"Establishment and persistence of dense stands of the introduced kelp *Undaria pinnatifida*"

by

Joseph Peter Valentine
BSc(Hons), University of Tasmania

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Statement of Originality

This thesis contains no material that has been accepted for a degree or diploma by the University or any other institution. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due acknowledgement is made in the text.

Joseph Peter Valentine

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Abstract

Despite high rates of occurrence of non-indigenous organisms in the marine environment, few studies have critically examined mechanisms underpinning the invasion process. In this study manipulative experiments and observations of a natural disturbance to native marine algae were used to examine the invasion dynamics of the Asian kelp *Undaria pinnatifida* on the east coast of Tasmania.

Disturbance to reduce cover of the native algal canopy was found to be a critical stage in the establishment of *U. pinnatifida*, while the presence of a stable canopy of native algae inhibited sporophyte development. In the first season of sporophyte growth following artificial canopy removal, *U. pinnatifida* recruited at high densities (up to 19 plants m^{-2}) while remaining rare or absent in unmanipulated plots. A similar response was recorded in areas where native macroalgae declined through natural processes. These results suggest that microscopic *U. pinnatifida* gametophytes or sporophytes presently occur throughout these native algal beds, but do not develop into visible sporophytes while the canopy is intact. The timing of disturbance was also an important factor. *U. pinnatifida* recruited in higher densities in plots where the native canopy was removed just prior to the sporophyte growth season (winter), compared to plots where the canopy was removed six months earlier during the period of spore release (spring). In the second year following canopy removal, *U. pinnatifida* abundance declined significantly, associated with a substantial recovery of native canopy-forming species. This supports the hypothesis that continued disturbance or stress to reduce cover of native algae is required for persistence of dense stands of *U. pinnatifida*.

Recovery of native algae after infestation by *U. pinnatifida* was investigated in greater detail in a large manipulative experiment conducted on a sea urchin 'barren' (*Heliocidaris erythrogramma*) seasonally dominated by dense cover of *U. pinnatifida*. This habitat was chosen as a model system to investigate persistence of *U. pinnatifida* for two reasons. Firstly, *U. pinnatifida* occurs most abundantly in Tasmanian waters on these urchin barrens and secondly, the level of disturbance could be easily manipulated in this system by controlling sea urchin density.

The experiment examined the response of *U. pinnatifida* and native macroalgae to treatments comprising all combinations of presence and absence of sea urchins, presence and absence of *U. pinnatifida* sporophytes, and presence and absence of fertile native macroalgae. *U. pinnatifida* not only persisted in the absence of sea urchin grazing, but was significantly more abundant compared to areas where urchin densities remained un-manipulated. Recovery of native canopy-forming species was minimal, even in treatments from which sea urchins and *U. pinnatifida* were removed, and an enhanced supply of native algal spores provided. Thus, factors other than urchin grazing were limiting development of native algae, consequently there was no evidence of inhibition of *U. pinnatifida* by native canopy species.

Recovery of native canopy-forming species was also examined in a transplant experiment. Settlement pavers colonised by high densities of native canopy-forming species were transplanted from an algal bed to sea urchin removal areas on an adjacent urchin barren. Following transplantation a marked reduction in cover of

canopy-forming algal recruits occurred in the absence of high densities of sea urchins, while cover was not affected on handling controls (pavers treated similarly but re-deployed into the algal bed).

These results suggest that *U. pinnatifida* may persist in the absence of disturbance in some circumstances, because other factors are limiting the recovery of native algae on the urchin barren. Canopy removal led to accumulation of a sediment matrix on the substratum, which is likely to influence settlement and development of early developmental stages of native algae. A consistent cover of sediment was observed on a large scale on the urchin barren, and rapidly developed on pavers transplanted to the urchin barren. Accumulation of sediment on the natural substratum, beneath dense algal cover was minimal by comparison. It appears that sediment accumulation plays a major role in inhibiting recruitment of native canopy-forming species.

The results of this work provide management options for control of *U. pinnatifida*. Where disturbance is linked to anthropogenic activity, managing the disturbance is likely to prove a more practical and cost-effective method of controlling invasion of *U. pinnatifida* at high densities than targeting the plant directly. On the east coast of Tasmania, preventing formation of *H. erythrogramma* barrens is of fundamental importance in this context.

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Chapter 1

General Introduction

The deleterious effects of non-indigenous species on native species and ecosystems have been widely recognised for decades (Elton, 1958; Lodge, 1993; Sakai *et al.*, 2001) and now represent one of the world's most serious conservation issues (Wilcove *et al.*, 1998). Coastal marine habitats are among the most heavily invaded systems, mainly due to human-assisted transport of marine organisms associated with international shipping, aquaculture and aquarium activities (Carlton and Geller, 1993; Meinesz *et al.*, 1993; Ribera and Boudouresque, 1995; Carlton, 1999).

Human-mediated range expansions (introductions) of marine organisms have the potential to cause significant economic and ecological damage. In the USA, introduced marine species have cost hundreds of millions of dollars in the twentieth century alone, due to direct costs and the loss of ecosystem services (Bax *et al.*, 2001). In ecological terms, non-indigenous species can have potentially catastrophic effects ranging from species-specific impacts to ecosystem level effects (Grosholz, 2002). For example, the impacts of the introduced Asian clam *Potamocorbula amurensis* in San Francisco Bay have been quantified at the ecosystem level, resulting in a shift from pelagic to benthic primary production with concomitant shifts in secondary production (Alpine and Cloern, 1992; Cloern, 1996).

While impacts of many introduced species are well understood, the process whereby new species invade an environment (i.e. invasion) is often less clear. A successful biotic invasion is the outcome of a multi-stage process that includes arrival,

establishment, spread and persistence (Mollison, 1986). The number of propagules entering the new environment, the life history characteristics of the new species, and the susceptibility of the environment to invasion by new species (invasibility) (Lonsdale, 1999) are the main factors thought to influence invasion success (Davis *et al.*, 2000). Invasibility itself is an emergent property of an environment, arising from the regions climate, levels of disturbance, along with the competitive ability and resistance to disturbance of native species.

In many cases it has been suggested that disturbance plays a critical role in facilitating the establishment and spread of exotic species, particularly for terrestrial plant communities where there is abundant evidence supporting the link between invasibility and disturbance (Elton, 1958; Cavers and Harper, 1967; Crawley, 1986, Crawley, 1987; Hobbs and Atkins, 1988). Understanding the role of disturbance in the invasion process is also an important stage in prioritising introduced species for management purposes (Byers *et al.*, 2002). Those species that establish and maintain persistent populations in the absence of disturbance represent a greater threat to the integrity of native communities than do species requiring disturbance for successful invasion (Hiebert, 1997).

Despite the recent rapid increase in occurrence of introduced marine organisms (see Bax *et al.*, 1999), few studies have investigated the role of disturbance in the invasion process for a marine species. Observations of the Asian clam *Potamocorbula amurensis* in San Francisco Bay, North America also provide evidence that disturbance can promote invasion of marine species. *P. amurensis* rose to dominance only after a major flood which caused densities of native species to

decline dramatically (Nichols *et al.*, 1990). Similarly, Reusch and Williams (1999) concluded that fragmentation of native eelgrass (*Zostera marina*) beds in California, which may reflect anthropogenically derived stress and disturbance, facilitates proliferation of the introduced bivalve *Musculista senhousia.* While these examples demonstrate that disturbance can promote invasion of introduced marine organisms, Sousa (2001) emphasises that there is insufficient information to generalize and that a more rigorous investigation of this relationship is required.

One of the few well studied examples of marine invasions is the Japanese fucoid alga *Sargassum muticum. S. muticum* has spread successfully to the shores of North America (Scagel, 1956) and several European countries (reviewed by Andrew and Viejo, 1998). Manipulative experiments indicate that *S. muticum* requires the provision of free space in order to establish successfully (Ambrose and Nelson, 1982; Deysher and Norton, 1982; Andrew and Viejo, 1998). Stable native algal canopies inhibit invasion, most likely by preventing *S. muticum* germlings from reaching the substratum (Deysher and Norton, 1982).

In recent years the kelp *Undaria pinnatifida* has undergone a global range expansion in temperate waters. Native to Japanese, Korean and Chinese coasts, *Undaria pinnatifida* has spread to the Atlantic and Mediterranean coasts of Europe (Castric-Fey *et al.*, 1993; Fletcher and Manfredi, 1995; Curiel *et al.*, 1998) as well as the shores of New Zealand (Hay and Luckens, 1987), Argentina (Casa and Piriz, 1996) and Australia (Sanderson, 1990; Campbell and Burridge, 1998). While the plant was intentionally introduced to the Atlantic Coast of Europe in 1983 (Floc'h *et al.*, 1991), the remaining introductions are all thought to have occurred accidentally via

international shipping activities, transported either as hull fouling or in ballast water, or in association 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 manipulative experimental studies conducted to date, undertaken on the Atlantic coast of France, local kelp species were shown to be resistant to invasion by *U. pinnatifida* (Floc'h *et al.*, 1996). Despite this result, it is widely speculated that *U. pinnatifida* is a highly invasive species, able to competitively displace native species and cause significant structural shifts in subtidal communities in sheltered to moderately exposed waters (Rueness, 1989; Fletcher and Manfredi, 1995).

In the Mercury Passage, where *U. pinnatifida* was first recorded in Tasmania, the plant occurs most abundantly in habitats subject to high levels of disturbance, particularly on 'urchin barrens'. These habitats are characterised by high densities of the sea urchin *Heliocidaris erythrogramma*, low cover of native macroalgae and seasonal abundance of *U. pinnatifida* which can exceed 100 % cover (Sanderson and Barrett, 1989; Johnson, unpublished). *U. pinnatifida* also occurs abundantly in other disturbed habitats including areas of sandscour at the base of reefs, shallow wave impacted sites, and unstable substrata such as small rocks and shell fragments (Johnson, unpublished). Previous observations suggest that *U. pinnatifida* does not encroach into dense native algal communities (J. Valentine, pers. obs.; Sanderson, 1997), consistent with reports from several other parts of the world where the alga has been introduced (Castric-Fey *et al.*, 1993; Hay and Villouta, 1993).

Given these observations it appears likely that disturbance to native algal communities is a key factor in determining the invasion success of *U. pinnatifida*. Understanding the role of disturbance is crucial in assessing the threat of an introduced species to native communities and defining appropriate control options. If *U. pinnatifida* is capable of competitively displacing native algal communities in the absence of disturbance, it represents a major threat to the integrity of native communities. Control options in this scenario should target the plant itself. Alternatively, if *U. pinnatifida* 'tracks' disturbance or requires continued disturbance to persist it presents less of a threat to native communities. In this scenario 'system management', rather than species management may be the most effective long-term strategy, applicable in circumstances where disturbance is linked to anthropogenic activity and where control efforts address the underlying cause of the disturbance rather than the plant itself (Mack *et al.*, 2000). In this study disturbance is defined as the loss of biomass of resident organisms from an area attributable to factors other than senescence (*sensu* Chapman and Johnson, 1990). The definition includes both physical (eg. wave action, sand abrasion) and biological (eg. herbivory, parasitism) effects. The primary objective of this study was to critically address the role of disturbance in two fundamental aspects of the invasion process, namely in the establishment and persistence of *U. pinnatifida*.

It is important to define what constitutes recruitment, establishment and persistence for *U. pinnatifida* in the context of this study. *U. pinnatifida* is a Laminarian kelp with an alternation of heteromorphic generations between a macroscopic sporophyte and a microscopic gametophyte. In this study recruitment refers to the development of macroscopic *U. pinnatifida* plants, while establishment of *U. pinnatifida* is defined

as the development of a mature canopy of adult sporophytes (> 30 cm in length) in an area that previously did not support sporophytes. Persistence (*sensu* Johnson and Mann, 1988) refers to more than one turnover of a canopy of adult *U. pinnatifida* sporophytes. The presence of microscopic gametophytes and or sporophytes was not considered to constitute establishment or persistence.

To examine the role of disturbance in the establishment of *U. pinnatifida*, two approaches were employed, including experimental manipulations and observations following disturbance to the native algal canopy. The experimental approach involved manipulating native algal canopy cover and proximity to a source of *U. pinnatifida* spores. These manipulations, presented in Chapter 2, were designed to address whether establishment of *U. pinnatifida* at high densities require both disturbance to reduce cover of native algae and a high density of *U. pinnatifida* spores. Observations following a natural canopy disturbance are presented in Chapter 3. The natural canopy decline occurred when one of the dominant canopy-forming species in the study area, *Phyllospora comosa*, suffered significant mortality during summer/autumn 2001. This decline provided the opportunity to observe the response of *U. pinnatifida* and native algae to a natural disturbance event and allowed comparison with the experiment involving artificial disturbance.

While disturbance may be required for the establishment of an introduced species, persistence may occur in the absence of the primary disturbance mechanism. For example, while disturbance to eelgrass (*Zostera marina*) habitats in California facilitates establishment of the bivalve *Musculista senhousia*, once established the mussel impedes eelgrass rhizome growth and vegetative propagation, allowing *M.*

senhousia to persist in the absence of continued disturbance (Reusch and Williams, 1998). Similarly, persistence of the introduced alga *Codium fragile* ssp *tomentosoides* in the NW Atlantic occurs in the absence of the disturbance that enables it to establish in the first place (Chapman *et al.*, 2002). Infestation of native kelps (*Laminaria* spp.) by an epiphytic bryozoan (*Membranipora membranaceae*) facilitates establishment of *C. fragile*, however, the dense stands of *C. fragile* that subsequently develop in turn inhibit recovery of *Laminaria* spp. (Chapman *et al.*, 2002). Furthermore, in terrestrial systems long-term dominance by invasive species may occur when invading plants change the disturbance regime (eg. fire frequency) to favour their own regeneration or introduce new forms of disturbance (Mack and D'Antonio, 1998).

The mechanism of persistence of *U. pinnatifida* was investigated (Chapter 4) using urchin barrens as a model system. The study concentrated on this habitat because urchin barrens are where *U. pinnatifida* occurs most abundantly in Tasmania (Sanderson and Barrett, 1989, Sanderson, 1997). In addition, since sea urchins are well known as an important source of disturbance to temperate subtidal communities (reviewed by Lawrence, 1975; Dayton, 1985; Chapman and Johnson, 1990), the level of disturbance could be manipulated in this system by controlling urchin density. A large manipulative experiment was designed to: (1) assess whether dense stands of *U. pinnatifida* are self-maintaining in the absence of high densities of sea urchins; and (2) identify those factors that influence the re-establishment of native canopy-forming species in areas dominated by *U. pinnatifida*.

While intensive sea urchin grazing may result in formation of urchin barrens, other factors may influence recovery of native canopy-forming species. For example, recovery of canopy-forming brown algae may be limited by their poor dispersal characteristics (Anderson and North, 1966; Ambrose and Nelson, 1982; Dayton, 1985; Andrew and Viejo, 1998). Persistence of barren areas in the absence of intensive sea urchin grazing was investigated using a transplant experiment (Chapter 5). Settlement pavers deployed in an algal bed and colonised by high densities of native canopy-forming species were transplanted to sea urchin removal plots on an adjacent urchin barren. This allowed an assessment of whether recruitment of native species on urchin barrens may be unsuccessful despite the absence of intense sea urchin grazing.

In Chapter 6 the role of disturbance in the ecology of *U. pinnatifida* is evaluated and discussed in light of present and anticipated disturbance regimes, with particular emphasis on *H. erythrogramma* dominated 'barren' habitats. Implications for management and the potential impact of *U. pinnatifida* on native communities are also considered. The reader should note that the chapters have been written as manuscripts for publication, consequently repetition in the introductions of several chapters was unavoidable.

Chapter 2

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

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2.1 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.

2.2 Introduction

The introduction of non-indigenous 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 non-indigenous 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 non-indigenous 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 in order 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* has undergone 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 (Castric-Fey *et al.*, 1993; Fletcher and Manfredi, 1995; Curiel *et al.*, 1998) and to shores of New Zealand (Hay and Luckens, 1987), Argentina (Casa and Piriz, 1996) and Australia (Sanderson, 1990; Campbell and Burridge, 1998). 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* 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. Alternatively, if *U. pinnatifida* requires disturbance to establish then there exists a greater 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.

This study investigated 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.

2.3 Materials and methods

2.3.1 Study site

The experiment was conducted at 7-12 m depth on rocky reef in the Mercury Passage, on the east coast of Tasmania (Figure 2.1). Reefs in this area support a variety of algal communities, ranging from sea urchin 'barrens' (dominated by *Heliocidaris erythrogramma*) seasonally dominated by *Undaria 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 away 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.

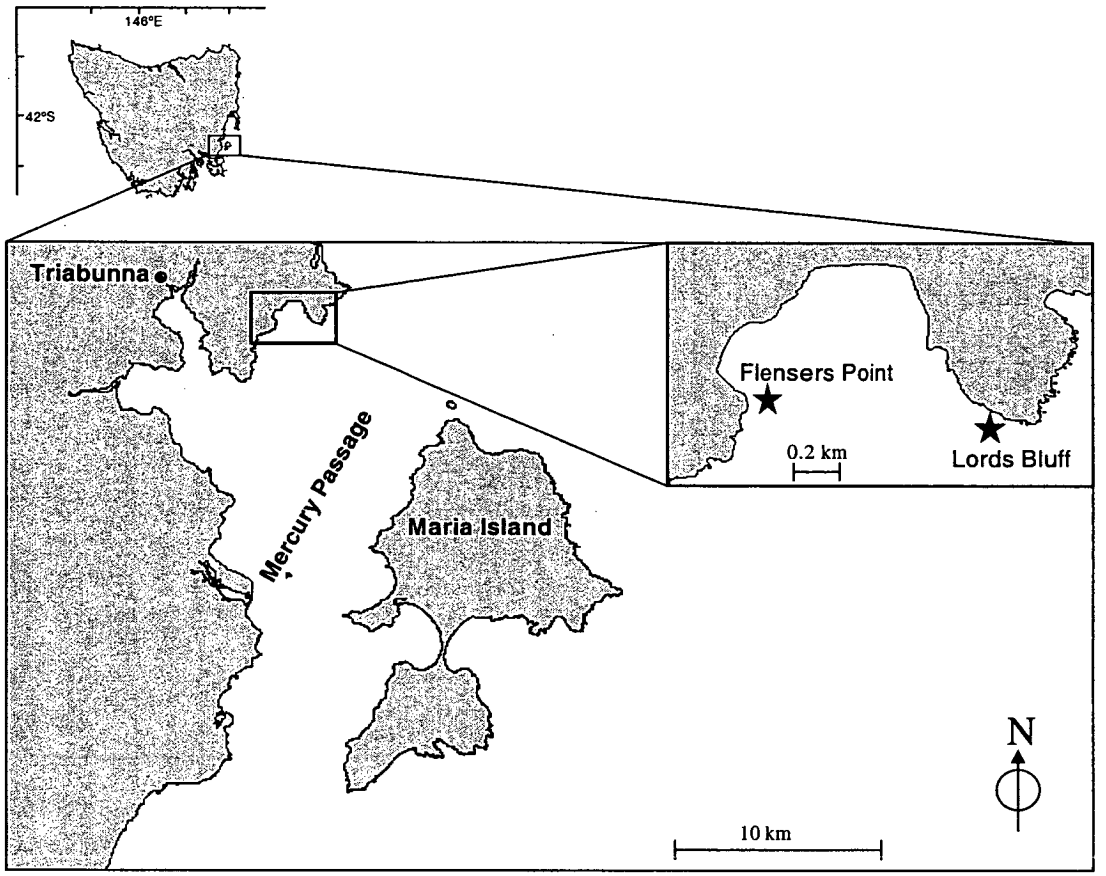


Figure 2.1. Map of Mercury Passage showing the location of study sites at Flensers Point and Lords Bluff.

Flensers Point was dominated by the fucoid *Seirococcus axillaris*, however, the common kelp *Ecklonia radiata* and the fucoids *Carpoglossum confluens, Cystophora retroflexa* and *Sargassum fallax* were also distributed patchily throughout the study area. At Lords Bluff a range of canopy-forming species were found including *Ecklonia radiata, Phyllospora comosa, Carpoglossum confluens* and *Seirococcus axillaris*. The understorey at both sites consisted of a diverse assemblage of turfing algal species, encrusting algae and invertebrates.

2.3.2 Experimental Manipulations

Experimental manipulations were applied to fixed 16 m^2 quadrats, while response variables were monitored only in the inner 4 m^2 of each quadrat to minimize edge effects. The experiment followed a 3-way factorial design representing all possible combinations of two levels of each of three factors, *viz.*:

1. Disturbance (2 levels; 100% removal of native algal canopy, no removal)
2. *Undaria pinnatifida* spore enhancement (2 levels; background, enhanced)
3. Site (2 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 understorey 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-Jan 2000 and from Sep 2000-Jan 2001.

To minimise confounding of treatments involving *U. pinnatifida* spores, experimental plots were separated by a minimum distance of ten metres. It was assumed that the 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 canopy 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.

2.3.3 Assessment of algal abundance

The algal community was assessed immediately prior to manipulation and at three monthly intervals hereafter 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 m^2 plot. Abundance of understorey algae, sessile invertebrates and sediment was assessed in terms of percentage cover. Percentage cover was estimated with a 0.25 m^2 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 understorey 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 (see Appendix I).

2.3.4 Analysis

Univariate analyses

Densities (i.e. stipe counts) were analysed using a 3-way Model I analysis of variance (ANOVA) with the main factors of canopy removal (2 levels), *U. pinnatifida* spore enhancement (2 levels) and site (2 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 (one year after the initial canopy removal) revealed no effect of *U. pinnatifida* spore enhancement on subsequent *U. pinnatifida* density (Table 2.1). In tests conducted on cover of native algae, the effect of *U. pinnatifida* spore enhancement was similarly highly non-significant. Consequently, treatments of ± *U. pinnatifida* spores were excluded from further analysis, enabling pooling of treatments and greater power to examine the effect of canopy removal.

Table 2.1. Three factor Model I ANOVA examining the response of *U. 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 non-significant.

Source of Variation	df	MS	F	P
Canopy removed (C)	1	38.48	64.27	0.001
Enhanced spores (E)	1	0.05	0.08	0.779
Site (S)	1	6.65	11.11	0.004
C*E	1	1.45	2.43	0.139
C*S	1	5.81	9.70	0.007
S*E	1	0.09	0.14	0.712
C*S*E	1	0.21	0.35	0.561
Error	16	0.60		

In subsequent analyses in which treatments of ± spore enhancement were pooled, data on stipe counts were analysed by a 2-way Model I ANOVA, while a 3-factor Model III nested ANOVA was used for cover data. Both analyses included canopy removal (3 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 ± *U. pinnatifida* spore enhancement). The 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, one and two 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 2000 canopy removal. The Dunn-Sidak adjustment ($\alpha_{adjusted} = 1-(1-\alpha)^p$, 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.

Multivariate analyses

To describe community responses to treatments and assess the significance of differences between treatments, non-metric multi-dimensional scaling (MDS) and non-parametric MANOVA (np-MANOVA) were used respectively. The relationship between controls and canopy removal plots was compared before manipulation and two 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 4^{th} 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 small number of permutations available to determine the distribution of the test statistic.

2.4 Results

2.4.1 The effect of canopy removal on density of *Undaria pinnatifida* and native canopy-forming algae

Canopy removal had a dramatic effect on *Undaria pinnatifida* density in the spring growth period of the following year (Figure 2.2a). While *U. pinnatifida* remained rare or absent in controls, canopy removal plots were characterized by the appearance of *U. pinnatifida* plants, up to 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 $_{2, 24}$, $P < 0.001$). 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 $_{1, 24}$, $P < 0.001$), but not at Flensers Point at the adjusted α level (F = 7.31, df $_{1, 24}$, $P < 0.012$; $\alpha_{adjusted}$ =0.009).

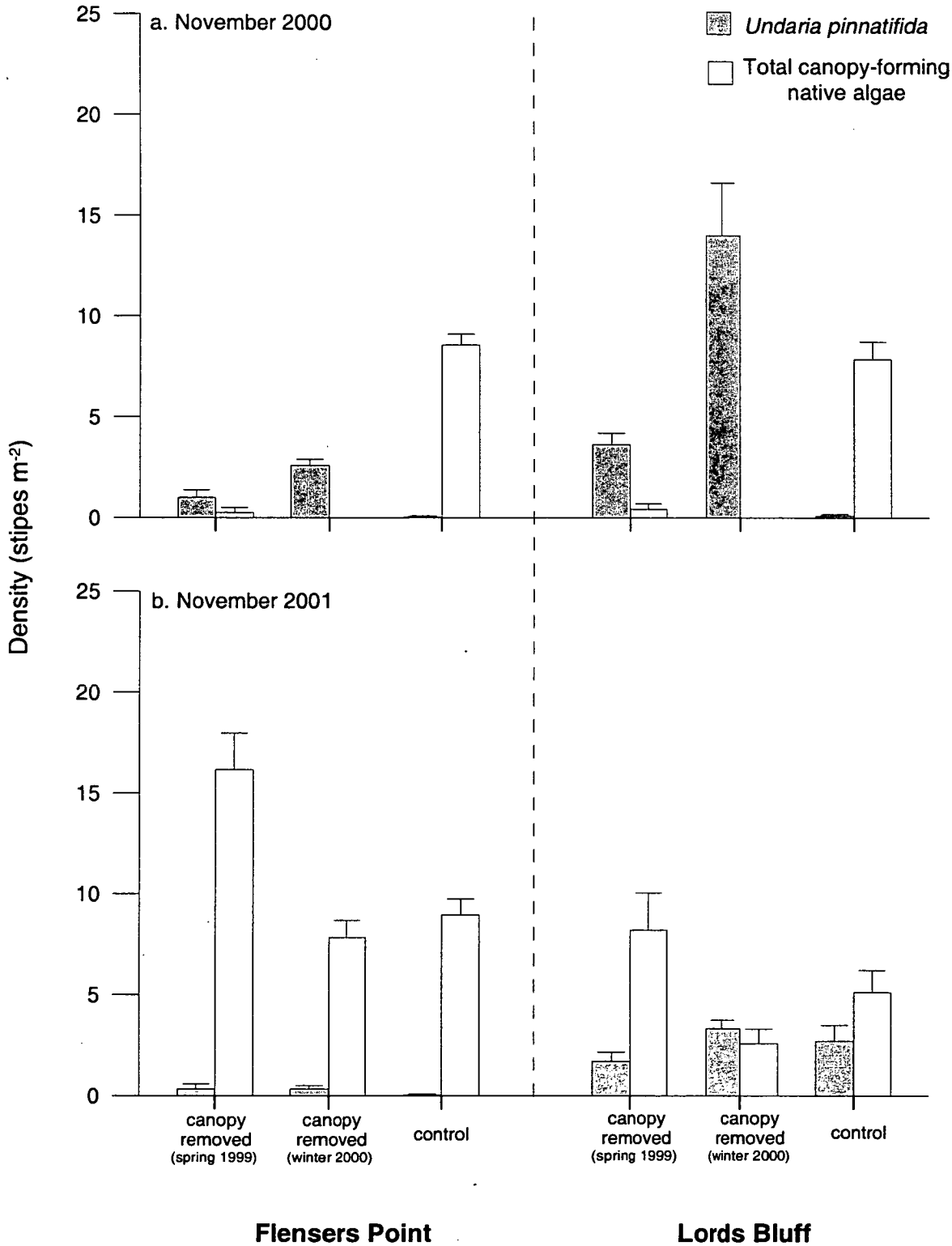


Figure 2.2. Effect of canopy removals on abundance of *Undaria pinnatifida* and total canopy-forming native algae assessed in (a) November 2000 and (b) November 2001. Data are means (± SE) of stipe counts (n=6 plots per treatment for spring canopy removal and controls; n=3 plots per treatment for winter 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*.

