3 d, seascape and treatment effects were significant ($F_{1,2} = 29.6, P = 0.032; F_{2,4} = 103.3, P = 0.0004$), and they also interacted strongly ($F_{2,4} = 81.35, P = 0.001$). There was no plot effect overall ($P = 0.11$), but its potential interaction with treatments was not testable in this model. By day 74, the treatment effect remained significant ($F_{2,4} = 7.78, P = 0.042$), and there was a significant site(within seascape) \times treatment interaction ($F_{4,48} = 2.77, P = 0.038$), due mainly to differences in survival rates within the partial cages, that were quite different between RR and BR (Fig. 3). There was still a relatively large contribution of seascape to the overall results, shown in particular by the differences in the fully exposed (no-cage) treatment between -SR and +SR sites. Predation effects at Black Rock (+SR site) were almost identical to those in the small-scale experiment over the first 30 d. There was a sharp drop in mussel numbers in the open treatment, slower mortality in partial cages, and greatest survival in the full cages (Fig. 3). At the other +SR site (RR), mussels in open areas disappeared rapidly but most of those in the partial cages (where only fish were excluded) survived well for 6 mo. At the two -SR sites (WB and 9MB), there was a gradual decline

in survival in the open treatment, but it was still around 40% after 150 d (Fig. 3). Mussels survived well in both caged treatments, although there appeared to be some predation in the partial cages, particularly at WB. This predation may be attributable to seastars that were abundant around experimental plots (within 2 m of plots there were 4.0 ± 1.9 seastars per circle of 2 m radius at WB and 2.8 ± 1.0 at 9MB). However, because survival was higher in the partial cages (which seastars can enter) compared to no-cage tiles, other predators potentially contributed to predation on the fully exposed mussels.

To illustrate the overall differences between seascapes from both the small and large scale experiments, data on mussel survival are summarized for days 13 (first experiment) and 15 (second experiment) (Fig. 4). It is evident that on both the west and east coasts, -SR sites behaved almost identically within this time frame, with no differences between coasts and between treatments. Survival at the +SR sites on the east coast was very low and similar among sites and between dates (for BR in both experiments) when exposed to all predators, and intermediate in most cases (except for RR) when fish were excluded (and large invertebrates were allowed entry; partial cage).

Long-term predation effects on early recruits.—Throughout most of the experimental period, the total number of mussel recruits found within barnacle patches was approximately three times greater when pro-

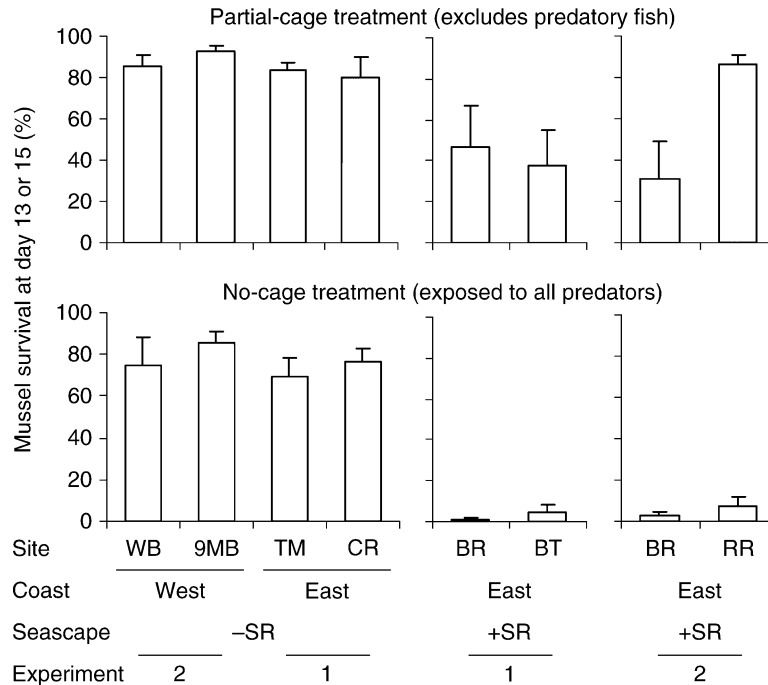


FIG. 4. Summary of small- and large-scale predation experiments. Small-mussel survival (mean + SE) at days 13 (first, small-scale, experiment) or 15 (second, large-scale, experiment) at all sites on the east and west coast. For site abbreviations, see *Methods: Study sites*.

