

Establishment of the introduced kelp *Undaria pinnatifida* in Tasmania depends on disturbance to native algal assemblages

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Abstract

Despite recent rapid increases in the occurrence of nonindigenous marine organisms in the marine environment, few studies have critically examined the invasion process for a marine species. Here we use manipulative experiments to examine processes of invasion for the Asian kelp *Undaria pinnatifida* (Harvey) Suringar at two sites on the east coast of Tasmania. Disturbance to reduce cover of the native algal canopy was found to be critical in the establishment of *U. pinnatifida*, while the presence of a stable native algal canopy inhibited invasion. In the first sporophyte growth season following disturbance of the canopy, *U. pinnatifida* recruited in high densities (up to 19 plants m⁻²) while remaining rare or absent in un-manipulated plots. The timing of disturbance was also important. *U. pinnatifida* recruited in higher densities in plots where the native canopy was removed immediately prior to the sporophyte growth season (winter 2000), compared with plots where the canopy was removed 6 months earlier during the period of spore release (spring 1999). Removal of the native canopy also resulted in a significant increase in cover of sediment on the substratum. In the second year following canopy removal, *U. pinnatifida* abundance declined significantly, associated with a substantial recovery of native canopy-forming species. A feature of the recovery of the native algal canopy was a significant shift in species composition. Species dominant prior to canopy removal showed little if any signs of recovery. The recovery was instead dominated by canopy-forming species that were either rare or absent in the study areas prior to manipulation of the canopy. © 2003 Elsevier B.V. All rights reserved.

Keywords: Invasion process; Introduced macroalgae; Establishment; Disturbance; Canopy removal; *Undaria pinnatifida*

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1. Introduction

The introduction of nonindigenous species into the marine environment is recognised as a major threat to marine ecosystems, with potentially dramatic effects on biological diversity, productivity, habitat structure and fisheries (Carlton, 1999; Bax et al., 2001). Over the past two decades there has been a vast increase in the worldwide spread of nonindigenous organisms, due mainly to dispersal via human-mediated transport (Bax et al., 2001). It is estimated that more than 15,000 species of marine organisms may be transported around the world in ships' ballast water each week (Carlton, 1999). This rapid acceleration in spread of nonindigenous marine organisms now poses a major challenge for management of marine ecosystems. When presented with a large number of introduced species, managers must decide which species have immediate priority for control, which to control if time and finances are available, and which to leave alone (Hiebert, 1997).

Knowledge of the threat posed by an introduced species is essential to effectively prioritise species for management purposes (Byers et al., 2002). One important aspect of threat is associated with the invasion process itself, particularly the role of disturbance in the establishment of an introduced species. While there is substantial evidence showing that disturbance can be a key mechanism in the invasion of both terrestrial and freshwater organisms (e.g. Hobbs and Adkins, 1988; Hobbs and Huenneke, 1992; Lodge, 1993; Moyle and Light, 1996; D'Antonio et al., 1999), relatively few examples exist for marine communities (but see Nichols et al., 1990; Reusch and Williams, 1999).

In recent years the kelp *Undaria pinnatifida* (Harvey) Suringar has experienced a global range expansion in temperate waters. Native to Japanese, Korean and Chinese coasts, *U. pinnatifida* has spread to the Atlantic and Mediterranean coasts of Europe (Curiel et al., 1998; Castric-Fey et al., 1993; Fletcher and Manfredi, 1995) and to shores of New Zealand (Hay and Luckens, 1987), Argentina (Casa and Piriz, 1996) and Australia (Campbell and Burrridge, 1998; Sanderson, 1990). While the plant was intentionally introduced to the Atlantic Coast of Europe in 1983 (Floc'h et al., 1991), introductions to other areas are all thought to have occurred accidentally via international shipping activity, mediated either through hull fouling or discharge of ballast water, or associated with translocation of aquaculture organisms (Perez et al., 1981).

While the occurrence and spread of *U. pinnatifida* has been well documented, the mechanism of its invasion and impact on native communities has received little attention. In one of the few experimental studies to date, local kelp species were shown to be resistant to invasion by *U. pinnatifida* on the Atlantic coast of France (Floc'h et al., 1996). Despite this result, it is speculated widely that *U. pinnatifida* is a highly invasive species, able to competitively displace native species in sheltered to moderately exposed waters (Rueness, 1989; Fletcher and Manfredi, 1995).

In the Mercury Passage, where the plant was first recorded in Tasmania, *U. pinnatifida* exhibits an annual growth pattern. Macroscopic sporophytes typically recruit in winter growing through spring to a length of up to 2 m. Reproduction is thought to occur during late spring–early summer, after which the plant degenerates. Sporophytes are generally absent from reefs by the end of summer (Sanderson and Barrett, 1989). *U. pinnatifida* occurs most abundantly on urchin 'barrens' characterized by high densities of the sea urchin

Heliocidaris erythrogramma and low cover of native algae. In these habitats *U. pinnatifida* forms monospecific stands during the sporophyte growth season (Sanderson, 1990). Recent work has demonstrated a significant negative correlation between sea urchin densities and native algae, but a significant positive correlation between sea urchins and *U. pinnatifida* (Johnson, unpublished). *U. pinnatifida* also occurs abundantly in other disturbed habitats such as areas of sandscour at the base of reefs and on unstable substrata, while it occurs rarely in established macroalgal stands (Sanderson, 1997; C. Johnson, pers. comm.).

Observations of *U. pinnatifida* occurring abundantly in disturbed habitats suggest disturbance is potentially playing a significant role in its establishment. *U. pinnatifida* also manifests many characteristics of an opportunistic species, such as short lifespan, high growth rate, a high biomass invested in reproduction, small propagule size and high number of propagules released, and a single reproductive episode (Grime, 1977; Clayton, 1990). Species with these features are commonly associated with disturbance (Clayton, 1990). If *U. pinnatifida* requires disturbance to establish, then there exists a range of management options, which include targeting the cause of the disturbance rather than the plant itself. If disturbance is linked to anthropogenic activity, then managing disturbance may prove a cost-effective option. Alternatively, if *U. pinnatifida* is capable of displacing native algae in the absence of any primary mechanism of facilitation such as disturbance, then it represents a major threat to the integrity of native algal communities. Under this scenario, management may need to target the plant directly.

In this study we investigate the role of disturbance as a process facilitating invasion of dense stands of *U. pinnatifida*. Manipulative experiments were used to examine the relationship between disturbance, establishment of *U. pinnatifida* and subsequent recovery of native species.

2. Materials and methods

2.1. Study sites

The experiment was conducted at 7–12 m depth on rocky reef in the Mercury Passage, on the east coast of Tasmania (Fig. 1). Reefs in this area support a variety of algal communities, ranging from sea urchin ‘barrens’ (dominated by *H. erythrogramma*) seasonally dominated by *U. pinnatifida*, to areas dominated by diverse stands of native canopy-forming algae. Our experiments were conducted at two sites (Flensers Point and Lords Bluff), dominated by native algal species and as far as practically possible from the nearest dense stands of *U. pinnatifida* (ca. 0.2 km at Lords Bluff and 1.0 km at Flensers Point).

Both sites are characterized by gently sloping rocky substratum to a depth of 12–14 m, with moderate topographic relief. Although there is slight variation in aspect between the two sites, they are similarly exposed to easterly swells, which although infrequent, can be large. Using the classification scheme proposed for Tasmanian subtidal communities by Edgar (1984), the sites are described as moderately exposed and support a mixed algal assemblage.

Flensers Point was dominated by the furoid *Seirococcus axillaris*, however, the common kelp *Ecklonia radiata* and the fucoids *Carpoglossum confluens*, *Cystophora*

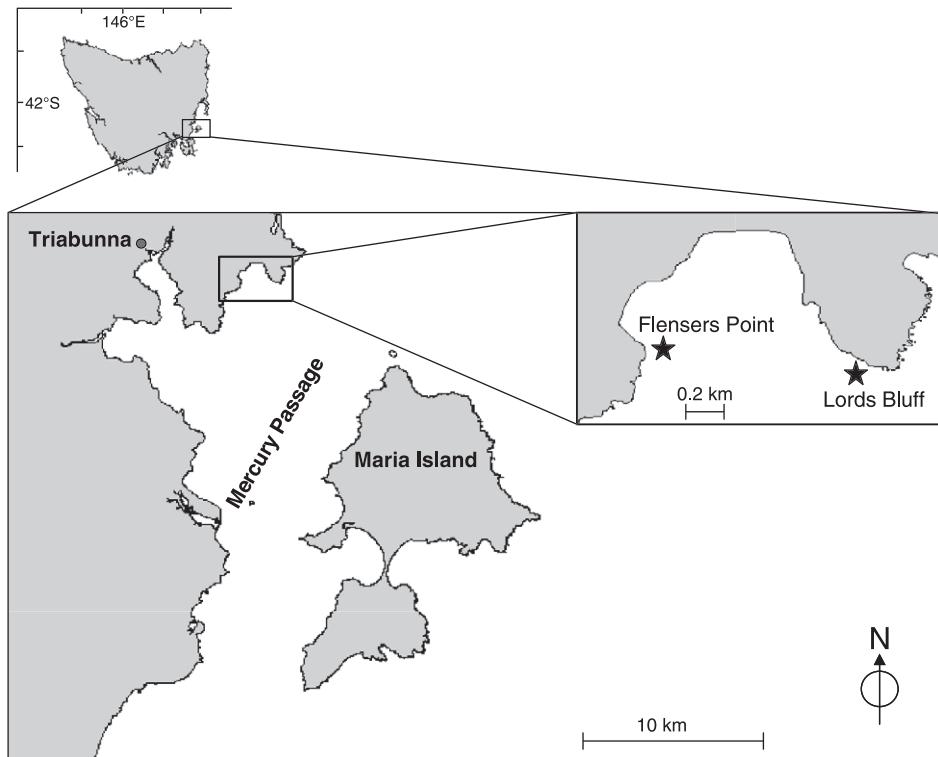


Fig. 1. Map of Mercury Passage showing the location of study sites at Flensers Point and Lords Bluff.

retroflexa and *Sargassum fallax* were also distributed patchily throughout the study area. At Lords Bluff, a range of canopy-forming species were found including *E. radiata*, *Phyllospora comosa*, *C. confluens* and *S. axillaris*. The understorey at both sites consisted of a diverse assemblage of turfing algal species, encrusting algae and invertebrates.

