COMMUNITY ECOLOGY

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Community effects following the deletion of a habitat-forming alga from rocky marine shores

Abstract Habitat-forming species increase spatial complexity and alter local environmental conditions, often facilitating a diversified assemblage of plants and animals. Removal of dominant species, therefore, can potentially lead to pronounced changes in diversity and community structure through a series of negative and positive interactions involving several components of the community. Here we test community responses to the deletion of the dominant, canopy-forming alga *Hormosira banksii* from the mid-intertidal zone of wave-protected rocky shores in southern New Zealand. This species was removed in winter (July) from three 3×3-m areas at each of two platforms (Kaikoura and Moeraki) on the east coast of the South Island. Initially, 59 taxa occurred in stands, but there were only four algal species with greater than 5% cover and three mobile invertebrate species with more than five individuals per 0.25 m². By 6 months after *Hormosira* removal, most fucoid and coralline algae had burned off, and there were blooms of ephemeral algae in the removal plots, but almost no change within controls. After 2 years, diversity declined by 44% relative to controls at Kaikoura and 36% at Moeraki, and the amount of bare space had increased by tenfold at Kaikoura and twofold at Moeraki. Few sessile or mobile invertebrates were present. Recruitment of *Hormosira* occurred after 14 months in the removal plots. At this time, a "press" disturbance was initiated into one half of each removal plot to test the effects of continued removal of *Hormosira* on diversity. Similar "end-points" of the control and "press" removal plots were not reached after 2 years, and even after *Hormosira* recruitment into the original "pulse" experiment there was little recovery of the community. In this mid-intertidal system with considerable thermal stress, and perhaps in others with few perennial species, diversity and community structure can critically depend on positive associations with a single dominant species.

Keywords Fucoid algae · *Hormosira banksii* · Intertidal · New Zealand · Positive interactions · Species deletion

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Introduction

Marine intertidal habitats are often characterised by species in dense aggregations. Algal canopies (Bertness et al. 1999), corals (Stimson 1985), seagrass (Connolly 1995), mussels (Seed 1996) and ascidians (Monteiro et al. 2002) can all modify habitats, increase spatial complexity and facilitate the presence of other species. Although the relationships between habitat and diversity have been studied for decades (e.g. Kohn and Leviten 1976), the role of key species in maintaining diverse local communities is not as well understood. For example, controversy exists over the relative importance of non-trophic, positive biotic interactions involving key species compared to negative interactions in structuring marine communities (Menge 2000; Shouse 2003), although a considerable amount of recent evidence has highlighted their importance (see reviews by Bruno and Bertness 2001; Stachowicz 2001; Bruno et al. 2003). Non-trophic positive interactions are defined as any direct or indirect biotic interaction between two or more species in which one or both organisms benefit through growth, reproductive output and/or survival, while neither is harmed (Bertness and Callaway 1994).

These processes work in two directions. As a community develops, some species can provide a critical habitat

that facilitates other species. For example, habitat-ameliorating positive interactions drive the coexistence of the salt marsh plants *Iva fructescens* and *Juncus gerardi* and their associated insect fauna (Bertness and Hacker 1994). *J. gerardi* canopies enhance the establishment of *I. fructescens* seedlings in potentially stressful conditions (Bertness and Hacker 1994), which increases insect diversity by up to 35% (Hacker and Gaines 1997). Conversely, the removal of a single species can lead to a cascading loss of other species in the community through a series of secondary extinctions (Dayton 1975; Pimm 1980). The processes following the deletion of key species and community recovery after key species recruit may be positive or negative, and they are not necessarily symmetrical. Some species may be far more responsive than others to changes to temperature (Tsuchiya 1983; Bertness et al. 1999), solar radiation (Figueiredo et al. 2000), wave action (Dayton 1971; Blanchette 1997), sedimentation (Airoldi and Cinelli 1997), consumer pressure (Paine 1971, 1974) and trophic relationships (Underwood 1999) that may follow removal of a key species. Recovery relies on the trajectories of recruitment, growth and developing relationships that may be quite different between disturbed and undisturbed communities, resulting in substantially different communities that persist over many years (Petraitis and Latham 1999; Foster et al. 2003; Jenkins et al. 2004; Schiel et al. 2004).

Large perennial algae form the bulk of biogenic habitat on many temperate rocky shores and are frequently affected by a wide range of natural (Dayton 1971; Blanchette 1997) and anthropogenic disturbances (Brown et al. 1990; Keough and Quinn 1998; Brown and Taylor 1999; Schiel and Taylor 1999). In the subtidal environment, numerous studies have shown that dense kelp canopies have suppressive effects on most understory algae, mainly through a severe reduction in light, and that canopy removals usually result in increased recruitment and growth of other species (e.g. Reed and Foster 1984; Clark et al. 2004). In the intertidal zone, however, the relationships between algal canopies and other species in the assemblage can be far more complicated, especially in the physically stressed mid- to high-shore zones. Although algal canopies can reduce light to the understory, the layering of algae at low tide can also have a positive influence on the local environment through the retention of moisture, reduction in temperature stress and protection from solar radiation (Bertness et al. 1999; Figueiredo et al. 2000). Studies involving the removal of intertidal canopy-forming algae have illustrated both that strong negative effects, for example through the loss of obligate understory species (e.g. Dayton 1975), and direct positive interactions, through recruitment and interspecific effects, can play integral roles in community structure (Bertness et al. 1999; Jenkins et al. 1999). The relative proportions and importance of these types of interactions are unknown for most communities (Menge 2000), and especially so when the total local diversity is considered (Hacker and Gaines 1997).