tected from predators compared to unprotected treatments (Fig. 5). This difference was significant already on the first monitoring day (day 37: $F_{1,4} = 11.6$, $P = 0.027$). All mussels were young recruits (<5 mm) at the start of the experiment (March 2003). By 200 d after the experiment began, there was an average of approximately 40 mussels per 100 m² in the caged treatment but only 10 in the open treatment within barnacle patches. By the end of October 2003 (day 217) new recruits started to appear in all experimental plots and this trend increased over time (Fig. 5b), but the total number of mussels in the cages was still more than twice that in the open plots (Fig. 5a). By day 259, the effect of predation exclusion was even stronger ($F_{1,4} = 85.0$, $P = 0.0008$). Many of the small recruits in caged areas steadily grew in size. By early October 2003, the number of larger mussels (5–10 mm) equaled the number of the small ones (Fig. 5b, c) and by March 2004 a few mussels were already >20 mm long. Only a few mussels in the open (no-cage) treatment survived long enough to recruit into the 5–10 mm size class (94% fewer than in the caged plots by day 300 in January 2004, Fig. 5c). Mussels that did survive and grow in open areas were located mostly inside tests of large dead barnacles. The average mussel cover in the caged plots tripled between March 2003 and March 2004 (from 5.6 ± 1 to 17 ± 8.3 [mean \pm SE]) while it did not change in the open plots (5 ± 1.2 and 6 ± 3 , respectively).

Mussel settlement

Among the four sites near Christchurch, the tuffies from the two -SR sites generally had higher mussel settlement rates than those at the two +SR sites in both March and April 2003 (Fig. 6). The two -SR sites, however, were quite different from each other. Settlement at CR was an order of magnitude greater than at TM and two orders of magnitude greater than at the +SR sites. Overall, there was greater settlement in April than in March, mainly at the -SR sites, and the relative composition of species also changed. At the -SR sites, the dominant species in the collectors was *Perna canaliculus*. During March, *M. galloprovincialis* was the second most abundant species and the other two species were rare. In April, *Xenostrobus pulex* became relatively abundant in the collectors at the -SR sites and was more abundant than *M. galloprovincialis* in TM. At the +SR sites, there was little difference between months (settlement levels were low at both months) but there were difference in species' abundances. Here, *M. galloprovincialis* was the most numerous species followed by *P. canaliculus* and then *X. pulex*, which occurred mostly in April. These complex differences among seascapes, sites, and months are reflected in their strong interactions in the multivariate analysis ($P < 0.0001$ for all factors and interactions; Appendix D, MANOVA table) using the different species (excluding *Aulacomya ater maoriana* that was very rare in the collectors) as the dependent variables.

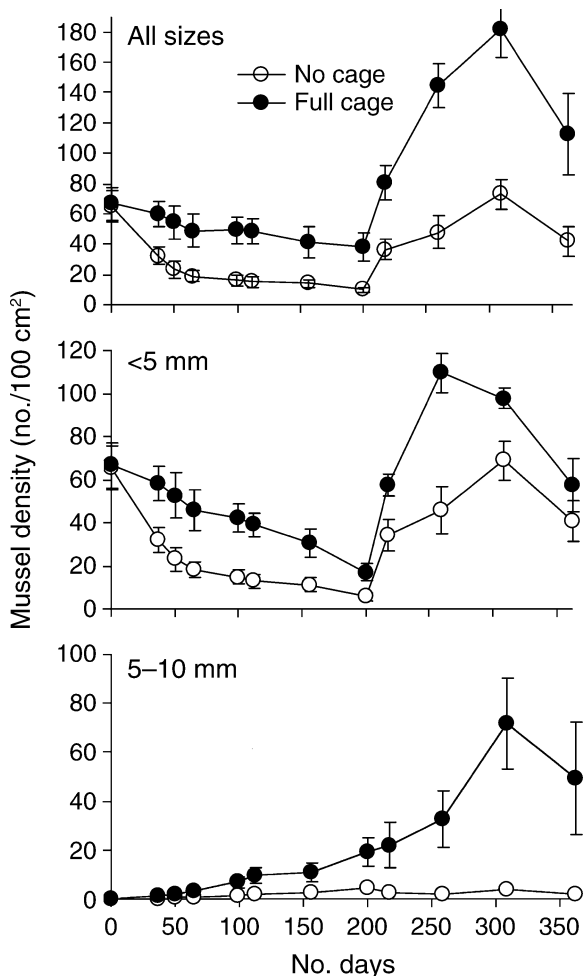


FIG. 5. Density of mussel recruits (mean \pm SE of two different size classes and of all sizes pooled) in 10 \times 10 cm plots within barnacle patches exposed to all predators (no cage) and protected from large predators (full cage) in the low shore of a +SR site (Black Rock) from March 2003 to March 2004.

The separate univariate ANOVAs, however, showed only a significant site(seascape) \times month interaction in *Mytilus* and *Perna* ($F_{2,32} = 4.23, P = 0.024$, and $F_{2,32} = 32.7, P < 0.0001$, respectively; Appendix D, ANOVA table).