Algal assessments conducted in November 2001 (during the second season of *U. pinnatifida* sporophyte growth following disturbance) revealed a significant effect of "site" ($F = 38.31$, df $_{1, 24}$, $P < 0.001$) but no significant response of *U. pinnatifida* to the canopy manipulations conducted 18 and 24 months previously (Figure 2.2b). 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 (Figure 2.2b). In contrast, *U. pinnatifida* plants were observed in moderate levels (mean 2.5 plants m^{-2}) in all treatments at Lords Bluff (including controls). The number of *U. pinnatifida* plants in canopy removal plots at Lords Bluff decreased significantly from November 2000 to the November 2001 assessment, while density of native species increased to levels comparable with controls (Figure 2.2b). 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 *Phyllospora comosa* and *Ecklonia radiata* associated with above average water temperatures during the 2000/2001 summer.

2.4.2 Native canopy-forming algae: species composition

Although densities of native canopy-forming algae had recovered in the canopy removal treatments 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 *Seiroccoccus axillaris* continued to dominate control areas throughout the experiment at Flensers Point, the assemblages that developed in canopy removal areas consisted mainly of Sarg*assum fallax*, *Cystophora retroflexa, Sargassum vestitum* and to a lesser extent *Cystophora moniliformis* (Figure 2.3). Similarly, at Lords Bluff, the assemblage in un-manipulated control plots dominated by *Ecklonia radiata*, *Phyllospora comosa*, *Seirococcus axillaris* and *Carpoglossum confluens* was replaced by *Cystophora retroflexa* and *Cystophora moniliformis* in the canopy removal treatments (Figure 2.3). At both sites species abundant in control areas were rare or absent in the canopy removal treatments, therefore differences between treatments could not be tested statistically.

2.4.3 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 data. Cover data can provide greater sensitivity than density data, largely reflecting the different growth forms and growth densities among algal species (Johnson and Mann, 1993).

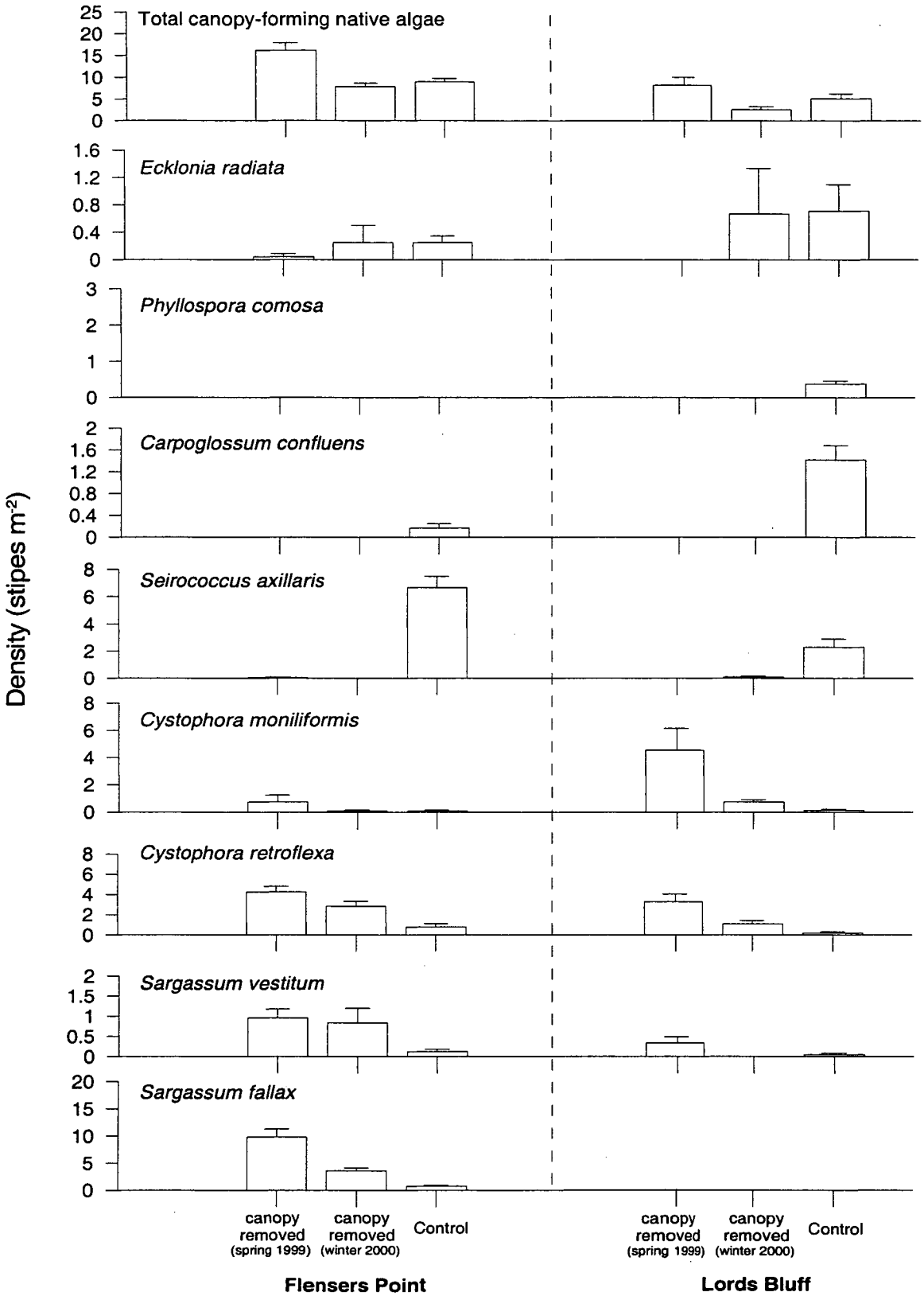


Figure 2.3. Abundance of dominant canopy-forming native algae in relation to canopy removal at two sites in Mercury Passage, November 2001. Data represent mean stipe densities (+SE) (n=6 replicate plots per treatment for spring canopy removals and controls; n=3 replicates plots per treatment for winter canopy removals).

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 % ± 6.5 SE) was still considerably greater than that in plots where canopy removals had been conducted in spring 1999 (28 % ± 5.2 SE) and winter 2000 (11 % ± 1.3 SE) (Figure 2.4; Table 2.2). 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, there was no significant difference in the cover of native canopy species in control (86 % ± 5.6 SE) and spring 1999 canopy removal (71 % ± 4.0 SE) plots, while cover in canopy removal plots conducted in winter 2000 had increased markedly (49 % ± 4.1 SE) but still remained significantly lower than that in controls (Figure 2.4; Table 2.3).

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 % ± 6.3 SE) and winter 2000 (9 % ± 2.1 SE) (Figure 2.5). The trend of recovery stalled somewhat in 2001, with spring 1999 (34 % ± 5.8 SE) and winter 2000 canopy removal plots (15 % ± 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 *Phyllospora comosa* and *Ecklonia radiata*. Despite this decline in cover in control plots, cover in canopy

removal plots was still significantly lower than controls by November 2001 (Figure 2.5; Table 2.3).

2.4.4 Response of understorey algae to canopy disturbance

In interpreting the response of *U. pinnatifida* and native canopy-forming algae to disturbance it is also important to consider understorey algal species, given that occupation of space by turfing algal species can inhibit recruitment of canopy-forming species (Dayton, 1975; Dayton *et al.*, 1984; Kennelly, 1987a; Airoldi, 1998). The response of turfing species to canopy removal, therefore, may have significant implications for both invasion of *U. pinnatifida* as well as the recovery of native canopy species.

Foliose red algae

There was a significant response of foliose red understorey algae to canopy removal, although the response varied significantly among sites and the time since canopy removal. At Flensers Point, foliose red algal cover remained at low levels (< 5 %) in control plots for the duration of the experiment while fluctuating significantly in canopy removal treatments (Figure 2.4). Cover increased to a peak in November 2000 for spring 1999 (38 % ± 9.8 SE) and winter 2000 (26 % ± 4.1 SE) canopy removal treatments, after which a gradual decrease was recorded. No significant effect of disturbance was detected on completion of the final assessment in November 2001, 18 and 24 months after implementation of canopy removals (Table 2.3).

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 % ± 3.7 SE) and winter 2000 (18 % ± 8.6 SE) relative to controls (1 % ±1.0 SE) (Figure 2.5). 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 (Figure 2.5). 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 in comparison with Flensers Point.

Brown turf algae

The guild of 'brown turf algae' represented less then 10 % cover in control plots at both sites (Figures 2.4, 2.5). A significant "canopy removal*site" interaction was evident from assessments in November 2000 and 2001. 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 (Figure 2.4). 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 (Figure 2.5). 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, associated with recruitment of *Colpomenia* spp. (Figure 2.5). This ephemeral species subsequently degenerated and comprised a minor component of algal cover in all further assessments.

Green algae

The green algal guild, comprising mainly species of *Caulerpa*, was a minor component of the Lords Bluff flora. While green algae contributed up to 20 % cover at Flensers Point, no significant treatment effects were detected, indicating that abundance of *Caulerpa* fluctuated in time and space independent of treatment (Figure 2.4).

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 double the cover of that in control plots (Figure 2.5; Table 2.3). Cover of this guild at Flensers Point was consistently higher than at Lords Bluff, however, differences between treatments at Flensers Point were not significant.

Encrusting algae

The encrusting algal guild, including non-geniculate coralline algae and *Peyssionnella* 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 (Figures 2.4, 2.5; Table 2.3). A canopy removal*site interaction was evident at the November 2000 assessment, demonstrating the reduction in cover of encrusting algae at Lords Bluff was more dramatic than at Flensers Point (Table 2.2).

2.4.5 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 (Figures 2.4, 2.5). 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 < 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.

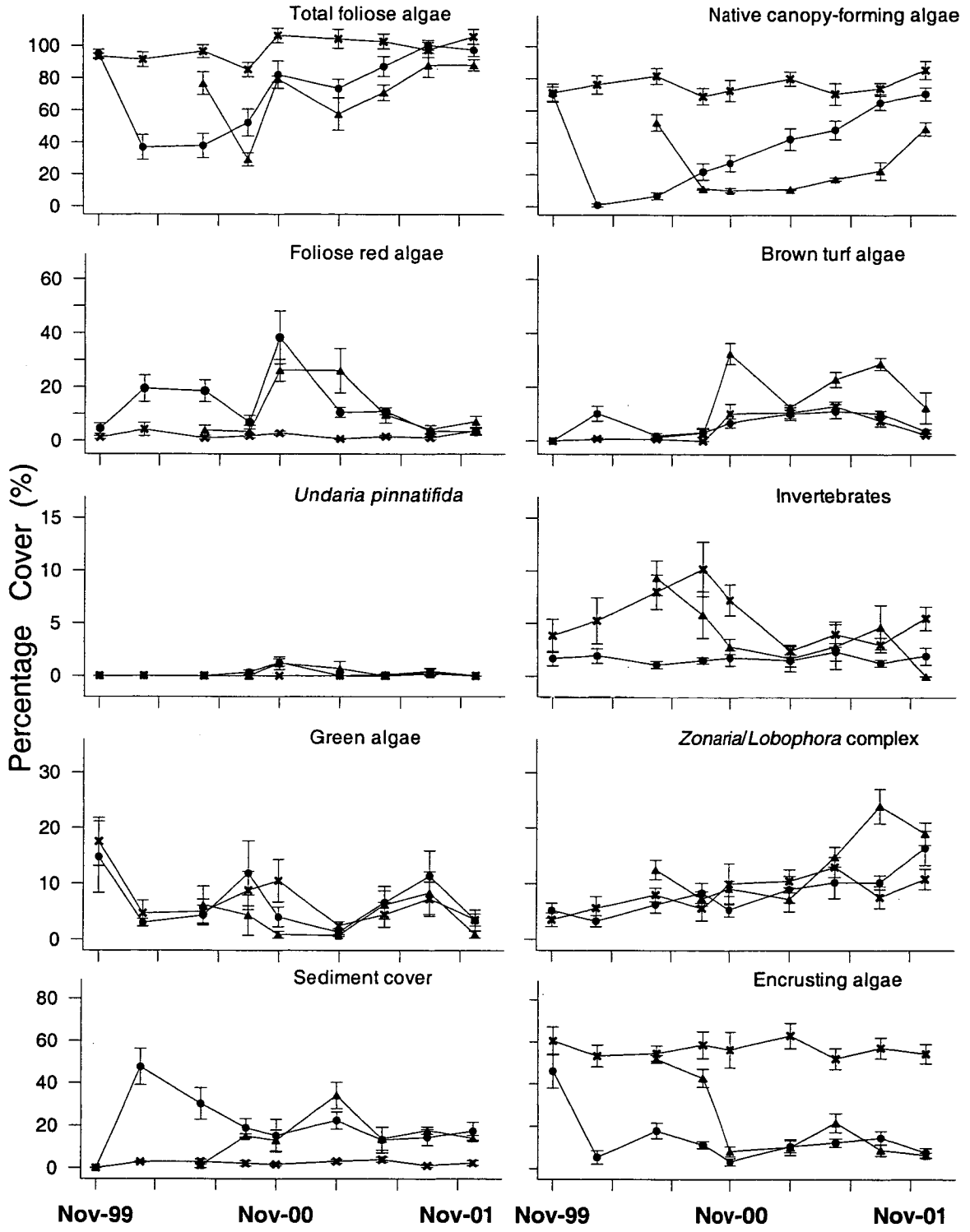


Figure 2.4. Effect of removal of native canopy-forming algae on the cover of various algal guilds, invertebrates and the sediment matrix at Flensers Point. Data are mean percentage cover (± SE) (n=6 plots per treatment for spring canopy removal and controls; n=3 plots per treatment for winter canopy removal). Circles=canopy removed spring 1999; triangles=canopy removed winter 2000; crosses=control).

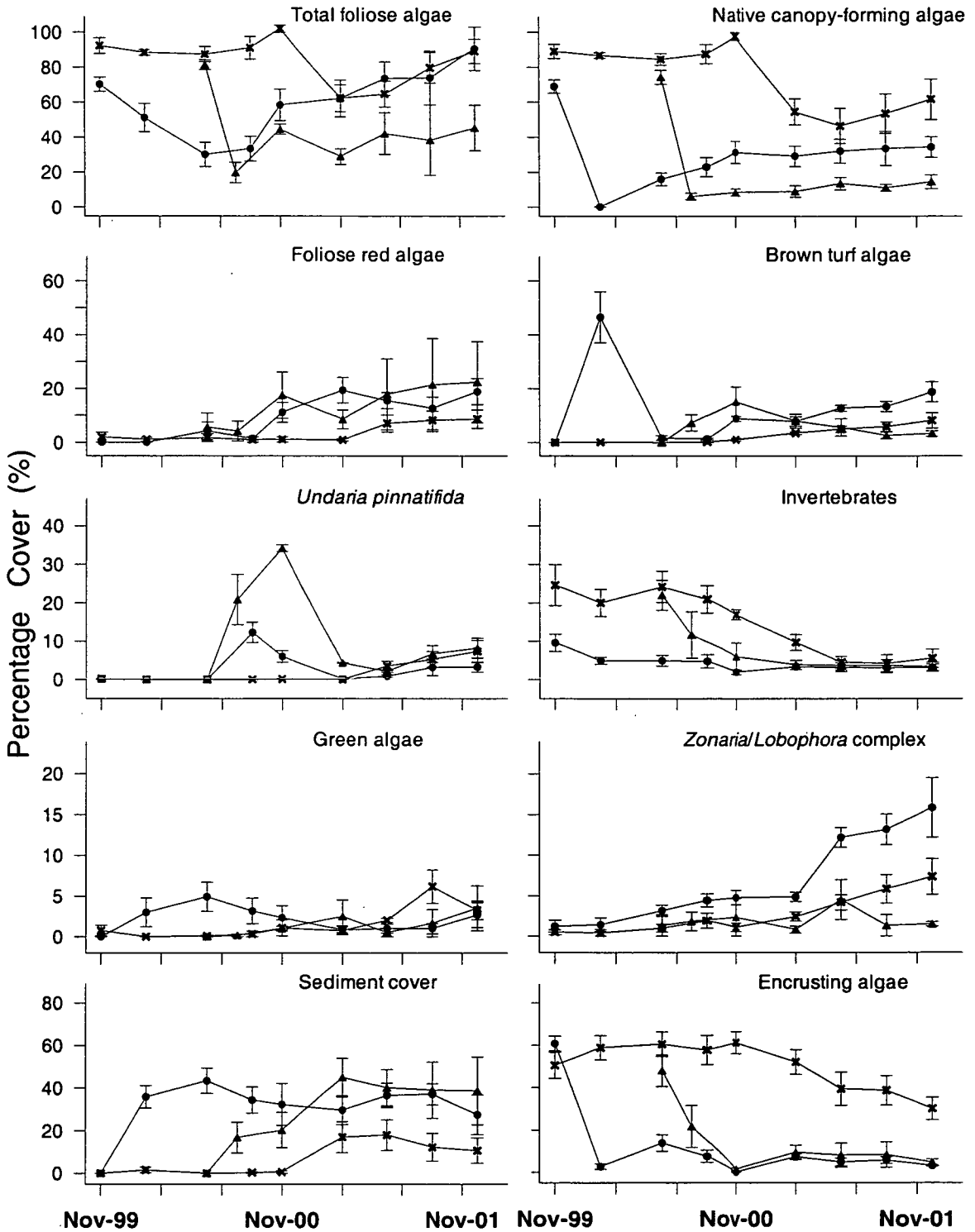


Figure 2.5. Effect of removal of native canopy-forming algae on the cover of various algal guilds, invertebrates and the sediment matrix at Lords Bluff. Data are mean percentage cover (± SE) (n=6 plots per treatment for spring canopy removal and controls; n=3 plots per treatment for winter canopy removal). Circles=canopy removed spring 1999; triangles=canopy removed winter 2000; crosses=control).

Table 2.2. 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 the 3 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 < 0.009 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 v sp	co v wi	sp v wi	co v sp	co v wi	sp v wi
	F P df = 2, 24	*F* P df = 1, 24	*F* P df =2, 24	*F* P df =24, 90	*F* P	*F* P	*F* P	*F* P	*F* P	*F* P
Sediment cover	18.50	1.58	1.79	5.05	17.46	19.20	0.94	73.71	42.20	0.25
[log (Y+1)]	**0.001**	0.221	0.1879	**0.001**	**0.001**	**0.001**	0.333	**0.001**	**0.001**	0.619
Encrusting algae	117.32	8.28	4.84	2.11	138.70	33.24	14.83	252.78	123.58	3.48
[log (Y+1)]	**0.001**	**0.008**	**0.0171**	**0.006**	**0.001**	**0.001**	**0.001**	**0.001**	**0.001**	0.065
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)	**0.001**	**0.002**	0.1136	**0.001**	**0.001**	**0.001**	0.709	**0.001**	**0.001**	0.062
Native canopy-forming algae	103.46	4.27	3.44	2.50	81.34	102.90	7.73	174.80	210.57	13.81
(no transformation)	**0.001**	**0.050**	**0.0487**	**0.001**	**0.001**	**0.001**	**0.006**	**0.001**	**0.001**	**0.001**
Foliose red algae	15.63	6.84	1.53	6.05	68.03	31.19	1.32	16.65	20.81	1.51
(sqrt)	**0.001**	**0.015**	0.2373	**0.001**	**0.001**	**0.001**	0.253	**0.001**	**0.001**	0.221
Brown turf algae	14.67	4.04	4.09	1.43	0.45	18.94	14.45	23.21	17.17	0.04
[log (Y+1)]	**0.001**	0.056	**0.0296**	0.114	0.502	**0.001**	**0.001**	**0.001**	**0.001**	0.834
Undaria pinnatifida	40.66	54.86	17.01	1.60	5.96	5.62	0.14	59.60	146.43	33.61
[log (Y+1)]	**0.001**	**0.001**	**0.0001**	0.059	0.016	0.019	0.707	**0.001**	**0.001**	**0.001**
Invertebrates	39.99	10.19	4.76	1.27	20.30	5.94	1.54	83.79	29.06	4.34
(sqrt)	**0.001**	**0.004**	**0.0181**	0.206	**0.001**	0.016	0.217	**0.001**	**0.001**	0.039
Green algae	1.94	3.86	2.45	1.40						
(no transformation)	0.165	0.061	0.1074	0.131						
Zonaria/Lobophora complex	0.06	9.46	2.54	1.65	4.41	0.09	1.99	2.72	0.21	0.79
(no transformation)	0.944	**0.005**	0.0997	**0.047**	0.038	0.760	0.162	0.102	0.647	0.376

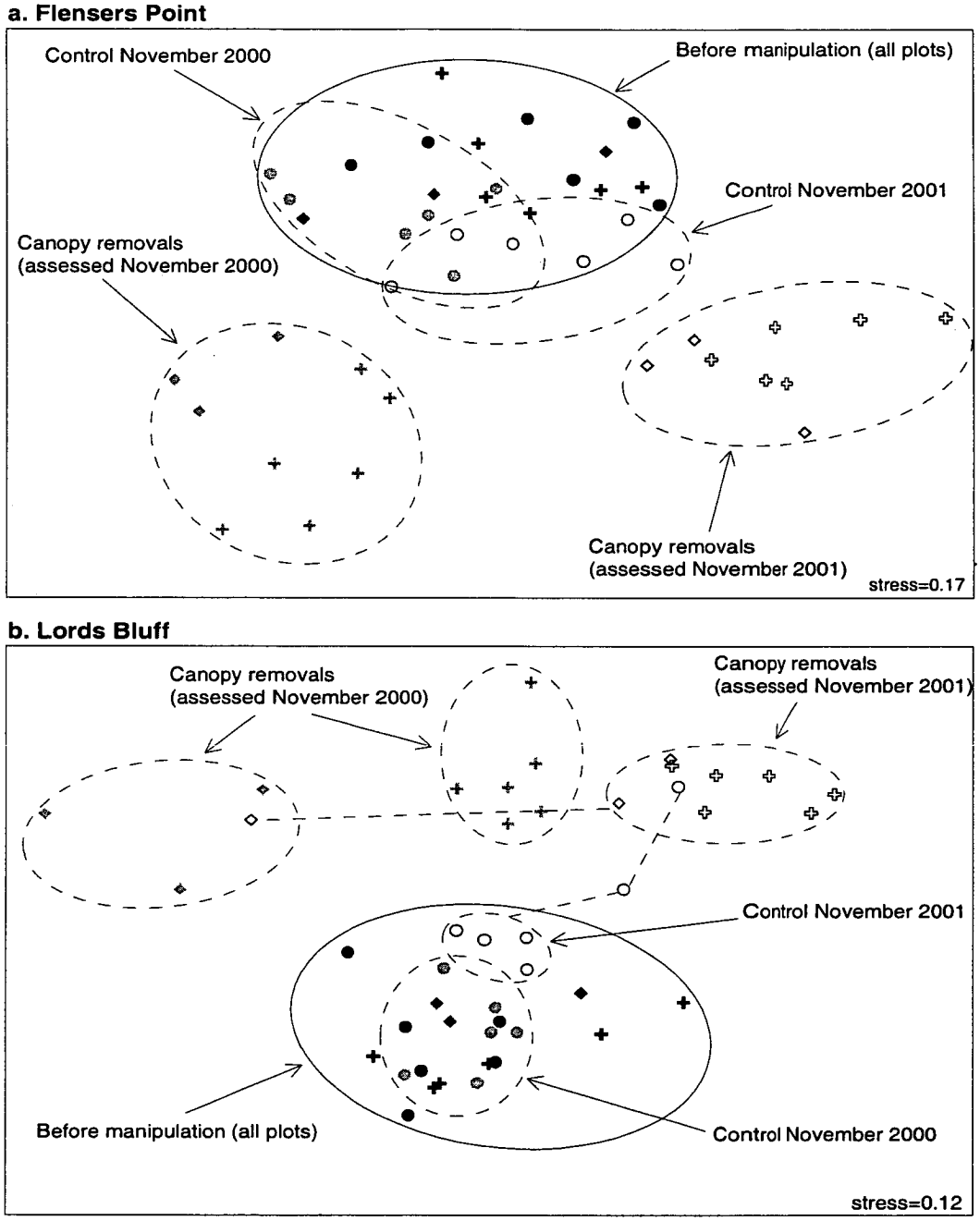
Table 2.3. Analysis of the effect of removing native canopy-forming algae on the cover of various algal guilds, invertebrates and the sediment matrix, assessed in November 2001. Results are of the overall ANOVA examining the effect of canopy removal and site, and the 3 planned comparisons for each site. 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 < 0.009 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 v sp	co v wi	sp v wi	co v sp	co v wi	sp v wi
	F	*F*	*F*	*F*	*F*	*F*	*F*	*F*	*F*	*F*
	P	P	P	P	P	P	P	P	P	P
	df = 2, 24	df = 1, 24	df =2, 24	df =24, 90						
Sediment cover	8.09	3.03	0.21	7.20	24.32	14.83	0.03	13.85	18.99	1.74
(sqrt)	**0.002**	0.095	0.809	**0.001**	**0.001**	**0.001**	0.860	**0.001**	**0.001**	0.190
Encrusting algae	85.18	14.28	1.60	1.62	125.82	86.21	0.02	89.02	39.98	1.90
(sqrt)	**0.001**	**0.001**	0.223	**0.054**	**0.001**	**0.001**	0.900	**0.001**	**0.001**	0.170
Total foliose algae	5.96	9.30	1.90	2.14	1.05	3.10	0.86	0.03	19.29	20.55
(no transformation)	**0.008**	**0.006**	0.172	**0.005**	0.309	0.081	0.356	0.862	**0.001**	**0.001**
Native canopy-forming algae	13.47	25.19	0.47	2.66	4.74	19.29	6.84	16.08	31.92	5.64
(no transformation)	**0.001**	**0.001**	0.633	**0.001**	0.032	**0.001**	0.010	**0.001**	**0.001**	0.019
Foliose red algae	1.94	11.04	1.02	4.17	0.05	2.46	3.10	8.71	7.30	0.09
(sqrt)	0.166	**0.003**	0.377	**0.001**	0.816	0.119	0.081	**0.004**	**0.008**	0.770
Brown turf algae	4.00	5.72	9.09	1.87	1.15	11.72	6.49	15.47	3.29	25.25
(sqrt)	**0.032**	**0.025**	**0.001**	**0.019**	0.285	**0.001**	0.012	**0.001**	0.072	**0.001**
Undaria pinnatifida	1.23	18.58	1.23	1.03	0.00	0.00	0.00	3.52	0.10	3.41
(no transformation)	0.296	**0.001**	0.296	0.440	1.000	1.000	1.000	0.063	0.755	0.068
Invertebrates	4.30	1.49	2.21	1.80	9.59	16.93	2.52	0.64	0.29	0.01
(sqrt)	**0.025**	0.235	0.131	**0.026**	**0.003**	**0.001**	0.116	0.426	0.590	0.912
Green algae	0.24	0.12	0.50	1.32						
(no transformation)	0.789	0.729	0.610	0.173						
Zonaria/Lobophora complex	5.81	10.68	5.98	1.36	4.35	4.96	0.27	7.59	6.18	22.41
(sqrt)	**0.009**	**0.003**	**0.008**	0.150	0.039	0.028	0.601	**0.007**	0.014	**0.001**

2.4.6 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 2.3). However, despite this recovery, 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 (Figure 2.6a) 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 2.4). 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 (Figure 2.6b). This reflects dieback and therefore decreased abundance of *Phyllospora comosa* and *Ecklonia 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.

