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FEATURE ARTICLE

Gradients of disturbance to an algal canopy and the modification of an intertidal community

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ABSTRACT: Disturbances over a range of intensities are common in intertidal communities, often causing partial removal of dominant species. However, most studies testing effects of disturbance on community structure use treatments where the dominant species is either present or absent, and usually record responses of only a few community components. Here, we test responses of the entire local community of benthic algae and invertebrates across a gradient of disturbance to a habitat dominant in southern New Zealand, the fucoid alga *Hormosira banksii*. Replicate 0.25 m^2 plots of 100% cover of *H. banksii* were manipulated and maintained at 0, 25, 50 and 75% cover at 2 sites for 13 mo. Throughout the experiment, communities in the complete removal and control plots were the most different from each other, but intermediate plots had varied responses and were usually not significantly different from each other. Generally, as cover of *H. banksii* decreased, community variability increased through time. Taxa richness declined with reduced *H. banksii* cover, with up to 77% of its variation explained by variation in canopy cover. Other fucoid algae declined across the gradient, with complete canopy removals having 92% less fucoid cover than control plots. Complete canopy removal had positive effects on ephemeral algae, especially at one site which exhibited large seasonal blooms. Bare space was greatest where canopies were completely removed and understory algae died. Diversity was greatest in plots with complete canopies rather than at intermediate levels, and there was no replacement of the dominant *H. banksii* by other species. There was no consistent effect on taxa across the gradient; some species responded linearly while others responded at threshold levels of canopy cover. This study shows the importance of disturbance gradients interacting with key species, which may have considerable bearing on reef community structure.
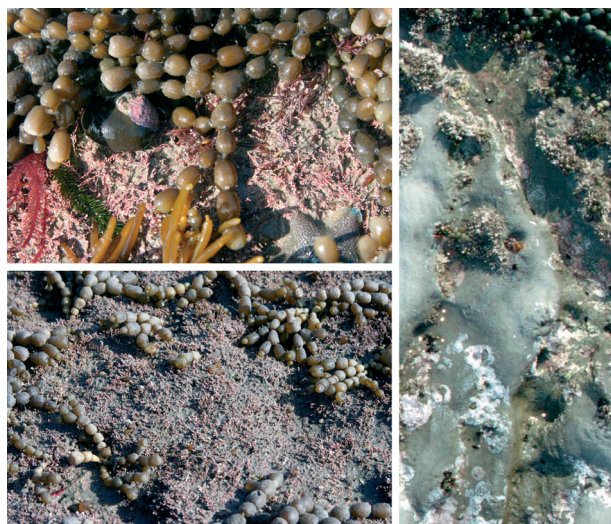
When algal canopies of *Hormosira banksii* (top left) are removed, this leads to nearly total loss of associated species (right); intermediate canopy losses (bottom left) result in species-specific density changes.

Photos: M. Hickford

KEY WORDS: Canopy · Disturbance · Gradient · Habitat-forming algae · *Hormosira banksii* · Positive interaction · Species removal · Threshold

INTRODUCTION

A change in the patterns of abundance of habitat-forming species can have large effects on associated assemblages (Strauss 1991, Brown et al. 2001). For example, the removal of dense algal canopies (Dayton 1975, Bertness et al. 1999, Jenkins et al. 1999a), corals (Stimson 1985), seagrass (Ramage & Schiel 1999), and mussels

(Paine 1985, Seed 1996) can modify the local habitat, alter spatial complexity and affect surrounding understory benthic species, both positively and negatively.

In intertidal communities dominated by macroalgae, disturbances naturally occur over a wide gradient, from small impacts that remove a few individual plants, to large storms that can remove entire canopies (Underwood 1998, 1999). The consequent effects on assemblage structure across such disturbance gradients are variable. Typically, complete removal of a competitively dominant species allows other species to recruit into available space and grow, thereby increasing total benthic diversity, at least until the dominant becomes re-established (Connell & Slayter 1977, Sousa 1979, Jenkins et al. 1999a, 2004). The loss of a dominant species can also lead to the loss of obligate understory species (Dayton 1975, Bertness et al. 1999, Jenkins et al. 2004, Lilley & Schiel 2006) or lead to changes in direct and indirect interactions within a community (Underwood 1998, 1999). Smaller disturbances of algal canopies, however, provide only partial gaps of space and light for other species to recruit into, which may also lead to increased benthic diversity (Sousa 1979, Shea et al. 2004), but the effects of disturbances over a gradient from small to large are poorly documented in temperate marine communities.

Because natural populations of species are temporally and spatially variable, fluctuations in the abundance or canopy cover of dominant macroalgal species may not correspond linearly with their effects on the associated community (Strauss 1991, Brown et al. 2001, Speidel et al. 2001). One major hypothesis, the Intermediate Disturbance Hypothesis, predicts that diversity will be greatest at intermediate levels of disturbance and least when impacts are either small or very large (Connell 1978). Sousa (1979), for example, tested this for an intertidal algal assemblage on boulders in southern California and found that when the dominant red alga *Gigartina canaliculata* was removed, the community went through a period of high diversity before *G. canaliculata* returned to dominance. Increased diversity of benthic species was a consequence of the frequency and intensity of storm and wave disturbances to the community and the resulting likelihood of canopy loss. It is also possible that increasing disturbance intensity in communities dominated by algal canopies may result in a positive linear response of the associated assemblage through the greater provision of bare space and light gaps. Conversely, diversity could decline with increasing impacts if understory species rely on an established algal canopy during low tide to reduce temperature stress (Bertness et al. 1999, Lilley & Schiel 2006) or solar radiation (Figueiredo et al. 2000). There may well be thresholds of responses that vary from species to species across a disturbance intensity gradient.