2.2. Experimental manipulations

Experimental manipulations were applied to fixed 16-m² quadrats, while response variables were monitored only in the inner 4-m² of each quadrat to minimize edge effects. The experiment followed a three-way factorial design representing all possible combinations of two levels of each of three factors, viz.:

1. Disturbance (two levels; 100% removal of native algal canopy, no removal)
2. *U. pinnatifida* spore enhancement (two levels; background, enhanced)
3. Site (two sites).

Treatments requiring manipulation were assigned at random at each site, and there were three replicates of each treatment. The disturbance treatment, involving physical removal

of the macroalgal canopy, mimics natural disturbance caused by urchin grazing and storms. Canopy removal was conducted initially in spring (November 1999), during the period of spore release by *U. pinnatifida* (Sanderson, 1997). Plants were removed by carefully cutting stipes immediately above the holdfast, while understory species were left intact.

In treatments involving enhancement of *U. pinnatifida* spores, mesh bags were filled with fertile sporophylls and hung over the plots. Fresh material was added every 4–6 weeks for as long as fresh sporophyll material was available in sufficient quantities. Containing the sporophylls in a coarse (20 mm) mesh bag prevented their grazing by toothbrush leatherjackets (*Acanthaluteres vittiger*) which caused significant damage to unprotected sporophylls. Spore enhancements were undertaken from Nov. 1999 to Jan. 2000 and from Sep. 2000 to Jan. 2001.

To minimise confounding of treatments involving *U. pinnatifida* spores, experimental plots were separated by a minimum distance of 10 m. We assumed that the effective spore shadow of *U. pinnatifida* is limited and predominantly within a few metres of the parent plant, as has been demonstrated for other large brown algae (Ambrose and Nelson, 1982; Dayton, 1985; Andrew and Viejo, 1998).

To examine the effect of timing of disturbance on invasion by *U. pinnatifida*, an additional canopy removal was employed in winter (June 2000). In contrast to the initial canopy removal in spring, this removal of native algae was immediately prior to the appearance of macroscopic *U. pinnatifida* sporophytes. At each site there were three replicate plots of this treatment.

2.3. Assessment of algal abundance

The algal community was assessed immediately prior to manipulation and at three monthly intervals thereafter for 24 months. Abundance of canopy-forming species was measured in terms of stipe counts (i.e. density) and percentage cover. Stipe counts involved recording all adult plants >30 cm in length in each 4-m² plot. Abundance of understory algae, sessile invertebrates and sediment was assessed in terms of percentage cover. Percentage cover was estimated with a 0.25-m² quadrat using a point intercept method. The quadrat was divided with a grid of 49 evenly spaced intersections and was laid flat on the reef during algal assessment. Algae occurring under each intercept and one corner of the quadrat were recorded, to give a total of 50 intersections per quadrat. Four randomly positioned quadrats were assessed in this way for each plot on every sampling occasion. Where a dense cover of canopy algae was present in a quadrat, cover was assessed in a two-stage process. First, cover of canopy algae was estimated. Secondly, the fronds of the canopy species were moved aside to allow assessment of the cover of understory algae, sessile invertebrates and sediment. Accordingly, the total percentage cover for individual quadrats can exceed 100%.

Organisms were identified in situ to the highest taxonomic resolution possible. For canopy algae, identification to species level was possible, however, it was necessary to allocate other species to species complexes or guilds (e.g. foliose red algae, brown turf algae).

2.4. Analysis

2.4.1. Univariate analyses

Densities (i.e. stipe counts) were analysed using a three-way Model I analysis of variance (ANOVA) with the main factors of canopy removal (two levels), *U. pinnatifida* spore enhancement (two levels) and site (two levels) all treated as fixed factors. Site was considered a fixed factor because possible sites available for the experiment (i.e. of similar depth, exposure, topography, extent of reef and proximity to nearest dense *U. pinnatifida* stand) was essentially limited to the two sites chosen.

Analysis of responses to treatments assessed in November 2000 (1 year after the initial canopy removal) revealed no effect of *U. pinnatifida* spore enhancement on subsequent *U. pinnatifida* density (Table 1). In tests conducted on cover of native algae, the effect of *U. pinnatifida* spore enhancement was similarly highly nonsignificant. Consequently, treatments of $\pm$ *U. pinnatifida* spores were excluded from further analysis, enabling pooling of treatments and greater power to examine the effect of canopy removal.

In subsequent analyses in which treatments of $\pm$ spore enhancement were pooled, data on stipe counts were analysed by a two-way Model I ANOVA, while a three-factor Model III nested ANOVA was used for cover data. Both analyses included canopy removal (three levels) and site (2 levels). There were three levels of canopy removal because these analyses included the treatment of winter canopy removal. The nested ANOVA included the effect of plot nested within all combinations of canopy removal*site as a random factor. The design was unbalanced since there were three replicates of each treatment for the winter canopy removal treatment, but six replicates of the remaining treatments (after pooling across treatments with $\pm$ *U. pinnatifida* spore enhancement). This analysis was conducted on data collected during assessment of algal community composition in November 2000 and November 2001. This allowed examination of the algal response to canopy removal during the peak period of *U. pinnatifida* sporophyte development, 1 and 2 years after the initial canopy removals. For both density and cover data, three planned comparisons were conducted for each site, viz. (i) control vs. spring 1999 canopy removal, (ii) control vs. winter 2000 canopy removal, and (iii) spring 1999 vs. winter

Table 1

Three-factor Model I ANOVA examining the response of *Undaria pinnatifida* in November 2000 to experimental treatments initiated during November 1999. The analysis was conducted on square root transformed stipe counts of all *U. pinnatifida* plants >30 cm in length in each experimental plot ($n=3$). Note that the effect of the *U. pinnatifida* spore enhancement treatment was highly nonsignificant

Source of variation	df	MS	F	P
Canopy removed (C)	1	38.4816	64.27	0.0001
Enhanced spores (E)	1	0.0487	0.08	0.7790
Site (S)	1	6.6502	11.11	0.0042
C*E	1	1.4553	2.43	0.1385
C*S	1	5.8066	9.70	0.0067
S*E	1	0.0846	0.14	0.7120
C*S*E	1	0.2115	0.35	0.5606
Error	16	0.5987		

2000 canopy removal. The Dunn–Sidak adjustment ($\alpha_{\text{adjusted}} = 1 - (1 - \alpha)^p$, where p = number of tests) was used to adjust the significance level associated with planned comparisons.

Prior to all univariate tests, transformations to stabilize variances were determined from the relationship between group standard deviations and means (Draper and Smith, 1981). Transformations are expressed in terms of the untransformed variate, Y . All univariate tests were undertaken using the SAS® statistical package.

2.4.2. Multivariate analyses

To describe community responses to treatments and assess the significance of differences between treatments, nonmetric multi-dimensional scaling (MDS) and nonparametric MANOVA (np-MANOVA) were used, respectively. The relationship between controls and canopy removal plots was compared before manipulation and 2 years after manipulation at each site. To identify species most responsible for any observed differences in community structure, SIMPER analysis was conducted. These analyses were based on Bray–Curtis similarity matrices derived from percentage cover data after a fourth root transformation to reduce the influence of dominant species. MDS and SIMPER analyses were undertaken using the PRIMER 4.0 software (Carr and Clarke, 1994), while np-MANOVAs were undertaken as outlined in Anderson (2001). For np-MANOVA, the winter canopy removals were excluded from the analysis because of the inherent problems of low power as a result of low replication ($n=3$) and, therefore, the small number of permutations available to determine the distribution of the test statistic.

3. Results

3.1. The effect of canopy removal on the density of *U. pinnatifida* and native canopy-forming algae

The effect of canopy removal had a dramatic effect on *U. pinnatifida* density in the spring growth period of the following year (Fig. 2a). While *U. pinnatifida* remained rare or absent in controls, plots from which the canopy was removed were characterized by the appearance of *U. pinnatifida* sporophytes, to a maximum density of 19 plants m^{-2} in some plots. The trend was qualitatively consistent among sites, however, there were significantly more *U. pinnatifida* plants associated with the Lords Bluff site, evidenced by a highly significant “canopy removal*site” interaction ($F=14.71$, $df_{2,24}$, $P<0.0001$). The timing of disturbance events also influenced *U. pinnatifida* abundance. Canopy removals conducted in winter 2000, at the onset of the period of sporophyte growth and development, exhibited higher numbers of *U. pinnatifida* plants compared to plots where the canopy was removed the previous spring. This trend was evident at both sites, although a statistically significant result was observed at Lords Bluff ($F=44.41$, $df_{1,24}$, $P<0.0001$), but not at Flensers Point at the adjusted α level ($F=7.31$, $df_{1,24}$, $P<0.0124$; $\alpha_{\text{adjusted}}=0.0085$).