The SIMPER routine (Carr and Clarke, 1994) was used to identify the species contributing to these differences in community structure (Note that the analysis did not include the winter 2000 canopy removal treatments, since total foliose algal cover had not recovered to that in the control plots by November 2001 at either site; see Table 2.3). The species contributing to the observed differences (Table 2.5) were



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

Figure 2.6. 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 4^{th} root transformed percentage cover data. The plots associated with canopy removals and controls have been outlined for clarity.

found to strongly reflect treatment effects described earlier for canopy-forming algae (see results 2.4.2). 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. *Seirococcus axillaris*, *Ecklonia radiata*, *Phyllospora comosa*) and an increase in cover of *Cystophora retroflexa* and *C. moniliformis* in canopy removal plots were the main contributors to the differences observed between treatments (Table 2.5).

Table 2.4. Comparison of community structure in relation to canopy removal before (November 1999) and 24 months after (November 2001) experimental manipulation. Results are 2-factor nested np-MANOVAs based on a Bray-Curtis matrix of 4th root transformed data (4999 permutations used for tests of significance). The level of significance was altered according to the Dunn-Sidak adjustment, $\alpha_{adjusted}$=0.013. Significant tests are shown in bold face. (Note that winter canopy removals were not included in the analysis due to low replication.)

Site	Source of Variation	Time						
			November 1999			November 2001		
		df	MS	F	P	MS	F	P
Flensers Point	Canopy removal	(1, 10)	2185.94	1.452	0.234	29204.38	21.421	**0.003**
	Plot (Canopy removal)	(10, 36)	1505.06	1.888	**0.006**	1363.33	1.941	**0.001**
Lords Bluff	Canopy removal	(1, 10)	655.91	0.318	0.8552	22443.06	9.482	**0.003**
	Plot (Canopy removal)	(10, 36)	2064.67	3.076	**0.001**	2366.92	1.912	**0.004**

Table 2.5. 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. 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.

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

2.5 Discussion

2.5.1 *Undaria pinnatifida*: opportunist or super competitor?

Patterns of abundance of *Undaria 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 *Ecklonia radiata* and *Phyllospora comosa* canopy at Lords Bluff in 2001 (Chapter 3).

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 four months after the period of spore release and 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 *Undaria 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. Either there was higher survivorship of *U. pinnatifida* gametophytes and/or microscopic sporophytes beneath the native canopy and/or increased competition of developing *U. pinnatifida* sporophytes with native algae that responded to the spring 1999 canopy removal. In plots where canopy removals were conducted in spring 1999, native algae had a six 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 *Sargassum 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 100s 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 (10s metres), drifting sporophylls or fragments enable dispersal in the scale of hundreds of metres to kilometres (Forrest *et al.*, 2000). Drift *U. pinnatifida* plants with intact sporophylls are commonly observed throughout the Mercury Passage. Similar multiple dispersal strategies have been described for *Sargassum 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 Santelices, 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 one 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 as 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 *Desmarestia 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 *Desmarestia 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.

2.5.2 Maintenance of *Undaria 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 issues that relate to ongoing maintenance of dense *U. pinnatifida* stands after they establish.

2.5.3 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. 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 six 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 timing of clearance 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. 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 the results of this study, removal of a canopy of *Ecklonia 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 establishment of dense mats of turf algae from the *Zonaria/Lobophora* complex, which persisted for up to two 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; Dayton *et al.*, 1992; Edwards, 1998; Dayton

et al., 1999). Given the patterns observed in response to manipulations in this study, it could be speculated that mechanisms similar to those maintaining patch dynamics on the Pacific coast of North America forests also act on the east coast of Tasmania.

2.5.4 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 would allow 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 may prevent the 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; Kennelly, 1987b; 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 (Airoldi *et al.*, 1995). Experiments have shown recruitment of some algal species to be negatively affected by sediment deposition (Devinny and Volse, 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. Despite the increase and persistence of sediment following canopy removal, however, 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, on nearby reefs in the Lords Bluff region where sediment accumulation occurs on a large spatial scale associated with urchin barren habitats, native algae did not recover over a two-year period in areas where urchins were removed (Chapter 4).

A feature of canopy removal areas at both sites was the increased abundance of *Cystophora 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).

2.5.5 Destructive sea urchin grazing: an important source of disturbance?

While it has been 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 the study area, destructive grazing by the sea urchin *Heliocidaris erythrogramma* is the most widespread form of disturbance to native algae. In the Mercury Passage the only large monospecific stands of *U. pinnatifida* are associated with urchin barrens (Johnson, unpublished). 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 - 7 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 which has facilitated establishment of dense *U. pinnatifida* stands.

2.5.6 Conclusions

This study demonstrates that disturbance to the native algal canopy facilitates establishment of *Undaria pinnatifida* sporophytes. 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* provides a potential management opportunity to control abundances of this introduced alga.

Chapter 3

"Establishment of the introduced kelp *Undaria pinnatifida* following dieback of the native macroalga *Phyllospora comosa*"

(submitted *to Marine and Freshwater Research*)

3.1 Abstract

The Asian kelp *Undaria pinnatifida* has recently been introduced to several countries in both hemispheres. While the occurrence and subsequent spread of the alga has been well documented, the process of its invasion remains poorly understood. Recent work involving artificial canopy manipulations has demonstrated that disturbance to the native algal canopy facilitates establishment of *U. pinnatifida* sporophytes at high densities, however, the kelp's response to a natural disruption of the canopy has not been assessed. This study examined the response of *U. pinnatifida* to significant dieback during summer/autumn 2001 of a common native canopy-forming macroalga, *Phyllospora comosa*, on the east coast of Tasmania. The response of *U. pinnatifida* and native algae to the dieback was observed during the following *U. pinnatifida* sporophyte growth season (spring 2001) and compared with adjacent areas where dieback did not occur. *U. pinnatifida* recruited in high densities (6.75 ± 1.99 plants m^{-2}) in dieback areas while remaining rare or absent in control areas where the native canopy was intact. The dieback also resulted in bleaching of encrusting algae, and increased cover of understorey algae and sediment. The results support the findings of recent artificial disturbance experiments, confirming the importance of disturbance events in the successful establishment of *U. pinnatifida*.

3.2 Introduction

As a consequence of human-mediated dispersal, the Asian kelp *Undaria pinnatifida* has recently become a conspicuous exotic component of subtidal algal communities in many temperate regions throughout the world (Rueness, 1989; Sanderson and Barrett, 1989; Hay, 1990; Castric-Fey *et al.*, 1993; Fletcher and Manfredi, 1995; Casa and Piriz, 1996; Campbell and Burridge, 1998), including the east coast of Tasmania (Sanderson and Barrett, 1989; Sanderson, 1990). While several studies have documented the occurrence and spread of *U. pinnatifida* few have examined the mechanisms facilitating invasion of *U. pinnatifida*.

It is speculated that *U. pinnatifida* is a highly invasive species capable of competitively displacing native algal species (Rueness, 1989; Fletcher and Manfredii, 1995). Our previous experiments suggest that in Tasmania *U. pinnatifida* requires disturbance to establish at high densities. In the absence of disturbance, stands of native algae were resistant to invasion by *U. pinnatifida* sporophytes (Chapter 2). Notably, on the east coast of Tasmania *U. pinnatifida* occurs at high densities only in disturbed habitats, particularly on sea urchin 'barrens', but also on areas of sandscour at the edge of rocky reefs and on unstable substrata, while it occurs rarely in established native algal communities (Johnson, unpublished; (Sanderson, 1997).

The distinction between *U. pinnatifida* as an opportunist or aggressive dominant competitor is an important component of defining the threat the plant poses to native algal communities. If *U. pinnatifida* is a dominant competitor it represents a major threat to the integrity of native communities and efforts to control the plant should

target the plant directly. Alternatively, if *U. pinnatifida* 'tracks' disturbance opportunistically, it represents less of a threat to native algal communities. Targeting the cause of the disturbance, rather than the alga itself, may be the most effective control option in circumstances in which disturbances are linked to human activities.

While experimental studies have demonstrated the potential importance of disturbance in the invasion process (Floc'h *et al.*, 1996; Chapter 2), naturally occurring disturbances ultimately leading to establishment of *U. pinnatifida* sporophytes have not been reported. This study outlines a natural (but uncommon) dieback of the dominant canopy-forming brown algae, *Phyllospora comosa*, on the east coast of Tasmania that provided an opportunity to observe the response of *U. pinnatifida* to a natural disturbance event. The response of *U. pinnatifida* and native algae is interpreted in light of our recent work using artificial disturbance treatments.

3.3 Materials and methods

3.3.1 Study site and decline of *Phyllospora comosa*

The study was conducted at Lords Bluff, in the Mercury Passage on the east coast of Tasmania (42° 32' S 147° 59' E). The algal community at the study site demonstrates clear zonation with depth (Figure 3.1). A narrow band of *Durvillea potatorum* occupies the sublittoral fringe, below which the prostrate canopy-forming algae *Phyllospora comosa* forms virtually monospecific stands to a depth of *ca.* 5-6 m. From 6-10 m a range of large brown algae form a "mixed assemblage" (Edgar, 1984) including the common kelp *Ecklonia radiata*, and the fucoids *Seirococcus axillaris*, *Carpoglossum confluens* and *P. comosa*. Below the mixed algal assemblage, *Seirococcus axillaris* dominates canopy structure at this site.

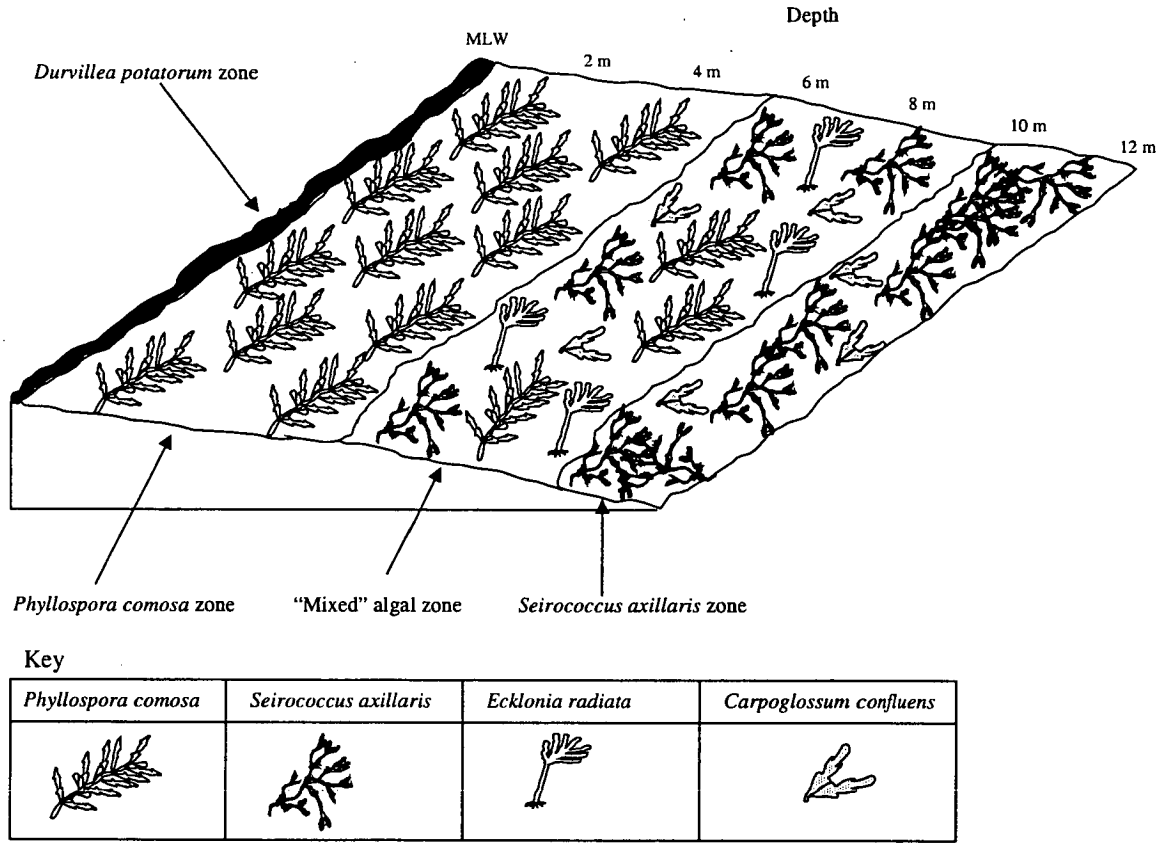


Figure 3.1. Generalised scheme of the distribution of canopy-forming brown algae in relation to depth at Lords Bluff. Not to scale.

We began monitoring the algal community at the Lords Bluff site in six permanent 16 m^2 quadrats in the mixed algal assemblage in November 1999 (Figure 3.2). The quadrats were randomly positioned within the mixed algal zone along 100 m of coastline. Deterioration of *E. radiata* and *P. comosa* was first evident in February 2001 when plants began to lose pigmentation and decay at the extremities. Morbidity became more severe over the next 2-3 months, culminating as a prominent dieback of *P. comosa* plants in large patches on the deeper edge of the *P. comosa* dominated assemblage and within the mixed algal assemblage. The decline in *E. radiata* was not

as extensive as for *P. comosa*, while there was no deterioration of *P. comosa* in shallow water (< 6 m) or of *C. confluens*, *S. axillaris* or any other large brown algae in the study area. *P. comosa* dieback was also observed in other areas of Mercury Passage, over at least 20 km of coastline, mainly associated with sheltered reefs. This is the first report of *P. comosa* decline and there is no evidence that it occurs commonly.

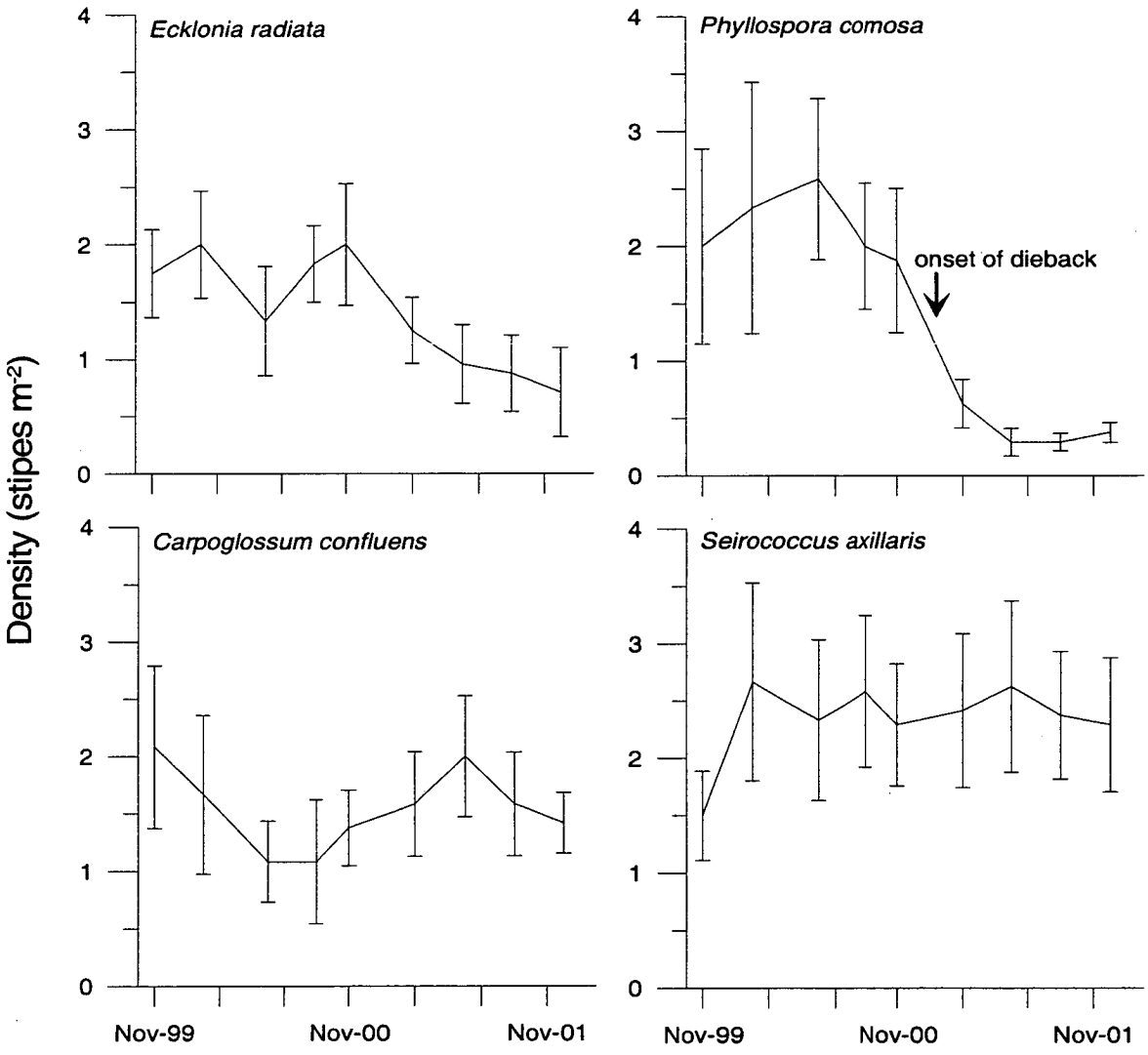


Figure 3.2. Results from routine monitoring of canopy-forming brown algal species in fixed quadrats within the mixed algal assemblage November 1999-2001. Data are means (± SE) of 6 replicate quadrats.

While identification of the cause of the *P. comosa* decline was beyond the scope of this study, it is likely that above average seawater temperatures on the east coast of Tasmania over the 2000/2001 summer/autumn period contributed to the decline. In surface waters adjacent to Lords Bluff more than 50 % of observations for the December-May 2000-2001 period exceeded 17.5 °C, compared to an average of only 27 % for the previous ten years.

A negative relationship between seawater temperature and nitrate (the nutrient most likely to limit macroalgal growth) is well recognized for North American coastal waters (Dayton *et al.*, 1992) and has been correlated with mortality or decline in macroalgal growth in several studies (Chapman and Craigie, 1977; Zimmerman and Kremer, 1984; Dayton *et al.*, 1999). Although the relationship between nitrate levels and canopy-forming algal abundance in Tasmanian waters has not been investigated, a similar negative relationship between temperature and nitrate levels in offshore waters has been previously identified (Harris *et al.*, 1987). It is possible therefore that nutrient stress during this period of high seawater temperature played a significant role in the *P. comosa* decline. The apparent influence of wave exposure on the distribution of dieback patches suggests that factors such as vertical mixing also contributed to the decline. We hypothesise that other algal species were not affected due to variability in tolerance to low nutrient conditions, as has been demonstrated previously in intertidal (Gunnill, 1985) and subtidal habitats (Dayton *et al.*, 1984; Tegner and Dayton, 1987; Tegner, 1997; Dayton *et al.*, 1999).

3.3.2 Establishment of dieback monitoring plots

In May 2001, prior to the annual appearance of *Undaria pinnatifida* sporophytes and when large patches of *P. comosa* dieback were evident, six replicate 16 m^2 fixed plots were established in the area of *P. comosa* decline. The plots were located at the boundary separating the deeper edge of the *P. comosa* assemblage from the shallow edge of the mixed algal assemblage.

The fixed plots had been dominated by *P. comosa*, evidenced by the decaying canopies and remaining stipes of affected plants. Small amounts of *E. radiata*, *S. axillaris* and *C. confluens* also occurred in some plots. The density of all canopy-forming algae was measured using the inner 4 m^2 of the permanent plots immediately after their establishment. The abundance of *P. comosa* and *E. radiata* prior to their decline was estimated from the density of decaying stipes, although it is likely that pre-decline densities were underestimated since some plants may have been dislodged from the substratum before assessment.

3.3.3 Algal assessment

Algal density and percentage cover in 'dieback' plots was measured in September 2001, during the peak period of *U. pinnatifida* sporophyte growth and compared to plots (16 m^2) in adjacent 'control' areas where there was no evidence of canopy decline. Control areas were selected to match conditions in the dieback area as closely as practically possible in relation to depth, reef topography and algal community structure.

Two control areas were selected, namely those located in patches of native algae in the same depth range as in the dieback area (7 - 8 m depth; n = 6 replicate plots)

dominated by *S. axillaris* and *C. confluens*, and those in patches of *P. comosa* in slightly shallower depths (5 - 6 m depth; n = 6 replicate plots) in which there was no evidence of morbidity. It should be noted that on adjacent sea urchin barrens *U. pinnatifida* is abundant from 5 m depth to the limit of available substratum (12 m).

In all plots algal density was measured by counting adult algae > 30 cm in length within the inner 4 m^2 of the plot. The percentage cover of algae, sediment and sessile invertebrates was also estimated within the inner 4 m^2 of the plot using five randomly positioned 0.25 m^2 quadrats. Cover was estimated using a point intercept method employing 50 equidistant points in each quadrat.

3.3.4 Data analysis

The algal response in the three 'areas' was compared using a single-factor model I analysis of variance (ANOVA) based on algal density (area = fixed factor, 3 levels) and a nested mixed model ANOVA based on algal cover (area = fixed factor, 3 levels; plot (area) = random factor, 6 levels). Where appropriate, *a posteriori* comparison of means was conducted using the Ryan-Einot-Gabriel-Welsch (REGW) multiple range test. For all tests, transformations required 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.

3.4 Results

3.4.1 *Undaria pinnatifida* response

The results show clearly that recruitment of *Undaria pinnatifida* into dieback areas was significantly greater than in plots with intact canopies, resulting in higher densities and cover of *U. pinnatifida* in areas where *Phyllospora comosa* was previously dominant but subsequently decimated (Figures 3.3, 3.4; Table 3.1, 3.2). In both types of control native algal patches where the canopy was intact, little or no recruitment of *U. pinnatifida* was observed. The density of *U. pinnatifida* sporophytes that developed in the dieback areas exceeded that of the *P. comosa* plants in those plots prior to the decline (estimated from assessments in May 2001). Although densities were comparable, *U. pinnatifida* sporophyte cover (28.1 % ± 6.8 SE) was significantly lower than the canopy cover of *P. comosa* prior to the dieback (estimated to be > 95 % based on pre-decline densities), due to the larger canopy area occupied by *P. comosa* individuals relative to *U. pinnatifida*.

3.4.2 Recovery of canopy-forming algae

Native canopy-forming algal species showed a slow recovery in the dieback areas, attaining 15.3 % (± 1.7 SE) cover in September 2001 (Figure 3.4). As a total measure of native algal cover 5.7 % was attributed to plants that survived the disturbance, with the remaining 9.6 % cover consisting of recruits. The most common recruits were of *Ecklonia radiata* and *Cystophora moniliformis*, while other canopy-forming species were rare (Figure 3.5).

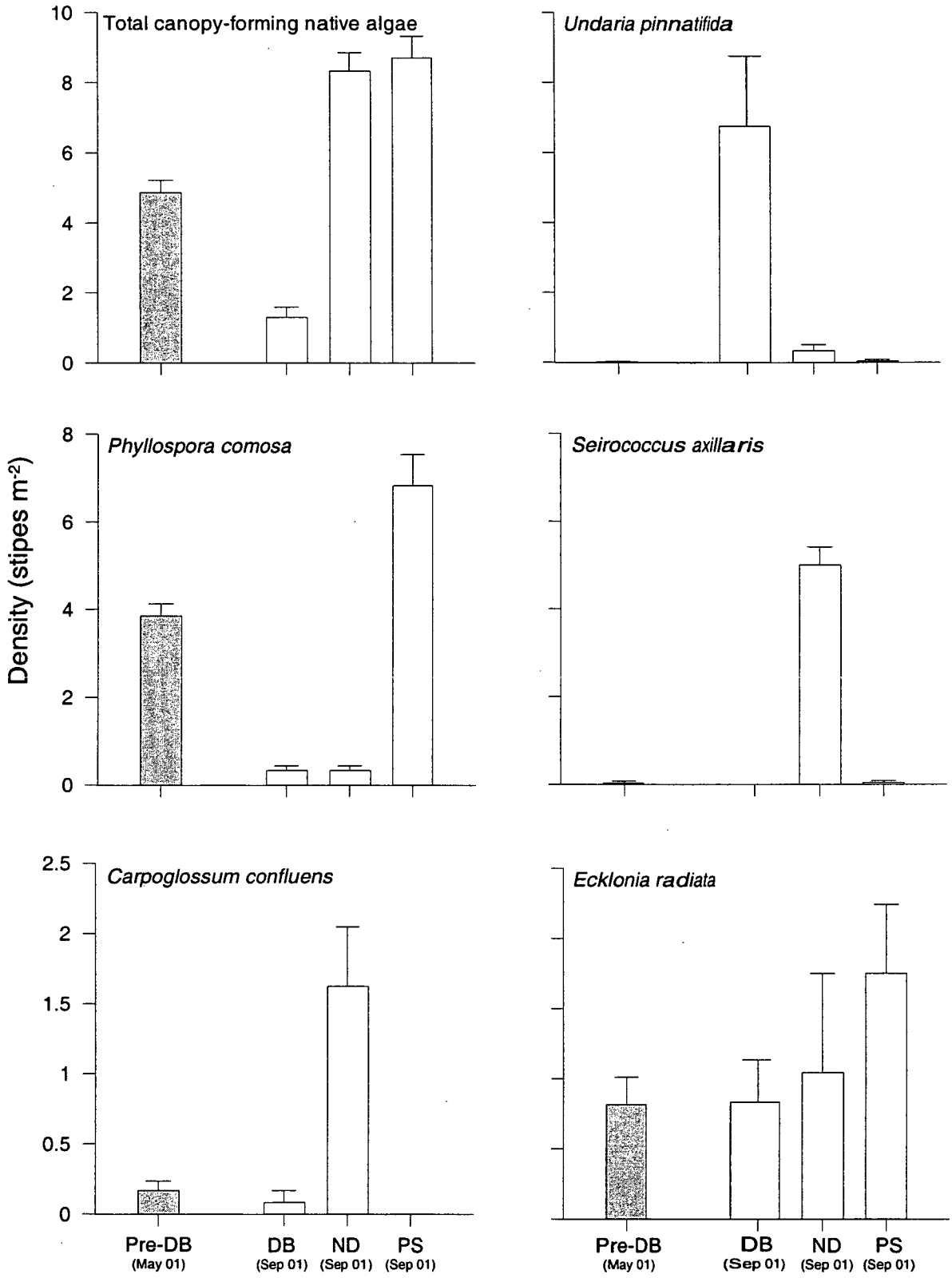


Figure 3.3. Density of canopy-forming brown algae in the three areas: DB = *Phyllospora comosa* dieback area; ND = Non-dieback area with intact canopy (dominated by *Seirococcus axillaris* and *Carpoglossum confluens*); PS = *Phyllospora* shallow area; Pre-DB = estimate of algal density in dieback area prior to dieback, conducted in May 2001. Data are means (+ SE) of six replicate plots within each area.