The relationships between the canopy cover of a habitat-dominating species and associated assemblages have some significance for understanding community structure and the impacts and recovery from disturbances in intertidal systems. Partial removal or thinning of macroalgal stands occurs frequently through anthropogenic disturbances, such as trampling (Brown & Taylor 1999, Schiel & Taylor 1999) or natural disturbances, such as wave action (Underwood 1998), 'burn-off' (i.e. destruction of parts of the organism from exposure-related stress) at low tide (Lilley & Schiel 2006), and burial and abrasion by sediments (Airoldi & Virgilo 1998, Schiel et al. 2006). Despite thinning occurring more frequently than complete removal of a stand (Strauss 1991), most experimental studies test canopy effects on communities by using treatments in which the dominant species is either present or absent, and typically focus on responses of a few components of interest in communities such as macroalgae and large molluscan grazers (Kennelly 1987, Bertness et al. 1999, Jenkins et al. 1999a,b, Speidel et al. 2001).

In southern New Zealand, moderately exposed rocky shores along much of the east coast are dominated by the fucoid alga *Hormosira banksii* (Turner) Decaisne. This species typically forms a dense canopy layer on the mid shore, with a standing biomass of up to 8 kg m^{-2}. Plants have a very small discoid holdfast and are often removed by waves and storms (Underwood 1999) or human effects such as trampling (Schiel & Taylor 1999). *H. banksii* is the only perennial, canopy-forming species able to survive in high abundance on the mid-shore (Schiel 2004). Lilley and Schiel (2006) showed that complete removal of *H. banksii* from 3 × 3 m areas had strong negative effects on the local benthic community over 2 yr. Up to 45% of species in *H. banksii* beds were lost or greatly declined in abundance following the removal of *H. banksii*. These species included epifauna associated with *H. banksii* and understory species that could not survive on the mid shore without the protective canopy layer, such as other fucoids (e.g. *Carpophyllum maschalocarpum* and *Cystophora* spp.) and small, delicate branching algae (e.g. *Chaetomorpha coliformis*, *Ceramium* spp., *Dictyota* spp., and *Laurencia thyrsifera*). However, as in most other studies, gradients of disturbances were not examined.

Here, we examine how differences in the canopy cover of a habitat-dominating species affects the structure of the associated benthic community. We hypothesized that increasing levels of disturbance to a macroalgal canopy would result in greater cover of opportunistic ephemeral algae, greater recruitment of less competitive perennial species, more grazers and a loss of obligate benthic understory species.

MATERIALS AND METHODS

In January 2003, fifteen 0.5×0.5 m plots were marked in the mid-littoral zone (0.85 to 1.0 m above lowest astronomical tide level, LAT), over a 30 m^2 area on each of 2 rocky reef sites (Mudstone Bay and Wairepo Flats) on the Kaikoura Peninsula (42°25′S, 173°41′E). Both reefs extend ca. 150 m from the upper intertidal to the subtidal zones, but are generally protected from severe wave action by offshore reefs and a coastal topography that deflects swells (Ramage & Schiel 1999). The mid-intertidal zone at both sites is covered with a dense canopy (typically 95 to 100% cover) of the fucoid alga *Hormosira banksii*. Plants of this species can reach up to ca. 35 cm in length in these habitats, are often densely packed and fused at the holdfast, and can be difficult to distinguish as individuals. To create consistent treatments, therefore, we used the percentage cover of canopy as the main factor to manipulate. Canopy treatments were: 0% complete removal (T0), 25% intact (T25), 50% intact (T50), 75% intact (T75) and unmanipulated controls (T100). Three replicates of each of the 5 treatments were randomly assigned to the pre-marked plots. To thin treatment plots, plants were removed haphazardly throughout a plot to avoid clumping of plants. Plants were removed at the holdfast with a knife to avoid damaging the understory and substratum. All plants overhanging the removal plots from outside were trimmed back to eliminate possible edge effects of the canopy. Treatments were initiated as plants lay over the reef at low tide; all plots were then visually re-checked using a quadrat on 2 subsequent tides to ensure that the initial treatment covers were consistently achieved. Plots were maintained at their treatment levels of canopy cover throughout the experiment because the primary factor of interest was canopy cover. A 0.25 m^2 strung quadrat was used to monitor the benthic community prior to removal and at 1, 4, 7, 10 and 13 mo after initial removal. Percentage cover estimates were made for all algae and sessile invertebrates, and mobile invertebrates were counted. Layering of species often resulted in >100% total cover of all algae. All benthic taxa larger than ca. 3 mm were included. To avoid destructive sampling of the understory, identification of all species was done in the field. Most organisms were identified to the species level, but many smaller algae could be identified only to genus; many of the smaller invertebrates (especially polychaetes and isopods) were identified by family (see Appendix 1).

Multivariate and univariate analyses were used. Non-metric multidimensional scaling (nMDS) using Bray-Curtis distances on 4th-root transformed data was used to visualise changes in the understory community across the disturbance gradient. Analysis of similarity (ANOSIM) was used to test for differences in community composition across sites, between treatments within sites, and through time. Where global R-statistics were statistically significant, pairwise ANOSIM tests were used to examine treatment differences. Because of the loss of power in pairwise tests, p-values were often not significant, and the R-value was used as an indicator of relative dissimilarity between treatments (Clarke 1993). Similarity of percentage (SIMPER) was used to demonstrate which species, or groups of species, were responsible for any patterns found between treatments and an index of multivariate dispersion (IMD) was calculated to compare the variability of communities across treatments through time (Clarke 1993, Clarke & Warwick 2001) using Primer v5.1.2 (Clarke & Gorley 2001). See Clarke (1993) for further discussion of the analyses used here.

Univariate analyses (repeated measures general linear models) were performed on the richness and abundance of specific groups of taxa. A repeated measures model was used to account for the variability through time of all treatments. However, it is noted that limitations can occur due to non-independence through time. We also used regression analyses to test for responses of variables to the disturbance gradient, on data from the last sampling date. Homogeneity of variances was tested by Cochran's *C*-test and, where necessary, percentage cover data were square-root arcsine transformed and counts of individuals were square-root transformed to fulfill the assumptions of ANOVA. Fisher's least significant difference (LSD) post-hoc analysis was used to examine differences within factors.