There is renewed interest in understanding where, when and under what circumstances positive interactions play a prominent role in community structure (see Stachowicz 2001; Bruno et al. 2003) and on what components of the community they act. The physically stressed conditions of the mid-intertidal zone of rocky shores provide a good environment in which to test models predicting that positive interactions are important where abiotic stress is high (e.g. Bertness and Callaway 1994; Bruno and Bertness 2001). Here we focus on these issues of positive and negative effects by testing community responses to the removal of a key habitat-forming alga on the shores of southern New Zealand.

The mid-shore region of wave-protected intertidal rocky reefs in New Zealand is dominated by a dense cover of the fucoid alga *Hormosira banksii*. Plants can reach 25 cm in length, have densities of several hundred per square metre, reach a standing crop of up to 8 kg/m^2 and are thickly layered on intertidal benches at low tide (Schiel and Taylor 1999). The aim of this study was to examine how the presence of this species affects the diversity and composition of the mid-shore community. We set out to test whether the removal of *Hormosira* has a negative effect on local diversity, whether its recovery has a positive effect on diversity, that sustained removal as a disturbance ("press" removal) has a different effect on diversity than a single, one-off disturbance ("pulse" removal) and whether community structure across disturbances converges through time.

Methods

The basic experimental unit was a 3×3-m plot. This size was chosen to ensure that the removal area was larger than the immediate propagule drop zone, as the great majority of *Hormosira* propagules settle beneath or near adult plants (D.R. Schiel, unpublished data) and so potential edge effects of neighbouring canopies would be reduced (cf. Southward 1965). In July 2002 (winter), six plots were marked at each of the two largest intertidal platforms covered by *Hormosira* on the South Island of New Zealand, located at Kaikoura (42°25′S, 173°41′E) and 350 km to the south at Moeraki (45°21′S, 170°51′E). The plots were located in the lower mid-littoral zone between 0.8 and 0.9 m above the lowest astronomical tide (LAT) at Kaikoura and between 0.9 and 1.1 m above LAT at Moeraki. Both reefs are moderately exposed to wave action and extend approximately 150 m from the upper intertidal to the subtidal zone. The substratum at Kaikoura is mudstone and at Moeraki it is basaltic rock. All plots had an initial *Hormosira* cover of approximately 95% and were at least 3 m from each other. The corners of each plot were marked with stainless steel bolts. Plots were randomly assigned to one of two treatments, either unmanipulated controls or *Hormosira* removal. In removal plots, a knife was used to remove all *Hormosira* tissue whilst avoiding damage to the understory and

substratum. All plants overhanging the removal plots from outside were trimmed back. Plots were monitored over a 2-year period, at 0.5, 1, 2, 4, 6, 10, 16, 20 and 24 months after removal, to include both immediate and longer term changes in the assemblages and the trajectories of recovery. They were carefully searched for all species, which were identified in the field to the greatest taxonomic resolution possible. Samples from some smaller species (approx. 2 mm) were taken back to the laboratory to be identified using a microscope. To estimate abundances of all species (greater than 2 mm) within the larger plots, five 0.25-m^2 quadrats were randomly placed throughout each plot not less than 30 cm from the plot edge. Percentage cover was estimated for algae and sessile invertebrates. Counts of individuals were recorded for mobile invertebrates. Disturbance from sampling was minimised by kneeling on sponge mats when it was necessary to be inside plot boundaries.

Recruitment of *Hormosira* did not occur until 14 months after the experiment began (see Results). At this time the 3×3-m treatment plots were subdivided into halves to test the effect of a "press" removal versus the original "pulse" removal. In each randomly chosen 1.5×3-m sub-plot, *Hormosira* recruits (visible to the naked eye, approximately 1–5 mm in length) were removed immediately after each recruitment period (to simulate a "press" disturbance). In the other half, *Hormosira* was allowed to recruit naturally ("pulse" disturbance), and plants were left to grow undisturbed. Five 0.25-m^2 quadrats within each half were used to determine species abundances, as above, during the 16-, 20- and 24-month monitoring times. After 24 months, the density and percentage cover of *Hormosira* were measured in the "pulse" removal halves and the controls.

To quantify the epifauna (e.g. gammarid amphipods, harpacticoid copepods, micro-gastropods) associated with *Hormosira*, five adult plants were bagged and removed during low and high tide from just outside each control plot. Epifauna larger than 100 μm were removed from plants by shaking them in 70% ethanol. Samples were then sorted under a microscope. Epifauna taxa were grouped into broad taxonomic groups at the start and end of the experiment.

To test for differences in temperature in the control and *Hormosira* plots, an i-button thermacron temperature logger was placed on the substratum in one control and one removal plot at each site between February and October 2003.