DISCUSSION

In recent years, the importance of trophic connectivity among adjacent habitats in different ecological systems is starting to emerge, requiring the integration of landscape and food web ecology (Polis et al. 1997). Our study integrates these two aspects of ecology and offers several insights into the processes that account for considerable variability in mussel-dominated, intertidal communities among sites at different spatial scales. We propose a conceptual model of seascape-dependent, top-down control through predation on mussel recruits by subtidal predators; we discuss the

question of scale in which those predators operate, compared to other less mobile predators; and we describe a context-dependent, interaction-web structure for southern New Zealand that highlights the role of mobile, subtidal predators. Finally, we point to a potential decoupling between prey supply and predation intensity, where predation involves subtidal predators.

Seascape-dependent predation

The importance of predation by subtidal predators, particularly fish, on recruit mussels was unequivocal. In most cases, predation was swift, occurring within a few days, and intense, removing 60–100% of small mussels. This predation pressure operated at a localized scale, in the order of hundreds of meters, and at broader scales of sites scattered around the South Island of New Zealand, but it was seascape dependent. Furthermore, the differences in predation intensity corresponded to the differences in domination of intertidal benches by mussels. The cover of mussels, particularly those in the smaller size classes, was significantly greater on intertidal benches without adjacent subtidal reefs than on those where the reef was contiguous from the intertidal to subtidal zones.

The ability to infer a far-ranging relationship between predation and seascapes depends not only on the predation intensity seen in our experimental results but also on the experimental arrays themselves. Site selection was limited in both the local- and broad-scale experiments. In the first experiment, the +SR and -SR sites were not interspersed, due to the nonrandom way the seascapes were arrayed along the peninsula. However, the predation effects were strong and consistent in this and in another related study (G. Rilov, unpublished data). Furthermore, the sites were distant enough from each other that the effects of mobile predators should have been independent. The main predators were undoubtedly fish, particularly the reef-associated labrids *Notolabrus celidotus* and *N. fucicola*, which are the most abundant nearshore predatory fishes around the South Island (Schiel and Hickford 2001). Both fish are generalist predators that eat a wide range of bivalves, gastropods, and small crustaceans (Denny and Schiel 2001). Around sites on the east coast of the South Island, the most abundant prey items of *N. fucicola* are small mussels, and 42% of fish sampled in one study had these in their gut (Jones 1984b, Denny and Schiel 2001). Both fish species show high fidelity to reef sites dominated by large brown seaweeds, feed mostly within circumscribed home ranges (Jones 1984a) and were seen foraging in the intertidal zone at the +SR sites of Banks Peninsula (G. Rilov, unpublished data). We therefore consider it to be highly likely that they were the primary agents of predation and also that their effects were localized and did not spill over between our study sites. We also surmise that large crabs (red rock crab, *Plagusia chabrus* and cancer crabs, *Cancer novaehelandiae*) foraging from the sub-

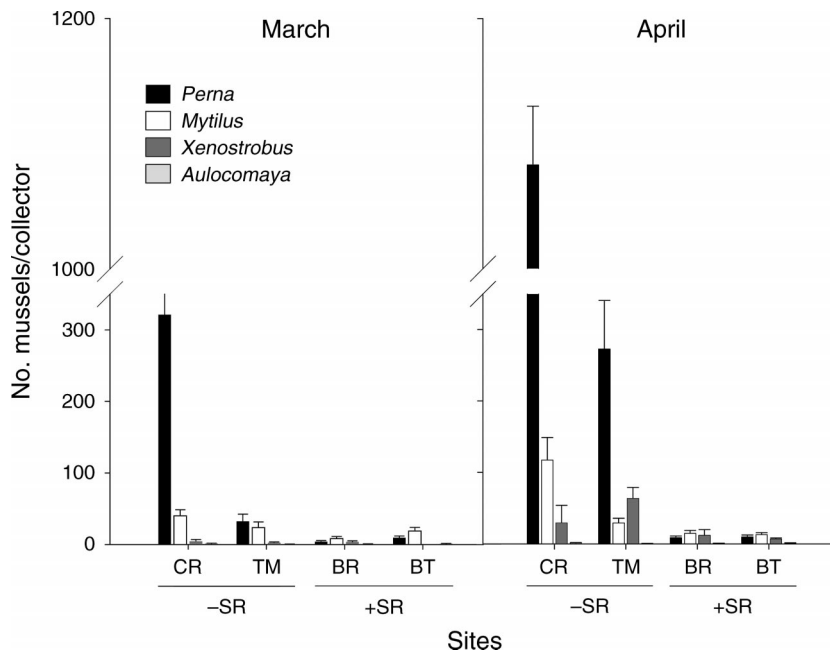


FIG. 6. Recruitment (mean \pm SE, number per collector) of four species of mussels into mussel collectors in the low shore at four sites near Christchurch in March and April 2003. For site abbreviations, see *Methods: Study sites*.

tidal zone had an influence on mussel survival, as evidenced by the smaller effects seen in the partial cages that excluded fish. These crabs were abundant at the +SR sites of Bank Peninsula at night (G. Rilov, *unpublished data*).