RESULTS

Prior to removal, *Hormosira banksii* cover was between 95 and 100% at both sites. The cover of *H. banksii* in the control plots did not vary from this over the study period. Taxa richness per 0.25 m^2 plot across all treatments ranged from 10 to 31, with a total of 71 taxa found at Mudstone Bay and 58 taxa at Wairepo Flats throughout the duration of the experiment (see Appendix 1). The distribution of species abundances was heavily skewed with only 2.4% (Mudstone Bay) and 4.5% (Wairepo Flats) of all taxa having >5% cover or 5 ind. plot^{-1}. Taxa with cover consistently greater than 5% were *Cystophora torulosa*, *Corallina officinalis* and nongeniculate corallines; the most abundant invertebrates were *Turbo smaragdus*, *Maorichiton caelatus* and *Chiton pelliserpentis*. The great majority of other species had <1% cover or <1 ind. plot^{-1}.

There were initial differences in the community composition of the 2 sites prior to the start of the experiment (ANOSIM; R = 0.55, p < 0.001). These differences were primarily due to greater richness and abundance of molluscan macrograzers (>5 mm shell length), especially *Cantharidella tesselata*, *Chiton pelliserpentis*, *Maorichiton caelatus*, *Melagraphia aethiops*, and *Turbo smaragdus* at Wairepo Flats; and greater richness and abundance of red algal species, particularly *Champia novae-zelandiae*, *Dipterosiphonia heteroclada*, *Gigartina chapmanii*, and *Polysiphonia decipiens* at Mudstone Bay. Because of these initial site differences, treatments were analysed separately for each site.

Community-wide effects

The canopy thinning treatments produced generally similar responses of the communities at both sites (Table 1). Over the entire 13 mo of the experiment, using combined data from all monitoring times, there was a gradient of community composition across the treatments. At Mudstone Bay, the complete canopy removals (T0) and controls (T100) were significantly different from each other and from all other treatments. The intermediate disturbance treatments (T25, T50, T75) had similar community composition over the course of the study, and the T75 and T100 treatments were also similar. At Wairepo Flats, there was a broad overlap across the treatments. T0 was significantly different from T75 and T100, T100 was different from all others except T75, and the 4 non-control treatments broadly overlapped in their community responses. Therefore, plots with full canopies and absent canopies

Table 1. Pairwise Analysis of Similarity (ANOSIM) between the canopy thinning treatments, combining all data over the 13 mo of monitoring. Significant p-values are in bold. Global R-statistics—Mudstone Bay: R = 0.35, p < 0.001; Wairepo Flats: R = 0.22, p < 0.001. Under the table is a representation of similar treatments based on the pairwise tests. Treatments connected by lines are not significantly different

Treatment	Mudstone Bay		Wairepo Flats	
	R	p	R	p
T0 vs. T25	0.259	**<0.001**	0.090	0.03
T0 vs. T50	0.312	**<0.001**	0.088	0.03
T0 vs. T75	0.342	**<0.001**	0.218	**<0.001**
T0 vs. T100	0.630	**<0.001**	0.542	**<0.001**
T25 vs. T50	0.004	0.38	0.061	0.08
T25 vs. T75	0.024	0.22	0.072	0.05
T25 vs. T100	0.296	**<0.001**	0.321	**<0.001**
T50 vs. T75	0.077	0.04	0.127	0.06
T50 vs. T100	0.328	**<0.001**	0.375	**<0.001**
T75 vs. T100	0.127	0.06	0.081	0.04

Mudstone Bay ——— ——————————————— —————————

Treatments   T0   T25   T50   T75   T100

Wairepo Flats ———————————————

tended to be different from each other and from most of the intermediate canopies, which themselves formed similar communities.

Differences in community composition after 13 mo were evident in the nMDS plots of treatments at each site (Fig. 1A,B). At both sites, the complete canopy removal and control plots formed distinct clusters, whereas the other treatments were interspersed in multivariate space. The tighter cluster of the 3 intermediate treatments at Mudstone Bay indicates their greater similarity of community responses than at Wairepo Flats.
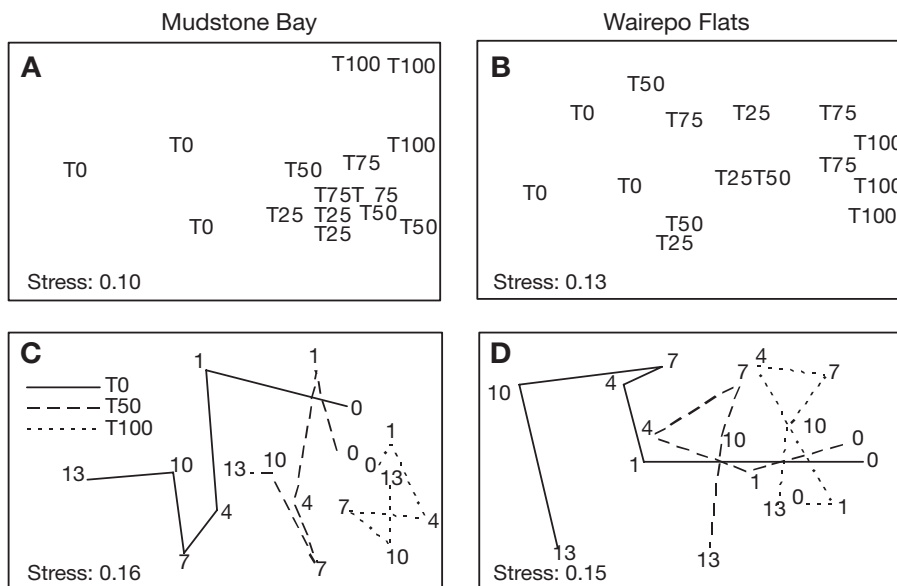

Fig. 1. 2-dimensional non-metric multidimensional scaling (nMDS) plots showing (A,B) differences in community composition for T0, T25, T50, T75 and T100 *Hormosira banksii* thinning treatments 13 mo after experimental initiation at (A) Mudstone Bay and (B) Wairepo Flats; and the temporal variation in the T0, T50 and T100 treatments at (C) Mudstone Bay and (D) Wairepo Flats (each numeral represents the month following initial removal)

The time trajectories of community responses among the treatments can be visualised in the nMDS plots (Fig. 1C,D). In both sites, the community composition in the complete canopy removal treatment (T0) quickly diverged from the other treatments in multivariate space. Controls showed little variation over time at Mudstone Bay, but at both sites the end points for controls were remarkably similar to the starting points (seen as the positions of 0 and 13 relative to each other for the T100 lines). The intermediate treatment T50 clearly produced an intermediate response in community development. The 2 other intermediate treatments (T25 and T75) did not significantly differ from T50 (Table 1), so were excluded to improve clarity of graphs.