Statistical analyses

A combination of multivariate and univariate analyses was used to test the effects of *Hormosira* removal. Nonmetric multidimensional scaling (nMDS) was used to visually examine the effect of *Hormosira* removal on the composition of the entire benthic community relative to the control situation. All analyses used Bray-Curtis distances on fourth-root transformed data (Clarke 1993). Distances between samples on the ordination represent relative dissimilarity between groups. Analysis of similarity (ANOSIM) was used to test the null hypotheses of no differences in community composition between sites, between treatments within sites and through time. ANOSIM uses rank-similarity Bray-Curtis matrices and randomised permutations to calculate the statistic R and a significance level for differences in the composition of sample groups (Clarke 1993). R usually lies between 0 and 1, with 0 indicating sample similarity and 1 indicating dissimilarity (Clarke 1993). ANOSIM does not test for interaction terms between main effects. Where global R values were significant, pairwise ANOSIM tests were used to examine treatment differences. Due to the loss of power in pairwise tests, P values were often not significant, and R was used as an indicator of relative dissimilarity between groups (Clarke 1993).

Similarity of percentage (SIMPER), a non-statistical technique that shows individual species' contributions to the separation of sample groups in nMDS analysis (Clarke 1993), was used to demonstrate which species, or groups of species, were responsible for the patterns found between treatments. An index of multivariate dispersion (IMD) was calculated to compare the variability of communities through time. IMD shows the relative variability based on the average distance among replicates in the rank similarity matrix. A higher IMD value indicates greater sample variability.

Analyses of variance were conducted on the richness, diversity and abundance of specific groups of taxa. Homogeneity of variances was tested by Cochran's tests and, where necessary, percentage cover data were arcsine square-root transformed and counts of individuals were square-root transformed to fulfil the assumptions of ANOVA (Sokal and Rohlf 1995). Fisher's LSD post-hoc analysis was used to examine differences within factors.

Results

Prior to removal, *Hormosira* cover was approximately 95% at both sites. Fifty-nine taxa were found between both sites over the duration of the experiment. Of these, only four algal species had greater than 5% cover, and only three benthic invertebrates had more than five individuals per 0.25 m^2 [see Appendix A of the electronic supplementary material (ESM)]. Consequently, bare space was relatively scarce, at less than 5% cover. There were differences in the communities at Kaikoura and Moeraki prior to experimental manipulation (ANOSIM $R = 0.78$, $p < 0.001$). Species with more southern distributions (e.g. the coralline alga *Jania micrathrodia*) were found only at Moeraki, which also had more small limpets (e.g. *Notoacmea* spp., *Siphonaria* spp.), fewer chitons (*Chiton pelliserpentis*, *Maorichiton caelatus*) and less cover of perennial brown algae other than *Hormosira* (*Carpophyllum maschalocarpum*, *Halopteris* spp.) than at Kaikoura. Because of these initial site differences, treatments were analysed within each site separately.

Effects of *Hormosira* removal on the community

The epifaunal community comprised an average of 63 individuals per adult *Hormosira* plant, which equalled approximately 15,000 individuals per 0.25 m^2. Three taxonomic groups accounted for 70% of the total individuals found: micro-gastropods (24%), harpacticoid copepods (24%) and gammarid amphipods (23%). These, along with isopods, ostracods and other planktonic organisms at high tide, declined in numbers when *Hormosira* plants were removed. The epifauna present on other macroalgae were not measured, and while some individuals may change hosts, there was an obvious decline in the total numbers of epifauna during low-tide monitoring (personal observation). The trajectory of community composition through time differed between control and *Hormosira* removal treatments (Fig. 1a, b). At both sites, the removal community was more variable than the controls through time. There was non-significant variation between treatments prior to removal, but through time the two trajectories diverged further in multivariate space. Indices of IMD showed the removal treatments at both sites to be more variable than the control plots (IMD values: Kaikoura, control = 0.69, removal = 1.26; Moeraki, control = 0.74, removal = 1.26). The controls at both sites varied between 2 and 24 months, but variation was not as great as in the removal treatments, which changed substantially over time (Fig. 1a, b). The "press" removals were more similar to the "pulse" removals at Moeraki than to those at Kaikoura.

After 24 months, the control, "press" and "pulse" removal plots at Kaikoura were different with respect to community composition (global $R = 1.0$, $p = 0.004$;