Algal assessments conducted in November 2001 (during the second season of *U. pinnatifida* sporophyte growth following disturbance) revealed a significant effect of

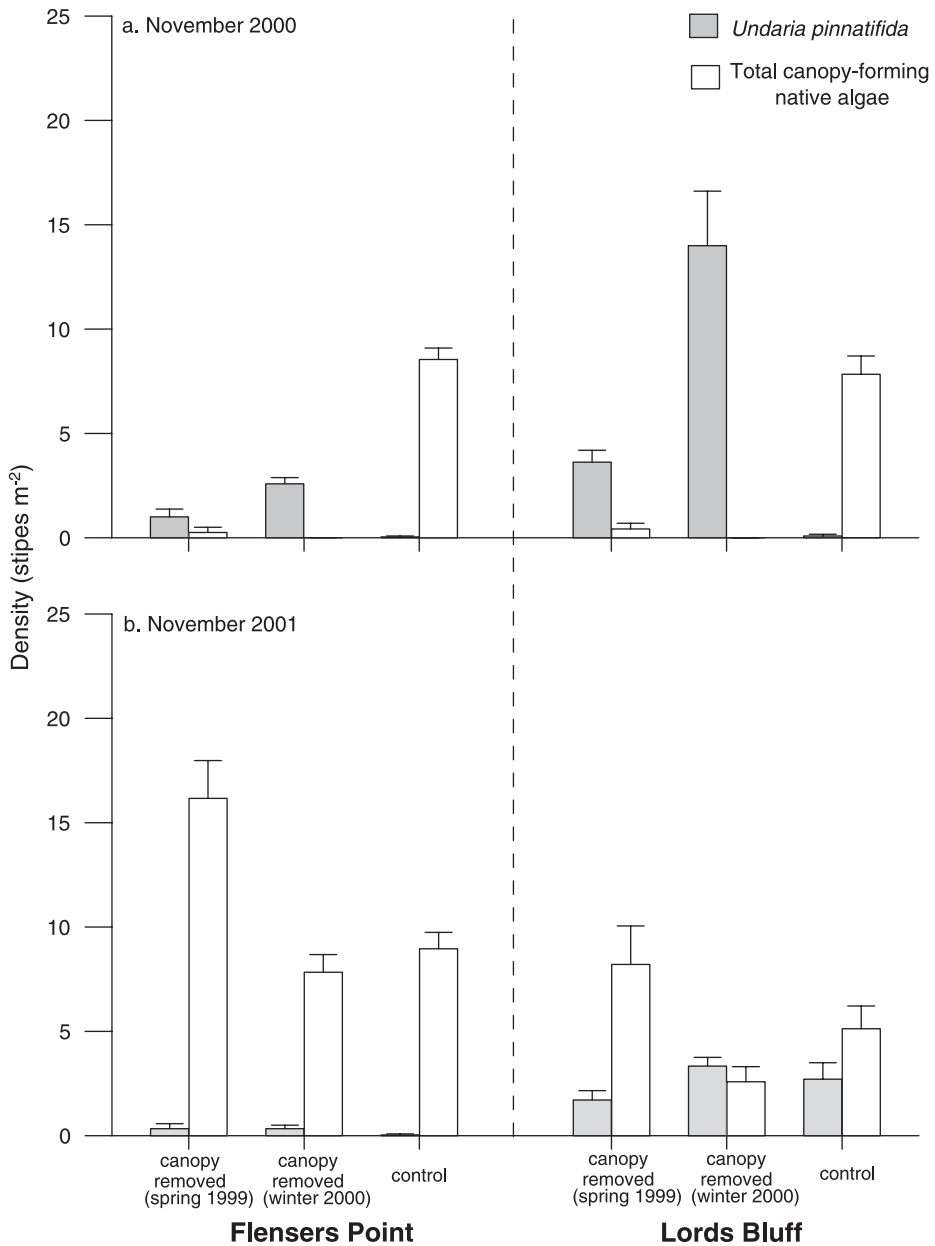


Fig. 2. Effect of canopy removals on abundance of *Undaria pinnatifida* and total canopy-forming native algae assessed in (a) November 2000 and (b) November 2001. Data are means ($\pm$ SE) of stipe counts ($n=6$ plots per treatment for spring canopy removal and controls; $n=3$ plots per treatment for winter canopy removal). Note that stipe counts represent plants >30 cm total length. Canopy-forming native species include *Ecklonia radiata*, *Phyllospora comosa*, *Seirococcus axillaris*, *Carpoglossum confluens*, *Cystophora moniliformis*, *C. retroflexa*, *Sargassum fallax* and *S. vestitum*.

“site” ($F=38.31$, $df_{1,24}$, $P<0.0001$) but no significant response of *U. pinnatifida* to the canopy manipulations conducted 18 and 24 months previously (Fig. 2b). At Flensers Point, very low levels of *U. pinnatifida* were observed in ‘canopy removal’ plots in November 2001 while the density of native species increased markedly (Fig. 2b). In contrast, *U. pinnatifida* plants were observed in moderate levels (mean 5 plants m^{-2}) in all treatments at Lords Bluff (including controls). The number of *U. pinnatifida* plants in plots from which the canopy was removed at Lords Bluff decreased significantly from November 2000 to the November 2001 assessment, while density of native species increased to levels comparable with controls (Fig. 2b). It should also be noted that the density of native canopy-forming algae declined in control plots at Lords Bluff between November 2000 (mean 7.8 plants m^{-2}) and November 2001 (mean 5.1 plants m^{-2}). This was due to a decline in *P. comosa* and *E. radiata* associated with above average water temperatures during the 2000/2001 summer.

3.2. Native canopy-forming algae: species composition

Although densities of native canopy-forming algae had recovered in plots from which the canopy was removed by November 2001 (24 months after the initial canopy removal), the species composition in control plots and recovered ‘canopy removal’ plots was distinctly different. While *Seirococcus axillaris* continued to dominate control areas throughout the experiment at Flensers Point, the assemblages that developed in areas where the canopy was removed consisted mainly of *S. fallax*, *C. retroflexa*, *Sargassum vestitum* and, to a lesser extent, *Cystophora moniliformis* (Fig. 3). Similarly, at Lords Bluff, the assemblage in un-manipulated control plots dominated by *E. radiata*, *P. comosa*, *S. axillaris* and *C. confluens* was replaced by *C. retroflexa* and *C. moniliformis* in the ‘canopy removal’ treatments (Fig. 3). At both sites, species abundant in control areas were rare or absent in plots from which the canopy was removed, so differences between treatments could not be tested statistically.

3.3. Recovery of native canopy algae: percentage cover

While stipe density was appropriate to examine some aspects of the response of *U. pinnatifida* and native canopy algae, a more detailed examination of recovery patterns of the entire community was based on plant cover. Cover can provide greater sensitivity than data describing density, largely reflecting the different growth forms and densities among algal species (Johnson and Mann, 1993).

There were substantial differences among sites in the response of native canopy-forming algae to canopy removal. During the first year following canopy removal there was a gradual increase in cover at Flensers Point, although by November 2000 cover in control plots ($73\% \pm 6.5$ SE) was still considerably greater than that in plots where canopy removals had been conducted in spring 1999 ($28\% \pm 5.2$ SE) and winter 2000 ($11\% \pm 1.3$ SE) (Fig. 4; Table 2). However, during 2001 the cover of native canopy-forming algae increased dramatically in plots from which the canopy had been removed in both spring 1999 and winter 2000, reflecting the trend shown for stipe counts. By November 2001,