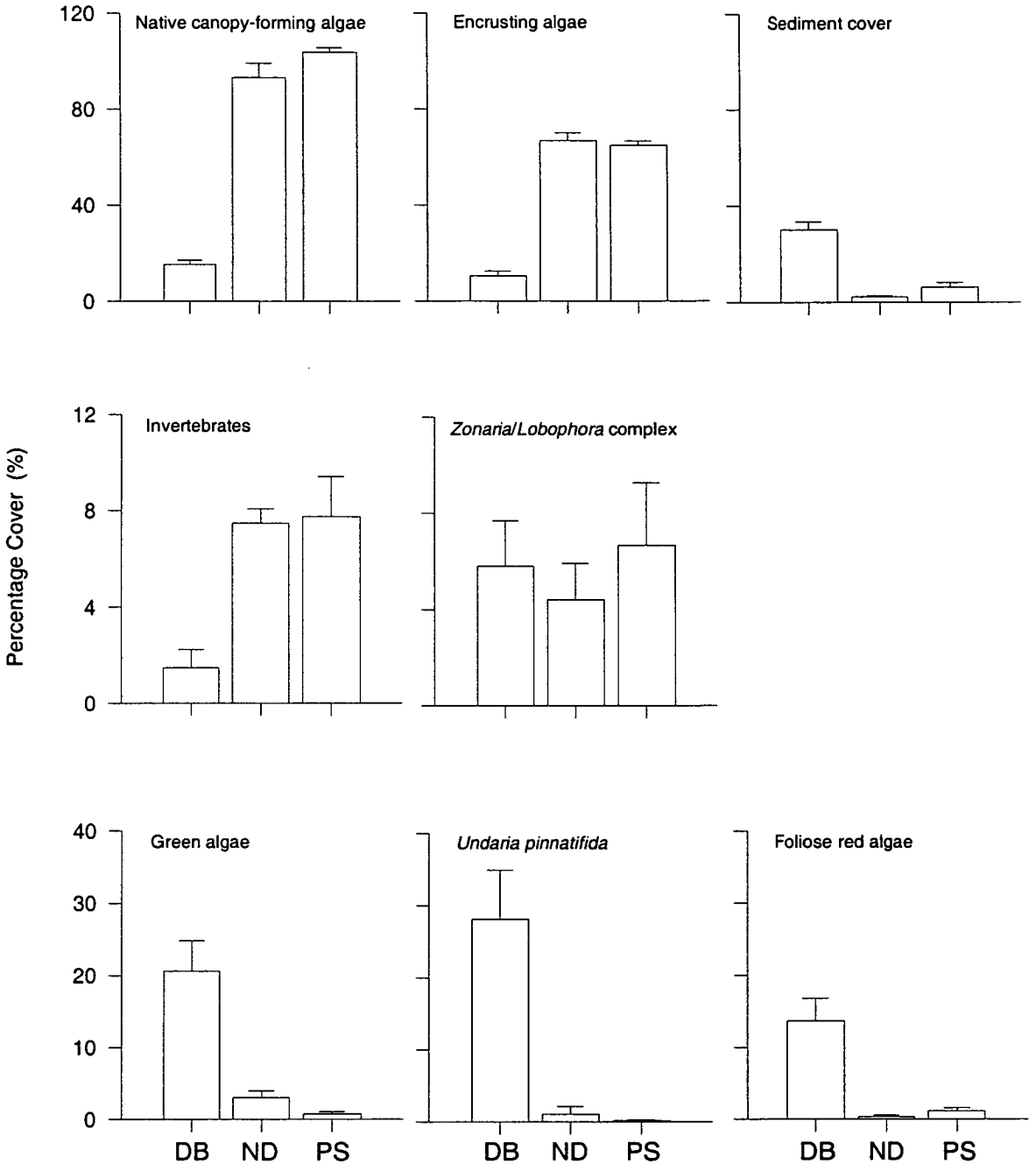


Figure 3.4. Cover of algae, invertebrates and sediment in the three algal areas, assessed in September 2001: DB = *Phyllospora comosa* dieback area; ND = Non-dieback area with intact canopy (dominated by *Seirococcus axillaris* and *Carpoglossum confluens*); PS = *Phyllospora* shallow area. Data are means (+ SE) of six replicate plots within each area.

Table 3.1. Results of univariate ANOVAs comparing density of canopy-forming macroalgae in the three algal areas, assessed in September 2001. Results are the overall ANOVA examining the effect of area and REGW multiple range tests examining differences between areas. Areas in which the density of algae are not significantly different (REGW tests, $\alpha = 0.05$) are indicated by a horizontal underline. Significant P-values in the main ANOVA are shown in bold face ($\alpha = 0.05$). Treatment codes are abbreviated as: DB = dieback area; ND = Non-dieback area with intact canopy (dominated by *Seirococcus axillaris* and *Carpoglossum confluens*); PS = *Phyllospora comosa* shallow area.

Taxon (transformation)	Source of variation		
	Area (df = 2, 15)		REGW Tests
	F	P	
Total canopy-forming native algae (no transformation)	69.93	**0.001**	DB ND PS
Undaria pinnatifida {log (*Y* + 0.1)}	26.81	**0.001**	DB ND PS
Phyllospora comosa (no transformation)	81.77	**0.001**	DB ND PS
Seirococcus axillaris (no transformation)	143.67	**0.001**	DB PS ND
Carpoglossum confluens (no transformation)	13.57	**0.001**	DB PS ND
Ecklonia radiata (no transformation)	0.83	0.455	

Table 3.2. Results of ANOVAs comparing cover of algae, invertebrates and sediment in the three algal areas as assessed in September 2001. Results are the overall ANOVA examining the effect of area and plot (area), along with REGW multiple range tests examining differences between areas. Areas where cover of algae is not significantly different (REGW tests, $\alpha = 0.05$) are indicated by a horizontal underline. Significant P-values in the main ANOVA are shown in bold face ($\alpha = 0.05$). Treatment codes are abbreviated as: DB = *Phyllospora comosa* dieback area; ND = Non-dieback area with intact canopy (dominated by *Seirococcus axillaris* and *Carpoglossum confluens*); PS = *Phyllospora* shallow area.

Taxon (transformation)	Source of variation				
	Area (df = 2, 15)		Plot (Area) (df = 15, 72)		REGW tests
	F	P	*F*	P	
Native canopy-forming algae (no transformation)	220.19	**0.001**	3.12	**0.001**	DB ND PS
Undaria pinnatifida ($Y^{0.32}$)	34.43	**0.001**	1.69	0.071	DB ND PS
Foliose red algae {log (*Y* + 0.1)}	23.03	**0.001**	1.91	**0.036**	DB ND PS
Fine green algae {log (*Y* + 0.1)}	14.87	**0.001**	1.55	0.109	DB ND PS
Zonaria/Lobophora complex {log (*Y* + 0.1)}	0.41	0.672	2.63	**0.003**	
Encrusting algae (no transformation)	198.19	**0.001**	0.95	0.511	DB ND PS
Invertebrates {log (*Y* + 0.1)}	13.54	**0.001**	1.67	0.076	DB ND PS
Silt cover ($\sqrt{Y}$)	39.09	**0.001**	2.16	**0.016**	DB ND PS

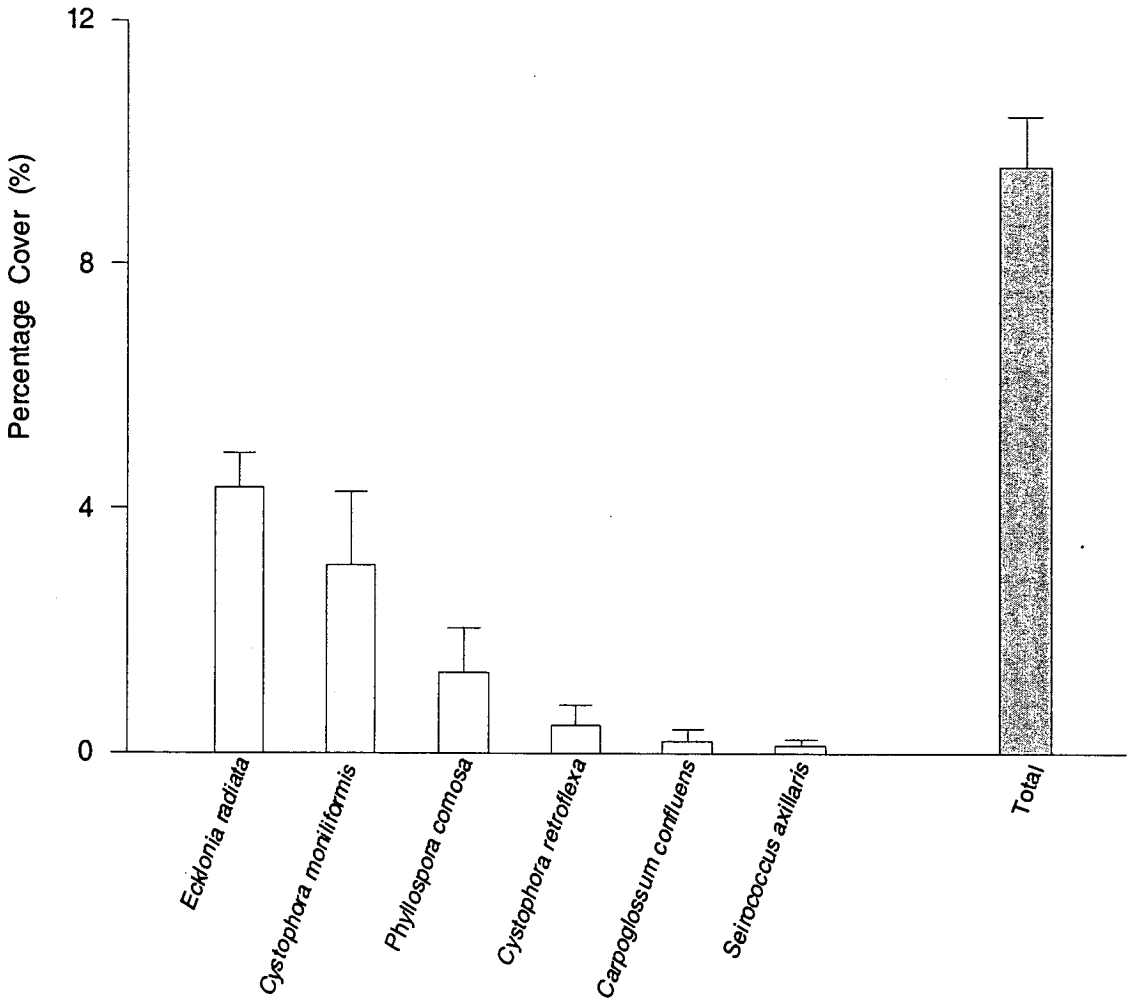


Figure 3.5. Percentage cover of recruits of canopy-forming brown algae in *Phyllospora comosa* dieback plots, assessed in September 2001. Data are means (+ SE) of six replicate plots.

3.4.3 Cover of understorey algae, sediment and invertebrates

The reduction in cover of the *P. comosa* canopy resulted in bleaching of encrusting algae and an increased cover of sediment and understorey algae (Figure 3.4; Table 3.2). Cover of healthy non-geniculate coralline algae and the crustose *Peyssionella* spp. was dramatically lower in the dieback area (10.5 % ± 1.9 SE) compared to that in non-dieback patches at the same depth (66.7 % ± 3.3 SE) and the shallow *P. comosa* plots (64.7 % ± 1.9 SE). Sediment cover in the dieback areas (30.1 % ± 3.3 SE) was an order of magnitude greater than that in non-dieback patches at the same

depth (2.2 % ± 0.5 SE) and significantly greater than that in the shallow *P. comosa* plots (6.3 % ± 1.8 SE).

Cover of both foliose red and green understorey algae was significantly greater in the dieback areas compared with adjacent control patches where the native canopy remained intact (Figure 3.4; Table 3.2). The green algal group, consisting entirely of the filamentous algae *Cladophora* sp., averaged 20.6 % (± 4.2 SE) cover in the *P. comosa* dieback area but was < 3 % in the two control areas. Similarly, the foliose red algal group, which included a range of ephemeral species (e.g. *Heterosiphonia* spp., *Polysiphonia* spp.) averaged 13.6 % (± 3.2 SE) cover in dieback plots compared with < 1.5 % in the control areas. In contrast, cover of the *Zonaria/Lobophora* complex was similar in all three areas.

Sessile understorey invertebrates were also influenced by the *P. comosa* decline. Cover was lower in the dieback area (1.5 % ± 0.8 SE) compared to that in non-dieback patches at the same depth (7.5 % ± 0.6 SE), and the shallow *P. comosa* plots (7.7 % ± 1.7 SE). These differences were associated with reduced cover of encrusting sponges, ascidians and the bryozans *Orthoscuticella ventricosa* and *Bugularia dissimilis* in the dieback plots (Figure 3.4; Table 3.2).

3.5 Discussion

3.5.1 Response of *Undaria pinnatifida* to canopy dieback

The clear response of *Undaria pinnatifida* following the dieback of *Phyllospora comosa* is consistent with results of manipulations demonstrating that experimental removal of the native algal canopy results in establishment of *U. pinnatifida* (Chapter 2). The results demonstrate that microscopic gametophytes and/or sporophytes were distributed beneath the dense *P. comosa* canopy prior to the decline, since the canopy deterioration occurred during autumn, when *U. pinnatifida* spores are not present in the water column (Sanderson, 1997). *U. pinnatifida* sporophytes responded opportunistically to the *P. comosa* decline, most likely by utilising the increased light levels associated with the reduction in canopy cover. These results are also consistent with previous observations of *U. pinnatifida*, correlating dense stands of *U. pinnatifida* with disturbed habitats (Sanderson, 1997; Johnson, unpublished), and casual observations of *U. pinnatifida* establishing in patches from which native algae are removed during storm swells (J. Valentine, pers. obs.).

The results also indicate that there is a relationship between timing of disturbance and subsequent *U. pinnatifida* sporophyte density. The *P. comosa* dieback occurred over the summer/autumn months of 2001, while in our artificial disturbance treatments canopy removals were conducted during spring 1999 and winter 2000. Whilst direct comparisons with these artificial disturbances need to be interpreted carefully (because the *U. pinnatifida* response was measured in different years), it is nonetheless interesting that the *U. pinnatifida* sporophyte densities that developed following *P. comosa* dieback (6.8 plants m^{-2} ± 2.0 SE) fell between the values observed for the spring (3.6 plants m^{-2} ± 0.6 SE) and winter (14.0 plants m^{-2} ± 2.6 SE) canopy removals in the artificial disturbance experiment (Chapter 2). These

combined data suggest that the closer the timing of disturbance is to the onset of sporophyte development, the greater the establishment density of *U. pinnatifida*. We speculate that as the period between disturbance and the onset of sporophyte development increases, competition with native species able to develop before *U. pinnatifida* sporophytes begin growing, leads to lower recruitment success of *U. pinnatifida*.

3.5.2 Response of native species to canopy dieback

The decline of encrusting algae and increase in sediment cover following dieback of the *P. comosa* canopy have been similarly observed in several studies in which algal canopies have been removed artificially (Kennelly and Underwood, 1993; Edwards, 1998; Melville and Connell, 2001). The bleaching of encrusting algae that followed the decline of the canopy may be caused either by increased light levels, increased sediment levels, or a combination of both. Although the detrimental effects of sediment on encrusting algae are largely unknown, it appears that the sweeping effect of large macroalgae on the benthos maintains encrusting algae largely free of sediment. A possible mechanism to explain this observation has been proposed by Melville and Connell (2001), suggesting that large macroalgae suppress the growth of filamentous algae, indirectly leading to the persistence of encrusting algal cover.

While *U. pinnatifida* is clearly able to recruit and grow when cover of encrusting coralline algae is reduced, there is limited understanding of the consequences of coralline algal decline for native species. Edwards (1998) concluded that the primary substratum upon which the brown alga *Desmarestia ligulata* recruits was non-geniculate coralline algae. Similarly, in rockpool habitats in the Mediterranean Sea it has been suggested that persistence of the canopy-forming alga *Cystoseira* sp. may

depend on the availability of encrusting coralline algae (Benedetti-Cecchi and Cinelli, 1992). In marked contrast to these results, others have shown that encrusting coralline algae inhibit the development of foliose and filamentous macroalgae either by shedding their epithallial cells (Johnson and Mann, 1986; Camus, 1994; Keats *et al.*, 1997) or through the production of allelopathic substances (Suzuki *et al.*, 1998).

The restricted temporal scale of the study limits the scope of inference in regard to the response of canopy-forming algae to the *P. comosa* decline. Despite this, the initial slow rate of recovery observed following artificial canopy removal (see Chapter 2) appears comparable to that observed in this study after natural canopy disturbance. Recovery of native canopy-forming species averaged 9.6 % in the present study, while averaging 12.3 % in assessments conducted 6 months after artificial canopy removals in the adjacent mixed algal zone (Chapter 2). We also note that there was some recruitment of *P. comosa* into dieback areas, despite the observation that this species did not recruit at all over the two-year period of the artificial clearance experiments (Chapter 2). This may reflect seasonal and annual variation in availability of *P. comosa* propagules. Alternatively the different mechanisms that lead to reduced canopy cover (i.e. artificial vs natural canopy removal) may explain this variation. For example, the increased light levels that follow canopy removal would have been more rapid in the artificial canopy removal compared with the natural canopy disturbance, where the canopy declined over a longer time period.

In terms of understorey foliose species, some similarities and conspicuous differences were evident between the present study and our recent work involving

artificial disturbance treatments (Chapter 2). For example, cover of the foliose red algal guild averaged 13.7 % (± 3.2 SE) following *P. comosa* dieback, a level comparable to that observed six months after artificial canopy removals (10.9 % ± 5.2 SE). In contrast, the significant response of green understorey algae (*Cladophora* sp.) following dieback of *P. comosa* was not observed in artificial canopy removals, either reflecting variability in availability of propagules or differences associated with the mechanism of canopy removal.

The loss of sessile invertebrate cover with dieback of *P. comosa* is comparable to that observed following artificial canopy removals in Tasmania and elsewhere (Kennelly, 1987b; Kennelly, 1989; Chapter 2). The observed decrease in cover was likely to be associated with the increased sediment levels, which effectively smothered these animals.

3.5.3 Conclusions

The results from this study highlight the opportunistic nature of *U. pinnatifida.* Following deterioration of the canopy, macroscopic sporophytes developed at high densities during the spring growth season, while remaining rare or absent in adjacent patches where the native canopy remained intact. These findings have significant implications for locations where *U. pinnatifida* has been introduced. Given results from our previous work to indicate that native algae can recover slowly in artificially disturbed areas after initial invasion by *U. pinnatifida*, the intensity and spatial and temporal distribution of disturbance is likely to be critical in determining abundance of *U. pinnatifida* on a local scale. If disturbance occurs at an appropriate frequency (e.g. annually or 2-yearly), it can be expected that *U. pinnatifida* will maintain large and persistent populations. There is growing evidence that disturbance as a result of

human activities is increasing, with potentially dramatic consequences on benthic communities (Harris and Tyrrell, 2001). The effects of stresses such as climate change (Coelho *et al.*, 2000), species removals (Pauly *et al.*, 2000) and habitat alteration due to fishing (Collie *et al.*, 1997; Watling and Norse, 1998) represent ongoing threats to native algal communities. Unless these disturbances can be mitigated, *U. pinnatifida* is likely to continue to colonise new areas and become a persistent and conspicuous component of temperate subtidal communities around the globe.

Chapter 4

"Does intensive grazing by the sea urchin *Heliocidaris erythrogramma* enable dense stands of the introduced kelp *Undaria pinnatifida* to persist?"

(submitted to *Marine Ecology Progress Series*)

4.1 Abstract

Few studies have addressed processes enabling persistence of an introduced species after its introduction in a marine system. In this study we investigate mechanisms enabling persistence of the introduced Asian kelp *Undaria pinnatifida* on sea urchin (*Heliocidaris erythrogramma*) 'barrens' on the east coast of Tasmania. Previous work has demonstrated that development of dense stands of *U. pinnatifida* requires disturbance to reduce cover of native algae. Observations of *U. pinnatifida* occurring abundantly on urchin barren habitats suggests that disturbance in the form of grazing urchins prevents recovery of native canopy-forming species, allowing dense stands of *U. pinnatifida* to persist. We examined this hypothesis over a 30-month period in a manipulative experiment in which the response of native algae and *U. pinnatifida* was examined in treatments comprising all possible combinations of +/- urchins, +/- *U. pinnatifida* and +/- enhanced native algal spore inoculum. The results demonstrated that the local sea urchin *H. erythrogramma* can have a significant impact on *U. pinnatifida* abundance. The response was most dramatic in the 2001 sporophyte growth season, when sea urchins destructively grazed *U. pinnatifida* sporophytes in experimental plots on the urchin barren. Removal of sea urchins resulted in a slow increase in cover of understorey red algae but only limited recovery of native canopy-forming species. In treatments where both sea urchins and *U. pinnatifida* were removed, cover of canopy-forming species did not exceed 6 % over the duration of the study. Consequently, in the absence of sea urchin grazing

there was no evidence of inhibition of *U. pinnatifida* by native algae. While the intensity of urchin grazing may directly influence persistence of *U. pinnatifida*, recovery of native canopy-forming species may be influenced by a combination of factors including sea urchin grazing, depth and most importantly, the degree of sediment accumulation.

4.2 Introduction

Biological introductions in the marine environment have increased significantly over the last two decades, mainly due to human assisted transport associated with international shipping, aquaculture and aquarium activities (Carlton and Geller, 1993; Meinesz *et al.*, 1993; Ribera and Boudouresque, 1995; Carlton, 1999). Introduced marine species now represent a major threat to native ecosystems with the potential to dramatically alter native communities by affecting biological diversity, productivity, habitat structure and fisheries (Carlton, 1999).

In defining the threat that an introduced species poses to native communities it is important to understand the role of disturbance in the invasion process (Hiebert, 1997). If an introduced species can establish and maintain persistent populations in the absence of disturbance, it potentially represents a major threat to the integrity of native communities. Conversely, if establishment and persistence of an exotic species relies on disturbance, the key threatening process is the disturbance rather than the introduced species itself.

While disturbance may facilitate establishment of an introduced species, its persistence may not require ongoing disturbance. For example, on the Atlantic coast

of Canada invasion by the introduced seaweed *Codium fragile* ssp. *tomentosoides* is facilitated by disturbance to the native kelp canopy in the form of either destructive urchin grazing or smothering of kelp laminae by the epiphyte *Membranipora membranacea* (Chapman *et al.*, 2002). Once *C. fragile* is established, however, it displaces kelp species by inhibiting recruitment (Chapman *et al.*, 2002). Similarly, invasion of San Francisco Bay by the introduced clam *Potamocorbula amurensis* followed a major flood disturbance, after which the introduced clam inhibited recovery of the native community during conditions of normal river flow (Nichols *et al.*, 1990).

Since its introduction to the port of Triabunna in the 1980's (Sanderson and Barrett, 1989), the annual Japanese kelp *Undaria pinnatifida* has become a conspicuous feature of subtidal communities in sheltered to moderately exposed habitats along much of the east coast of Tasmania. Recent experiments have demonstrated clearly that disturbance to the native algal canopy is an essential process facilitating successful establishment of *U. pinnatifida* (Chapter 2; Chapter 3). Following both artificial and natural disruption of the canopy, *U. pinnatifida* sporophytes recruited in high densities, while the presence of an intact native canopy inhibited sporophyte development in the same area.

While these recent experiments are illuminating in defining mechanisms of establishment, factors responsible for the persistence of dense *U. pinnatifida* stands have not been adequately addressed. Sea urchin grazing may represent a continuous source of disturbance that effectively maintains dense *U. pinnatifida* stands. In Tasmania, *U. pinnatifida* occurs most abundantly on urchin 'barrens' characterised

by high densities of the sea urchin *Heliocidaris erythrogramma*, low cover of native algae, and seasonal abundance of *U. pinnatifida* which often exceeds 100 % cover (Sanderson and Barrett, 1989; Sanderson, 1997; Johnson, unpublished). It has been suggested that *U. pinnatifida* maintains high densities on urchin barrens as a result of high reproductive output and rapid spring growth of the sporophyte which exceeds the grazing capabilities of the urchin (Sanderson and Barrett, 1989). Based on these observations and the role of sea urchins as a major source of disturbance to temperate subtidal communities elsewhere (Mann, 1977; Schiel and Foster, 1986; Andrew, 1993; Hagen, 1995; Palacin *et al.*, 1998), our hypothesis is that maintenance of dense stands of *U. pinnatifida* on urchin barrens requires continual disturbance in the form of intensive grazing by sea urchins.

In this study we report on a large manipulative experiment designed to identify (1) whether dense stands of *U. pinnatifida* are self-maintaining in the absence of high densities of sea urchins; and (2) those factors that affect the re-establishment of native canopy-forming species in sea urchin/*U. pinnatifida* dominated areas.

4.3 Materials and methods

4.3.1 Study site

The study was conducted between June 1999 and November 2001 in the Mercury Passage, on the east coast of Tasmania. In this area a variety of subtidal communities are found, ranging from 'urchin barrens' to habitats dominated by native perennial brown algae. Urchin barrens in the Mercury Passage area are characterised by relatively high densities (4-8 m^{-2}) of the sea urchin *Heliocidaris erythrogramma*, low

cover of native algae, and seasonal dominance by *Undaria pinnatifida*. We conducted the experiment in an extensive area of urchin barren habitat on a reef at Lords Bluff in the Mercury Passage (42°31' S 147°59' E). At this site the urchin barren extended along approximately 250 m of coast at depths greater than 5 m.