In addition to a gradient of community development, there was a gradient in the variability of responses over 13 mo (Table 2). The IMD values at Mudstone Bay declined linearly from the complete removal plots (T0) to the control plots (T100), indicating more variability through time with increasing levels of disturbance to the canopy. The IMD values were more variable among disturbance treatments at Wairepo Flats, but the controls with a full canopy were the least variable of all treatments.

The species that accounted for differences among treatments tended to be similar between the sites. At both sites, SIMPER identified the control plots (T100) as having more molluscan macrograzers (particularly the chitons *Chiton pelliserpentis* and *Maorichiton caelatus*) and perennial fucoid algal cover (*Carpophyllum maschalocarpum*, *Cystophora scalaris* and *Cystophora torulosa*) than the other treatments. Plots with complete canopy removal (T0) had more ephemeral algae (especially *Adenocystis utricularis*, *Colpomenia sinuosa*, *Leathesia difformis* and *Ulva/Enteromorpha* complex) than the T25–T100 plots. At Wairepo Flats, the predatory gastropod *Haustrum haustorium*, the crabs *Halicarcinus cookii* and *Halicarcinus varius* and the sea star *Patiriella regularis* were all less abundant in T0, T25 and T50 compared to the T75 and T100 plots.

Table 2. Index of multivariate dispersion (IMD) values of each canopy thinning treatment showing the relative variability between disturbance treatments 13 mo after initiation at Mudstone Bay and Wairepo Flats

| Treatment | IMD value | |
	Mudstone Bay	Wairepo Flats
T0	1.35	1.08
T25	1.07	1.13
T50	0.94	0.94
T75	0.78	1.05
T100	0.57	0.81

Taxon-specific responses through time

The taxa richness of communities in the disturbance treatments varied significantly by site and treatment (Table 3). The number of taxa in treatments fluctuated considerably through time (Fig. 2A,B). There was an initial decrease in the number of taxa in most removal treatments at both sites. The intensity of this response increased with increasing levels of disturbance and was particularly evident in the T0 plots. Repeated measures analysis of variance and Fisher's LSD post-hoc tests showed that complete removal plots (T0) generally had significantly fewer taxa than all other treatments, and T100 plots had significantly more taxa than all other treatments at both sites. The treatments T25, T50 and T75 were positioned mostly in step-wise fashion between T0 and T100. There was a significant Treatment × Time interaction, with taxa richness steadily increasing in T100, while T0 declined after winter at Mudstone Bay and during summer at Wairepo Flats. In the T0, T25 and T50 treatments at both sites, there was a tendency for taxa richness to be greatest during the intermediate period of 4–10 mo. This was largely a reflection of an increase in ephemeral algal species which tend to bloom during the winter–spring months (see paragraph below). Control plots, however, generally increased in richness through time.

Algal species were grouped into ephemerals and perennials. The most abundant ephemeral species were the browns *Colpomenia sinuosa* and *Ectocarpus* spp. and a green *Ulva/Entermorpha* complex. Mudstone Bay had significantly greater ephemeral cover than Wairepo Flats, but this varied by treatment (Table 3). The significant effects of treatment, Site × Treatment, and Time × Site × Treatment were all driven by the increased cover in complete removal plots (T0) during late winter (7 mo after removal) at Mudstone Bay (Fig. 2C,D). The treatments at Wairepo Flats were similar through time; the cover of ephemeral algae showed only a slight increase midway through the study. Overall, there was no evidence of a gradient of response to the disturbance levels. Complete removal of the canopy was necessary for a bloom to occur.

Fucoid algal cover, excluding *Hormosira banksii,* was comprised of *Carpophyllum maschalocarpum*, *Cystophora retroflexa*, *Cystophora scalaris* and *Cystophora torulosa.* Their cover varied significantly among treatments which had varying effects through time (Table 3). Overall, sites were not significantly different. As for previous groupings, the T0 and T100 treatments tended to be separate from all others, with T0 plots showing the greatest decrease in fucoids as they burned off after the canopy was removed, and T100 plots showing an increase as fucoids (especially *C.*

Table 3. Three-factor RMANOVA (repeated measures analysis of variance) results of the effects of site, canopy treatment and monitoring time on the number of taxa, and percentage cover of ephemeral algae, perennial fucoid algae, bare space and turfing coralline algae. *p ≤ 0.05, **p ≤ 0.01, ***p ≤ 0.0001