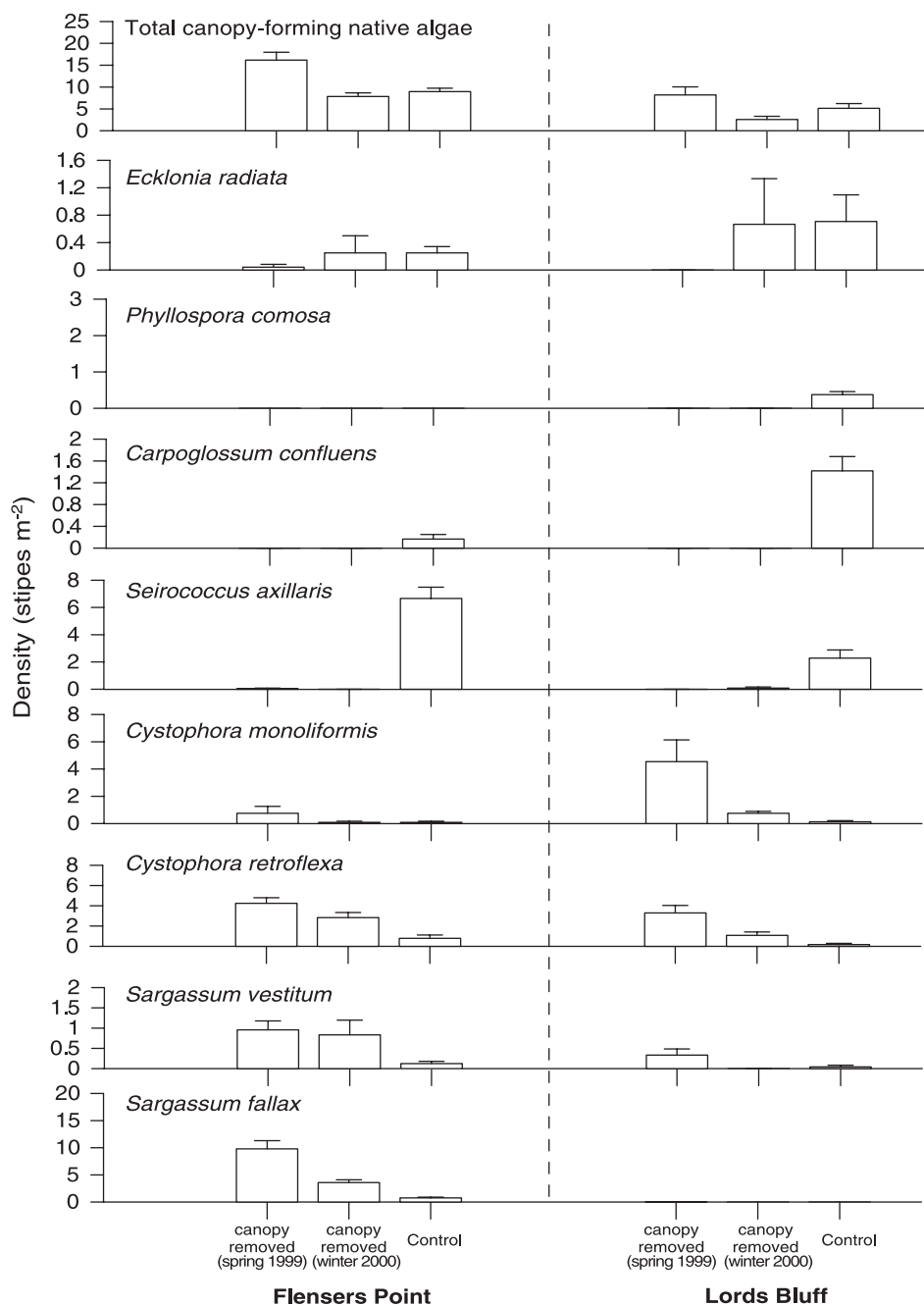


Fig. 3. Abundance of dominant canopy-forming native algae in relation to canopy removal at two sites in Mercury Passage, November 2001. Data represent mean stipe densities (+ SE) ($n = 6$ replicate plots per treatment for spring canopy removals and controls; $n = 3$ replicates plots per treatment for winter canopy removals).

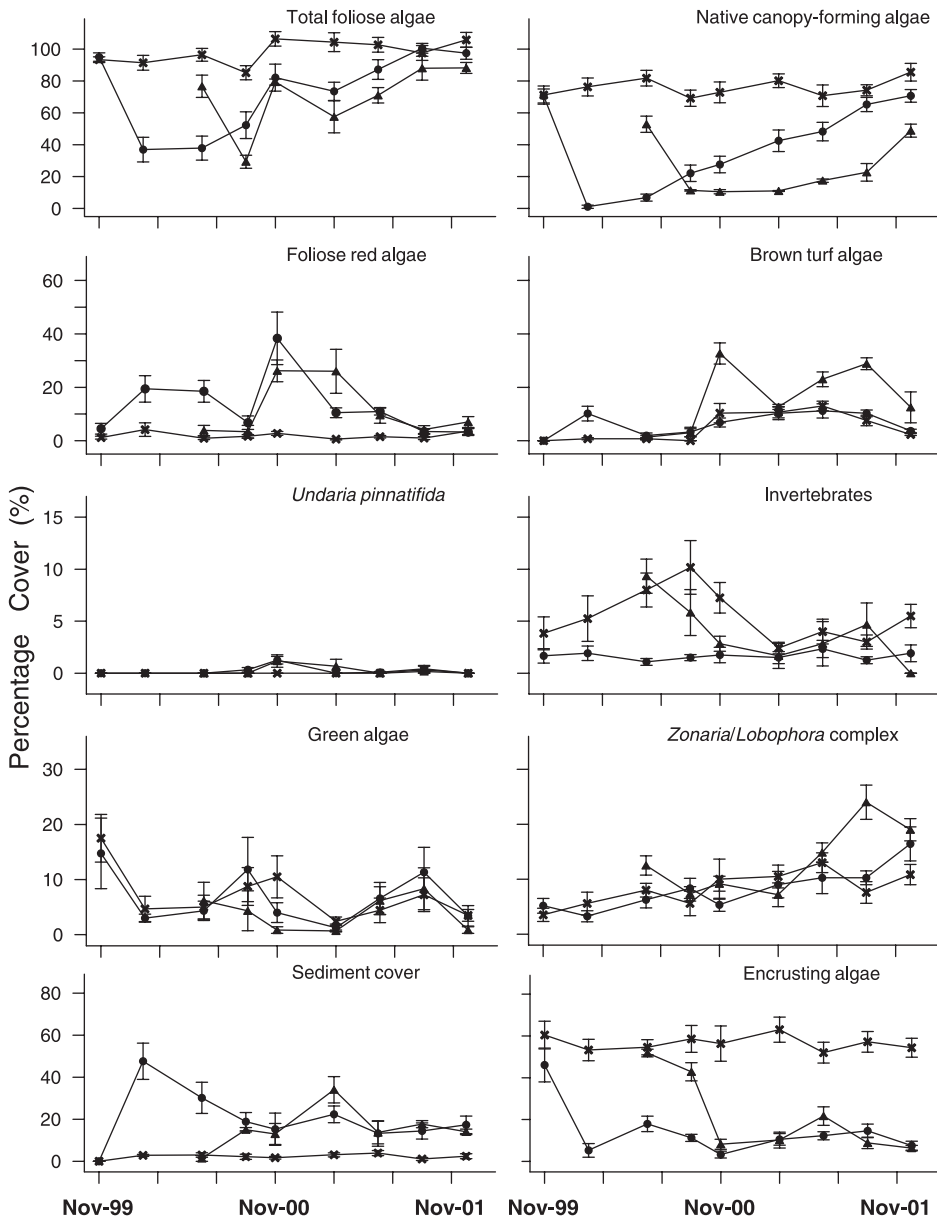


Fig. 4. Effect of removal of native canopy-forming algae on the cover of various algal guilds, invertebrates and the sediment matrix at Flensers Point. Data are mean percentage cover ($\pm$ SE) ($n=6$ plots per treatment for spring canopy removals and controls; $n=3$ plots per treatment for winter canopy removals). Circles = canopy removed spring 1999; triangles = canopy removed winter 2000; crosses = control.

Table 2

Analysis of the effect of removing native canopy-forming algae on the cover of various algal guilds, invertebrates and the sediment matrix, assessed in November 2000. Results are of the overall ANOVA examining the effect of canopy removal and site, and of the three planned comparisons for each site. For planned comparisons, “co”= control, “sp”=spring canopy removal, while “wi”= winter canopy removal. Significant *P*-values are shown in bold face: *P*-values < 0.05 are significant for the main analysis; *P*-values < 0.0085 are significant for the planned comparisons (α adjusted using Dunn–Sidak method). All of the tests presented use the MS Plot (C*S) as the error term

Guild (transformation)	Source of variation				Planned comparisons					
					Flensers point			Lords Bluff		
	Canopy removal (C)	Site (S)	C*S	Plot (C*S)	co vs. sp	co vs. wi	sp vs. wi	co vs. sp	co vs. wi	sp vs. wi
	<i>F</i> (<i>df</i> = 2,24)	<i>F</i> (<i>df</i> = 1,24)	<i>F</i> (<i>df</i> = 2,24)	<i>F</i> (<i>df</i> = 24,90)	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>
	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>
Sediment cover	18.50	1.58	1.79	5.05	17.46	19.20	0.94	73.71	42.20	0.25
[log (<i>Y</i> + 1)]	0.0001	0.2205	0.1879	0.0001	0.0001	0.0001	0.3337	0.0001	0.0001	0.6189
Encrusting algae	117.32	8.28	4.84	2.11	138.70	33.24	14.83	252.78	123.58	3.48
[log (<i>Y</i> + 1)]	0.0001	0.0083	0.0171	0.0061	0.0001	0.0001	0.0002	0.0001	0.0001	0.0648
Total foliose algae	22.14	12.93	2.38	2.95	16.44	13.57	0.14	52.93	61.18	3.54
(no transformation)	0.0001	0.0015	0.136	0.0001	0.0001	0.0004	0.7090	0.0001	0.0001	0.0624
Large brown algae	103.46	4.27	3.44	2.50	81.34	102.90	7.73	174.80	210.57	13.81
(no transformation)	0.0001	0.0498	0.0487	0.0010	0.0001	0.0001	0.0064	0.0001	0.0001	0.0003
Foliose red algae (sqrt)	15.63	6.84	1.53	6.05	68.03	31.19	1.32	16.65	20.81	1.51
	0.0001	0.0152	0.2373	0.0001	0.0001	0.0001	0.2527	0.0001	0.0001	0.2212
Brown turf [log (<i>Y</i> + 1)]	14.67	4.04	4.09	1.43	0.45	18.94	14.45	23.21	17.17	0.04
	0.0001	0.0559	0.0296	0.1143	0.5018	0.0001	0.0002	0.0001	0.0001	0.8335
<i>Undaria pinnatifida</i>	40.66	54.86	17.01	1.60	5.96	5.62	0.14	59.60	146.43	33.61
[log (<i>Y</i> + 1)]	0.0001	0.0001	0.0001	0.0586	0.0162	0.0194	0.7065	0.0001	0.0001	0.0001
Invertebrates (sqrt)	39.99	10.19	4.76	1.27	20.30	5.94	1.54	83.79	29.06	4.34
	0.0001	0.0039	0.0181	0.2060	0.0001	0.0164	0.2171	0.0001	0.0001	0.0394
Green algae	1.94	3.86	2.45	1.40						
(no transformation)	0.1654	0.0612	0.1074	0.1310						
<i>Zonaria/Lobophora</i> complex	0.06	9.46	2.54	1.65	4.41	0.09	1.99	2.72	0.21	0.79
(no transformation)	0.9435	0.0052	0.0997	0.0471	0.0379	0.7599	0.1615	0.1016	0.6468	0.3762

there was no significant difference in the cover of native canopy species in control plots ($86\% \pm 5.6$ SE) and plots from which the canopy was removed in spring 1999 ($71\% \pm 4.0$ SE). Cover in plots from which the canopy was removed in winter 2000 had increased markedly ($49\% \pm 4.1$ SE) but still remained significantly lower than that in controls (Fig. 4; Table 3).