The influence of habitat structure on predation intensity is well documented for some intertidal communities, but most studies have focused on within-habitat effects of microhabitats on predator abundance and foraging. For example, In North America, Menge (1978) described bare zones around crevices occupied by whelks *Thais (Nucella) lapillus*. Fairweather (1988b) found that the whelks *Morula marginalba* and *Thais orbita* in Australia quickly moved away from areas without shelter even when prey were abundant. Predation by these whelks was greatly reduced in areas where shelter was scarce (Fairweather 1988c, a). Similarly, in the eastern Mediterranean, food availability is a poor predictor for density of the large whelk *Stramonita haemastoma* while refuge (holes and crevices) appeared to be the limiting factor (Rilov et al. 2001, 2002). Within a short distance (<100 m) this whelk is abundant on benches with ample suitable refuge and is rare on benches where suitable refuge is scarce but its favorite prey (mussels) is abundant. The interactions between structure, distribution and predation effects in these studies were highly localized, mainly because whelks are relatively small, slow, and usually forage only on the scale of tens of centimeters to a few meters. The effects of mobile predators foraging from subtidal reefs are documented in only a few studies. For example, Menge et al. (1986a) showed predation effects

by fish and crabs on sessile invertebrates in the low intertidal zone in Panama. Robles (1997) showed that lobsters in southern California maintained a distinctive algal turf by feeding extensively on juvenile intertidal mussels that otherwise grow and replace the algae on wave-exposed shores. Fish and crabs, like lobsters, are relatively large and can move rapidly between habitats across a seascape and, therefore, have the potential to be more effective predators on a larger spatial scale than intertidal-dwelling invertebrate predators. Their presence and influence in the intertidal zone seem to be restricted primarily by the presence or absence of subtidal reefs.

Because of the reported differences in predation intensity between the east and west coasts of New Zealand (Menge et al. 1999, 2002, 2003), we had intended to test the effects of seascapes across these two coastlines using a fully balanced design. However, we could find no accessible sites on the northern west coast that had contiguous subtidal reefs similar to those on the east coast. Much of the South Island west coast has a shallow bathymetry near the shoreline that extends into sand and gravel. Subtidal reefs nearshore are rare and the patches that exist are unlikely to support large populations of reef-associated species. In this, the sites without subtidal reefs on the west coast are similar to those on the east coast. However, there are also considerable differences between coastlines in upwelling (Stanton 1976) and frequency of intense wave action. Despite these differences, the survival rate of small mussels at the -SR sites on the west coast was very similar to those on the east coast, lending a degree of

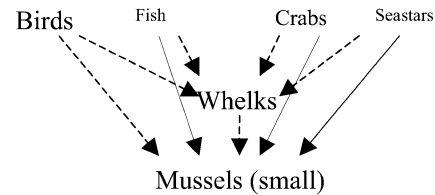
confidence that predation effects on small mussels were more site dependent and seascape dependent than coast dependent.

A modified structure of the New Zealand intertidal trophic interaction web

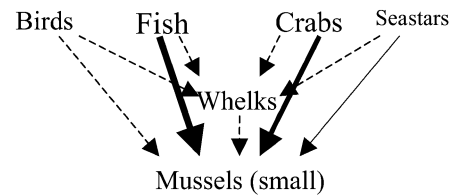
The results presented by Menge et al. (1999, 2002, 2003) led to a coast-dependent, oceanographic-linked, food web structure with only one important predator in the system—a seastar. There are clearly differences in the potential predators between the east and west coasts, and they also appear to operate on different size classes of mussels. The large seastar *Stichaster australis* is far more common on the west coast than on the east coast, but its abundance is highly site specific (Morton and Miller 1968, Menge et al. 1999, 2003). Menge et al. (1999, 2003) showed that this seastar was responsible for most of the predation on large mussels, leading to the conclusion that predation was more intense along the west coast. Although there may have been a minor effect of seastars at west coast sites in our experiments, as evidenced by the lower survival in partial cages at one site compared to full cages (Fig. 3), there were major contrasts in our assessment of predation intensity on this coast compared to that of Menge et al. (1999, 2003). The major reason for this is that we experimented with smaller mussels, which are far more susceptible to predation by fish (e.g., Denny and Schiel 2001) than the larger mussels used by Menge et al. (1999, 2003), and the fact that predation by seastars can be highly localized. There may also have been a seasonal effect in seastar feeding rates. Our experiment was begun in the early austral winter (May) and lasted until spring (October), and *Stichaster* may reduce their activity during winter as *Pisaster* do on the U.S. west coast (Menge et al. 1994). On a population scale, the high rates of mussel settlement on the west coast compared to the east coast (Menge et al. 1999, 2003) could ameliorate the effects on seastars on mussel recruits (“swamping” effect, see Dayton 1971).