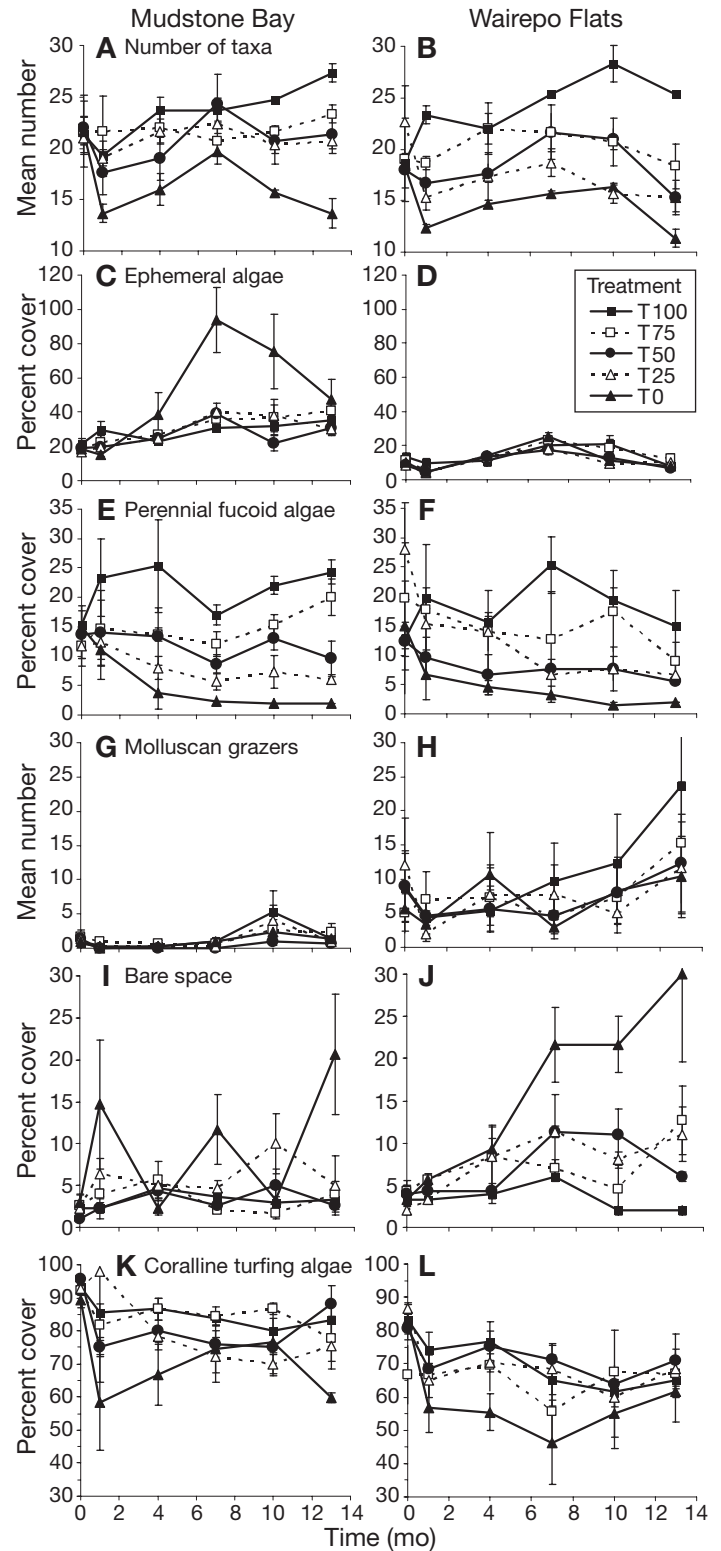| Source of variation	df	Number of taxa MS	F	Ephemeral algae MS	F	Perennial algae MS	F	Grazers MS	F	Bare space MS	F	Coralline turf MS	F
Between effects													
Site	1	145.80	6.58*	2.45	92.61***	41.09	0.23	2163.20	104.22***	424.20	10.7**	0.99	26.7***
Treatment	4	292.16	13.19***	0.09	3.52*	1029.00	5.77**	27.76	1.34	430.99	10.9***	0.12	3.24*
Site × Treatment	4	18.18	0.82	0.08	3.32*	85.66	0.48	15.18	0.73	43.05	1.08	0.03	0.76
Error	20	22.16		0.03		178.39		20.76		39.73		0.04	
Within effects													
Time	5	47.28	8.27***	1.25	155.50***	179.68	5.08***	121.70	13.89***	175.90	10***	0.20	19.9***
Time × Site	5	13.32	2.33*	0.12	14.37***	86.80	2.45*	83.65	9.55***	65.05	3.71*	0.01	1.11
Time × Treatment	20	22.91	4.01***	0.03	3.85***	15.09	1.72*	15.09	1.72*	77.09	4.39***	0.02	1.61
Time × Site × Treatment	20	7.23	1.27	0.03	3.14***	27.78	0.79	13.79	1.57	30.35	1.73*	0.01	0.91
Error	100	5.72		0.008		35.35		8.76		17.54		0.01	

Fig. 2. Temporal variation in: (A,B) the number of taxa, (C,D) percentage cover of ephemeral algae; (E,F) percentage cover of perennial fucoid algae, (G,H) number of molluscan grazers, (I,J) percentage cover of bare space, and (K,L) coralline turfing algae in the 5 *Hormosira banksii* partial removal treatments, at Mudstone Bay and Wairepo Flats. Values are mean (±SE)

torulosa) recruited beneath the canopy (Fig. 2E,F). The partial removal treatments generally responded in a step-wise fashion, although the T25 and T50 plots grouped together at Wairepo Flats throughout most of the study.

The different treatments produced no overall effect on grazers, but Wairepo Flats had more grazers than Mudstone Bay (Table 3, Fig. 2G,H). The most common molluscan grazers at both sites were *Chiton pelliserpentis*, *Maorichiton caelatus* and *Turbo smaragdus*. At Wairepo Flats, increased numbers of grazers after 10 mo in all treatments, particularly the control plots, were due to recruitment of *Cantharidella tesselata*, *M. caelatus* and *T. smaragdus*.

Primary space was mostly bare rock or covered by geniculate coralline algae (*Corallina officinalis* and *Jania* sp.) and nongeniculate coralline algae. Bare space varied significantly by treatment and site, but there were no consistent effects through time across the treatments and sites (Table 3). The complete removal plots had the most bare space throughout most of the study at both sites, and the controls the least (Fig. 2I,J). Post-hoc tests showed that the T25 plots had significantly more bare space than controls (T100) at both sites. *C. officinalis* was the most abundant of the coralline species. Its cover varied among treatments, sites and through time (Table 3). Within one month of treatment initiation, the coralline cover decreased in all treatments at both sites, but the effect was especially great in the T0 plots where it decreased by 25 to 30% as burn-off occurred (Fig. 2K,L). All other treatments fluctuated through time with no clear pattern.