At Lords Bluff there was also a gradual increase in cover of native canopy-forming species in the year following canopy removals in spring 1999 ($31\% \pm 6.3$ SE) and winter 2000 ($9\% \pm 1$ SE) (Fig. 5). The trend of recovery stalled somewhat in 2001, with spring 1999 ($34\% \pm 5.8$ SE) and winter 2000 ‘canopy removal’ plots ($15\% \pm 4.0$ SE) showing only slight increases in cover. Unlike Flensers Point, where cover in controls remained consistently high (mean 69–86%) over the entire 24 months of the study, the cover in control areas at Lords Bluff declined significantly during the study period, averaging 98% in November 2000 but declining to 54% in February 2001. This was mainly associated with the declines in *P. comosa* and *E. radiata*. Despite this decline in cover in control plots, cover in ‘canopy removal’ plots was still significantly lower than in controls by November 2001 (Fig. 5; Table 3).

3.4. Response of understory algae to canopy disturbance

In interpreting the response of *U. pinnatifida* and native canopy-forming algae to disturbance, it is also important to consider understory algal species given that occupation of space by turfing algal species can inhibit recruitment of canopy-forming species (Dayton et al., 1984; Kennelly, 1987a; Airoidi, 1998). Thus, the response of turfing species to canopy removal may have significant implications for both invasion of *U. pinnatifida* as well as the recovery of native canopy-forming species.

3.4.1. Foliose red algae

There was a significant response of foliose red understory algae to canopy removal, although the response varied significantly among sites and with the time since canopy removal. At Flensers Point, foliose red algal cover remained at uniformly low levels ($< 5\%$) in control plots for the duration of the experiment while fluctuating significantly in treatments in which the canopy was removed (Fig. 4). Cover increased to a peak in November 2000 for canopy removals conducted in both spring 1999 ($38\% \pm 9.8$ SE) and winter 2000 ($26\% \pm 4.1$ SE), after which a gradual decrease was recorded. No significant effect on foliose red algae of disturbance to the canopy was detected on completion of the final assessment in November 2001, 18 and 24 months after implementation of canopy removals (Table 3).

At Lords Bluff, cover of foliose red algae remained at low levels in all treatments prior to November 2000, when cover increased in plots from which the canopy was removed in spring 1999 ($11\% \pm 3.7$ SE) and winter 2000 ($18\% \pm 8.6$ SE) relative to controls ($1\% \pm 1.0$ SE) (Fig. 5). Cover in canopy removal treatments remained significantly higher than in controls for the remainder of 2001, despite a slight increase in cover in the control areas (Fig. 5). The significant “site” effect evident in the November 2001 assessment reflected the higher cover of foliose red algae observed in all treatments at Lords Bluff compared with Flensers Point.

Table 3

Analysis of the effect of removing native canopy-forming algae on the cover of various algal guilds, invertebrates and the sediment matrix, assessed in November 2001

Guild (transformation)	Source of variation				Planned comparisons					
					Flensers point			Lords Bluff		
	Canopy removal (C)	Site (S)	C*S	Plot (C*S)	co vs. sp	co vs. wi	sp vs. wi	co vs. sp	co vs. wi	sp vs. wi
	<i>F</i> (<i>df</i> =2,24)	<i>F</i> (<i>df</i> =1,24)	<i>F</i> (<i>df</i> =2,24)	<i>F</i> (<i>df</i> =24,90)	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>
	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>	<i>P</i>
Sediment cover (sqrt)	8.09 0.0021	3.03 0.0948	0.21 0.8093	7.20 0.0001	24.32 0.0001	14.83 0.0002	0.03 0.8607	13.85 0.0003	18.99 0.0001	1.74 0.1898
Encrusting algae (sqrt)	85.18 0.0001	14.28 0.0009	1.60 0.2230	1.62 0.0541	125.82 0.0001	86.21 0.0001	0.02 0.8997	89.02 0.0001	39.98 0.0001	1.90 0.1702
Total foliose algae (no transformation)	5.96 0.0079	9.30 0.0055	1.90 0.1720	2.14 0.0053	1.05 0.3087	3.10 0.0808	0.86 0.3560	0.03 0.8623	19.29 0.0001	20.55 0.0001
Large brown algae (no transformation)	13.47 0.0001	25.19 0.0001	0.47 0.6328	2.66 0.0005	4.74 0.0316	19.29 0.0001	6.84 0.0101	16.08 0.0001	31.92 0.0001	5.64 0.0192
Foliose red algae (sqrt)	0.1658 4.00 0.0316	0.0028 5.72 0.0249	0.3765 9.09 0.0012	0.0001 1.87 0.0186	0.8158 1.15 0.2854	0.1193 11.72 0.0009	0.0810 6.49 0.0122	0.0038 15.47 0.0001	0.0079 3.29 0.0723	0.7704 25.25 0.0001
<i>Undaria pinnatifida</i> (no transformation)	1.23 0.2960	18.58 0.0001	1.23 0.2960	1.03 0.4400	0.00 1.0000	0.00 1.0000	0.00 1.0000	3.52 0.0630	0.10 0.7550	3.41 0.0675
Invertebrates (sqrt)	4.30 0.0253	1.49 0.2346	2.21 0.1311	1.80 0.0255	9.59 0.0025	16.93 0.0001	2.52 0.1155	0.64 0.4261	0.29 0.5896	0.01 0.9116
Green algae (no transformation)	0.24 0.7893	0.12 0.7290	0.50 0.6100	1.32 0.1731						
<i>Zonaria/Lobophora</i> complex (sqrt)	5.81 0.0088	10.68 0.0033	5.98 0.0078	1.36 0.1498	4.35 0.0393	4.96 0.0279	0.27 0.6013	7.59 0.0069	6.18 0.0144	22.41 0.0001

Results are of the overall ANOVA examining the effect of canopy removal and site, and of the three planned comparisons for each site. For planned comparisons, “co”= control, “sp”=spring canopy removal, while “wi”=winter canopy removal. Significant *P*-values are shown in bold face: *P*-values < 0.05 are significant for the main analysis; *P*-values < 0.0085 are significant for the planned comparisons (α adjusted using Dunn–Sidak method). All of the tests presented use the MS Plot (C*S) as the error term.