Unlike the more simplified, subsidies-dependent, trophic-interaction web of high predation on the west coast and low on the east coast (Menge et al. 2003; noted by Palumbi 2003), a revised trophic-interaction web, which incorporates differential effects by different guilds of predators, is more appropriate (Fig. 7). Sites without subtidal reefs, which encompass most of those on the central to northern west coast, have weak predation by fish, while the opposite applies to sites with subtidal reefs. On a coast-wide basis, predation by seastars is strong and by fish and crabs is weak on the west coast, and predation by seastars is weak and by fish and crabs is strong on the east coast (in +SR sites), but only on small mussels (size selective predation, see also Ojeda and Dearborn 1991). On the east coast, once mussels reach a refuge size (approximately 15 mm shell length), or if protected within crevices or

a) East coast, –SR sites



b) East coast, +SR sites



c) West coast, –SR sites

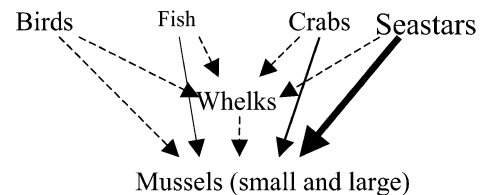


FIG. 7. A seascape-dependent trophic interaction-web structure for southern New Zealand east and west coasts. (a) –SR bench on the east coast, (b) +SR bench on the east coast, (c) –SR bench on the west coast. Size of taxa names indicates relative abundance and thickness of arrows indicates relative strength of the interaction. Dashed lines are assumed interactions that have not been measured.

mussel beds, they are generally free from most predators. This refuge in size and micro-habitat probably allows mussels to establish the beds seen at some sites with subtidal reefs on the east coast. Whelks, which are known to be important predators in other parts of the world (Connell 1961, Menge 1976, Castilla and Duran 1985, Hunt and Scheibling 1998, Johnson et al. 1998), are abundant on both coasts (up to hundreds per m²), although most are small, concealed in crevices and mussel beds, and tend to be slow in feeding (B. Menge, *personal communication*; D. Schiel, *unpublished data*).

Settlement and predation: a potential decoupling

The differential supply of recruits undoubtedly plays a major role in determining community structure in New Zealand (supply-side ecology, sensu Lewin 1986), and is probably greater on parts of the west coast (Menge et al. 2003), although we demonstrated that very high supply occurs locally on the east coast as well. The high supply rates on sites with no subtidal reefs near Christchurch may be a result of a localized retention mechanism near an estuary just north of Banks

Peninsula. This area could also be a sink for larvae coming from more southern populations via the Southland Current, as trajectories of drift cards and circulation in that area seem to suggest (Carter and Herzer 1979, Reynolds-Fleming and Fleming 2005). Alternatively, or in conjunction with this, there may be seascape-dependent settlement. Banks Peninsula is known to be an area with large numbers of sessile invertebrates in the shallow subtidal zone (Schiel and Hickford 2001) as well as throughout the intertidal zone. Where shallow subtidal reefs are present, mussel larvae may settle throughout an extensive reef system. Where subtidal reefs are absent, settling larvae could potentially be concentrated on intertidal benches, the only hard substrata available. Regardless of the mechanism, if the higher rate of settlement seen on seascapes without subtidal reefs in our study is a more general phenomenon, it would interact synergistically with lower predation pressure to produce the greater cover of mussels seen at most of these sites.

This apparent inverse relationship between predation intensity and settlement rate is an intriguing result of our study. Although settlement into collectors was measured in only two months, the sites without subtidal reefs (particularly one of them) had far more recruits than those with subtidal reefs. This contrasts with recent bottom-up/top-down models (Connolly and Roughgarden 1999) and the conclusions of studies both around these New Zealand sites (Menge et al. 1999, 2002, 2003) and on the west coast of North America (e.g., Menge et al. 1994) where a positive feedback between the rate of settlement and predation intensity has been suggested. This discrepancy is probably related to the fact that, unlike intertidal seastars and whelks, predators such as fish and crabs are not entirely reliant on intertidal subsidies because they also feed subtidally.

In conclusion, our study shows the necessity of considering the entire suite of predators and the different sizes/life stages of prey before valid conclusions can be drawn on trophic interactions and their effects on community structure. Intertidal benches frequently do not occur in isolation from subtidal reefs and, therefore, present a contiguous seascape to mobile, foraging species. Settlement and nutrient supply, the "subsidies" from offshore (Palumbi 2003), are likely to interact with these localized seascapes in complex ways.