4.3.2 Experimental design

The experiment consisted of a total of eight treatments, comprising factorial combinations of three factors, *viz.* (1) abundance of *Heliocidaris erythrogramma* (2 levels; 0 % and 100 % removal); (2) extent of *Undaria pinnatifida* canopy (2 levels; 0 % and 100 % removal of sporophytes); and (3) level of native algal spore inoculum (2 levels; background and enhanced).

There were four replicates of each experimental treatment, yielding a total of 32 plots. Treatments were assigned at random to permanent plots established in the 7-12 m depth range in the urchin barren habitat in June 1999. The experimental plots were 4 x 4 m, although response variables were estimated from the inner 2 x 2 m area to minimize edge effects.

4.3.3 Manipulations

The initial removal of sea urchins (*H. erythrogramma*) commenced in June 1999. Thereafter plots were maintained clear of immigrating urchins every 4-6 weeks for the 30 month duration of the experiment. Fences were not used to restrict urchin access, since *H. erythrogramma* showed low rates of movement in an earlier study conducted on a nearby reef (Sanderson *et al.*, 1996) and in a pilot study we conducted to assess immigration rates.

U. pinnatifida sporophytes were removed by cutting plants immediately above the holdfast. In the first season of the experiment (1999), plants were removed once they could be readily identified as *U. pinnatifida* recruits, at around 5 cm in total length. In subsequent seasons (2000 and 2001) plants were removed when they reached 15 cm in length. Removals were conducted approximately monthly during the *U. pinnatifida* sporophyte growth season (i.e. August-December).

The native algal spore inoculum was enhanced by placing fertile native species collected from an adjacent reef in mesh bags attached to star pickets at the perimeter of plots. Several individuals (6-10 depending on the species and size of plants) of a single species were placed in each mesh bag. This technique has proved effective in seeding macroalgae in other experiments (Dayton *et al.*, 1984). A range of canopy-forming brown algae (*Phyllospora comosa, Ecklonia radiata, Carpoglossum confluens, Seirococcus axillaris*) were used for the seeding treatment depending on their availability and the presence of fertile reproductive material. Fresh material was added to experimental plots every 6-8 weeks during 1999 and 2000. In addition to using plants in mesh bags for the enhancement treatment, algae transplanted to concrete bricks were also used as a spore source (*Macrocystis pyrifera* and *Ecklonia radiata*). For algal transplants, whole plants were carefully removed from the substratum, attached to bricks using heavy-duty rubber bands and placed at the perimeter of plots. To ensure separation of treatments receiving an enhanced spore inoculum from those that did not receive the enhancement, plots were separated by a minimum distance of 15 m. We assumed that the effective spore shadow of the algal species we used was limited to < 15 m, as has been demonstrated for other large brown algae (Ambrose and Nelson, 1982; Anderson and North, 1966; Andrew and

Viejo, 1998; Deysher and Norton, 1982). Species used in the spore enhancement treatments and the dates of replenishment of fresh material are included in Table 4.1.

4.3.4 Algal assessment

Assessment of experimental plots was conducted approximately every three months, during which the density of canopy-forming species and urchins was recorded, along with cover of understorey algae, sessile invertebrates and sediment. A census of the density of canopy-forming algae (> 30 cm total length) and urchins was made by direct counts in the inner 2 x 2 m of each plot. Cover of understorey species was estimated from five 0.10 m^2 photoquadrats positioned randomly in each plot. Photographs were taken using Ektachrome 100 ASA slide film and slides were scanned to determine the cover of algae using a point intercept method. Each image was overlayed with 100 equally spaced dots using Imagepro® computer software. Organisms were identified from photographs to the highest taxonomic resolution possible. For large brown algae identification to species level was possible, however, for most of the understorey species, photographs could only be used to separate algal cover into guilds (e.g. red algae, brown turf algae, green algae). An estimate of sediment depth was also obtained during algal assessments, measured to the nearest millimetre in five random positions in each plot.

Table 4.1 Details of spore enhancement manipulations, indicating the species 'seeded', the enhancement technique and dates of deployment.

Enhancement Methodology	Date(s) Conducted	Species "seeded"
Mesh bag	26/6/99	*Seirococcus axillaris*, *Carpoglossum confluens*, *Ecklonia radiata*
	4/8/99	*Seirococcus axillaris*, *Carpoglossum confluens*, *Ecklonia radiata*
	8/11/99	*Seirococcus axillaris*, *Carpoglossum confluens*, *Ecklonia radiata*
	14/1/00	*Ecklonia radiata*, *Phyllospora comosa*
	22/3/00	*Ecklonia radiata*, *Phyllospora comosa*
	23/6/00	*Seirococcus axillaris*, *Carpoglossum confluens*, *Ecklonia radiata*
	21/9/00	*Seirococcus axillaris*, *Carpoglossum confluens*, *Ecklonia radiata*
	20/11/00	*Seirococcus axillaris*, *Carpoglossum confluens*, *Ecklonia radiata*
Transplant	13/4/00 10-11/5/00	*Ecklonia radiata* *Macrocystis pyrifera*

Photographic sampling did not allow quantifying more than one structural layer of the algal community. The primary aim of the photoquadrat assessment was to estimate cover of understorey species and recruits of canopy-forming species. If a canopy was present in the quadrat (mainly *Undaria pinnatifida*), larger plants were moved aside before the photograph was taken. The photoquadrat assessment had limitations when estimating cover of encrusting algae, sessile invertebrates and sediment when there was significant cover of understorey algae present.

As a result of these issues, at the conclusion of the experiment in November 2001, destructive sampling was conducted to investigate algal community structure in more detail. All foliose macroalgae in each plot were removed by hand and placed in mesh bags before being transported to the laboratory (filamentous algae occurring in the sediment matrix were not collected). Samples were sorted to the highest taxonomic resolution possible and dried (70 °C for 48 hours) before weighing.

4.3.5 Statistical analysis

Analysis of the response of algal community was conducted separately for assessments made in November 2000 and November 2001, approximately 15 and 27 months after all treatments were initiated. Rather than using a repeated measures approach, we decided *a priori* to conduct analyses during the peak period of *U. pinnatifida* sporophyte growth for each year of the experiment. We also analysed the response of *U. pinnatifida* in November 1999 as the urchin density manipulation had been in place for five months prior to this assessment.

Of the five species that were used in the native spore enhancement treatment, only macroscopic recruits of *Carpoglossum confluens* were ever observed in the study area. None of these recruits, however, reached the criterion of 30 cm minimum length used in density assessments during the course of the experiment and their cover averaged < 1 % across all treatments. We tested whether cover of *C. confluens* recruits was influenced by the spore enhancement treatment in preliminary analyses using a 4-factor Model III nested ANOVA. This analysis included main effects of urchin removal, *U. pinnatifida* removal and spore enhancement (all fixed effects) as well as the nested term of 'plots within all combinations of urchin**Undaria**spore

enhancement' (a random effect). In both November 2000 ($F = 1.33$; $df_{1, 24}$; $P < 0.26$) and November 2001 ($F = 1.05$; $df_{1, 24}$; $P < 0.23$) the effect of spore enhancement was highly insignificant.

As a consequence of the very low cover values and lack of any effect of spore enhancement, this treatment was ignored in the main analysis, providing greater power to examine the effects of sea urchin and *U. pinnatifida* removal. For the main analysis density data were analysed using a 2-factor Model I ANOVA while for cover data a 3-factor Model III nested ANOVA was used. Both analyses included urchin and *U. pinnatifida* removal. For the nested ANOVA, 'plots within (urchin removal**Undaria* removal)' was included as a random factor.

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. Variances of some variables remained heterogeneous after transformation which usually occurred when mean abundance (and variance) of a guild was zero in several experimental plots. In these instances the analysis was still carried out, recognizing that with a balanced design heteroscedasticity has little effect on Type I error, but can increase Type II error (Scheffé, 1959).

4.4 Results

4.4.1 Maintenance of sea urchin removal treatment

During the first 18 months of the experiment, physical removal maintained urchin densities at very low levels in removal treatments, averaging 0.5 individuals m^{-2} compared to 7.1 individuals m^{-2} in unmanipulated plots (Figure 4.1). Between January and April 2001, however, some re-invasion of cleared plots occurred with densities reaching an average of 5.8 individuals m^{-2} in April 2001. For the remainder of the experimental period the number of animals in removal plots remained at very low levels.

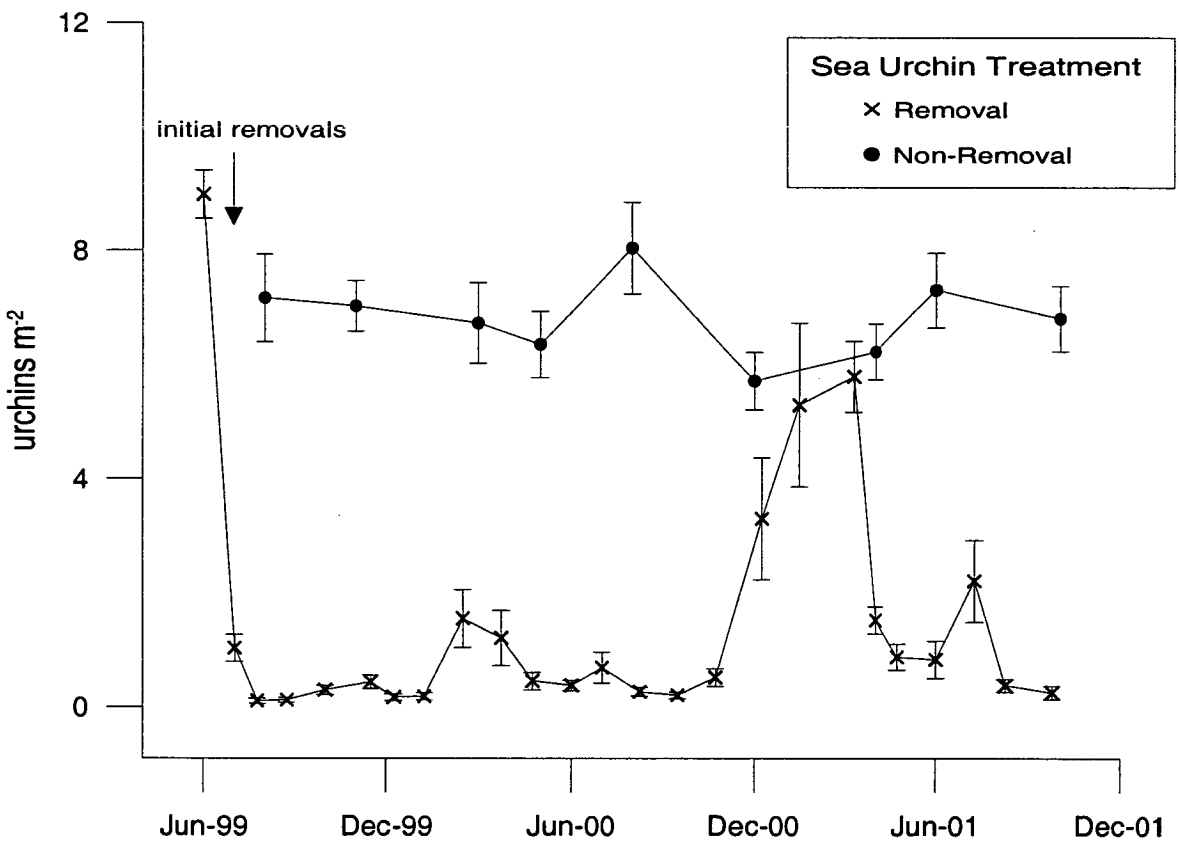


Figure 4.1. Mean density (± SE) of sea urchins in removal and non-removal plots (n = 16). Removal plots were visited approximately every four weeks for the duration of the study. Data associated with the urchin removal treatment represents the number of animals cleared from plots while maintaining the treatment. For the non-removal treatment densities are derived from data collected during routine assessments of algae and sea urchins (conducted at three monthly intervals).

4.4.2 Response of *Undaria pinnatifida* to experimental manipulations

Undaria pinnatifida densities were higher in plots from which urchins were removed than in plots containing sea urchins (Figure 4.2). In urchin removal plots, average densities of *U. pinnatifida* sporophytes were 3-4 plants m^{-2} higher than in controls in 1999 and 2000, however, these differences were not statistically significant (1-way ANOVAs, 1999: $F = 3.27$, $df_{1, 14}$, $P = 0.092$; 2000: $F = 3.74$, $df_{1, 14}$, $P = 0.074$). In 2001 the effect of urchin removal was statistically significant (1-way ANOVA, $F = 8.41$, $df_{1, 14}$, $P = 0.012$) resulting in a mean *U. pinnatifida* density of 5.2 plants m^{-2} compared to less than 0.1 plant m^{-2} in controls. This result corresponded to an average biomass (dry weight) of 54.5 g m^{-2} *U. pinnatifida* in urchin removal plots compared to 0.4 g m^{-2} in controls (Figure 4.6).

The effect of sea urchins was also evident from the number of *U. pinnatifida* plants taken from removal treatment plots. In all years there were fewer *U. pinnatifida* plants removed from plots with urchins than in treatments free of urchins (Table 4.2). Examination of the number of plants in experimental plots prior to the initial removal of *U. pinnatifida* in August 2001 allowed an assessment of the cumulative effects of the previous 2 years of manipulation on *U. pinnatifida* abundance (Figure 4.3). The results clearly show that the presence of urchins had considerable detrimental effects on *U. pinnatifida* density (2-way ANOVA, $F = 14.93$, $df_{1, 28}$, $P = 0.001$), while the *U. pinnatifida* removal treatment had no significant effect on abundance in the subsequent 2001 sporophyte growth season (2-way ANOVA, $F = 0.57$, $df_{1, 28}$, $P = 0.455$).

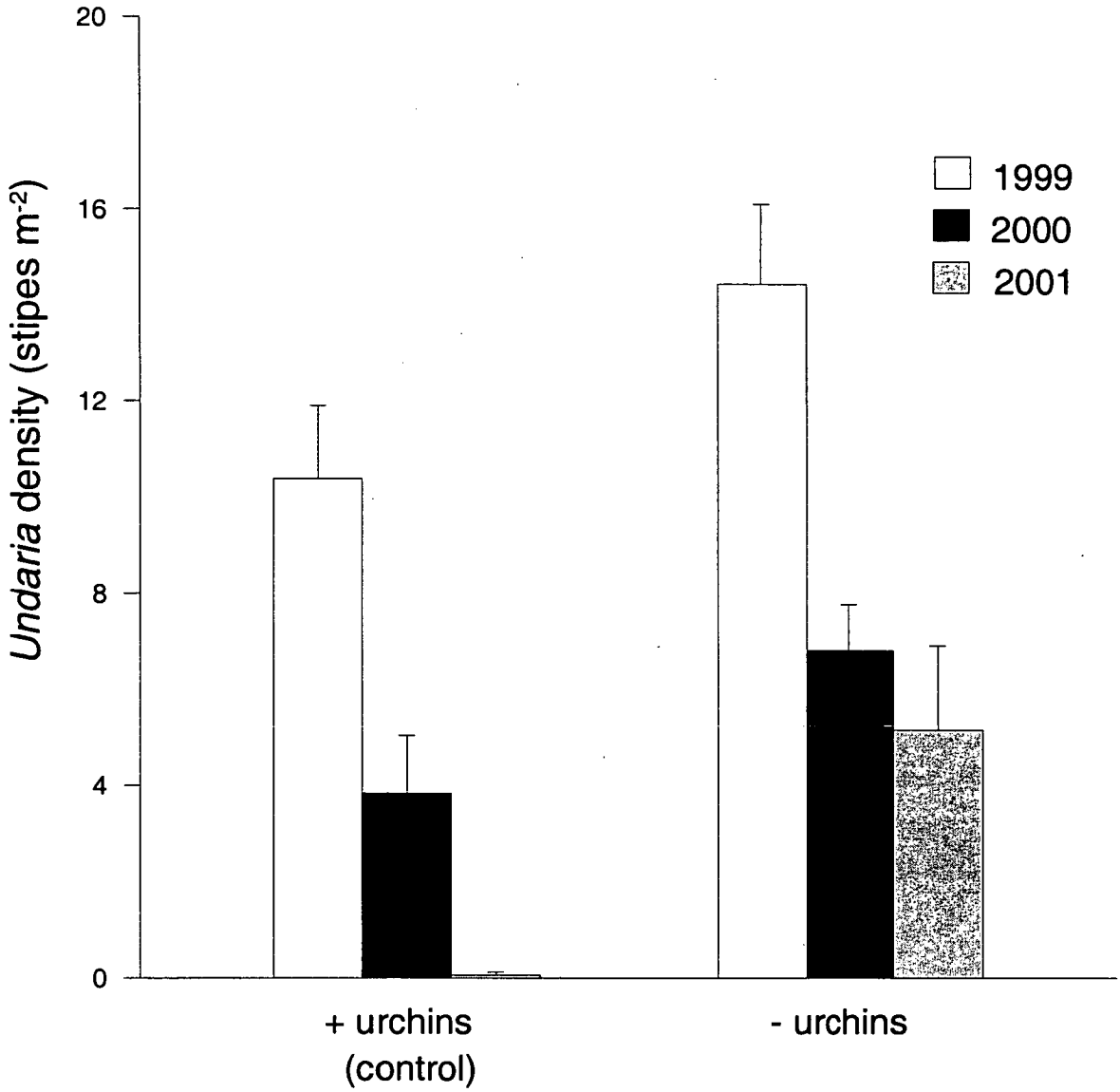


Figure 4.2. Effect of sea urchin manipulations on abundance of *Undaria pinnatifida* assessed in November 1999, 2000 and 2001. Data represent mean (+ SE) stipe counts of all adult plants > 30 cm in size in each 4 m^2 experimental plot (n = 8 replicates per treatment).

Table 4.2. Number of *Undaria pinnatifida* plants removed from experimental '*Undaria* clearance' plots. In 1999 plants were removed as soon as they could be identified as *U. pinnatifida*, which was around 5 cm in total length. In 2000 and 2001, plants were removed on reaching 15 cm in total length. During each year plots were visited regularly during the sporophyte growth season (August-December) to remove any new recruits. Data are means (± SE).

1999*		2000		2001	
+urchin	-urchin	+urchin	-urchin	+urchin	-urchin
996 ± 158.1	1719 ± 136.3	165 ± 51.4	217 ± 44.8	2 ± 1.0	47 ± 11.4

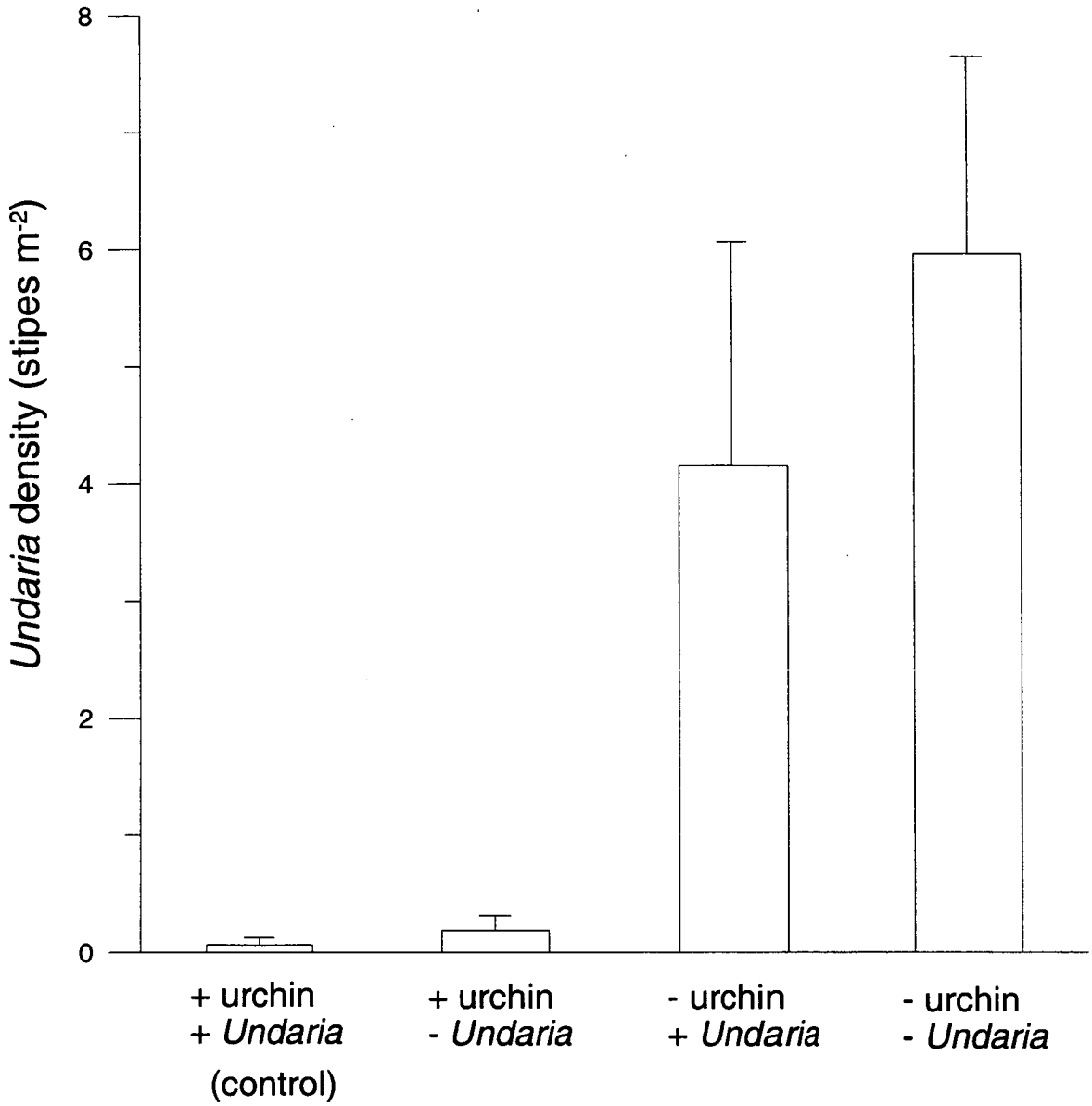


Figure 4.3 Response of *Undaria pinnatifida* to experimental manipulations assessed in August 2001, prior to the commencement of the 2001 *U. pinnatifida* canopy manipulations. Data represent means (+ SE) of all *U. pinnatifida* plants > 15 cm in total length within each 4m^2 experimental plot (n = 8 replicates per treatment).

4.4.3 Response of native algae to sea urchin removal

Total native algal cover

Total native algal cover in plots with sea urchins remained < 20 % during experimental period (Figures 4.4; 4.5). The community was characterised by very low cover of both brown and green algae and moderate cover of foliose red algae. Cover of canopy-forming species remained < 2 % throughout the experiment. The persistent presence of a high cover of sediment (> 50 %) up to 10 mm in depth was also a feature of control areas (Figure 4.4).

A significant increase in cover of native algae was detected in response to removal of sea urchins in both the November 2000 and 2001 assessments (Figure 4.4; Table 4.3). While total algal cover was comparable between urchin removal and non-removal plots for the first year of the study, cover increased steadily in urchin removal treatments after July 2000 (Figure 4.5). This pattern is reflected clearly in the biomass (dry weight) of plants determined at the conclusion of the experiment, with an average of 36.2 g m^{-2} in urchin removal treatments compared with < 2 g m^{-2} when urchins were present (Figure 4.6, Table 4.4).

Response of native canopy-forming species

While native canopy-forming species never exceeded 6 % in any treatment over the 30-month experimental period, significantly greater cover developed in urchin removal plots than in controls in November 2000 (Figure 4.4, Table 4.3). The magnitude of this difference was small, however, with cover increasing from 0.7 % in the presence of urchins to 4.8 % in urchin removal plots. For data collected in November 2001 no canopy-forming species were recorded in the presence of

urchins, compared with an average of 1.6 % in urchin removal plots. This difference was marginally non-significant (P = 0.0570, see Table 4.3). The predominate canopy-forming species that were observed during the study were *Cystophora retroflexa* and *C. moniliformis*, as well as occasional individuals of a range of *Sargassum* species.

Data describing the biomass (dry weight) of canopy-forming species at the end of the experimental period exhibited the same trend as cover. Across urchin removal treatments, biomass of canopy species averaged 7.2 g m^{-2} (Figure 4.6). This value was strongly influenced by the presence of a single large *Seirococcus axillaris* plant present in one of the urchin removal plots at the beginning of the experiment that persisted throughout the study period (Appendix II). If this individual was excluded from analysis, the average biomass was reduced to 4.1 g m^{-2}.

Response of understorey algae and invertebrates

Urchin density had significant effects on cover of the red algal guild which consisted of both foliose and filamentous species. In November 2000 average red algal cover was 14.2 % in the presence of urchins, while it increased to 23.5 % in urchin removal plots (Figure 4.4; Table 4.3). Data collected during November 2001 showed even greater differences with cover averaging 14.3 % in the presence of urchins, compared to 41.5 % in urchin removal treatments. The temporal trend indicates that the greatest divergence in treatments occurred in the second year after manipulation of urchins (Figure 4.5). Native algal cover was clearly dominated by the guild of red algae (Figures 4.4 and 4.5) which showed stronger interannual variation than seasonal fluctuations.

The biomass (dry weight) of foliose red algae collected during destructive sampling at the end of the experiment reflected the patterns observed in cover (Figure 4.6; Table 4.4). Average biomass in urchin removal plots was 24.9 g m^{-2}, while in the presence of urchins this value was 1.9 g m^{-2}. The dominant red algal species occurring in urchin removal plots in the destructive sample was *Dasya ceramiodes*, which contributed more than 50 % of total algal biomass in urchin removal plots (see Appendix II). The biomass of *Echinothamnion* sp., *Dictymenia harveyii* and *Heterosiphonia* sp. also reached moderate levels in urchin removal plots.

In plots where urchins were present the average cover of green algae did not exceed 0.1 %. Sea urchin removal resulted in very small but statistically significant increases in cover of green algae in November 2000 and November 2001 (Figure 4.4; Table 4.3). These increases were mainly associated with the presence of *Codium* sp. or unidentified filamentous algae. Green algae were not collected in sufficient quantity during destructive sampling to warrant analysis.

The guild of brown turf-forming algae did not respond to a decrease in urchin density during the first year of the experiment (assessment in November 2000). A year later in November 2001, however, the effect of urchins was significant but small, resulting in an additional 3 % cover in removal plots. In destructive samples no representatives from the brown turf guild were collected in the presence of urchins, while biomass averaged 4.1 g m^{-2} in urchin removal treatments. The main species collected during destructive sampling were *Zonaria angustata* and *Dictyopteris muelleri*. Ephemeral species that were absent during destructive sampling but relatively abundant at

various times during the study included *Asperococcus* sp., *Scytosiphon* sp. and *Colpomenia* sp.