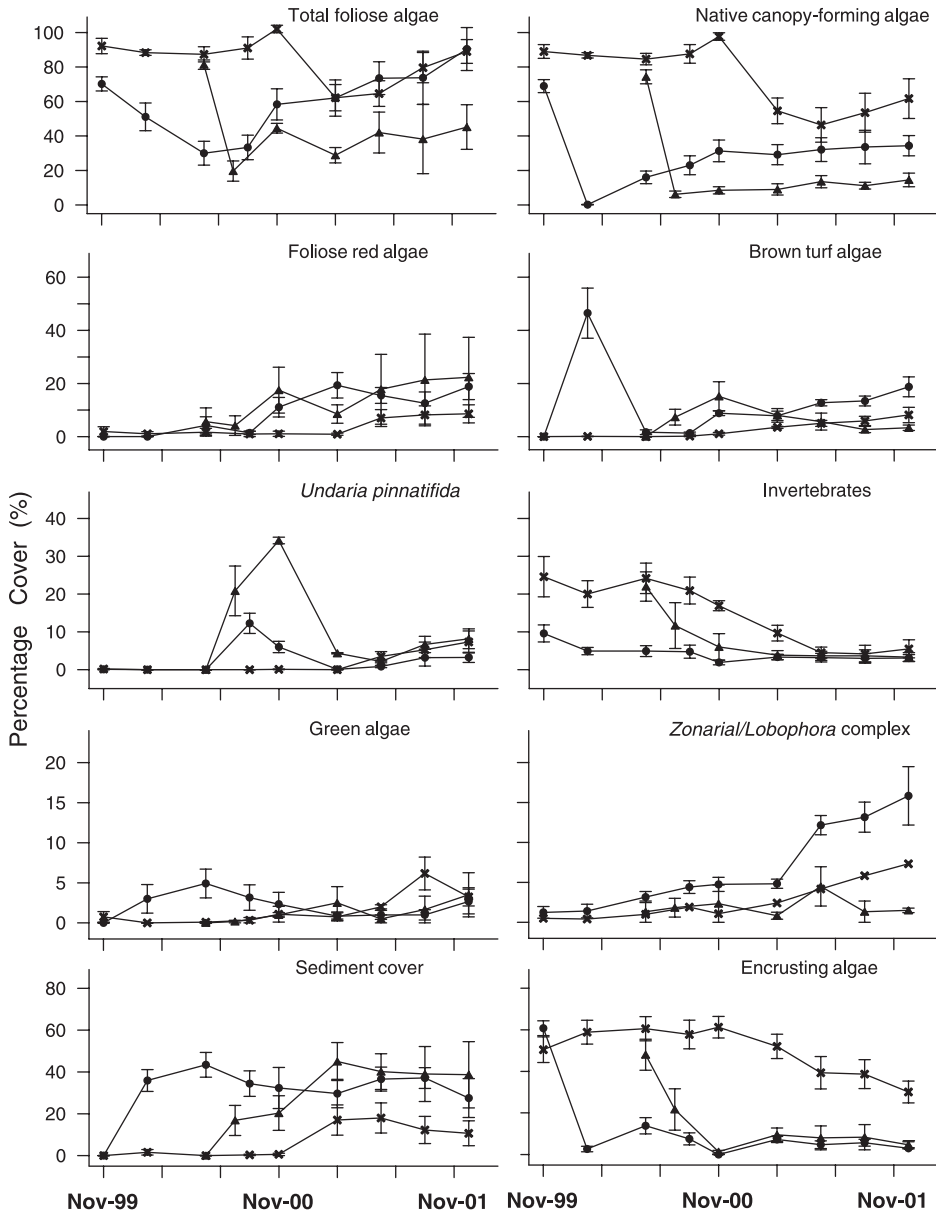


Fig. 5. Effect of removal of native canopy-forming algae on the cover of various algal guilds, invertebrates and the sediment matrix at Lords Bluff. Data are mean percentage cover ($\pm$ SE) ($n=6$ plots per treatment for spring canopy removals and controls; $n=3$ plots per treatment for winter canopy removals). Circles = canopy removed spring 1999; triangles = canopy removed winter 2000; crosses = control.

3.4.2. Brown turf algae

The guild of ‘brown turf algae’ represented less than 10% cover in control plots at both sites (Figs. 4 and 5). Cover in plots at Flensers Point subject to canopy removal in winter 2000 displayed consistently higher cover of brown turf than in control plots and in plots where the canopy was removed in spring 1999 (Fig. 4). In contrast, at Lords Bluff cover of brown turf in plots from which the canopy was removed in spring 1999 was higher than in control plots and in plots where canopy removals occurred in winter 2000 (Fig. 5). These differences are reflected in a significant “canopy removal*site” interaction evident for assessments in November 2000 and 2001. A notable feature at Lords Bluff was the major peak in brown turf cover observed in the first assessment following the spring 1999 canopy removal, which was associated with recruitment of *Colpomenia* spp. (Fig. 5). This ephemeral species subsequently degenerated and comprised a minor component of algal cover in all further assessments.

3.4.3. Green algae

The green algal guild, comprising mainly species of *Caulerpa*, was a minor component of the Lords Bluff flora. While they contributed up to 20% cover at Flensers Point, no significant treatment effects were detected, indicating that abundance of *Caulerpa* fluctuated patchily in time and space independent of our experimental treatments (Fig. 4).

3.4.4. *Zonaria/Lobophora* complex

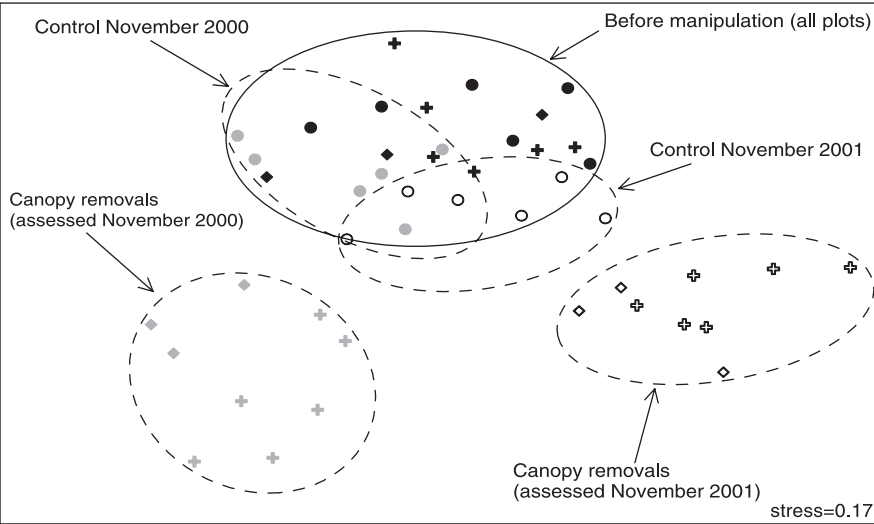
In general, responses of algae in the *Zonaria/Lobophora* complex to experimental treatments were relatively small. A significant effect of canopy removal was detected during the November 2001 assessment at Lords Bluff, with cover in plots cleared of canopy species eventually developing approximately twice the cover of that in control plots (Fig. 5; Table 3). Cover of this guild at Flensers Point was consistently higher than at Lords Bluff, however, differences between treatments at Flensers Point were not significant.

3.4.5. Encrusting algae

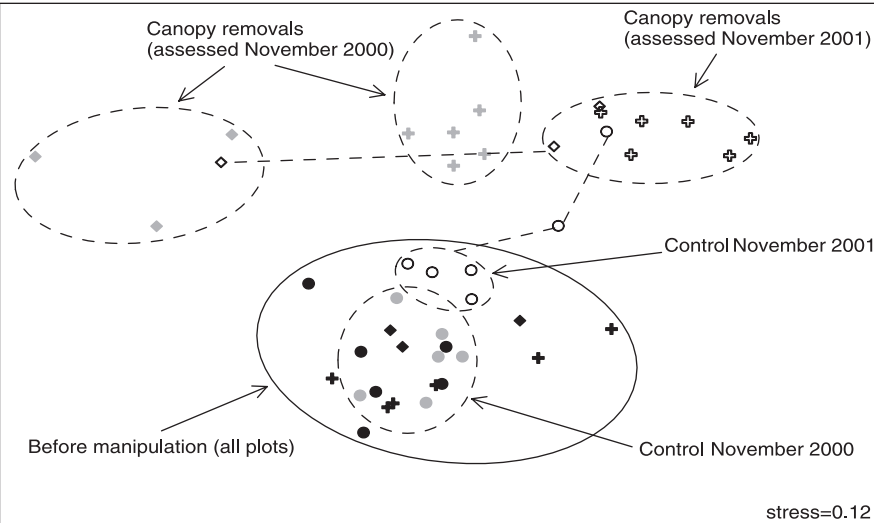
The encrusting alga guild, including nongeniculate coralline algae and *Peyssonnela* spp., showed clear responses to experimental manipulations. Removal of the algal canopy resulted in bleaching of the vast majority of encrusting algae present in experimental plots, with no subsequent recovery observed over the 24-month study period (Figs. 4 and 5; Table 3). A “canopy removal*site” interaction was evident at the November 2000 assessment, reflecting that the reduction in cover of encrusting algae at Lords Bluff was more dramatic than at Flensers Point (Table 2).

Fig. 6. Ordination (MDS) showing relationship between experimental plots from which the algal canopy was removed (in spring 1999 and winter 2000) and un-manipulated plots over the duration of the study (November 1999–November 2001) at Flensers Point and Lords Bluff. The analysis is based on a Bray–Curtis matrix of fourth root transformed percentage cover data. The plots associated with canopy removals and controls have been outlined for clarity.

a. Flensers Point



b. Lords Bluff



Treatment	Time of assessment		
	November 1999 (before manipulation)	November 2000	November 2001
Control	●	●	○
Canopy removed spring 1999	+	+	+
Canopy removed winter 2000	◆	◆	◆

3.5. Effect of canopy removal on sediment cover

Cover of sediment, forming a loose matrix on the substratum of variable depth ca. 1–10 mm, increased significantly immediately after canopy removal at both sites (Figs. 4 and 5). Sediment cover remained significantly higher in canopy removal plots than in controls throughout the study period (Table 3). Sediment cover was low in control plots, averaging less than 4% in control areas at Flensers Point for the duration of the study, while at Lords Bluff cover was <2% during 2000, after which there was a slight increase to an average of 7% by November 2001.

3.6. Community level effects

By November 2001, the total cover of foliose algae in plots from which the canopy was removed initially (i.e. in spring 1999) had recovered to levels comparable with controls at both sites (see Table 3). However, despite the recovery of cover, there were significant differences between treatments in algal community structure. At Flensers Point in November 2001, algal community structure in control plots and in plots from which the canopy was removed were clearly separated in MDS space (Fig. 6a) despite supporting similar cover. Although not as clear as the patterns observed at Flensers Point, significant patterns in community structure were also apparent at Lords Bluff, with np-MANOVA indicating differences among treatments in algal community composition 24 months after the initial canopy removal (Table 4). An interesting anomaly in algal composition at Lords Bluff was the increased variation in control treatments in November 2001 relative to the two previous years (Fig. 6b). This reflects dieback and therefore decreased abundance of *P. comosa* and *E. radiata*, which occurred in the control plots after November 2000. Those control plots subject to dieback, which initially supported a dense canopy of *P. comosa* and *E. radiata*, were more similar to canopy removal treatments after the dieback, indicating that the changes associated with the natural decline of these algae were similar to those observed in artificial disturbances.