Fig. 1c). SIMPER showed the differences in composition to be a combination of reduced richness and abundance of delicate and branching algae (e.g. *Ceramium* spp., *Chaetomorpha coliformis*, *Gelidium caulacantheum*, *Dictyota* spp., *Laurencia thyrsifera*), an increase in opportunistic ephemeral brown algae (*Adenocystis utricularis*, *Colpomenia sinuosa*, *Leathesia difformis*, *Splachnidium rugosum*) and a decrease in perennial fucoids (*Carpophyllum maschalocarpum*, *Cystophora scalaris*, *C. torulosa*) in the removal plots. The grazers *Chiton pelliserpentis* and *Cantharidella tesselata* decreased in the removal plots, while the topshell *Melagraphia aethiops* and limpets *Siphonaria* spp. increased. It was the difference in abundance of these taxa that drove the differences between the "press" and "pulse" removal plots. The effects in the "pulse" plots were more subtle than those in the "press" plots. At Moeraki, the composition of control, "press" and "pulse" removal plots also differed after 24 months, but the two removal treatments were more similar than at Kaikoura (global $R = 0.63$, $p = 0.014$; Fig. 1d). SIMPER showed that the same general groups of taxa were responsible for the treatment dissimilarity as at Kaikoura. At Moeraki, the delicate and branching algal species that were reduced in abundance were *C. coliformis*, *Echinothamnion sp.*, *L. thyrsifera*, *Pleonosporium hirtum* and *Plocamium microcladiodes*. Ephemeral brown algae showed the same pattern as at Kaikoura. The change in perennial fucoid cover was caused by a reduction in *Cystophora retroflexa* and *C. torulosa* in the removal plots. The molluscan grazers *C. pelliserpentis*, *Cellana radians* and *C. tesselata* all decreased in the removal plots, while the small limpet *Notoacmea* spp. increased. The abundances of these taxa in both removal treatments were similar.

Fig. 1 Two-dimensional non-metric multidimensional scaling plots showing variation in community composition through time due to the treatment (each *numeral* represents the month after initial removal) atKaikoura (**a**) and Moeraki (**b**) and the differences between treatments 24 months after initial removal at Kaikoura (**c**) and Moeraki (**d**)
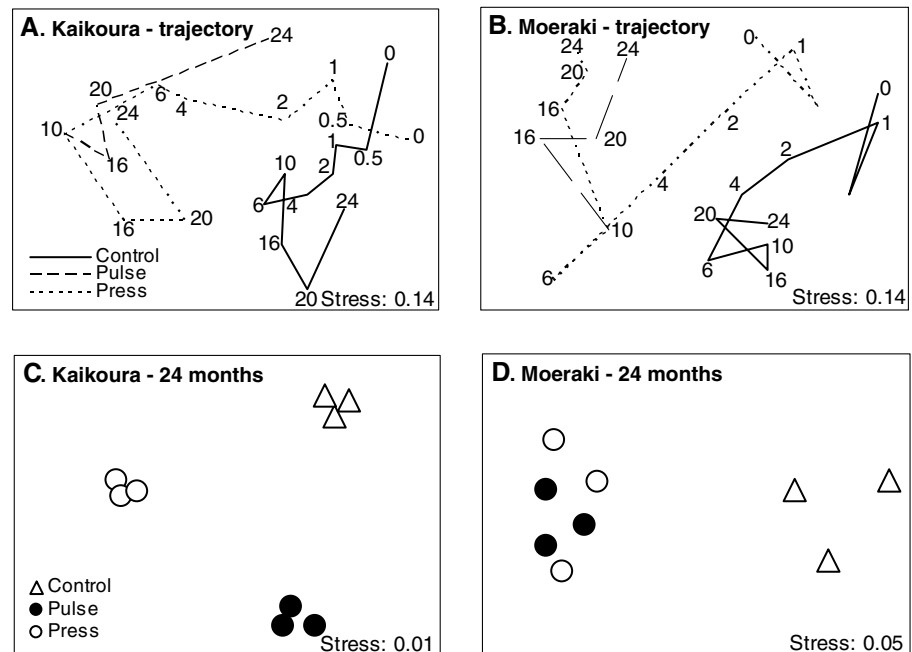
Taxon-specific responses to *Hormosira* removal

The differences between treatments were not consistent over time or between sites (Table 1). Generally there were fewer taxa in removal plots than in control plots, but the difference was greater at Kaikoura than at Moeraki (Table 1; Fig. 2a, b). Twenty-four months after initiation, removal plots had 44 and 34% fewer taxa than the control plots at Kaikoura and Moeraki, respectively.

There were occasional blooms of opportunistic ephemeral brown algae (especially *Adenocystis*, *Colpomenia* and *Leathesia*), primarily in the removal plots (Table 1; Fig. 2c). Ephemeral cover was usually less than 20%, but increased to 70% at Kaikoura and 40% at Moeraki during the spring of 2002, 4 months after removal. This bloom died off within 2 months.

Four fucoid species (excluding *Hormosira*) were initially present: *Carpophyllum maschalocarpum*, *Cystophora retroflexa*, *C. scalaris* and *C. torulosa*. Within several weeks of *Hormosira* removal at Kaikoura, there was a decrease in fucoid cover and richness as the understory fucoids were exposed to thermal and desiccation stress and died. After 4 months, the low-shore fucoids *C. maschalocarpum* and *C. scalaris* were gone at both sites. The subsequent recruitment and cover of fucoids (excluding *Hormosira*) were far greater at Kaikoura than Moeraki and greater in control plots than in removal plots, and these fluctuated through time (Table 1; Fig. 2d). After 24 months, the removal plots had 83 and 71% less cover than the control plots at Kaikoura and Moeraki, respectively. Fucoid cover increased the most in control plots at Kaikoura after recruitment of the low-shore fucoid *C. torulosa* under the *Hormosira* canopy during the spring/summer period (6 months after treatment initiation).