Responses after 13 mo

Regression analyses were used to test for trends in response variables over the disturbance gradient at the end of our experiment. The average number of taxa had a highly significant response across the canopy levels of *Hormosira* at both sites (Fig. 3A). Between 72 (Mudstone Bay) and 77% (Wairepo Flats) of the variation in taxa numbers was explained by the treatment levels. The slopes were the same for both sites (b = 0.12) but there were more species across all treatments

at Mudstone Bay. Ephemeral algae showed no significant trend across treatments at either site (Fig. 3B). Neither slope was significant, but there was far greater ephemeral cover overall at Mudstone Bay (mean = 36.9%) than at Wairepo Flats (mean = 8.9%). Fucoid cover showed significant responses at both sites, but the magnitude of the response was less at Wairepo Flats than at Mudstone Bay (test of slopes: $F_{1,26} = 6.4$, p = 0.017). Less of the variation in fucoid cover was accounted for by the treatments at Wairepo Flats ($R^2 = 86$% at Mudstone Bay, 38% at Wairepo Flats). At both sites, however, there was generally a step-wise increase in fucoid cover with increasing cover of the *Hormosira* canopy.
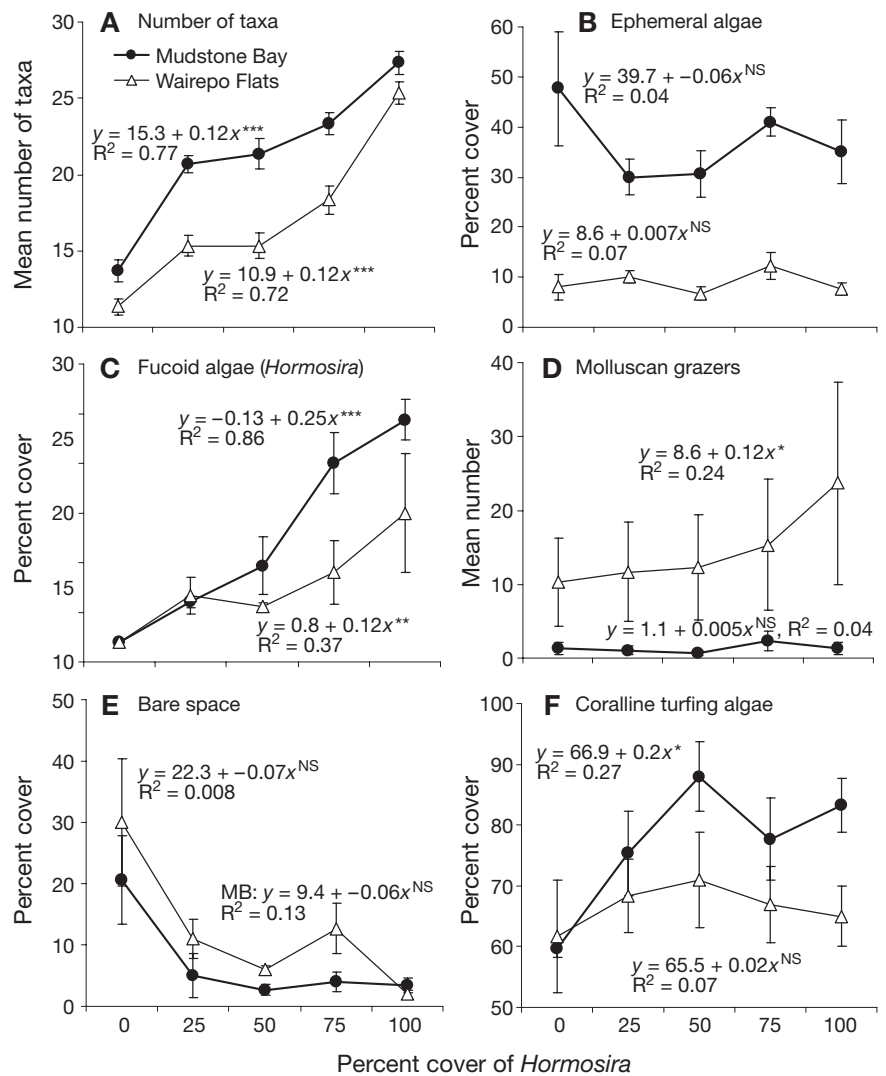

Fig. 3. (A) Number of taxa; (B) abundance of ephemeral algae; (C) abundance of perennial fucoid algae, excluding *Hormosira banksii*; (D) number of molluscan grazers; (E) percentage cover of bare space; and (F) percentage cover of coralline turfing algae, in the *Hormosira banksii* partial removal treatments (all treatments combined) 13 mo after experiment initiation at Mudstone Bay and Wairepo Flats. Values are mean (±SE). Regression equations and R^2 values for each trajectory are shown. ns: not significant, *p ≤ 0.05, **p ≤ 0.01, ***p ≤ 0.0001

Molluscan grazers showed a positive response to canopy cover at Wairepo Flats but not at Mudstone Bay (Fig. 3D), but the variation was high and little of it was accounted for by the treatment levels (R^2 = 24 % at Wairepo Flats). Across all treatments there were far more grazers at Wairepo Flats (mean = 14.7) than at Mudstone Bay (mean = 1.3).

Bare space was highly variable, particularly in the T0 treatments, and there was no significant trend across the treatments at either site (Fig. 3E). Over all treatments, there was more bare space at Wairepo Flats (mean = 18.6 %) than at Mudstone Bay (mean = 6.5 %). Turf-forming coralline algae increased significantly across the disturbance gradient at Mudstone Bay to T50 but not at Wairepo Flats (Fig. 3F). The significant effect was due mostly to the reduced cover of corallines in the T0 treatment. Over all treatments, there was a greater cover of corallines at Mudstone Bay (mean = 76.8 %) than at Wairepo Flats (mean = 66.6 %).