Table 4

Comparison of community structure in relation to canopy removal before (November 1999) and 24 months after (November 2001) experimental manipulations

Site	Source of variation	Time						
		November 1999				November 2001		
		<i>df</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
Flensers point	Canopy removal	(1,10)	2185.94	1.4524	0.2338	29,204.38	21.4214	0.0026
	Plot (canopy removal)	(10,36)	1505.06	1.8880	0.0058	1363.33	1.9413	0.0008
Lords Bluff	Canopy removal	(1,10)	655.91	0.3177	0.8552	22,443.06	9.482	0.0026
	Plot (canopy removal)	(10,36)	2064.67	3.0763	0.0004	2366.92	1.9121	0.0038

Results are two-factor nested np-MANOVAs based on a Bray–Curtis matrix of fourth root transformed data (4999 permutations used for tests of significance). The level of significance was altered according to the Dunn–Sidak adjustment, $\alpha_{\text{adjusted}} = 0.013$. Significant tests are shown in bold face. (Note that winter canopy removals were not included in the analysis due to low replication.)

Table 5

SIMPER analysis identifying individual species or guilds responsible for the differences in community structure between treatments assessed in November 2001 at Flensers Point and Lords Bluff

Species	Average abundance (% cover)		% Contribution	Cumulative %
	Canopy removal	Control		
Flensers Point				
<i>Seirococcus axillaris</i>	1.16	66.34	13.19	13.19
<i>Sargassum fallax</i>	35.92	2.50	10.55	23.73
Encrusting algae	7.50	54.34	7.87	31.60
<i>Sargassum vestitum</i>	6.92	1.16	7.76	39.37
<i>Caulocystis cephalornithos</i>	3.84	0.00	6.35	45.72
Lords Bluff				
<i>Seirococcus axillaris</i>	0.66	29.66	10.02	10.02
<i>Cystophora monoliformis</i>	12.26	2.00	8.11	18.13
<i>Ecklonia radiata</i>	0.00	12.84	8.03	26.16
<i>Cystophora retroflexa</i>	10.66	1.42	8.02	34.18
<i>Phyllospora comosa</i>	0.00	4.00	7.34	41.52
<i>Caulocystis cephalornithos</i>	2.76	0.00	6.53	48.06
Encrusting algae	3.00	30.08	6.14	54.20

The column ‘% Contribution’ quantifies the breakdown of the contributions from each species to the difference in community structure between canopy removals and controls. Species were included in the table if they contributed to >5% of the difference in community structure. The analysis does not include plots where the canopy was removed in winter because the total cover of foliose algae in this treatment was still significantly lower than in controls by November 2001.

We used the SIMPER routine (Carr and Clarke, 1994) to identify the species contributing to these differences in community structure (note that the analysis did not include treatments in which the canopy was removed in winter 2000, since total foliose algal cover had not recovered to that in the control plots by November 2001 at either site; see Table 3). The species contributing to the observed differences (Table 5) were found to strongly reflect treatment effects described earlier for canopy-forming algae (see results in Section 4.2). At Flensers Point, of the five macroalgal groups observed to contribute >5% to the difference between treatments, four were the canopy-forming algae that proliferated in response to the initial canopy removal. The remaining group, encrusting algae, contributed 7.60% to the difference between treatments due to the high percentage cover in control relative to canopy removal plots. At Lords Bluff, lack of recovery of species dominating control areas (i.e. *S. axillaris*, *E. radiata*, *P. comosa*) and an increase in cover of *C. retroflexa* and *C. moniliformis* in canopy removal plots were the main contributors to the differences observed between treatments (Table 5).

4. Discussion

4.1. *U. pinnatifida*: opportunist or super competitor?

Patterns of abundance of *U. pinnatifida* observed in this study demonstrate clearly that disturbance resulting in removal of the native algal canopy is a critical step in the process

leading to establishment. The results indicate that microscopic *U. pinnatifida* gametophytes and/or sporophytes were dispersed throughout the native algal assemblages at both sites during the study period. These microscopic phases responded opportunistically to the artificial disturbance of canopy removal at both sites, and to the natural decline of the *E. radiata* and *P. comosa* canopy at Lords Bluff in 2001 (Valentine and Johnson, unpublished data).

Given that high densities of *U. pinnatifida* sporophytes recruited soon after disturbance to the canopy, the density of microscopic gametophytes present on the reef must have been sufficiently high to enable fertilisation. Clearly, there is no evidence to suggest that *U. pinnatifida* is capable of displacing native algal species through direct competition. A similar response to canopy removal has been observed for the introduced seaweed *Sargassum muticum* in northern Spain (Andrew and Viejo, 1998). In the present study, two lines of evidence suggest that it is competition for light, rather than for space, that is the major barrier to invasion. Firstly, *U. pinnatifida* recruited most strongly to plots where canopy removals were conducted 4 months after the period of spore release, just prior to the period of development of the macroscopic sporophyte (i.e. winter 2000). This demonstrates that the native canopy does not represent a physical barrier preventing spores from reaching the reef. Secondly, under the native algal canopy there was ample availability of hard substratum suitable for attachment of *U. pinnatifida* propagules and development of sporophytes given that cover of understorey species was generally less than 20%.

In relation to the supply of *U. pinnatifida* propagules, it is also important to consider the lack of any effect associated with the “spore enhancement” treatment. The most likely explanation for this result is that high densities of *U. pinnatifida* propagules had reached the reef via natural dispersal, so that the additional spores associated with the treatment had negligible effects on subsequent sporophyte density. An alternative explanation is that the treatment was unsuccessful in delivering high numbers of viable propagules to the reef. A problem of this nature might arise if the handling process had a detrimental impact on source plants, or if spores were released but were carried away from experimental plots by currents or surge. We consider this unlikely, however, given that a similar technique has been used previously to successfully seed *U. pinnatifida* (Saito, 1975).

The higher levels of *U. pinnatifida* recruitment observed in November 2000 in plots where the canopy was removed immediately prior to the sporophyte growth period (winter 2000), compared to canopy removals 6 months earlier during the period of spore release (spring 1999), raise two possibilities. There may have been higher survivorship of *U. pinnatifida* gametophytes and/or microscopic sporophytes beneath the algal canopy than in the cleared areas, or increased competition of developing *U. pinnatifida* sporophytes with native algae that also responded to the spring 1999 canopy removal. In plots where canopy removals were conducted in spring 1999, native algae had a 6-month window of development before commencement of the growth phase of the annual *U. pinnatifida* sporophyte generation. Proliferation of native species inhibiting the establishment of an introduced species has been demonstrated previously in experimental manipulations involving *S. muticum* (Deysher and Norton, 1982).

These observations raise key questions relating to dispersal of spores and longevity of the gametophyte stage in *U. pinnatifida*. Since there were no macroscopic *U. pinnatifida*

plants within the study areas at the beginning of the study, dispersal of spores from nearby plants over distances of at least several hundreds of metres must have occurred (the site at Flensers Point was ~ 1 km, and Lords Bluff was ~ 0.2 km, from the nearest stand of *U. pinnatifida*). Recent work conducted in New Zealand has suggested that *U. pinnatifida* possesses multiple strategies for natural dispersal. Laboratory experiments and field observations of spore dispersal confirmed that while spore dispersal is likely to be important for short-range dispersal (tens of metres), drifting sporophylls or fragments enable dispersal in the scale of hundreds of metres to kilometres (Forrest et al., 2000). Drift plants with intact sporophylls are commonly observed throughout the Mercury Passage. Similar multiple dispersal strategies have been described for *S. muticum* and it is thought that they may provide a mechanism to utilize the advantages of both long- and short-distance dispersal (Andrew and Viejo, 1998; Deysher and Norton, 1982; Kendrick and Walker, 1991).

The longevity of the *U. pinnatifida* gametophyte generation is also a critical question for managers. While analogies between gametophytes and seed banks in terrestrial plants have been proposed (Hoffman and Santelics, 1991), there is no experimental evidence of the phenomenon. Gametophytes of the perennial kelps *Macrocystis pyrifera* and *Pterygophora californica* in Southern California appear to live for <4 weeks, while for the annual kelp *Desmarestia ligulata* dormancy of up to 3–4 months has been observed (Reed et al., 1997). If *U. pinnatifida* gametophytes have similar properties to *D. ligulata*, disturbance would need to occur during this short period of gametophyte viability for *U. pinnatifida* sporophytes to establish. Alternatively, if gametophytes are capable of surviving for more than 1 year then it is possible that there could be an accumulation of these stages over successive years. In this scenario, the timing of disturbance would be less important since there would be a high likelihood that viable gametophytes would be present in any particular year. In the Mercury Passage, our experiments indicate that the longevity of gametophytes and/or microscopic sporophytes is at least 4–5 months.