ACKNOWLEDGMENTS

We thank B. Menge, two anonymous reviewers, and the subject editor for extensive and useful comments on this paper. Many thanks to our Marine Ecology Research Group colleagues: D. Taylor, M. Hickford, M. Novak, S. Lillie, S. Goldstein, P. South, and R. Taylor for invaluable help in the field work and comments on the manuscript, and to N. Ethridge for help in the workshop. This research was financially supported by the Andrew Mellon Foundation, including a post-doctoral fellowship to G. Rilov, and the New Zealand Foundation for Research, Science, and Technology.

LITERATURE CITED

- Barros, F., A. J. Underwood, and M. Lindegarth. 2001. The influence of rocky reefs on structure of benthic macrofauna in nearby soft-sediments. *Estuarine Coastal and Shelf Science* **52**:191–199.
- Burrows, M. T., K. Kawai, and R. N. Hughes. 1999. Foraging by mobile predators on a rocky shore: underwater TV observations of movements of blennies *Lipophrys pholis* and crabs *Carcinus maenas*. *Marine Ecology-Progress Series* **187**:237–250.
- Bustamante, R. H., and G. M. Branch. 1996. Large scale patterns and trophic structure of southern African rocky shores: the role of geographic variation and wave exposure. *Journal of Biogeography* **23**:339–351.
- Caffey, H. M. 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs* **55**:313–332.
- Carter, L., and R. H. Herzer. 1979. The hydraulic regime and its potential to transport sediment on the Canterbury continental shelf. *New Zealand Oceanographic Institute Memoir* **83**:1–32.
- Castilla, J. C., and L. R. Duran. 1985. Human exclusion from the rocky intertidal zone of central Chile—the effects on *Concholepas concholepas* (Gastropoda). *Oikos* **45**:391–399.
- Choat, J. H., and A. M. Ayling. 1987. The relationship between habitat structure and fish faunas on New Zealand reefs. *Journal of Experimental Marine Biology and Ecology* **110**:257–284.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stelattus*. *Ecology* **42**:710–723.
- Connell, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pages 460–499 in M. L. Cody and J. M. Diamond, editors. *Ecology and evolution of communities*. Belknap Press and Harvard University Press, Cambridge, Massachusetts, USA and London, UK.
- Connolly, S. R., and J. Roughgarden. 1998. A latitudinal gradient in northeast pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. *American Naturalist* **151**:311–325.
- Connolly, S. R., and J. Roughgarden. 1999. Theory of marine communities: competition, predation, and recruitment dependent interaction strength. *Ecological Monographs* **69**:277–296.
- Davis, N., G. R. Vanblaricom, and P. K. Dayton. 1982. Man-made structures on marine sediments: effects on adjacent benthic communities. *Marine Biology* **70**:295–303.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs* **41**:351–389.
- Denny, C. M., and D. R. Schiel. 2001. Feeding ecology of the banded wrasse *Notolabrus fucicola* (Labridae) in southern New Zealand: prey items, seasonal differences, and ontogenetic variation. *New Zealand Journal of Marine and Freshwater Research* **35**:925–933.
- Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* **78**:2064–2075.
- Fairweather, P. G. 1988a. Correlations of predatory whelks with intertidal prey at several scales of space and time. *Marine Ecology-Progress Series* **45**:237–243.
- Fairweather, P. G. 1988b. Movements of intertidal whelks (*Morula marginalba* and *Thais orbita*) in relation to availability of prey and shelter. *Marine Biology* **100**:63–68.
- Fairweather, P. G. 1988c. Predation creates haloes of bare space among prey on rocky seashores in New South Wales. *Australian Journal of Ecology* **13**:401–409.