There were generally more molluscan grazers (larger than 5 mm) in the control plots than in the removal plots, but this varied between sites and times (Table 1; Fig. 2e). At Kaikoura, both plots were similar until 10 months after removal, following which time the abundances in control plots increased due to an influx of chitons (*C. pelliserpentis* and *M. caelatus*) and the

turbinid gastropod *T. smaragdus*, which has a positive association with coralline turf (Walker 1998). These grazers also increased in the removal plots after 20 months. At Moeraki, mollusc densities were the same until 16 months after initial removal, following which time the densities increased in the control plots due to higher abundances of *C. tesselata*. Overall, however, grazer abundance was low, rarely exceeding eight per 0.25 m^2.

The primary substratum was predominantly a combination of bare space and cover by geniculate "turfing" and nongeniculate "encrusting" coralline algae. Their abundances were not independent, as an increase in one of these groups resulted in a decrease in another. There was more bare space at Kaikoura than at Moeraki, and more in the removal plots than in the controls (Table 1; Fig. 2f). Bare space increased dramatically at Kaikoura between 6 and 10 months after removal, corresponding with a decrease in the cover of nongeniculate algae in the removal plots. The cover of geniculate corallines did not differ between treatments.

"Press" versus "pulse" disturbance and recovery of *Hormosira*

There were far more *Hormosira* recruits in the removal areas than in the controls, but the magnitude of recruitment varied between sites. By far, the greatest number of recruits occurred in the clearances at Kaikoura (means: 171 at Kaikoura and 27 at Moeraki per 0.25 m^2; Fig. 3). Few recruits appeared in the control plots (means: six at Kaikoura and two at Moeraki per 0.25 m^2). Although reproduction occurs year-round in *Hormosira*, most recruits appeared in a single episode during their peak reproductive season of spring/summer (October/November; 14 months after the experiment was initiated). Differences in recruitment were reflected in the percentage covers at the end of the experiment, which varied by site and treatment. Controls remained almost completely covered by *Hormosira* at both sites, but this was mostly by large plants. The new recruits in the "pulse" removal half

Table 1 Results of a three-way analysis of variance on the number of total taxa per 0.25 m^2, the Shannon diversity index values, the percentage cover of ephemeral algae, perennial fucoid algae and bare space and the abundance of molluscan macrograzers. Site, treatment and time were all treated as fixed factors

Source of variation	df	Number of taxa		Shannon index		Ephemeral algae		Fucoid algae		Molluscan grazers		Bare space	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Site	1	567.67	80.05***	2.74	82.51***	0.61	42.06***	0.52	323.59***	0.013	12.44***	0.24	77.78***
Time	9	37.27	5.26***	2.63	79.20***	0.14	1.49	0.01	3.54***	0.005	4.20***	0.02	7.66***
Treatment	1	414.41	58.44***	0.74	22.33***	0.07	0.77	0.41	254.44***	0.012	10.95***	0.09	30.72***
Site × time	9	3.27	0.46	0.08	2.39	0.01	2.16	0.03	2.03*	0.003	2.55**	0.01	4.35***
Site × treatment	1	7.01	0.99	0.05	1.48	0.05	7.77*	0.03	15.58***	0.005	4.59*	0.06	18.35***
Time × treatment	9	22.41	3.16**	0.32	9.70***	0.08	12.43***	0.02	14.05***	0.001	0.90	0.02	6.73***
Site × time × treatment	9	21.23	2.99**	0.06	1.76	0.07	1.78	0.010	8.17***	0.003	2.48*	0.01	3.25**
Error	80	7.09		0.03		0.004		0.002		0.001		0.003	

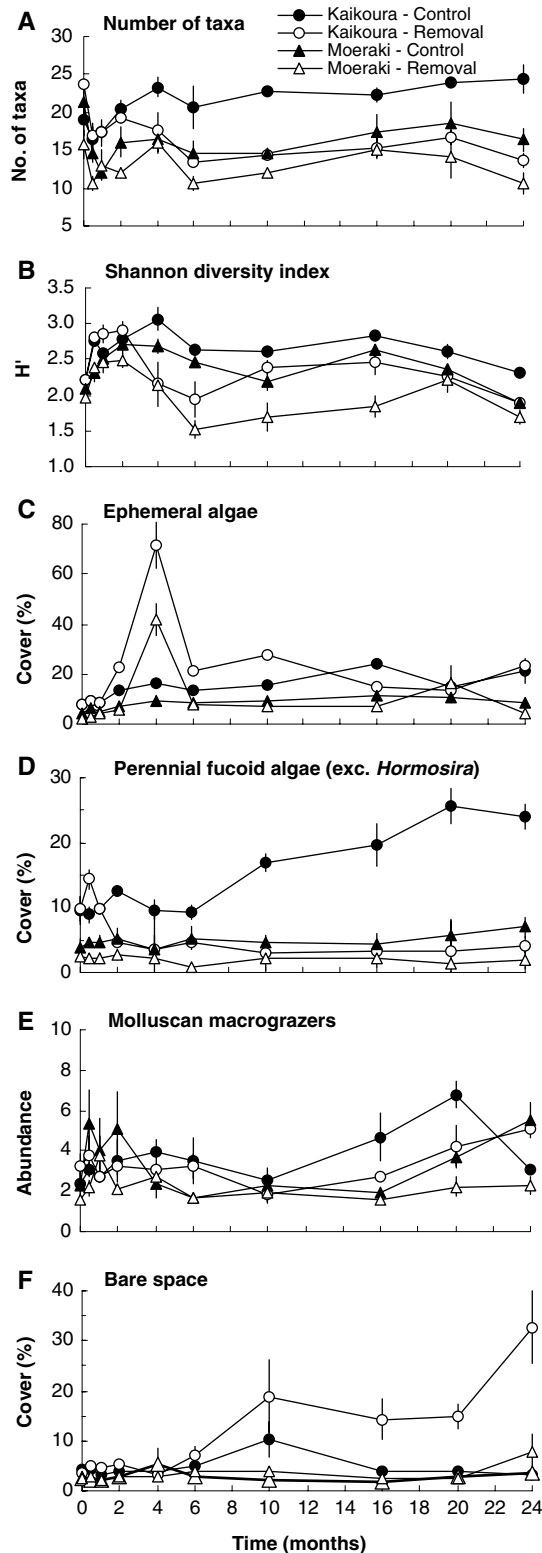*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$