DISCUSSION

Our study showed that thinning of a canopy of a dominant fucoid alga produced variable responses on associated species, and that these varied between sites. After 13 mo over a gradient of canopy cover, the number of taxa and the perennial fucoid cover (other than the original dominant) decreased across the disturbance gradient from a full *Hormosira banksii* canopy to complete canopy removal. Ephemeral algae bloomed in complete removal plots of one site and, perhaps surprisingly, primary bare space increased only in complete removal plots. These responses varied throughout the 13 mo of the study. In no treatments or individual plots, however, did another species establish dominance. This is consistent with longer term community effects of canopy removals on these shores (Lilley & Schiel 2006, Schiel 2006).

At different times of the year there was no significant difference between the 3 intermediate treatments in the multivariate responses. The structural changes in the community were driven more by the addition or loss of understory species than by changes in their abundances. The intermediate response of partial removal of *Hormosira banksii* on the understory was evident in the responses of specific groups of taxa. Fucoid algae, the largest of the space-occupiers with the greatest biomass on these shores (Schiel 2006), varied by treatment. *Carpophyllum maschalocarpum, Cystophora scalaris* and *Cystophora torulosa* are low-shore species, and seem capable of surviving in the mid-shore region only under a dense protective layer of *H. banksii*, which reduces heat and temperature stress during emersion (Lilley & Schiel 2006). In con-

trast to other studies in which a dominant canopy was removed (Jenkins et al. 2004) there was no replacement of *H. banksii* by any other fucoid. There are at least 4 other fucoid species that occur within several metres of *H. banksii* at the study sites, yet none of these can survive alone over most of the tidal range inhabited by *H. banksii* (Schiel 2006).

Ephemeral algae often bloom following disturbances (Connell 1972, Sousa 1979, Farrell 1991, Benedetti-Cecchi & Cinelli 1992a), but this was highly variable in our study. The opportunistic species *Colpomenia sinuosa*, *Ectocarpus* spp., *Leathesia difformis* and an *Ulva/ Enteromorpha* complex at Mudstone Bay bloomed following complete canopy removal. This bloom was seasonal and died off during late spring. There were clear site-related differences. Mudstone Bay, which is suspected of having a higher nutrient load because of riverine input and the large number of fur seals present, had greater cover of ephemeral algae than Wairepo Flats, which had no treatment effect. It appears, therefore, that the response of ephemeral algae relies on a combination of canopy removal, the provision of bare space and specific site characteristics relating to productivity (cf. Foster et al. 2003).

Studies elsewhere have shown that ephemeral algae can delay the development of a perennial community through the pre-emption of space during critical times of the year when other species could recruit (Lubchenco & Menge 1978, Sousa 1979, Coleman 2003, Foster et al. 2003). In our study, however, it appears that the main mechanism limiting the richness and abundance of understory fucoids is not competitive effects between algal species, but the lack of a dense algal canopy (see also Lilley & Schiel 2006), outside of which perennial low-shore species and smaller finely branching algal species are unable to survive. There was no evidence of competitive effects between algal species. The only treatment that had a great influx of ephemerals (T0 at Mudstone Bay) had an almost identical response in fucoid recruitment as the other treatments in which few ephemerals were present. Ephemeral algae, therefore, do not seem to be a key component in the recruitment of longer-lived species in the community in these mid-shore regions.

There was no effect of canopy thinning on the abundance of molluscan macrograzers, which commonly increase in abundance following complete removal of macroalgae (Connell 1972, Jenkins et al. 1999a,b, 2004). For example, Jenkins et al. (1999a,b, 2004) found that an influx of limpets following the removal of an *Ascophyllum* canopy persisted over 12 yr. On the shores near Sydney, Australia, Underwood (1998, 1999) found that grazing and predatory relationships were altered after removal of *Hormosira* canopies. Following large-scale removal of *H. banksii*, whelks de-

creased in abundance leading to an increase in the abundance of barnacles, which affected the recovery of *H. banksii*. There was little evidence of these types of responses in our study. There were few predatory whelks and the majority of grazing species found at Wairepo Flats and Mudstone Bay (e.g. *Chiton pelliserpentis*, *Maorichiton caelatus* and *Turbo smaragdus*) tend to reside in small cracks. Habitat heterogeneity in the form of surface rugosity may be more important to these species than the presence of an overlying algal canopy. Furthermore, the dominant grazer of this zone, the turbinid gastropod *Turbo smaragdus*, has little effect on fucoid recruitment, although it may affect ephemeral algae (Schiel 2006).

Several studies in subtidal habitats and tide pools have documented an inverse relationship between the cover of turfing algae (particularly coralline algae) and canopy cover; when canopies are removed, turfing algae tend to increase (Benedetti-Cecchi & Cinelli 1992b, Melville & Connell 2001). However, we found a clear reduction in the percentage cover of *Corallina officinalis* following complete removal of the canopy. The principal mechanism underlying this decline may be the increase in light and temperature following the canopy removal. A high proportion of *C. officinalis* became bleached white and then died off. The dieback of coralline algae corresponded to the increase (and associated variability) in bare space. Intermediate densities of *Hormosira banksii* had an intermediate level of bare space between controls and complete removal. This bare space was not colonised except for the bloom of ephemeral *Ulva/Enteromorpha* species during spring at Mudstone Bay, illustrating the functional importance *H. banksii* in the community as the only large, perennial canopy-forming species able to survive throughout the mid shore.

There have been only a few other studies in the marine environment that have examined the effects of partial canopy removal on the understory. Kennelly (1987) reduced the cover of the subtidal kelp *Ecklonia radiata* in Australia by removing various sections of the plants (fronds, fronds plus stipe and complete plants). The partial removal treatments had similar effects to complete removal, with an increase in turfing algae and a decrease in encrusting algae. This effect was due to the die-off of damaged plants in the partial canopy treatments. Speidel et al. (2001) manipulated the canopy of the intertidal fucoid *Fucus gardneri* to 20, 40, 60, 80 and 100% cover, and examined the effects on the number of germlings, recovery of adult plants, grazing molluscs and ulvoid cover. Similar to our study, a reduction in the *F. gardneri* canopy resulted in no effect on molluscan macrograzers. *F. gardneri* recovery showed a non-linear response to partial removal of the adult canopy. Removal of all

plants set recovery back by several months, but if some plants remained (20 to 80% cover), recruitment and recovery occurred at a faster rate (Speidel et al. 2001). In our study, there was a significant linear response in fucoid algae and the number of taxa to disturbance levels (Fig. 3). However, multivariate analyses showed non-linear effects across the entire community, with the 3 intermediate levels having a similar response that was intermediate between the 0 and 100% levels of disturbance. Therefore, there appears to be 2 thresholds of responses of the community to disturbance.