- Foster, M. S. 1990. Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia* **192**:21–33.
- Gaines, S., S. Brown, and J. Roughgarden. 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* **67**:267–272.
- Hayden, B. J. 1995. Factors affecting recruitment of farmed greenshell mussels, *Perna canaliculus* (Gmelin) 1791, in Marlborough Sounds. Dissertation. University of Otago, Dunedin, New Zealand.
- Hickford, M. J. H., and D. R. Schiel. 1995. Catch vs. count: effects of gill-netting on reef fish populations in southern New Zealand. *Journal of Experimental Marine Biology and Ecology* **188**:215–232.
- Hunt, H. L., and R. E. Scheibling. 1998. Effects of whelk (*Nucella lapillus* (L.)) predation on mussel (*Mytilus trosulus* (Gould), *M. edulis* (L.)) assemblages in tidepools and on emergent rock on a wave-exposed rocky shore in Nova Scotia, Canada. *Journal of Experimental Marine Biology and Ecology* **226**:87–113.
- Johnson, M. P., R. N. Hughes, M. T. Burrows, and S. J. Hawkins. 1998. Beyond the predation halo: small scale gradients in barnacle populations affected by the relative refuge value of crevices. *Journal of Experimental Marine Biology and Ecology* **231**:163–170.
- Jones, G. P. 1984a. Population ecology of the temperate reef fish *Pseudolabrus celidotus* Bloch and Schneider (Pisces, Labridae). 1. Factors influencing recruitment. *Journal of Experimental Marine Biology and Ecology* **75**:257–276.
- Jones, G. P. 1984b. Population ecology of the temperate reef fish *Pseudolabrus celidotus* Bloch and Schneider (Pisces, Labridae). 2. Factors influencing adult density. *Journal of Experimental Marine Biology and Ecology* **75**:277–303.
- Jones, G. P. 1988. Ecology of rocky reef fish of northeastern New Zealand: a review. *New Zealand Journal of Marine and Freshwater Research* **22**:445–462.
- Jones, G. P., and N. L. Andrew. 1993. Temperate reefs and the scope of seascape ecology. Pages 63–76 in C. N. Battershill, D. R. Schiel, G. P. Jones, R. G. Creese, and A. B. MacDiarmid, editors. Second International Temperate Reef Symposium. NIWA Marine, Auckland, New Zealand.
- Kitching, J. A., and F. J. Ebling. 1967. Ecological studies at Lough Ine. *Advances in Ecological Research* **4**:198–291.
- Kollman, J., and M. Buschor. 2003. Edges effects on seed predation by rodents in deciduous forests of northern Switzerland. *Plant Ecology* **164**:249–261.
- Levings, S. C., S. D. Garrity, and L. R. Ashkenas. 1986. Feeding rates and prey selection of oystercatchers in the Pearl Islands of Panama. *Biotropica* **18**:62–71.
- Lewin, R. 1986. Supply-side ecology. *Science* **234**:25–27.
- Lindquist, D. G., L. B. Cahoon, I. E. Clavijo, M. H. Posey, S. K. Bolden, L. A. Pike, S. W. Burk, and P. A. Cardullo. 1994. Reef fish stomach contents and prey abundance on reef and sand substrata associated with adjacent artificial and natural reefs in Onslow Bay, North Carolina. *Bulletin of Marine Science* **55**:308–318.
- Lively, C. M., and P. T. Raimondi. 1987. Desiccation, predation, and mussel–barnacle interactions in the northern gulf of California. *Oecologia* **74**:304–309.
- Marsh, C. P. 1986. Rocky intertidal community organization: the impact of avian predators on mussel recruitment. *Ecology* **67**:771–786.
- McQuaid, C. D., and G. M. Branch. 1985. Trophic structure of rocky intertidal communities: response to wave action and implications for energy flow. *Marine Ecology Progress Series* **22**:153–161.
- Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecological Monographs* **46**:355–393.
- Menge, B. A. 1978. Predation intensity on a rocky intertidal community. Relation between predator foraging activity and environmental harshness. *Oecologia* **34**:1–16.
- Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamada. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* **64**:249–286.
- Menge, B. A., B. A. Daley, J. Lubchenco, E. Sanford, E. Dahlhoff, P. M. Halpin, G. Hudson, and J. L. Burnaford. 1999. Top-down and bottom-up regulation of New Zealand rocky intertidal communities. *Ecological Monographs* **69**:297–330.
- Menge, B. A., J. Lubchenco, L. R. Ashkenas, and F. Ramsey. 1986a. Experimental separation of effects of consumers on sessile prey in the low zone of a rocky shore in the Bay of Panama: direct and indirect consequences of food web complexity. *Journal of Experimental Marine Biology and Ecology* **100**:225–269.
- Menge, B. A., J. Lubchenco, M. E. S. Bracken, F. Chan, M. M. Foley, T. L. Freidenburg, S. D. Gaines, G. Hudson, C. Krenz, H. Leslie, D. N. L. Menge, R. Russell, and M. S. Webster. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. *Proceedings of the National Academy of Sciences (USA)* **100**:12229–12234.
- Menge, B. A., J. Lubchenco, S. D. Gaines, and L. R. Ashkenas. 1986b. A test of the Menge–Sutherland model of community organization in a tropical rocky intertidal food web. *Oecologia* **71**:75–89.
- Menge, B. A., and A. M. Olson. 1990. Role of scale and environmental factors in regulation of community structure. *Trends in Ecology and Evolution* **5**:52–57.
- Menge, B. A., E. Sanford, B. A. Daley, T. L. Freidenburg, G. Hudson, and J. Lubchenco. 2002. Inter-hemispheric comparison of bottom-up effects on community structure: insights revealed using the comparative-experimental approach. *Ecological Research* **17**:1–16.
- Menge, B. A., and J. P. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *American Naturalist* **130**:730–757.
- Morton, J., and M. Miller. 1968. The New Zealand sea shore. Collins, London, UK and Auckland, New Zealand.
- Navarrete, S. A., and J. C. Casilla. 1993. Predation by Norway rats in the intertidal zone of central Chile. *Marine Ecology Progress Series* **92**:187–199.
- Navarrete, S. A., and B. A. Menge. 1996. Keystone predation and interaction strength: interactive effects of predators on their main prey. *Ecological Monographs* **66**:409–429.
- Ojeda, F. P., and J. H. Dearborn. 1991. Feeding ecology of benthic mobile predators—experimental analyses of their influence in rocky subtidal communities of the gulf of Maine. *Journal of Experimental Marine Biology and Ecology* **149**:13–44.
- Palumbi, S. R. 2003. Ecological subsidies alter the structure of marine communities. *Proceedings of the National Academy of Sciences (USA)* **100**:11927–11928.
- Petraitis, P. S., and S. R. Dudgeon. 2004. Detection of alternative stable states in marine communities. *Journal of Experimental Marine Biology and Ecology* **300**:343–371.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* **28**:289–316.
- Reynolds-Fleming, J. V., and J. G. Fleming. 2005. Coastal circulation within the Banks Peninsula region, New Zealand. *New Zealand Journal of Marine and Freshwater Research* **39**:217–225.