Fig. 2 Temporal variation in the mean (±SE) number of taxa (**a**), Shannon-Weiner diversity index values (**b**), percentage cover of ephemeral algae (**c**), percentage cover of perennial fucoid algae (excluding *Hormosira banksii*) (**d**), number of molluscan macrograzers (more than 5 mm in length) per 0.25 m^2 (**e**) and percentage cover of bare space (**f**) in control and *H. banksii* "press" removal plots at Kaikoura and Moeraki from treatment initiation in July 2002
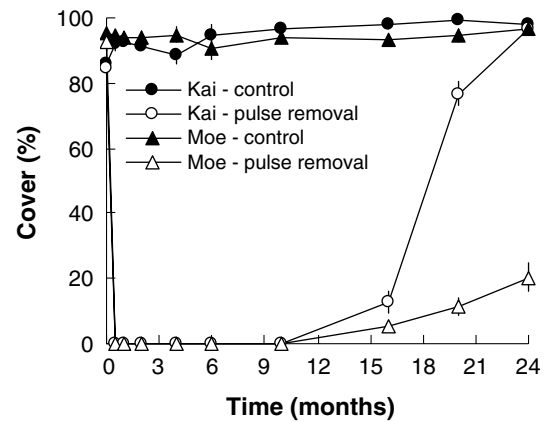

Fig. 3 Percentage cover (±SE) of *H. banksii* per 0.25 m^2 in control and "pulse" removal plots (cover in "press" removal was nil) at Kaikoura (*Kai*) and Moeraki (*Moe*)

covered virtually all (96±4.9%) of the 1.5×3-m plots at Kaikoura by the end of the experiment, but only 20% (±5.4) at Moeraki (Fig. 3, see also Appendix B of the ESM).

Despite the increase in cover of *Hormosira* in the "pulse" removal plots, there was little recovery of the wider community after 2 years (Fig. 1c–e). The "press" and "pulse" removal treatments were different at Kaikoura but not at Moeraki (Table 1; Fig. 1), with the "press" removal plots of the former having a greater cover of ephemeral algae (*Enteromorpha/Ulva* complex, *Leathesia difformis*), macrograzers (e.g. *Turbo smaragdus*) and nongeniculate and geniculate corallines, and a lower cover of perennial fucoid algae than the "pulse" removal treatments at Kaikoura.

Temperature

Temperature extremes at low tide were greater in the removal plots during the summer months, and this difference was greater at Kaikoura than at Moeraki (Fig. 4). There were no major differences in temperatures between control and removal plots during the cooler months (Fig. 4). Maximum temperatures reached 35.5°C at Kaikoura and 28.5°C at Moeraki in the removal plots during low tide, an increase of 9.5° and 4°C, respectively, on the temperatures in the control plots at the two sites (Fig. 4).

Discussion

This study tested and clarified the role of a dominant, habitat-forming species in maintaining the diversity and structure of mid-intertidal communities. There were comprehensive changes following the removal of the alga *H. banksii* that persisted for the 2-year duration of the study. Unlike most intertidal studies done elsewhere, no barnacles, and few mussels, grazers and whelks recruited into the treatments (Keough and Quinn 1998; Underwood 1999). Most of the changes were apparently driven
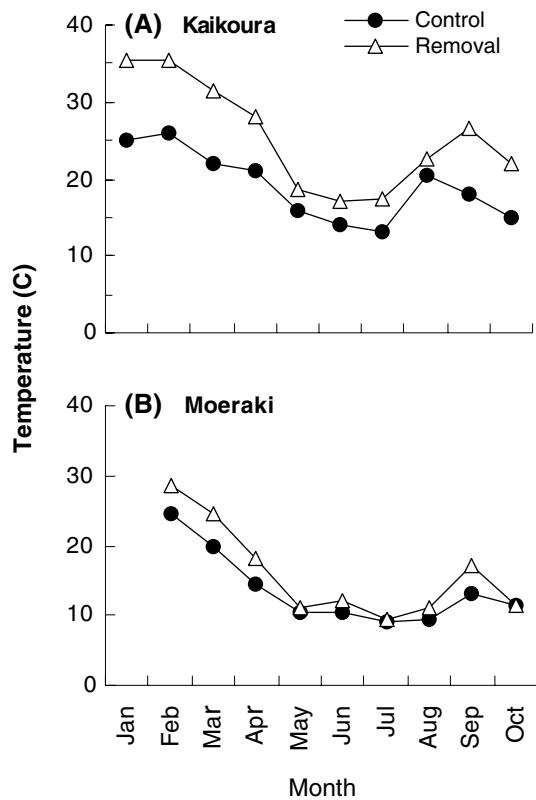
Fig. 4 The maximum monthly temperatures (°C) during periods of emersion in control and *H. banksii* removal plots between January and October 2003 at Kaikoura (**a**) and between February and October at Moeraki (**b**)