Small decreases in the cover of encrusting algae and sessile invertebrates were recorded in November 2001 in response to sea urchin removal (Figure 4.4; Table 4.3). Although significant, it is likely that these differences are misleading given limitations of the photoquadrat assessment, which sampled only a single structural layer of the algal community (see methods and materials). Consequently, the increased levels of understorey algae that occurred as a result of urchin removal inevitably lead to lower estimates of encrusting algae and invertebrate cover, despite the fact that the abundance of these organisms may not have changed.

4.4.4 Response of native algae to *Undaria pinnatifida* removal

In contrast to responses to urchin removal, manipulation of *U. pinnatifida* had limited effects on native algae. Significant treatment effects due to either *U. pinnatifida* removal or the 'urchin removal**Undaria* removal' interaction were rarely detected, with the exception of brown turf algae (Table 4.3). Removal of the *U. pinnatifida* canopy resulted in approximately 3 % greater cover of brown turf for data collected in November 2000. A year later in November 2001 there was no evidence that any algal group responded to the removal of the *U. pinnatifida* canopy.

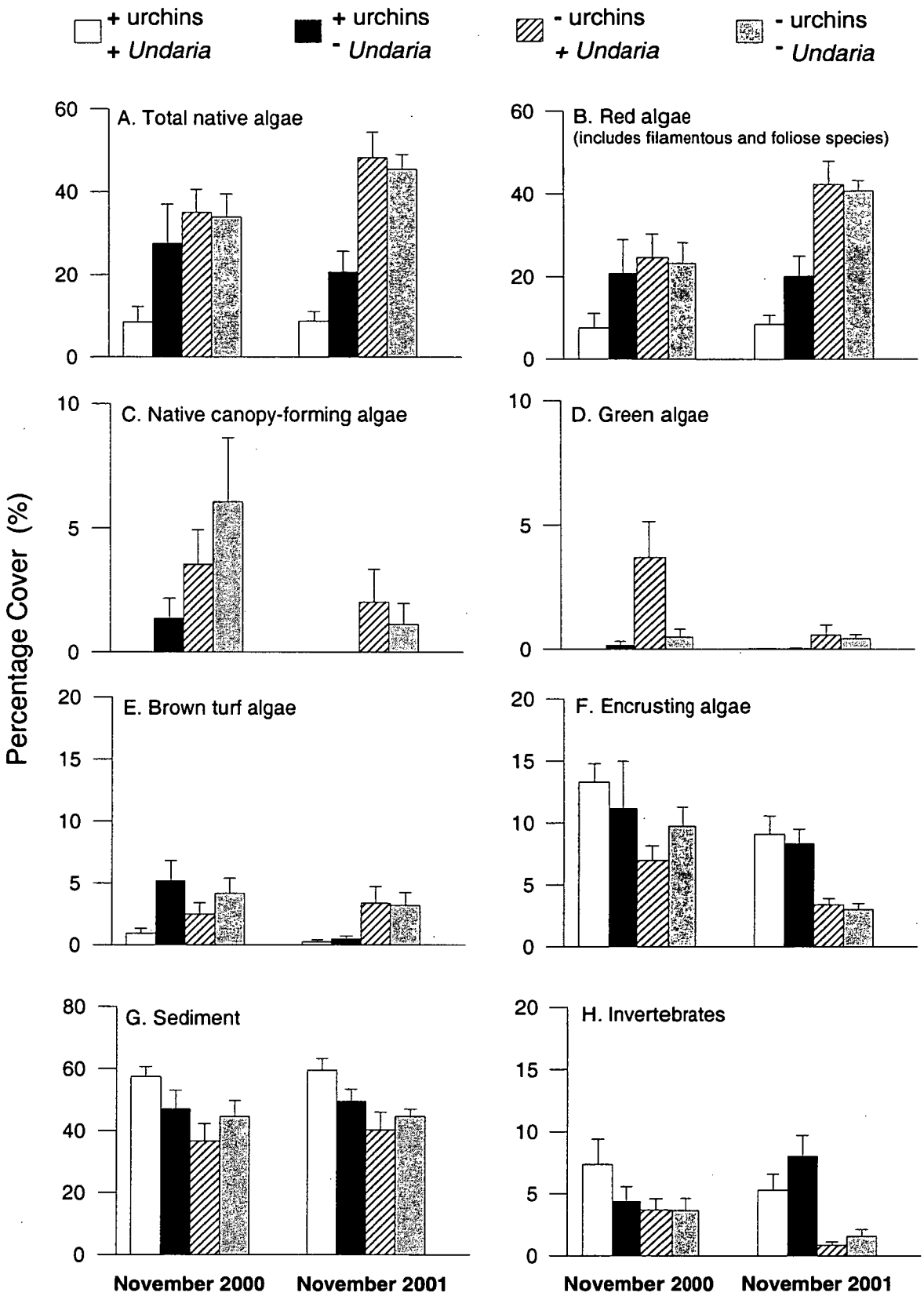


Figure 4.4. Effect of experimental manipulations on cover of various algal guilds, invertebrates and sediment, assessed in November 2000 and November 2001. Data represent mean (+SE) percentage cover (n = 8 replicates per treatment) determined from five randomly positioned 0.10 m^2 photoquadrats within each experimental plot. Note the different scales on the *Y*-axes.

Table 4.3. Effect of experimental manipulations on cover of algal guilds at the November 2000 and November 2001 assessments. Results are of the overall ANOVA examining the effect of sea urchin (*Heliocidaris erythrogramma*) removal and *Undaria pinnatifida* removal. Significant *P*-values (α = 0.05) are shown in bold face.

Guild (transformation)	Source of Variation							
	urchin		*Undaria*		urchin**Undaria*		Plot (urchin **Undaria*)	
	F (df = 1, 28)	P	*F* (df = 1, 28)	P	*F* (df = 1, 28)	P	*F* (df = 28, 128)	P
November 2000								
Total native algae ($\sqrt{Y}$)	12.66	**0.001**	2.12	0.157	2.62	0.117	5.45	**0.001**
Red algae {ln (*Y*+0.1)}	12.35	**0.002**	1.07	0.310	1.73	0.199	3.67	**0.001**
*Native canopy-forming algae (arcsin $\sqrt{0.01*Y}$)	7.37	**0.011**	1.63	0.213	0.15	0.704	3.00	**0.001**
*Green algae (arcsin $\sqrt{0.01*Y}$)	7.30	**0.012**	4.20	**0.050**	5.10	**0.032**	0.83	0.704
*Brown turf algae (arcsin $\sqrt{0.01*Y}$)	0.05	0.823	6.88	**0.014**	1.30	0.264	1.06	0.395
Encrusting algae ($Y^{*0.54}$)	2.47	0.127	0.03	0.853	2.22	0.147	4.38	**0.001**
Sediment (no transformation)	5.18	**0.031**	0.06	0.807	3.27	0.082	3.44	**0.001**
Invertebrates {ln(*Y*+0.1)}	2.71	0.111	0.48	0.493	0.35	0.561	2.54	**0.001**
November 2001								
Total native algae ($Y^{*0.42}$)	56.06	**0.001**	2.50	0.125	3.38	0.077	3.03	**0.001**
Red algae ($\sqrt{Y}$)	49.14	**0.001**	3.05	0.092	2.80	0.106	2.59	**0.001**
*Native canopy-forming algae (arcsin $\sqrt{0.01*Y}$)	3.94	0.057	0.32	0.577	0.32	0.577	1.55	0.053
*Green algae (arcsin $\sqrt{0.01*Y}$)	4.49	**0.043**	0.10	0.760	0.09	0.762	0.95	0.539
*Brown turf algae (arcsin $\sqrt{0.01*Y}$)	11.38	**0.002**	0.00	0.963	0.06	0.805	1.47	0.080
Encrusting algae ($\sqrt{Y}$)	29.07	**0.001**	0.20	0.661	0.68	0.417	1.38	0.115
Sediment (no transformation)	8.65	**0.007**	0.46	0.503	3.07	0.091	2.39	**0.001**
Invertebrates {ln(*Y*+0.1)}	35.60	**0.001**	2.46	0.128	0.04	0.852	1.55	0.053

* Transformation improved data structure considerably but did not achieve normality and homoscedasticity

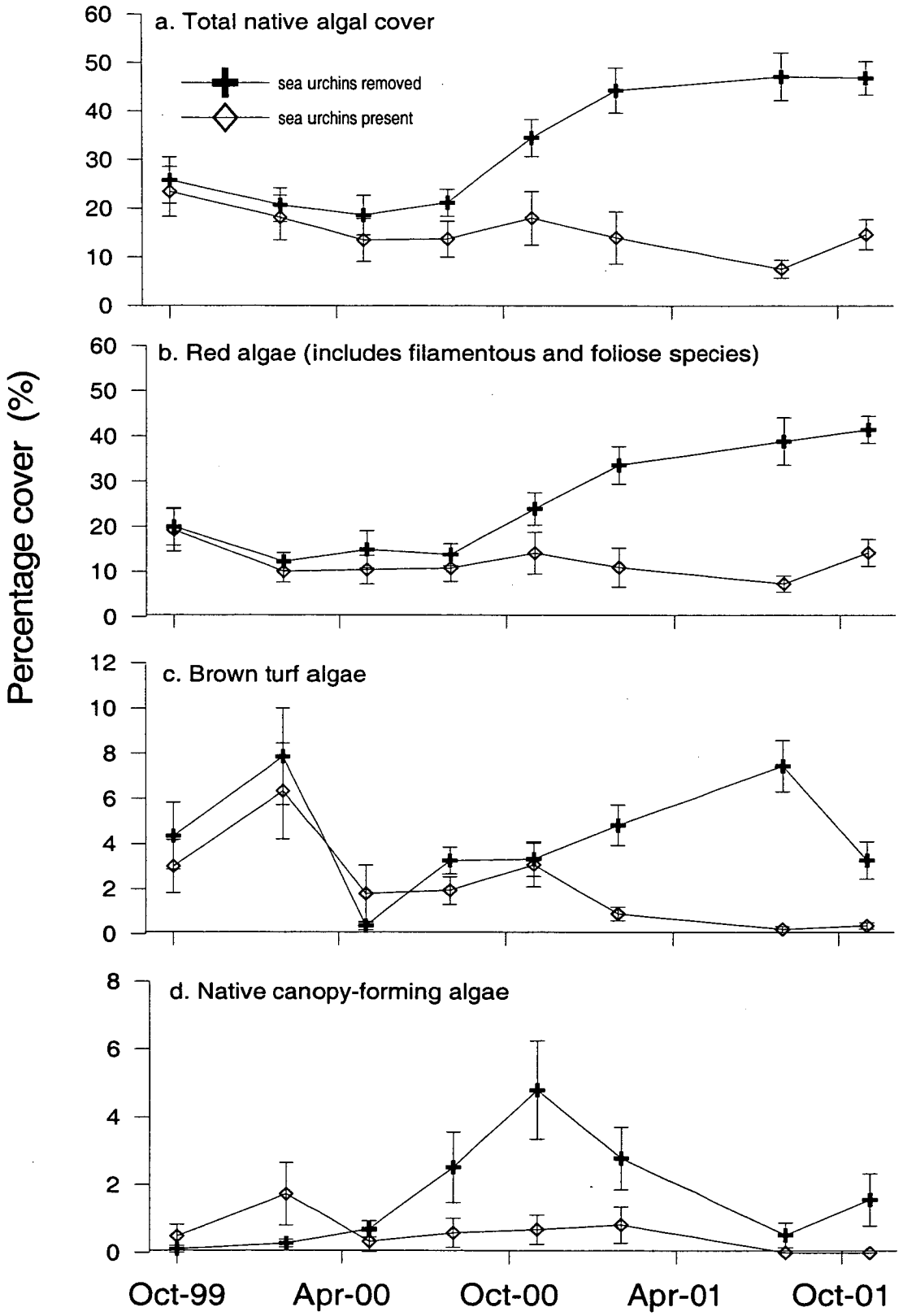


Figure 4.5. Effect of sea urchin removal on cover of algal guilds from October 1999 to November 2001. Data represent mean (± SE) percentage covers, pooled across treatments involving manipulation of *Undaria pinnatifida* (∴ n = 16) determined from 5 randomly positioned 0.10 m^2 photoquadrats within each experimental plot. Crosses represent sea urchin removal treatments, while diamonds indicate the presence of sea urchins. Note the different scales on the *Y*-axes.

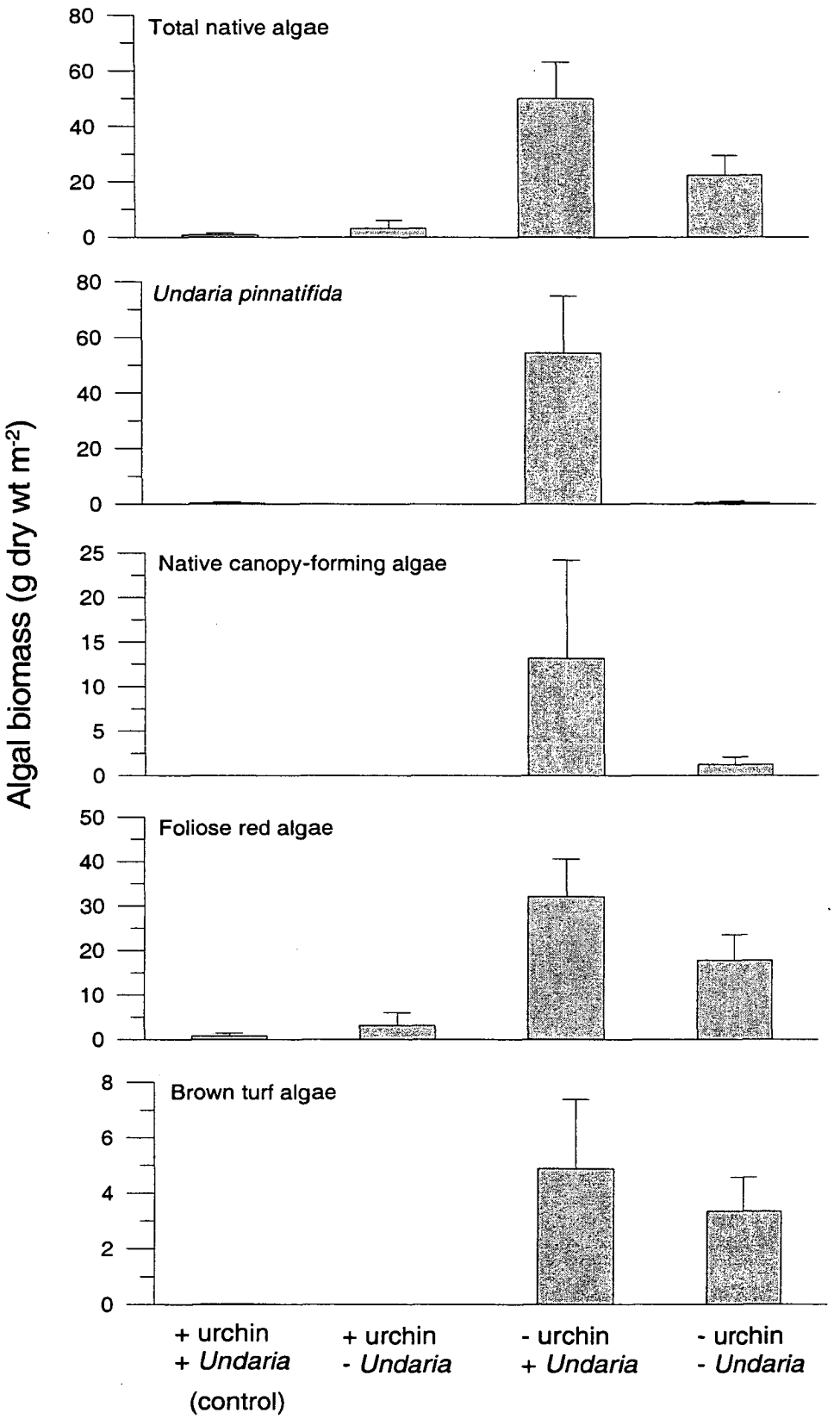


Figure 4.6. Effect of manipulations of sea urchins (*Heliocidaris erythrogramma*) and the canopy of *Undaria pinnatifida* on the biomass (g dry weight m^{-2}) of major algal groups following completion of the experiment in November 2001. Data represent means (+ SE) for each treatment (n=8). Biomasses were obtained by removing all macroalgae from each experimental plot (4 m^2 per plot). Note the different scales on the *Y*-axes.

Table 4.4 Effect of experimental manipulations on biomass of algal guilds collected at the end of the experiment (November 2001). Results are of the overall ANOVA examining the effect of sea urchin (*Heliocidaris erythrogramma*) and *Undaria pinnatifida* removals. Significant P-values ($\alpha = 0.05$) are shown in bold face. Note that for the *U. pinnatifida* response, the table includes the results of a 1-way ANOVA on the effect of urchin removal, as it was not appropriate to examine the effect of *U. pinnatifida* canopy removal on *U. pinnatifida* biomass.

Algal Guild (transformation)	Source of Variation					
	urchin		*Undaria*		urchin**Undaria*	
	F (df = 1, 28)	P	*F* (df = 1, 28)	P	*F* (df = 1, 28)	P
Total native algal cover {ln(*Y*+0.1)}	52.97	**0.001**	0.20	0.658	0.87	0.358
Undaria pinnatifida (no transformation)	6.98	**0.019**				
Native canopy-forming algae *{ln(*Y*+0.1)}	7.26	**0.012**	0.16	0.693	0.16	0.693
Foliose red algae ($Y^{*0.32}$)	42.76	**0.001**	0.29	0.595	1.58	0.220
Brown turf algae ($Y^{*0.14}$)	58.83	**0.001**	0.07	0.798	0.23	0.633

* Transformation improved data structure considerably but did not achieve normality and homoscedasticity

4.4.5 Effect of experimental manipulations on sediment

Cover of a sediment matrix was consistently high in all treatments throughout the experiment, averaging > 45 % across all treatments. Cover was slightly lower in the urchin removal plots when assessed in November 2000 and November 2001 (Figure 4.4; Table 4.3). Although statistically significant, it is likely that this difference is not biologically meaningful, for the same reasons outlined for encrusting algal and sessile invertebrate cover (i.e. the increase in algal cover in urchin removal plots inevitably lead to lower values of sediment cover, due to the fact that the photoquadrat technique only sampled a single structural layer of the community). In addition, a significant proportion of red algal cover was comprised of filamentous forms growing on the surface of the sediment matrix and not replacing the sediment itself. Thus it is likely sediment cover was under-estimated.

In plots containing sea urchins, the depth of sediment was significantly lower (2-way ANOVA, F = 18.84, $df_{1, 28}$, P = 0.001) than in plots from which the urchins were removed (3.8 mm ± 0.74 SE in removal plots, 1.4 mm ± 0.32 SE in un-manipulated plots)(Figure 4.7). Removal of the *U. pinnatifida* canopy had no detectable effect on either the cover or depth of sediment.

A prominent feature of the sediment matrix during summer 2001 was the presence of a cyanobacterial mat, dominated by the rod forming species *Microcoleus* sp.. Although the extent of the cyanobacterial mat was not affected by experimental manipulations, across all treatments an average of 25 % of the sediment was colonised by this organism.

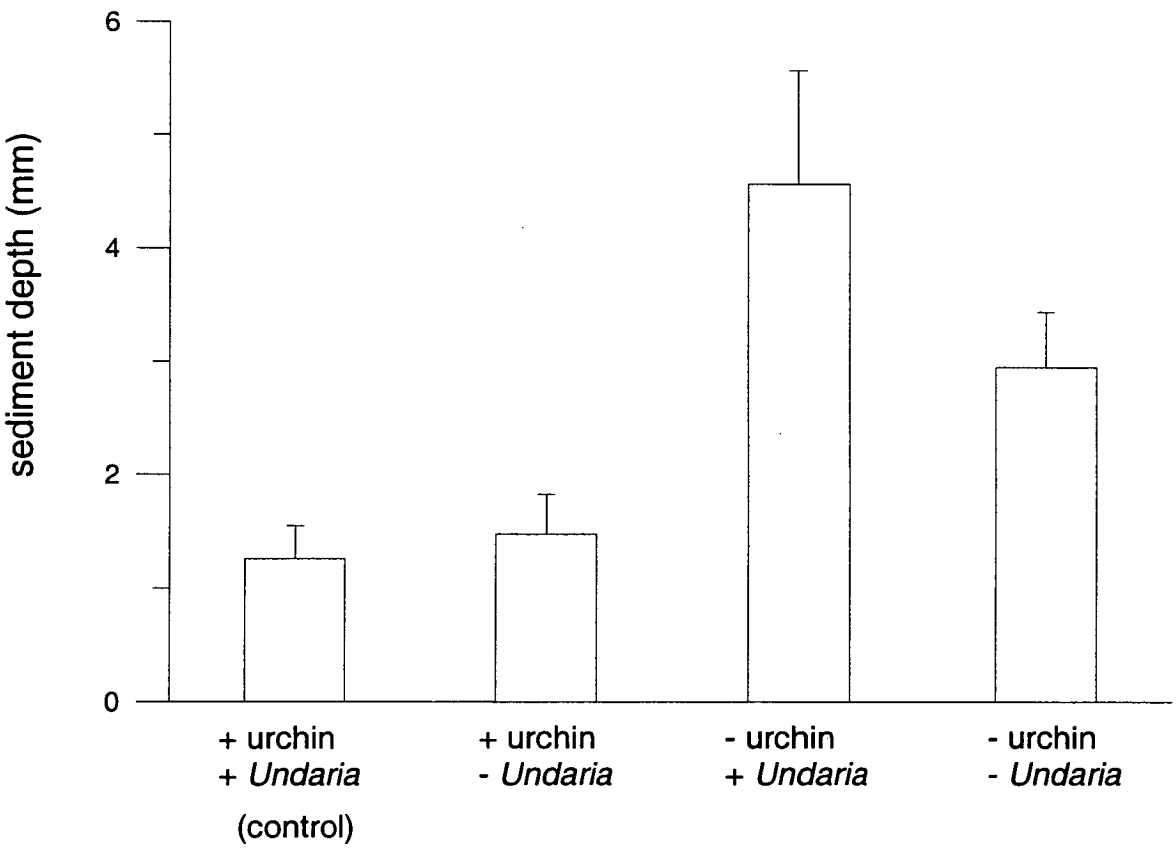


Figure 4.7. Effect of experimental manipulations on sediment depth, assessed in November 2001. Data represent mean (+SE) depth (n = 8 replicates per treatment) determined from five random positions within each experimental plot.

4.4.6 Spatial variability of algal guilds

A feature of the analysis associated with cover of the various algal guilds was the consistent significance of the 'plot (urchin**Undaria*)' term (Table 4.3), indicative of differences between replicate plots of the same treatment. Given that replicate plots were separated by a range of 15-180 m, this result reflects patchiness in the cover of these guilds at this spatial scale.

4.5 Discussion

In assessing the threat *Undaria pinnatifida* poses to native algal communities, it is essential to identify the factor(s) that maintain persistent populations. Two possible scenarios can explain long-term persistence of *U. pinnatifida* on urchin barrens. Firstly, persistence of dense *U. pinnatifida* stands may require continuous intervention by agents (eg. sea urchin grazing) to restrict development of native algal competitors. Alternatively, once established dense *U. pinnatifida* stands may be self-maintaining in the absence of sea urchin grazing or other mechanisms that limit cover of native algae. Self-maintenance could occur if the *U. pinnatifida* canopy inhibits recruitment of native canopy-forming species (eg. Ambrose and Nelson, 1982; Chapman *et al.*, 2002), which may also be limited by their poor dispersal abilities (Anderson and North, 1966; Amsler and Searles, 1980; Schiel and Foster, 1986; Santelices, 1990; Fletcher and Callow, 1992). The experimental approach used in this study incorporates manipulations of disturbance (i.e. urchins), the level of *U. pinnatifida* canopy, and the level of native algal propagule supply, providing key insights into the persistence of the 'urchin barren/*U. pinnatifida*' community state.

4.5.1 Does persistence of *Undaria pinnatifida* depend on grazing intensity?

While sea urchins have previously been observed grazing *U. pinnatifida* sporophytes (Sanderson and Barrett, 1989), the dramatic consequences of sea urchin grazing seen in 2001, where *U. pinnatifida* plants were recorded only in sea urchin removal plots, was unexpected. It is likely that this response was caused either by an increase in grazing intensity by *H. erythrogramma*, decreased recruitment success of *U. pinnatifida*, or a combination of both.

While no significant change in *H. erythrogramma* density occurred in the present study in control areas, a possibility is that a change in urchin behaviour in response to variation in food availability lead to increased grazing pressure on *U. pinnatifida*. If drift algae are the predominant food of this urchin (Connolly, 1986; Constable, 1989), then it is possible that a decrease in drift algae resulted in *H. erythrogramma* grazing *U. pinnatifida* with greater intensity during the course of the study. Whenever present, urchins were observed feeding on drift algae on the urchin barren.

Another explanation for the observed decline in *U. pinnatifida* is variable recruitment success. Data associated with the *U. pinnatifida* canopy removal treatment shows that abundance of *U. pinnatifida* was significantly lower in 2001 compared to the previous two years (Table 4.2). Under these conditions, *U. pinnatifida* abundance could be reduced significantly while the grazing rate of *H. erythrogramma* remains unchanged. Clearly lower recruitment success combined with a higher grazing rate would result in even greater impact on the abundance of *U. pinnatifida* sporophytes.

Our results (summarised in a conceptual model, Figure 4.8) show that when grazing pressure is low (i.e. in urchin removal plots), *U. pinnatifida* and understorey native species recruit successfully. When grazing pressure is high and/or *U. pinnatifida* recruitment is reduced, as occurred in treatments where urchin densities were not manipulated in 2001, all algae including *U. pinnatifida* will be destructively grazed. We suggest that when grazing intensity is at an intermediate level between these two extremes, *U. pinnatifida* persists while native algal species do not. It is likely that recruitment and growth rates of *U. pinnatifida* are much higher than that of native species, so that *U. pinnatifida* is able to outstrip the capacity of the urchin to consume it. The grazing preference of *H. erythrogramma* for *U. pinnatifida* relative to native algae remains unknown.

Grazing preference of sea urchins has been suggested previously as an important mechanism regulating stands of an introduced alga. In the northwest Atlantic, the sea urchin *Stronglyocentrotus droebachiensis* can consume the introduced algae *Codium fragile*, however, the alga lacks chemical attractants present in native algae (*Laminaria* spp.), which are the preferred food source (Prince and LeBlanc, 1992; Scheibling and Anthony, 2001). Based on laboratory feeding preference experiments, it is suggested that in moderate densities urchins will graze native species creating a mosaic of barren and *C. fragile* dominated areas, while at higher urchin densities all seaweeds will be grazed destructively (Scheibling and Anthony, 2001). Clearly similar experiments to elucidate feeding preference of *H. erythrogramma* would be useful in understanding the patterns of *U. pinnatifida* abundance that we have observed.