Much research has been done on how variability in size (Farrell 1989, Kim & DeWreede 1996), frequency (Sousa 1979) and intensity (Schiel & Taylor 1999, Speidel et al. 2001) of disturbance affects communities. According to the non-equilibrium disturbance paradigm, the removal of a dominant species can prevent the monopolisation of limiting resources by a small number of species (Connell & Slayter 1977, Sousa 1979, Benedetti-Cecchi & Cinelli 1992a,b). The intermediate disturbance hypothesis predicts that maximum diversity should occur at intermediate intensities of disturbance (Connell 1978), although these intermediate responses are known to be complex and variable (Johst & Huth 2005). Consistent with this model, highest diversity in our experiment should have occurred with a 50% reduction of canopy cover, which left some plants laying over the substratum during periods of emersion and sheltering those species in the understory, while still providing space for new species to colonise. However, with taxa richness as a proxy for diversity, there was no 'intermediate disturbance' response. We found that the greatest diversity occurred in the unmanipulated control plots and, at the end of the experiment, there was a significant decrease in diversity with increasing levels of disturbance (Fig. 3). It appears in this system, therefore, that the dominance of a single species has mostly a positive effect on the local benthic community. In contrast to other studies in which the partial removal or thinning of a dominant species resulted in the creation of a mixed species matrix (Sousa 1979), on the southern shores of New Zealand it mostly results in a decline in taxa richness and changes in the composition of the surrounding community. Positive effects on a wide range of species from habitat modification by a dominant species clearly has a major influence on diversity and community structure (cf. Bertness et al. 1999, Bruno & Bertness 2001). Furthermore, the dominant species is resistant to invasion and replacement by other species. There are no large perennial, canopy-forming species that are physiologically capable of invading these areas. *Hormosira banksii* is a key species that is crucial to the overall diversity and maintenance of community structure on these shores. In other

such situations, with one or few dominant species and weak trophic interactions, it is likely that these sorts of positive interactions on associated species will be important to community processes and structure. Future studies could investigate how these may be altered by varying levels of disturbance and the extent to which there are gradient or threshold responses.

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Appendix 1. List of macroscopic benthic understory taxa found at Mudstone Bay (MB) and Wairepo Flats (WF) throughout the duration of the experiment. *Denotes presence of taxa

	MB	WF		MB	WF
Perennial algae			**Molluscan grazers**		
Fucoids			*Cantharidella tesselata*	*	*
Carpophyllum maschalocarpum	*	*	*Chiton glaucus*	*	*
Cystophora retroflexa	*		*Chiton pelliserpentis*	*	*
Cystophora scalaris	*	*	*Maorichiton caelatus*	*	*
Cystophora torulosa	*	*	*Margarella* spp.	*	*
Hormosira banksii	*	*	*Melagraphia aethiops*	*	
Coralline turfing algae			*Notoacmea* spp.		*
Corallina officinalis	*	*	*Risellopsis varia*		*
Haliptilon roseum		*	*Siphonaria* spp.	*	*
Jania micrarthrodia	*		*Turbo smaragdus*	*	*
Jania sp.	*	*	*Zeacumantus* spp.	*	*
Other algae			**Anemones**		
Echinothamnion sp.	*	*	*Actinia tenebrosa*	*	
Encrusting algae	*		*Actinothoe albens*	*	*
Gelidium caulacantheum	*	*	*Anthopleura* spp.	*	*
Halopteris spp.	*	*	*Cricophorus nutrix*	*	*
Laurencia thyrsifera	*	*	*Epiactis thompsoni*	*	
Non-geniculate corallines	*	*	*Isactinia olivacea*	*	*
Notheia anomala	*	*	**Other**		
Ephemeral algae			*Aulacomya maoriana* (Bivalvia)		*
Adenocystis utricularis	*	*	*Buccinulum* spp. (Gastropoda)	*	*
Blue-green algae	*	*	*Cancer novaezelandiae*	*	
Bryocladia ericoides	*		*Chamaesipho columna* (Cirripedia)		
Bryopsis vestia	*		*Cominella glandiformis* (Gastropoda)		*
Centrocerus spp.	*		*Cominella maculosa* (Gastropoda)	*	*
Ceramium spp.	*	*	*Halicarcinus* spp. (Decapoda)	*	*
Chaetomorpha aerea	*		*Haustrum haustorium* (Gastropoda)	*	*
Chaetomorpha coliformis	*	*	*Mytilus galloprovincialis* (Bivalvia)		*
Chaetomorpha valida	*		Nereidae	*	*
Champia novae-zealandiae	*	*	*Ophionereis fasciata* (Echinodermata)	*	*
Codium convalutum	*		Opisthobranchs	*	*
Colpomenia sinuosa	*	*	*Patiriella regularis* (Echinodermata)		*
Dictyota spp.	*	*	Sabellariidae	*	
Dipterosiphonia heteroclada	*		Serpulidae	*	*
Ectocarpus spp.	*	*	Sphaeromatidae (Isopoda)	*	*
Enteromorpha bulbosa	*	*	Terebellidae	*	*
Gigartina chapmanii	*		UID Sponge	*	*
Hymenena sp.	*	*	UID Whelk A	*	*
Leathesia difformis	*	*	Valvifera (Isopoda)	*	
Lophurella caespitosa	*				
Petalonia fasciata	*				
Pleonosporium hirtum	*	*			
Polysiphonia spp.	*				
Scytosiphon lomentaria	*	*			
UID Red Filament	*				
Ulva spp.	*	*			