by strong non-trophic, habitat-associations and relationships between understory species and *Hormosira*.

Canopy-community interactions

Removal of *Hormosira* resulted in the immediate loss of almost the entire epifaunal community, which clearly had an obligate association with the canopy alga as habitat. The loss of species that live on, under and among primary space holders such as dominant algae and mussels may compose most of the taxa in communities, and these typically disappear or are greatly reduced in abundance following large disturbances (Dayton 1971). Two other major effects occurred within a few months of *Hormosira* removal which were taxon-specific. The first was that other species of fucoid algae in the understory darkened, became desiccated and died. These species later had a period of recruitment, but only beneath the canopies in the control plots. These desiccation-intolerant perennials form dense stands only a few meters away and 0.1 m lower on the shore than the experimental areas, but in the mid-intertidal zone they clearly have a positive association with the *Hormosira* canopy. Several other species of red, green and delicately branched brown algae beneath the canopy also died back, a response similar to that seen in other studies for obligate understory species (Dayton 1971). Conversely, opportunistic ephemeral

algae responded positively to the removal of the *Hormosira* canopy; this was especially the case for *Ulva*, *Adenocystis*, *Colpomenia* and *Leathesia*, which often appear after disturbances (Sousa 1979; Reed and Foster 1984; Jenkins et al. 1999). However, this surge lasted for only a few months. Blooms of ephemeral algae may slow the development of longer-lived perennials (Sousa 1979), but there was no evidence of this in our study. These die-offs and ephemeral blooms led to far more variable communities in the removal areas than in the control plots at both sites.

Of the physical factors affecting understory assemblages in the intertidal zone, the most important here appeared to be the provision of light gaps, leading to algal blooms, and temperature stress, leading to the demise of many species. Following the removal of the *Hormosira* canopy, the understory temperature during periods of emersion rose by as much as 9.5°C relative to similar areas under the canopy. During the summer months, this elevation took temperatures beyond 35°C in the understory, which may have exceeded lethal limits for some species (see Helmuth 1998; Schiel et al. 2004). While other mechanisms were not examined here, there was no obvious change in other factors, such as sediments, that could have caused the reduction in understory species (see Airoldi and Cinelli 1997).

Apart from the fucoids, the only other perennial component of the community was coralline algae. Other intertidal studies have found that turfing coralline algae increase in abundance following canopy removal (e.g. Benedetti-Cecchi and Cinelli 1992a; Bulleri et al. 2002). In our study, there was only a slight response in coralline cover to canopy removal. Corallines became bleached within a few months of canopy removal, but they recovered and formed the major component of benthic cover.

The poor response of sessile invertebrates and gastropods provides considerable contrast to most other studies of a similar nature. Studies in the eastern USA (Lubchenco and Menge 1978; Bertness et al. 1999), western USA (Foster et al. 2003), Europe (Jenkins et al. 2004) and Australia (Keough and Quinn 1998; Underwood 1999) have consistently shown an influx of invertebrates, with associated trophic relationships, into areas where dominant algal species have been removed. For example, removal of *Hormosira* in Australia resulted in an increase in the densities of herbivorous molluscs, especially limpets (Keough and Quinn 1998), removal of *Corallina* in Irish tide pools led to an increase in the abundance of *Patella vulgata* (Goss-Custard et al. 1979), removal of a *Durvillaea* canopy resulted in an influx of *Nacella macquariensis* (Simpson 1977), removal of *Ascophyllum nodosum* canopies caused an increase of *Littorina littorea* on the east coast of the USA (Bertness et al. 1999) and a three- to sixfold increase in the numbers of *Patella vulgata* on the Isle of Man (Jenkins et al. 1999, 2004). In our study, canopy removal generally resulted in fewer molluscan macrograzers. Although the poor recruitment of invertebrates in our study could have been affected by fish (Anderson

and Connell 1999) or bird (Marsh 1986) predation, it is consistent with numerous other experiments in this region (cf. Schiel 2004). Furthermore, the recruitment of barnacles and mussels is generally poor on the eastern South Island (Menge et al. 2003) and invariably poor or non-existent within algal-dominated areas on the east coast.