The opportunistic nature of *U. pinnatifida* observed in this study is also characteristic of other annual canopy-forming algae from the North American coast. These include the annual laminarian kelps *Alaria fistulosa* and *Nereocystis luetkeana* and the annual brown alga *D. ligulata*. These species appear unable to invade established kelp beds, but colonize rapidly when kelp canopies are removed (Vadas, 1972; Duggins, 1980; Reed and Foster, 1984; Edwards, 1998). The establishment of *D. ligulata* following severe storms can inhibit recruitment of other kelps, often causing local or patchy delays in kelp recovery (Dayton et al., 1992). It could be expected that *U. pinnatifida* establishment may cause similar delays in the establishment of native canopy-forming species. It should be noted that there is no native annual canopy-forming algal species in temperate waters in Australia.

4.2. Maintenance of *U. pinnatifida* stands post-establishment

Critical to understanding its invasion dynamics and defining the threat it poses is whether continued disturbance is required for *U. pinnatifida* to maintain persistent populations. While disturbance may be a requirement for its establishment, it does not necessarily follow that continued disturbance is required for *U. pinnatifida* populations to

persist. For example, on the Atlantic Coast of North America, disturbance to native kelps either due to destructive urchin grazing or infestation by an epiphyte (*Membranipora membranacea*) facilitates establishment of the introduced alga *Codium fragile* subsp. *tomentosoides*. Once established, dense stands of *C. fragile* subsp. *tomentosoides* appear to inhibit kelp recruitment in the absence of continued disturbance, eventually displacing it (Chapman et al., 2002). Research associated with terrestrial plant invasions also indicates that persistence may occur in the absence of continued disturbance if an introduced species changes the disturbance regime to favour its own reproduction, or if there are no species-specific herbivores or pathogens (Luken, 1997).

In the present study, *U. pinnatifida* declined in the second season following canopy removal, corresponding with the recovery of native canopy-forming species. These results suggest that, on the east coast of Tasmania, continued disturbance is required to maintain dense stands of *U. pinnatifida*, although this conclusion should be viewed with caution given that only two seasons of *U. pinnatifida* growth were observed. Further research should specifically address the ongoing maintenance of dense *U. pinnatifida* stands after they establish.

4.3. Recovery of native canopy-forming species following disturbance

The decline in the abundance of *U. pinnatifida* after its initial establishment is most likely explained by recovery of native species, in particular canopy-forming brown algae. However, while the native species that recruited to cleared areas (predominately *Cystophora* and *Sargassum* species) are ostensibly competitors of *U. pinnatifida*, they were markedly different to the canopy species dominating control plots. A possible explanation for differences in the long-established and newly developed canopies of native algae is the timing of disturbance. The availability of propagules is known to determine early succession in other algal assemblages (Foster, 1975; Emerson and Zedler, 1978; Dayton et al., 1984; Kim and DeWreede, 1996), but unfortunately the phenology of the majority of the native canopy-forming species observed in this study remains poorly understood. We note, however, that while canopy manipulations were 6 months apart, the species composition of the resultant canopy was similar for both seasons of canopy removal, at both sites. Therefore it appears likely that the timing of canopy removal had only a minor influence on native algal succession and that species which successfully colonized cleared patches were opportunistic and may represent the initial stages of algal succession. Interestingly, spatial patchiness in algal community composition at scales of 10^2 m is a feature of Mercury Passage, possibly reflecting patches at varying stages of algal succession.

Comparison of similar experiments conducted elsewhere reveals that patterns of recovery of canopy-forming species vary substantially. Similar to our results, removal of a canopy of *E. radiata* in Western Australia realised a shift in dominance from *E. radiata* to *Sargassum* spp. (Kirkman, 1981). In contrast, canopy removal in *E. radiata* forests on the New South Wales coast facilitated the establishment of dense mats of turf algae from the *Zonaria/Lobophora* complex, which persisted for up to 2 years for canopy removals conducted in all seasons except winter (Kennelly, 1987a). Canopy removals conducted in winter were colonized by both turf and *E. radiata*, with the kelp

rapidly developing a closed canopy, eventually resulting in the decline of turf (Kennelly, 1987a).

Examples from the Northern Hemisphere also reveal a wide variation in response to canopy disturbances. On the Atlantic Coast of North America, the canopy of *Laminaria longicuris* can redevelop rapidly after disturbance, irrespective of timing, dominating both early and late stages of community development (Johnson and Mann, 1988). In contrast, on the Pacific coast of North America where a high diversity of canopy-forming species are present, the canopy is often a mosaic of species depending on the frequency and intensity of disturbance and proximity to reproductive plants (Dayton et al., 1984, 1992, 1999; Edwards, 1998). Given the patterns observed in response to our manipulations of the canopy, we speculate that mechanisms similar to those maintaining patch dynamics on the Pacific coast of North America forests also act on the east coast of Tasmania.

4.4. Canopy removal and the sediment matrix

There are several mechanisms that may increase sediment deposition on the substratum following canopy removal. First, the algal canopy represents a large surface area and removing it allows sediment that would otherwise be trapped in the canopy to be deposited on the substratum. Additionally, the sweeping motion of canopy algae on the substratum caused by surge prevents sediment from accumulating on exposed surfaces of the reef (Kennelly, 1989). This is consistent with observations of higher levels of sediment in the centre of clearings compared with the edges (Kennelly and Underwood, 1993). It has also been suggested that the presence of the kelp canopy prevents colonization by small filamentous algae that facilitate accretion and consolidation of sediment (Melville and Connell, 2001).

Previous work has also observed an increase in sediment cover after canopy removal (Kennelly, 1987a,b; Kennelly and Underwood, 1993; Melville and Connell, 2001). The increased sediment levels observed in this study persisted throughout the study period in plots from which the canopy was removed. This is in contrast to previous research where persistence of the sediment layer after clearing was short-lived, decreasing to similar levels as that in control areas within a few months (Kennelly, 1987a; Kennelly and Underwood, 1993).

Sediment accumulation is a potentially important process in the ecology of rocky reefs for a number of reasons. Sediment burial and scour may affect algal communities by removing whole organisms, by physically preventing settlement of propagules on stable substrata, or by limiting newly settled propagules by reducing inputs of light and oxygen (Airoidi et al., 1995). Experiments have shown recruitment of some algal species to be negatively affected by sediment deposition (Devlinny and Vols, 1978; Kendrick, 1991; Umar et al., 1998). It is possible that the significant increase in sediment levels observed in canopy removal plots might influence the response of the algal community. However, despite the increase and persistence of sediment following canopy removal, both *U. pinnatifida* and some native species were able to recruit to these patches. This suggests that these particular species can tolerate a degree of sediment stress. Increased sediment may explain the lack of recovery of several of the native canopy-forming species, which may be more sensitive to sediment stress. Notably, at other sites at Lords Bluff where

sediment accumulation occurs on a large spatial scale associated with sea urchin ‘barrens’, native algae did not recover over a 2-year period in areas where both urchins and *U. pinnatifida* were removed (Valentine and Johnson, unpublished data).

A feature of canopy removal areas at both sites was the increased abundance of *C. moniliformis* relative to controls. *C. moniliformis* is known to grow in a variety of stressed habitats, including areas subject to sediment stress, while apparently being outcompeted in more favourable habitats (Edgar, 1984). In South Australia, *C. moniliformis* is abundant on sand scoured reefs including those covered by several centimetres of sediment (Shepherd and Wommersley, 1981).

4.5. Destructive sea urchin grazing: an important source of disturbance?

While we have shown that disturbance is necessary for successful establishment of *U. pinnatifida* at high densities, an important question is to identify the natural disturbance(s) facilitating *U. pinnatifida* establishment. Within our study area, destructive grazing by the sea urchin *H. erythrogramma* is the most widespread form of disturbance to native algae, and in Mercury Passage the only large monospecific stands of *U. pinnatifida* are associated with urchin barrens (Johnson, unpublished data). While *H. erythrogramma* can feed on *U. pinnatifida*, the recruitment and growth rates of the kelp clearly exceed the urchins’ capacity to graze the plant at mean urchin densities of $6\text{--}7\text{ m}^{-2}$.

Understanding the mechanisms of urchin barren formation by *H. erythrogramma* is therefore an important step in understanding the process of *U. pinnatifida* invasion. In temperate seas elsewhere in the world there is evidence supporting the link between overfishing of sea urchin predators and barren formation (Estes and Palmisano, 1974; Harrold and Reed, 1985; Watanabe and Harrold, 1991; Estes and Duggins, 1995; Vadas and Steneck, 1995; Sala et al., 1998; Steneck, 1998; Shears and Babcock, 2002). Recent work in Tasmania has indicated that the spiny lobster *Jasus edwardsii* is more important than reef fishes as a predator of *H. erythrogramma* and, moreover, that reduced abundances of lobsters as a result of fishing activity is sufficient to account for barren formation (Pederson and Johnson, unpublished). It is therefore possible that overfishing of sea urchin predators is the ultimate cause of reduced native algal cover in the Mercury Passage that has facilitated the establishment of dense *U. pinnatifida* stands.

4.6. Conclusions

This study demonstrates that disturbance to the native algal canopy facilitates the establishment of *Undaria pinnatifida* sporophytes, while in the absence of disturbance native algal communities resist invasion by this introduced kelp. The results suggest that management of *U. pinnatifida* populations may be most effective by targeting the cause of canopy disturbance, rather than the plant itself. Whilst it is not practical to manage natural disturbances in subtidal habitats such as storm damage, if disturbance is linked to human activity then options for control may exist. In our study area, the demonstrated links between fishing of sea urchin predators, urchin barren formation and subsequent establishment of *U. pinnatifida* provide a potential management opportunity to control abundances of this introduced alga.

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