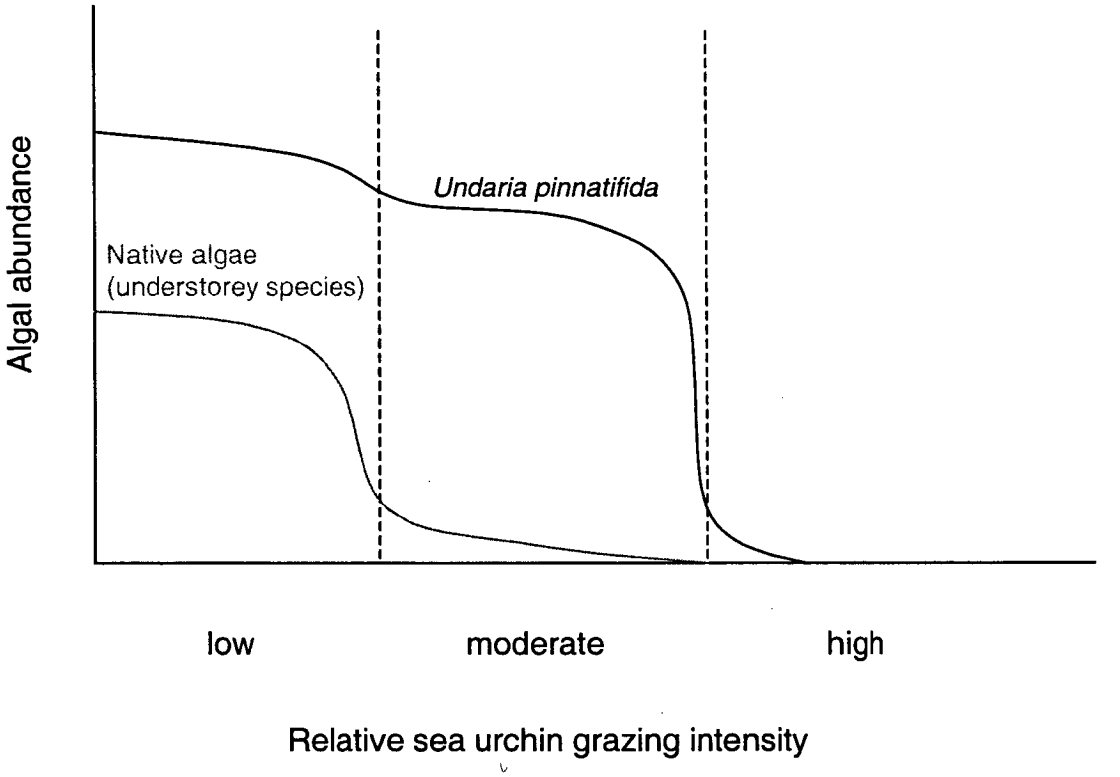


Figure 4.8. Conceptual model detailing the effect of sea urchin grazing intensity on the abundance of *Undaria pinnatifida* and native understorey algae. In sea urchin removal plots (i.e. low relative sea urchin grazing intensity) filamentous and foliose understorey species develop beneath a seasonal *U. pinnatifida* canopy. At moderate grazing intensity, characteristic of urchin barrens in the Mercury Passage, *U. pinnatifida* remains abundant while understorey species are destructively grazed. At high grazing intensity, as observed in experimental plots where sea urchins were not manipulated during 2001, all algae are destructively grazed. Note that relative sea urchin grazing intensity can be mediated by algal recruitment success (i.e. reduced algal recruitment success can lead to increased relative sea urchin grazing intensity).

4.5.2 Why did canopy-forming species fail to recover?

A key point is that under conditions of low grazing pressure, inhibition of *U. pinnatifida* by native algae was not observed because a dense canopy of native algal species did not develop, even after 30 months of urchin removals. This is in contrast to the rapid recovery (typically within 12 months) of canopy-species observed in previous studies in response to urchin removal (Duggins, 1980; Chapman, 1981; Andrew and Choat, 1982; Himmelman *et* al., 1983; Dayton *et al.*, 1984; Keats *et al.*, 1990; Leinnas and Christie, 1996; Agatsuma *et al.*, 1997; Shears and Babcock,

2002). Even removing both sea urchins and *U. pinnatifida*, as well as providing an immediate source of fertile material, resulted in a maximum of only 6 % cover of native canopy-forming species over the 30-month experiment. Although sea urchin removal resulted in a statistically significant increase in cover of canopy-forming species, the magnitude of increase was small. Several explanations may account for this limited recovery, related to factors inhibiting supply of algal propagules or post-settlement processes that may have inhibited early developmental stages.

Canopy-forming species: propagule supply

The failure of the spore enhancement treatment to initiate development of native algae in the absence of sea urchins and *U. pinnatifida* poses several questions. Although the technique has been used successfully elsewhere (Dayton *et al.*, 1984), it may be that in the present study the treatment was unsuccessful in delivering high densities of propagules to the substratum. Although we selected plants with fertile material, the presence of fertile material does not guarantee propagules will reach the substrate in high densities. Propagules may have been released but settled away from experimental plots due to current or surge, or alternatively, propagules may not have been released at all if the handling process affected the viability of source plants.

Whether or not the spore enhancement was effective in delivering high densities of spores to the substrate, it is likely that propagules of native canopy-forming species reached the reef via natural dispersal. A number of observations support this view. Firstly, on several occasions throughout the study large quantities of drift plants (predominately *Phyllospora comosa* and *Ecklonia radiata)* were swept onto the barren, often bearing fertile tissue. Secondly, dispersal via spores should have

occurred from plants in shallower water at the study site where a dense cover of native species was evident. Dispersal from a shallow algal fringe where macroalgae have refuge from sea urchin grazing has been attributed to the rapid recovery of kelp beds on barren grounds in the northwest Atlantic following mortality of sea urchins (Scheibling, 1986; Johnson and Mann, 1988, 1993). Finally, although it is widely held that effective dispersal by large brown algae is limited to within a few metres of the parent plants (Dayton, 1985; Schiel and Foster, 1986; Santelices, 1990; Norton, 1992), long distance spore dispersal in kelps may occur generally, particularly if spore release coincides with storms and associated turbulent mixing (Reed *et al.*, 1988). More recently, a modelling approach has demonstrated a much greater potential for long-range dispersal, suggesting that dispersal distance is determined more by processes related to fluid dynamics rather than the biological characteristics of propagules, particularly under conditions of high flow and large waves (Gaylord *et al.*, 2002). Even under calm conditions, 50 % of propagules of the kelp *Macrocystis pyrifera* were predicted to disperse greater than 100 m (Gaylord *et al.*, 2002). Consequently it is likely that dispersal to the study site from nearby (*ca.* 100 m distance) dense stands of canopy-forming species would have occurred during the 30 month study period.

Intrusion of sea urchins in 2001

The unexpected immigration of *Heliocidaris erythrogramma* into urchin removal plots in 2001 may have impacted canopy-forming species. It is possible that during the brief incursion of urchins, their grazing may have affected native canopy-forming species sufficiently to prevent recovery. We suggest, however, that this is unlikely given that prior to the incursion there was a period of 18 months where the densities

of sea urchins remained low while there was little recruitment of native species. During the period when urchins were at low levels, we observed significant recruitment of native canopy-forming species at an adjacent site, indicating that conditions were suitable for macroalgal growth. We note that in similar experiments conducted elsewhere, significant recruitment of large brown algae has occurred in the initial 12 months following urchin removal (Duggins, 1980; Chapman, 1981; Andrew and Choat, 1982; Himmelman *et al.*, 1983; Dayton *et al.*, 1984; Keats *et al.*, 1990; Leinnas and Christie, 1996; Agatsuma *et al.*, 1997; Villouta *et al.*, 2001; Shears and Babcock, 2002).

Inhibition by understorey algae and the effects of depth

While understorey algae can inhibit recruitment of canopy-forming species (Dayton, 1975; Dayton *et al.*, 1984; Kennelly, 1987; Airoldi, 1998), total cover of understorey species never exceeded 50 % in the present study and was often much lower. Thus, it is unlikely to account for the limited recovery of canopy species. The depth of our experimental removals (7 - 12 m) may have influenced the response of native canopy-forming species. Experimental removal of sea urchins in a New Zealand study has demonstrated that colonisation of large brown algae was much slower in a deeper zone (6.5 – 11.5 m) compared with two shallower zones (0 – 3.5 m and 3.5 – 6.5 m) (Villouta *et al.*, 2001).

The type of algae that colonises after urchin removal can also be significantly affected by depth. Experimental removal of the sea urchin *Centrostephanus rodgersii* from barren habitats in New South Wales, Australia showed that shallow (1-3 m) habitats were subsequently dominated by large brown algae (*Sargassum* spp.), while

deeper habitats (7 - 10 m) were dominated by filamentous red algae. The absence of brown algae at the deeper site was not due to the decreased light levels since forests of large brown algae were present at similar depths in adjacent areas (Fletcher, 1987). Our results parallel some of the findings from Fletcher (1987), in that depth alone does not explain the lack of recovery of canopy-forming species, given that diverse communities dominated by large brown algae are common at similar depths in other regions of the Mercury Passage, including reef within 100 m of the study site.

Impact of sediment matrix

The consistent cover of sediment across all treatments is likely to have contributed to the poor recovery of canopy-forming and other algal species. It is well established that sediment can inhibit recruitment of macroalgae (Devinny and Volse, 1978; Kendrick, 1991; Umar *et al.*, 1998). Sediment burial and scour influence algal communities by removing whole organisms, by physically preventing settlement of propagules on stable substrata, or by limiting newly settled propagules via reduced inputs of light and oxygen (Airoldi *et al.*, 1995; Chapman and Fletcher, 2002). Interestingly, the depth of the sediment matrix increased significantly after removal of sea urchins in the present study. It is likely that this was due to increased cover of filamentous algae occurring in the sediment matrix, subsequently facilitating sediment accretion (Melville and Connell, 2001).

While a high cover of sediment was a persistent feature of the barren habitat, clearly *U. pinnatifida* and small foliose understorey species were relatively abundant at times during the study, and therefore must be tolerant to a degree of sediment stress.

Opportunistic species that rapidly recolonise the substratum following mortality caused by burial and scour are characteristic of sediment stressed habitats (Littler *et al.*, 1983). Hence, the opportunistic nature of *U. pinnatifida* observed in our previous experiments (Chapter 2; 3) indicate that it is also likely to be adapted to establish in habitats subject to relatively high sediment accumulation.

The colonisation of the sediment matrix by a dense cyanobacterial mat in 2001 may also have had a significant negative influence on recruitment of canopy-forming species. Although the impact of cyanobacterial mats on macroalgal recruitment is unknown, the mat effectively smothered large patches of reef and would have almost certainly inhibited macroalgal growth.

The presence of a significant cover of sediment has not been reported from urchin barren habitats elsewhere. Typically 'urchin barrens' are characterised by high cover of crustose coralline algae in association with low macroalgal cover and high sea urchin density and are often referred to as 'coralline flats' or 'coralline barrens' (Breen and Mann, 1976; Ayling, 1981; Jones and Andrew, 1990; Johnson and Mann, 1993; Andrew, 1994). The *H. erythrogramma* barren at our study site appears to differ markedly from this general pattern, with only low cover of coralline algae (averaging 9.6 % in control areas) and a high cover of sediment. Indeed, a high accumulation of sediment is a notable general feature of *H. erythrogramma* barrens on the east coast of Tasmania, probably reflecting that these barrens typically arise on sheltered coastal reefs.

The likely effect of sediment in structuring the algal community in the present study warrants further research. Estimates of sediment cover and depth used in this study gave a general snapshot of abundance, however, more precise estimates of spatial and temporal variability, combined with analysis of sediment composition could be achieved using sediment traps (Airoldi *et al.*, 1995). Experiments employing novel techniques to manipulate sediment levels on rocky reefs (Airoldi and Cinelli, 1997) would also be valuable to test the effects of sediment on algal community structure.

4.5.3 Conclusions

While our previous experiments clearly demonstrated that disturbance is required for establishment of *Undaria pinnatifida* (Chapter 2; Chapter 3), the present study illustrates that persistence of *U. pinnatifida* stands associated with the urchin barren habitat is more complex. While dense stands of *U. pinnatifida* have been observed in the presence of relatively high sea urchin densities (Sanderson and Barrett, 1989; Sanderson, 1997; Johnson unpublished), our results demonstrate that urchins also have the ability to destructively graze *U. pinnatifida*, as observed in the 2001 sporophyte growth season. In the absence of sea urchin grazing, *U. pinnatifida* persisted, despite an increase in understorey algae, suggesting that self-maintenance can occur in the absence of sea urchin mediated disturbance. The fact that *U. pinnatifida* persisted in the absence of sea urchins is likely to reflect the poor recovery of native canopy-forming species. Our results suggest that factors other than sea urchin grazing contributed to this poor recovery. While the depth of the barren habitat and limited propagule supply may slow recruitment of canopy-species on the urchin barren, the main factor preventing recovery appears to be the high cover of sediment. Further research is required to critically investigate the

importance of sedimentation as a process inhibiting recovery of canopy-forming native species on these 'urchin barren/*U. pinnatifida*' dominated habitats.

Chapter 5

"Persistence of sea urchin barrens (*Heliocidaris erythrogramma*) on the east coast of Tasmania: inhibition of macroalgal recovery in the absence of high densities of sea urchins"

5.1 Abstract

Sea urchin barrens occur commonly in temperate regions throughout the world. Persistence of urchin barren habitats has significant implications for the ecology of subtidal reefs because they constitute areas of low productivity and diversity compared to habitats dominated by macroalgae. On the east coast of Tasmania the occurrence of urchin barrens has additional implications in that they represent a critical habitat of the introduced kelp *Undaria pinnatifida*. Identifying the factors responsible for maintenance of the barren habitat is essential in defining management options to promote recovery of native canopy-forming species. In this study a transplant approach is used to investigate whether inhibition of recovery of native canopy-forming algae can occur in the absence of intense sea urchin grazing. High densities of canopy-forming species successfully colonised settlement pavers deployed in a dense algal bed adjacent to a sea urchin barren. Transplanting these pavers to plots on the urchin barren from which urchins were removed resulted in > 80 % mortality of recruits after 3 months, and 100 % mortality after 7 months. The decline in macroalgal recruits on pavers transplanted to the urchin barren was associated with an increase in the cover and depth of sediment. A persistent cover of sediment was also a feature of pavers deployed on the urchin barren, where no canopy-forming algal recruits were observed. While sea urchins are undoubtedly important in creating urchin barrens, our results suggest that other mechanisms can

influence recovery of native canopy species. On the east coast of Tasmania sedimentation appears to play a critical role in inhibiting early developmental stages of macroalgae, thereby maintaining the barren habitat.

5.2 Introduction

The occurrence of sea urchin 'barrens' characterised by high densities of sea urchins and low cover of fleshy algae on rocky reefs has been widely reported from temperate regions across the globe (Lawrence, 1975; Choat and Schiel, 1982; Fletcher, 1987; Chapman and Johnson, 1990; Watanabe and Harrold, 1991; Andrew and Underwood, 1993; Hagen, 1995; Sivertson, 1997; Agatsuma *et al.*, 2000; Shears and Babcock, 2002). Urchin barrens are unproductive habitats compared to reefs dominated by seaweeds, with primary productivity *ca.* two orders of magnitude lower than comparable vegetated habitats (Chapman, 1981).

In southeast Tasmania, urchin 'barren' habitats dominated by the purple sea urchin *Heliocidaris erythrogramma* comprise an estimated 25 % of reef area in sheltered waters (Sanderson *et al.*, 1996). *H. erythrogramma* barrens are also a critical habitat for the introduced Asian kelp *U. pinnatifida*, which forms dense stands in these areas during the sporophyte growth season (Sanderson and Barrett, 1989; Sanderson, 1990; Sanderson, 1997).

Given the ecological implications of formation of sea urchin barrens and their importance as a critical habitat to *Undaria pinnatifida*, they represent a serious issue for management of the coastal zone. Re-establishment of native canopy-forming species on urchin barren habitats will not only lead to higher productivity and

biodiversity but it is also likely to result in the subsequent inhibition of development of *U. pinnatifida* sporophytes (Chapter 2). To determine whether management options exist to promote recovery of native canopy-forming species, it is vital to identify the factors responsible for persistence of the barren state.

Persistence of urchin barrens may not necessarily be dependent on continued grazing of sea urchins. We recently removed sea urchins from experimental plots on an urchin barren in Tasmania, and despite the lack of significant grazing saw no evidence for recovery of macroalgae after 30 months (Chapter 4). An alternative reason for the maintenance of urchin barren habitats relates to supply of native algal propagules. Dispersal of large brown algae is generally thought to be limited, with most recruits occurring within a few metres of the parent plants (Anderson and North, 1966; Ambrose and Nelson, 1982; Dayton, 1985; Andrew and Viejo, 1998;). Consequently, recovery of canopy-forming species on urchin barrens may be restricted by their poor dispersal capabilities.

In a previous paper (Chapter 4), we addressed possible factors responsible for maintaining the 'sea urchin/*U. pinnatifida*' dominated habitat, including native algal propagule supply. An enhanced supply of native algal spores was provided by regularly placing fertile species in mesh bags, which were subsequently attached to the perimeter of experimental plots. When combined with both sea urchin removal and removal of the *U. pinnatifida* canopy, the addition of this source of native algal spores failed to produce significant recovery of canopy-forming species (Chapter 4). Despite the fact that a similar technique has been used successfully to seed macroalgae (Dayton *et al.*, 1984), the subsequent failure of native canopy-forming

species to recover in our study area raised a number of uncertainties, including the possibility that the treatment itself was unsuccessful in delivering high densities of propagules to the substrate.

In this study we investigate the issue of macroalgal recovery critically using a transplant approach. We seeded settlement pavers with native propagules by deploying them in a habitat dominated by native canopy-forming species. These pavers were subsequently transplanted to plots in an adjacent sea urchin/*U. pinnatifida* dominated habitat, from which sea urchins were removed. Combined with appropriate handling controls, this approach allowed assessment of whether recovery of native canopy-forming algae on urchin barrens can be inhibited despite the absence of intense sea urchin grazing.

5.3 Materials and methods

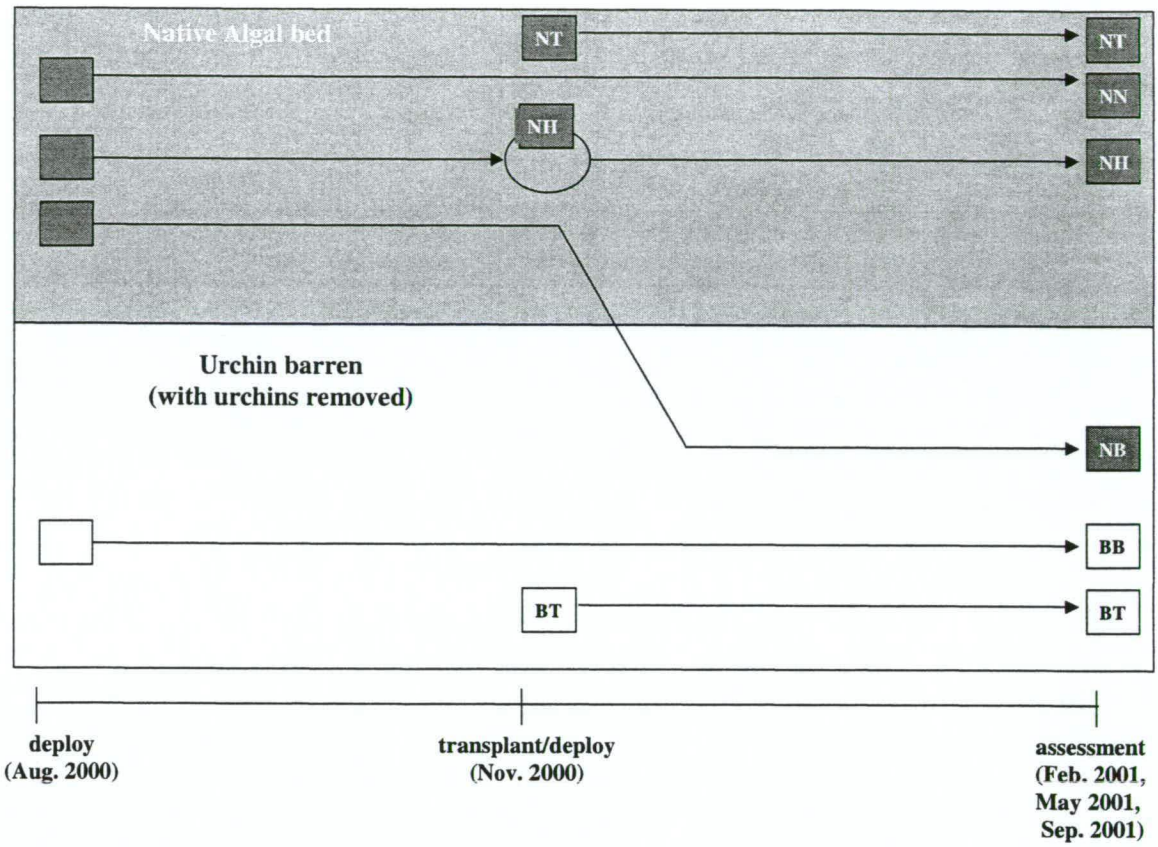
5.3.1 Study site

The experiment was conducted at Lords Bluff, situated at the northern extremity of the Mercury Passage on the east coast of Tasmania (42° 32' S, 147° 59' E). At this site a large area of 'urchin barren' habitat is found adjacent to reef dominated by native canopy-forming species (hereafter termed 'algal bed'). The urchin barren habitat is seasonally dominated by dense stands of the introduced Asian kelp *Undaria pinnatifida*. These two habitats or 'zones' formed the basis of the experimental manipulations. A more detailed description of the algal flora found at the site is provided elsewhere (Chapter 3; Chapter 4).

5.3.2 Experimental manipulations

Concrete pavers (29 cm x 19 cm x 9 cm) were used as settlement substrata, each giving a horizontal area of 551 cm^2 on the top surface for algal recruitment. Concrete has been used previously in studies of algal succession and is suitable in mimicking natural reef surfaces (Foster, 1975). Within each habitat individual pavers were randomly deployed along approximately 100 m of coastline, at least 30 m away from the 'algal bed'-'urchin barren' boundary, at a depth of 7-10 m. The initial deployment occurred in August 2000. After deployment pavers were randomly assigned to experimental treatments (see Figure 5.1). For each treatment, ten replicate pavers were deployed.

Transplantation of pavers took place approximately three months after deployment, while assessment of macroalgal abundance was carried out 3, 7 and 11 months after transplantation. During the transplant process, pavers were placed carefully into a large bin by divers, then slowly hauled to the surface. On the surface pavers were placed in bins containing fresh seawater and immediately covered with hessian sacks to minimize exposure to direct sunlight. Pavers were transplanted within 45 minutes of reaching the surface. Ten replicate pavers were also deployed in each habitat at the time of transplantation (i.e. NT and BT) to assess algal recruitment after the time of transplant. The handling control treatment (NH) was included to investigate potential artefacts associated with the transplantation process. This involved lifting pavers from the algal bed and re-deploying them in the same area.



TREATMENT	PURPOSE
NN	Assesses recruitment of macroalgae to pavers in the dense algal bed from Aug. 2000 to assessments.
NH	Handling control. Comparison with NN allows assessment of the effects of handling during the transplantation process on macroalgal survival.
NT	Assesses recruitment of macroalgae in algal bed after transplantation (Nov. 2000).
BB	Assesses recruitment of macroalgae to pavers on the urchin barren.
NB	Assesses change in macroalgae following transplant from the algal bed to the urchin barren.
BT	Assesses recruitment of macroalgae on the urchin barren after transplantation.

Figure 5.1. Experimental design and transplant protocol. Ten replicate pavers were deployed for each treatment.

5.3.3 Sea urchin removal

Settlement pavers deployed or transplanted to the urchin barren were positioned in areas where sea urchins were manually removed every 4-6 weeks (removal areas were 16 m^2 in area). This maintained an urchin density of < 0.5 m^{-2} in removal areas compared to an average of 7.1 m^{-2} on adjacent un-manipulated reef. An unexpected and brief intrusion of sea urchins into removal areas occurred in the barren zone during the summer period (January-April 2001), when densities temporarily exceeded 5 m^{-2}. Despite this intrusion, we assumed that sea urchin grazing had negligible effects on macroalgal recruitment (see Discussion, section 5.5). In the algal bed where sea urchins were not manipulated, densities averaged 2.7 m^{-2} ± 0.51 SE.

5.3.4 Assessment of algal abundance

The percentage cover of algae, sessile invertebrates and sediment on settlement pavers was estimated by recording taxa occurring under 50 regularly spaced intercepts of a point intercept quadrat. The quadrat covered the entire upper surface of the settlement paver and was positioned above the algae by a frame. Organisms were identified *in situ* to the highest taxonomic resolution possible. For canopy-forming algae identification to species level was possible, however, it was necessary to allocate other species to guilds (eg. foliose red algae, brown turf algae). The density of recruits of canopy-forming species was also measured on each paver by recording all recruits once they could be identified to species level. When recruitment was particularly dense, recruits were counted in each of four replicate 7 cm x 7 cm quadrats randomly positioned on each paver. At the conclusion of the

experiment in September 2001 the depth of accumulated sediment on the pavers was also measured to the nearest millimetre.

5.3.5 Analysis

The effect of the various 'treatments' on algal abundance was analysed using a one-way analysis of variance (ANOVA), with 6 levels of "treatment" (see Figure 5.1). Where appropriate, differences between treatments were investigated using the Ryan-Einot-Gabriel-Welsch (REGW) multiple range test. Analysis was conducted for data collected at the conclusion of the experiment in September 2001, 11 months after the transplantation occurred. This allowed sufficient time for recruitment patterns of macroalgae to be observed, as well as allowing enough time for development of *U. pinnatifida* sporophytes. 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*. Univariate tests were undertaken using the SAS® statistical package.

The relationship between sediment abundance and algal cover on settlement pavers was examined by plotting values of cover across all treatments against both sediment cover and an index of sediment load. This analysis also utilized data collected from additional settlement pavers deployed as part of a broader experiment. The index of sediment load (SL) was defined as: SL = (% cover*depth)/100. Linear regression was used to investigate the relationship between sediment cover and foliose algal cover, while quantile regression was used to examine the upper bounds of the relationship between sediment load and foliose algal cover. Coefficients and

confidence intervals for the quantile regression were estimated using the *R* statistical package (http://www.r-project.org/).