In addition to providing contrasting results to those obtained in northern hemisphere studies, our work shows that superficially similar communities in different geographic regions may have different ecological mechanisms affecting structure. *Hormosira* also forms canopies on mid-shore reefs in southeastern Australia. Underwood (1999) found that direct and indirect biological interactions between the canopy and understory organisms maintain the understory community. *Hormosira* had an indirect negative effect on the abundance of barnacles by providing predatory whelks with shelter. Following widespread removal of the *Hormosira* canopy, the foraging efficiency of whelks decreased, and following release from predation, barnacles became the dominant species (Underwood 1999). In New Zealand, very different mechanisms maintain the understory community of *Hormosira*. In the absence of species that can have strong trophic interactions, the recruitment, demographics, sensitivities to habitat modification and population dynamics of the dominant algae assume a more important role (cf. Schiel 2004).

Recruitment and recovery of *Hormosira*

One of the only species that responded positively to the removal of the canopy was *Hormosira* itself. The suppression of recruitment of conspecifics by canopies has been seen in most studies where canopies have been removed: for example, *Ascophyllum nodosum* (Jenkins et al. 1999), *Cystoseira* spp. (Benedetti-Cecchi and Cinelli 1992b), *Silvetia compressa* (Johnson and Brawley 1998), *Lessonia nigrescens* (Santelices and Ojeda 1984) and *Macrocystis pyrifera* (Reed et al. 1988). Most studies ascribe this effect to increased light (Reed and Foster 1984; Santelices and Ojeda 1984), the reduction in competition for space (Paine 1988), reduction in grazing (Santelices and Ojeda 1984; Benedetti-Cecchi and Cinelli 1992b; Johnson and Brawley 1998), reduction in abrasion by adult fronds (Leonard 1999) and increased coralline turf which provides microhabitat protection from desiccation and grazing (Benedetti-Cecchi and Cinelli 1992b; Johnson and Brawley 1998). Few of these apply to our study, other than temperature and light changes and the provision of more primary space. Grazers were more abundant beneath canopies, but these were small and in very low abundances. Whiplash effects have not been seen in *Hormosira* (Underwood 1999); this species has a buoyant, beaded form and tends to stay off the substratum during submergence. The major increase in primary space following canopy removal was because of the demise of understory species. Furthermore, the vast majority of *Hormosira* propagules settle beneath or near

adults (D.R. Schiel, unpublished data), so control plots probably had ample settlers. It seems likely, therefore, that the provision of bare space and increased light, acting on the early stages of *Hormosira*, led to its increase in the removal plots. However, there were important site-specific differences in community recovery that involved the differences in *Hormosira* recruitment. The Kaikoura "pulse" removal plots had 96% cover by recruits after 24 months, whereas at Moeraki there was only 20% cover at the same time point. Despite the almost complete cover of the "pulse" areas at Kaikoura, the *Hormosira* recruits were small (approx. 25 mm in length), and most of the control community was still absent. In time, it would be expected for the "pulse" plots to converge in their structure with the control plots. It seems likely, however, that the communities in the removal plots at Kaikoura will recover more quickly than those in the removal plots at Moeraki, where there was poor recruitment, dense corallines and little bare space. The slow recovery of *Hormosira* following disturbance is consistent with other studies on *Hormosira*. For example, Schiel and Taylor (1999) found that understory algae did not recover 2 years following trampling in New Zealand, Keough and Quinn (1998) found recovery took up to 4 years in Australia and Underwood (1998) found that *Hormosira* in Australia can take up to 5 years to recover after a major storm.

Conclusions

Our study provides several contrasts to studies elsewhere. Although disturbance to the key habitat-forming species resulted in highly variable communities through time, this did not involve sessile or grazing invertebrates (cf. Schiel et al. 2004) or whelks (Lubcheno and Menge 1978; Petraitis and Latham 1999). Throughout the mid-intertidal zone of semi-protected shores of New Zealand, *Hormosira* is the only large perennial alga that forms a significant canopy and dominates space (Morton and Miller 1968). There was no replacement of *Hormosira* following removal, unlike many other places where replacement by a less competitive, but functionally similar species can occur (Hawkins and Harkin 1985; Foster et al. 2003; Jenkins et al. 2004). For example, canopies of *Fucus serratus* and *F. vesiculosus* persisted 12 years after the removal of the intertidal alga *A. nodosum* (Jenkins et al. 1999, 2004) and in the western USA, the removal of *Hedophyllum* led to colonisation by *Laminaria* and *Lessoniopsis* (Dayton 1975). Clearly, the recovery of the full community depends on *Hormosira* recovery, as there is no species capable of replacing *Hormosira* in the mid-intertidal zone of platforms in New Zealand (Schiel 2004). Its morphology of mucilage-filled beads enable it to withstand far greater temperature stress than other fucoids (Brown 1987), which survive in the stressed conditions of the mid-tide zone only under the *Hormosira* canopy. Because no replacement by a functionally similar species is possible, disturbance to its canopy or its deletion from portions of reef have profound effects on

the entire structure of the community, with long-term consequences. We have shown here that non-trophic, positive interactions are important in structuring communities. We would anticipate that higher on the shore the effects of removal on the understory community would increase as habitat-amelioration from increasing physical stress becomes more important to the survival of species there (Bertness and Callaway 1994; Bruno and Bertness 2001). In such situations with one or few competitive dominants and weak trophic interactions, positive interactions and associations of species are likely to assume increased importance.

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