- Rilov, G., Y. Benayahu, and A. Gasith. 2001. Low abundance and skewed population structure of the whelk *Stramonita haemastoma* along the Israeli Mediterranean coast. *Marine Ecology Progress Series* **218**:189–202.
- Rilov, G., Y. Benayahu, and A. Gasith. 2002. Effect of an exotic prey on the feeding pattern of a predatory snail. *Marine Environmental Research* **54**:85–98.
- Robles, C. 1987. Predator foraging characteristics and prey population structure on a sheltered shore. *Ecology* **68**:1502–1514.
- Robles, C. D. 1997. Changing recruitment in constant species assemblages: implications for predation theory in intertidal communities. *Ecology* **78**:1400–1414.
- Robles, C., and R. Desharnais. 2002. History and current development of a paradigm of predation in rocky intertidal communities. *Ecology* **83**:1521–1536.
- Schiel, D. R. 2004. The structure and replenishment of rocky shore intertidal communities and biogeographic comparisons. *Journal of Experimental Marine Biology and Ecology* **300**:309–342.
- Schiel, D. R., and M. J. H. Hickford. 2001. Biological structure of nearshore rocky subtidal habitats in southern New Zealand. *Science for Conservation* **182**:5–54.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry*. W. H. Freeman and Co., New York, New York, USA.
- Stanton, B. R. 1976. Circulation and hydrology off the west coast of the South Island. *New Zealand Journal of Marine and Freshwater Research* **10**:445–467.
- Stapp, P., and G. A. Polis. 2003. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. *Oecologia* **134**:496–504.
- Underwood, A. J. 1997. *Experiments in ecology; their logical design and interpretation using analysis of variance*. Cambridge University Press, Cambridge, UK.
- Underwood, A. J., M. G. Chapman, and S. D. Connell. 2000. Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology* **250**:97–115.
- Underwood, A. J., and E. J. Denley. 1984. Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. Pages 151–180 in D. R. Strong, D. Simberloff, L. G. Abele, and A. B. Thistle, editors. *Ecological communities, conceptual issues and the evidence*. Princeton University Press, Princeton, New Jersey, USA.
- Underwood, A. J., and P. S. Petraitis. 1993. Structure of intertidal assemblages in different locations: how can local processes be compared? Pages 38–51 in R. E. Ricklefs and D. Schluter, editors. *Historical and geographical determinants of community diversity*. University of Chicago Press, Chicago, Illinois, USA.
- Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* **277**:102–104.
- Wootton, J. T. 1991. Direct and indirect effects of nutrients on intertidal community structure—variable consequences of seabird guano. *Journal of Experimental Marine Biology and Ecology* **151**:139–153.

APPENDIX A

Nested MANOVA on the effect of seascape, site, and shore height on percentage of cover of three size classes of mussels on the rock surface, and the separated ANOVA on the cover of the patches of the different size classes (*Ecological Archives* E087-043-A1).

APPENDIX B

ANOVA testing the effect of seascape, site, and treatment on survival of 5–15 mm mussels at four sites in the small-scale experiment (*Ecological Archives* E087-043-A2).

APPENDIX C

ANOVA testing the effect of seascape, site, plot, and treatment on survival of 5–15 mm experimental mussels at four sites in the large-scale experiment (*Ecological Archives* E087-043-A3).

APPENDIX D

Nested MANOVA on the effect of seascape, site, and month on mussel recruitment to collectors, and a similar ANOVA on the separated species (*Perna canaliculus*, *Mytilus galloprovincialis*, and *Xenostrobus pulex*) (*Ecological Archives* E087-043-A4).