5.4 Results

5.4.1 Response of canopy-forming algae to experimental manipulations

Native canopy-forming species

Native canopy-forming algae showed a clear response to experimental treatments (Figure 5.2b; Table 5.1). A range of macroalgae, including canopy-forming species, recruited successfully to pavers deployed in the algal bed (Figure 5.3). In contrast, canopy-forming species did not recruit to pavers deployed in the nearby barren habitat (Figure 5.2b). While we did not assess algal abundance immediately prior to transplantation, high densities of brown algal recruits were observed on transplanted pavers. These recruits were generally < 1 mm in size and were too small to identify to species level. Three months after transplant, when canopy-forming algal recruits were approximately 10 mm in size, average densities (all species combined) on un-manipulated (NN) pavers exceeded 1.2×10^4 recruits m^{-2}.

Transplantation of pavers from the algal bed to the barren habitat resulted in a dramatic reduction in cover of canopy-forming species (Figure 5.2b). Three months after transplant, cover averaged 62.8 % ± 6.3 SE on un-manipulated (NN) pavers, compared to 11.8 % ± 5.0 SE for transplanted (NB) pavers. Only a small proportion of canopy-forming algal cover on un-manipulated pavers could be attributed to recruitment after the time of transplant, since the NT treatment averaged only 3.4 % ± 1.8 SE cover at the February 2001 assessment. In subsequent assessments, cover declined to undetectable levels on the transplanted pavers, while gradually increasing

for control pavers. Development of macroalgae on pavers treated as handling controls was not statistically different to that on the undisturbed pavers (NN) (Table 5.1).

The results also indicate that recruitment success for canopy-forming species was dramatically lower in the period following transplantation compared with the previous 3 months. Data collected 7 months after transplant for controls (NN), which was comparable to data collected 11 months after transplant for the NT treatment (both treatments were deployed for 11 months), showed 67.2 % ± 5.7 SE in the NN treatment, while only 16.6 % ± 6.7 SE was recorded in the NT treatment.

Table 5.1. Results of one-way ANOVA's examining the effect of experimental manipulation on cover of algae and sediment, assessed in September 2001. For REGWQ tests, a horizontal underline indicates treatments that are not significantly different from each other ($\alpha = 0.05$). Refer to Figure 5.1 for treatment codes.

Guild (transformation)	df	MS	*F*	P	REGWQ tests
Total foliose algae (no transformation)	5, 54	8252.80	20.99	**0.001**	NN NH NT BB BT NB
Native canopy-forming algae {log (*Y*+0.1)}	5, 54	72.54	56.74	**0.001**	NN NH NT BB BT NB
Brown turf algae ($Y^{0.33}$)	5, 54	5.16	14.61	**0.001**	NN NT NH NB BB BT
Foliose red algae (sqrt)	5, 54	1.54	1.48	0.213	
Sediment cover (no transformation)	5, 54	1361.87	12.88	**0.001**	NN NH NT BB BT NB
Sediment load (no transformation)	5, 54	19.70	6.43	**0.001**	NN NH NT BB BT NB

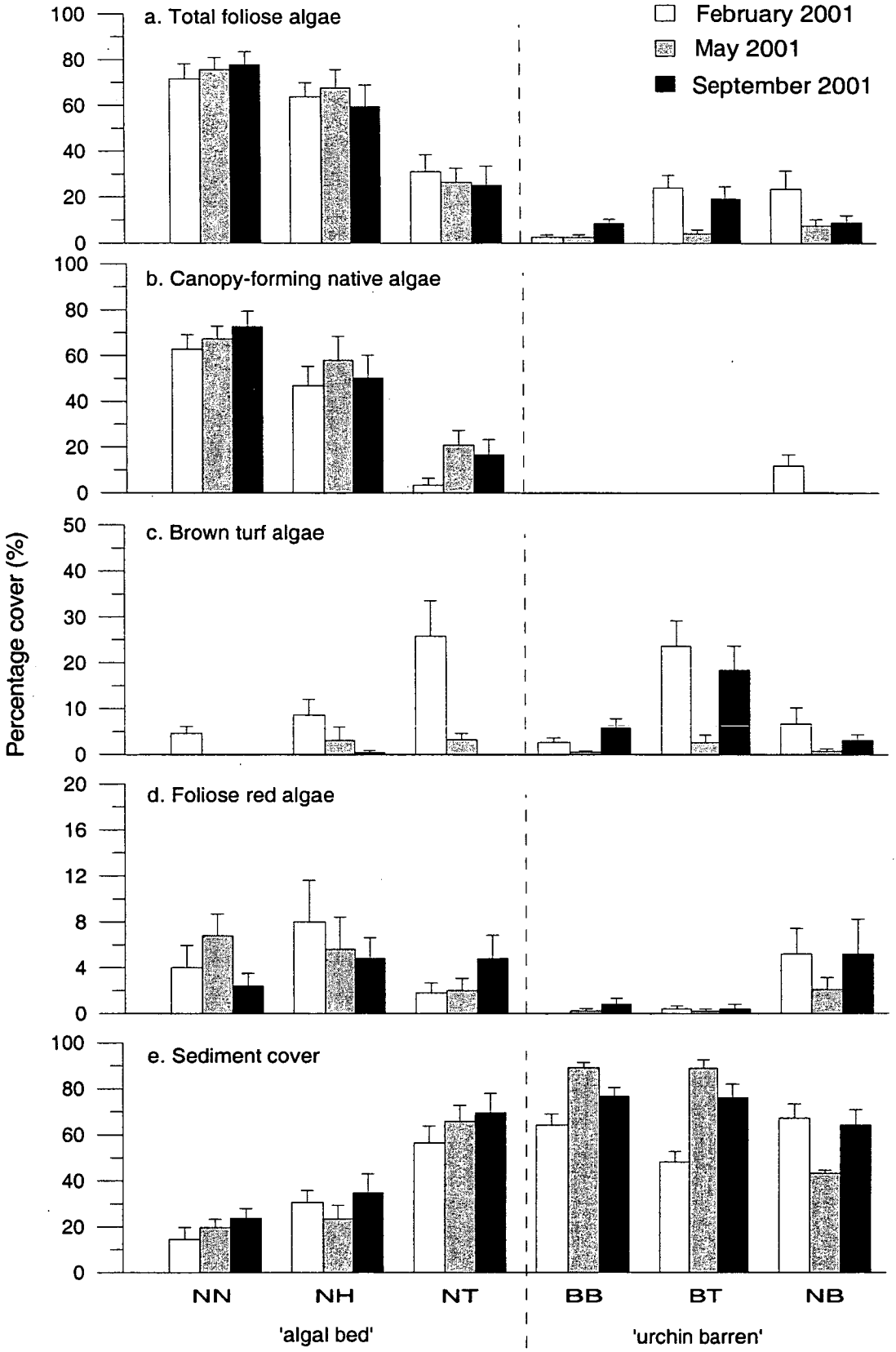


Figure 5.2. Response of algae and sediment to experimental manipulations. Data are mean percentage cover (+ SE) of 10 replicate pavers per treatment. The dotted vertical line separates pavers present in the two habitats at the time(s) of assessment. Treatment codes are as follows: NN-un-manipulated pavers in algal bed; NH-handling control; NT-measures recruitment of macroalgae in algal bed after transplantation; BB-un-manipulated pavers in urchin barren; BT-measures recruitment of macroalgae in urchin barren after transplantation; NB-Measures change in macroalgae following transplant from algal bed to the urchin barren.

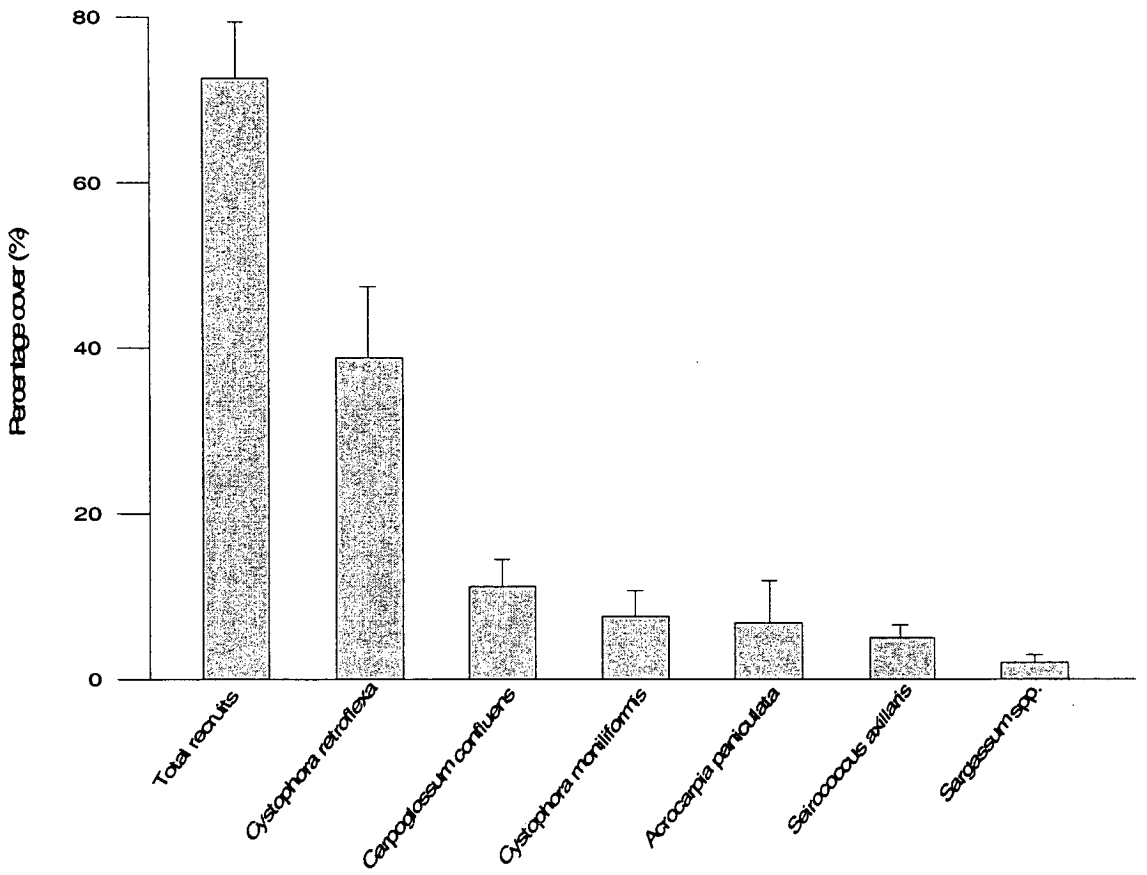


Figure 5.3. Relative abundance of native canopy-forming algae occurring on undisturbed (i.e. NN) pavers deployed in the native zone, assessed in September 2001. Data are mean percentage cover (+ SE) of 10 replicate pavers.

5.4.2 Response of understorey species

The guild of brown turf algae, comprising a range of ephemeral species including *Asperococcus* spp., *Colpomenia* spp., *Scytosiphon* spp. and several other unidentified species was generally low in cover for most treatments, usually averaging less than 10 % (Figure 5.2c). There were, however, some notable exceptions. At the February 2001 assessment, more filamentous brown turfing algae developed in both habitat types on pavers deployed at the time of transplant (NT and BT) than on those established at the beginning of the experiment (i.e. NB and NN). Cover declined in both NT and BT treatments in the May assessment, before increasing again on those pavers on the barren (BT) but not in the algal bed (NT). At the conclusion of the

experiment, cover of brown turf algae was higher in the BT treatment than in all other treatments (Figure 5.2c, Table 5.1).

Cover of foliose red algae was also very low across all treatments, averaging < 5 % (Figure 5.2d). Although cover of foliose red algae was generally higher on pavers deployed in the algal bed than on those deployed on the urchin barren, these differences were not significant at the completion of the experimental period (Table 5.1).

5.4.3 Patterns of sediment abundance

Pavers in the various treatments accumulated different amounts of sediment (Figure 5.2e; Table 5.1). The undisturbed pavers (NN) and handling controls (NH) in the algal bed recorded dramatically lower sediment cover compared to all other treatments over the entire period of the experiment. This trend was also reflected for sediment load data collected in September 2001 (Figure 5.4; Table 5.1).

Transplantation of pavers from the algal bed to the barren habitat (NB) resulted in a significant increase in sediment cover that persisted throughout the experimental period (Figure 5.2e; Table 5.1). Although we did not assess settlement pavers prior to transplantation, it was noted that pavers from the initial deployment on the algal bed were observed with low cover and depth of sediment, while pavers on the barren habitat possessed high cover and depths (up to 10 mm). After transplanting pavers from the algal bed to the barren area, sediment up to 10 mm in depth was observed on transplanted pavers two weeks after transplantation.

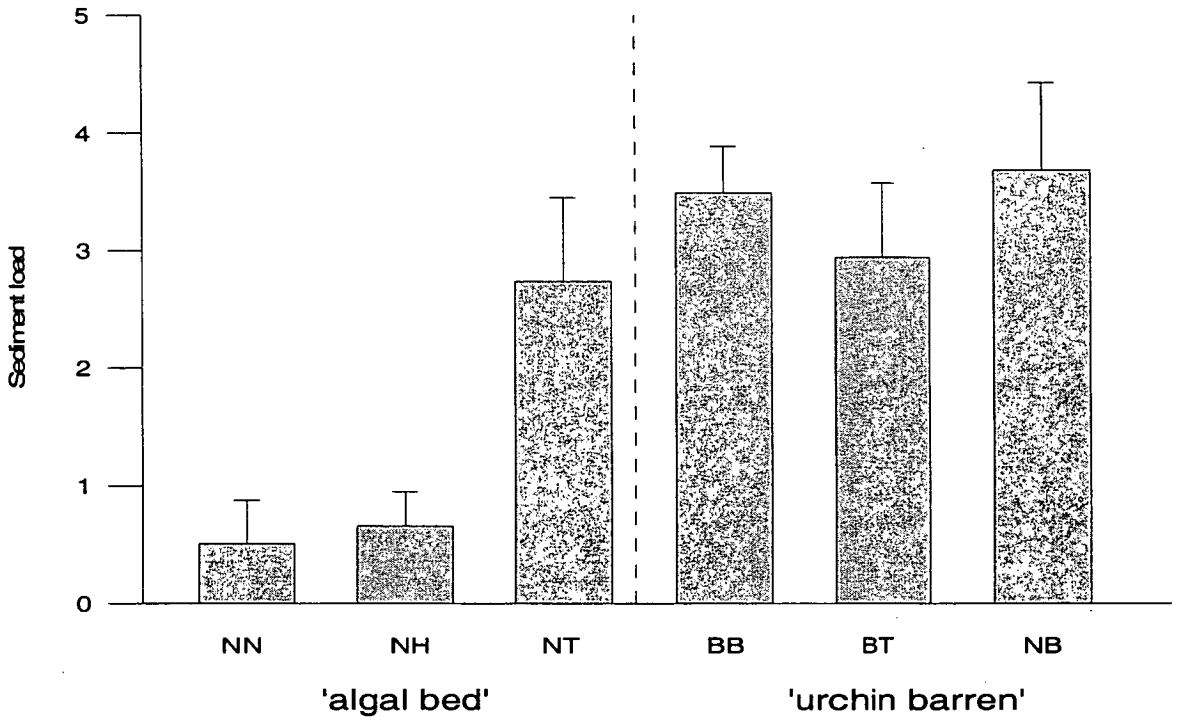


Figure 5.4. Effect of experimental manipulations on sediment accumulation following September 2001 assessment. Data represent mean sediment loads (+ SE) of 10 replicate pavers per treatment. Sediment load (SL) is an index of sediment accumulation and is calculated SL = (% cover*depth)/100. The dotted vertical line separates pavers present in the two habitats at the time of assessment. For treatment codes refer to Figure 5.1.

The pattern of sediment cover was generally the reciprocal of that observed for canopy-forming algae. When cover of canopy-forming algae was high, cover of sediment was low and vice-versa. We examined this trend in more detail by plotting values of sediment cover against total foliose algal cover, across all treatments (note that NT and BT treatments were excluded because they were deployed part way through the experiment). This analysis revealed a significant negative relationship between the cover of sediment and total foliose algae (Figure 5.5). Although sediment cover provided some useful patterns to explore in relation to algal abundance, a better indicator of the amount of sediment on the pavers was given by the index of sediment load which includes components of both sediment depth and cover (see methods and materials).

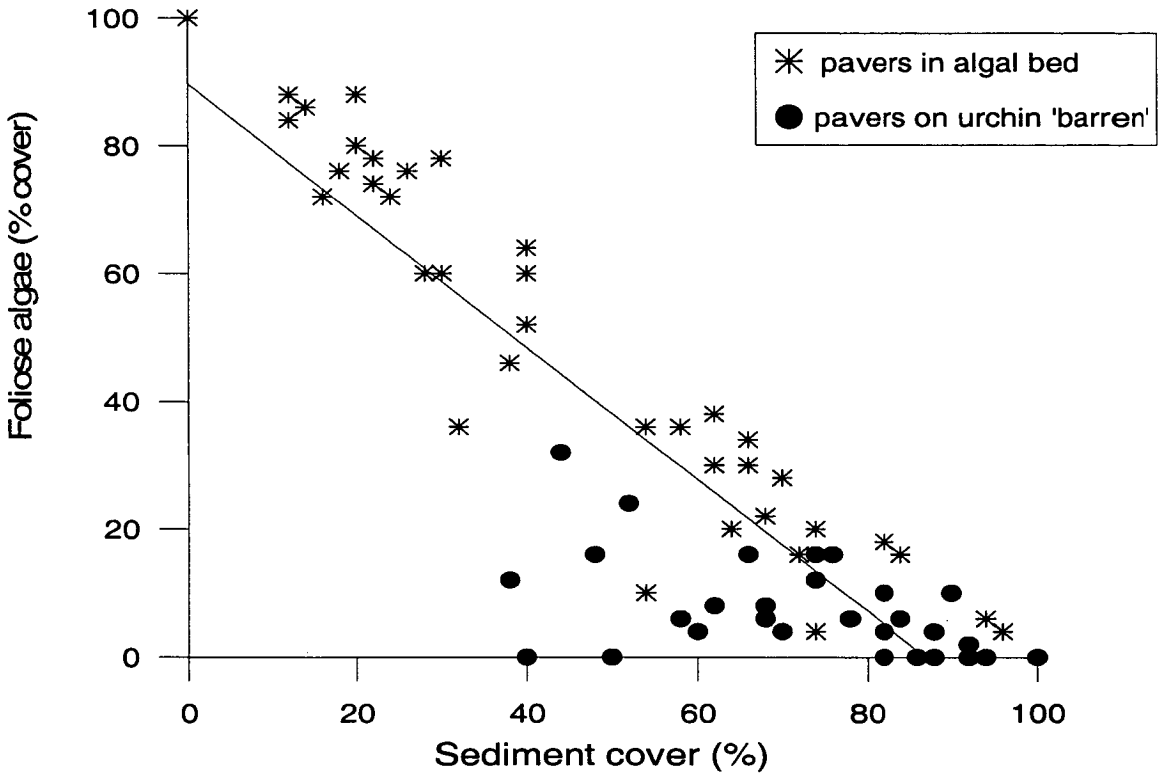


Figure 5.5. Relationship between sediment cover and total cover of foliose algae on settlement pavers, assessed in September 2001. Pavers in each habitat include transplanted pavers. Regression equation: $y = -1.031x + 89.62$, $n = 70$, $r^2 = 0.79$, $p < 0.0001$.

The relationship between algal cover and sediment load (Figure 5.6) was different to that for sediment cover (Figure 5.5). While cover of foliose algae varied substantially under conditions of low sediment load, high cover of foliose algae was only observed when sediment load was low. Under conditions of high sediment load, only low cover of foliose algae was observed. It should also be highlighted that in general, sediment load was higher on pavers either deployed or transplanted to the urchin barren compared with those in the algal bed, however, there were examples of high sediment load occurring on particular pavers in the native zone (Figure 5.6).

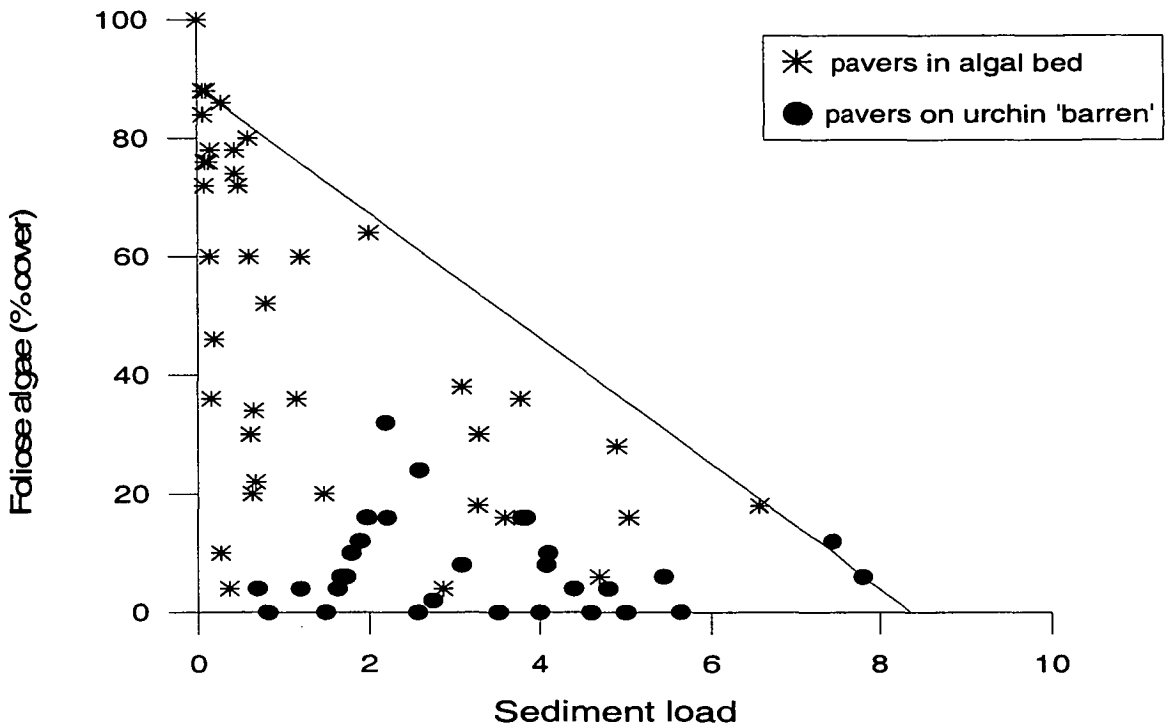


Figure 5.6. Upper bounds of the relationship between sediment load and foliose algal cover on settlement pavers, assessed in September 2001. The line represents a linear regression on the 90th quantile. Confidence intervals (70 %) were plotted but could not be distinguished from the regression line. Sediment load (SL) is an index of sediment accumulation and is calculated SL = (% cover*depth)/100. Pavers in each habitat include transplanted pavers. Quantile regression equation: $y = -10.594x + 88.636$, n=70, $p < 0.0001$.

5.5 Discussion

Strong experimental evidence indicates that sea urchin grazing can prevent re-establishment of canopy-forming algae on sea urchin barrens (Duggins, 1980; Chapman, 1981; Himmelman *et al.*, 1983; Keats *et al.*, 1990; Leinnas and Christie, 1996; Agatsuma *et al.*, 1997; Shears and Babcock, 2002). The results of our experiments, however, have shown low recruitment and a marked reduction in cover of canopy-forming algal recruits transplanted to barrens in the absence of high densities of sea urchins. Furthermore, while we regularly observed *H. erythrogramma* feeding during our frequent dives on the urchin barren (predominately on drift algae), we never observed sea urchins grazing the horizontal surface of the settlement pavers. Although on one occasion we observed a small number of urchins grazing on the vertical surface of pavers, this was only during the

brief incursion of urchins that occurred during January-April 2001. These results suggest that other mechanisms may operate to prevent recovery of macroalgae on urchin barrens.

5.5.1 Decline of algal recruits transplanted to pavers

The question then remains: If sea urchins were not the primary cause of the decline in canopy species then what other mechanisms are important? While the presence of turfing algae has been demonstrated to prevent re-establishment of large brown macroalgae (Dayton *et al.*, 1984; Kennelly, 1987a), only low cover of foliose red algae and brown turf was recorded on pavers deployed on the urchin barren which is unlikely to account for inhibition of native canopy species. We can also discount the potential inhibitory effects of a dense *Undaria pinnatifida* canopy on native algal abundance. The 2001 sporophyte growth season saw a significant decline in *U. pinnatifida* in our study area (see Chapter 4) such that *U. pinnatifida* cover was negligible both on the pavers themselves and in the immediate area surrounding them. This is also consistent with our previous work demonstrating that removal of the *U. pinnatifida* canopy on the urchin barren did not significantly affect cover of native foliose algae, even in the absence of sea urchins (Chapter 4).

Although the handling process itself did not result in a significant decline in canopy-forming algal abundance, the change in light environment associated with transplant from the algal bed to the barren could have contributed to mortality of macroalgal recruits. Many pavers deployed in the algal bed were subject to shading by canopy-forming algae and would have experienced increased light levels following transplantation, potentially leading to photoinhibition for algal recruits (eg. Hanelt,

1996; Hanelt *et al.*, 1997). There were also other pavers in the algal bed, however, that were not subject to shading by canopy species and would not have experienced a dramatic change in light environment after transplant. If the altered light environment contributed to algal mortality we would not have recorded mortality across all pavers. Consequently, a change in light environment is unlikely to account for the observed patterns of algal mortality.

The effects of sediment accumulation on settlement pavers in the barren habitat appears the most likely explanation for the observed inhibition of canopy-forming algal recruits. Previous studies have demonstrated the inhibitory effects of sediment on rocky reef organisms (reviewed by Airoldi, 2003). It seems likely the rapid accumulation of sediments on pavers transplanted to the barren zone would have resulted in burial and consequent reduction in irradiance and hence the photosynthetic capabilities of recruits. In addition, the combination of water motion (scour) with sediment on the substrate is also likely to have inhibited early developmental stages (Coelho *et al.*, 2000).

5.5.2 Lack of recruitment to pavers on urchin barren

The lack of recruitment of canopy-forming species on pavers deployed on the urchin barren is also likely to have been affected by sediment accumulation. In addition to the detrimental effects of sediment burial and scour on macroalgal propagules, recruitment of canopy-forming species would be limited as a consequence of the replacement of stable hard substrata with unstable sediment particles (Airoldi, 2003). Laboratory experiments conducted with *Macrocystis pyrifera* have demonstrated that effective recruitment can be reduced by spores attaching to sediment grains, which

are subsequently washed away from the benthos by waves and water motion (Devinny and Volse, 1978). Similarly, experiments have demonstrated that insertion, germination, survival and maturation of gametophytes of *Undaria pinnatifida* and *Ecklonia cava* were inhibited in the presence of sediment particles (Arakawa and Matsuike, 1992).

Another possible reason for the lack of recruitment on the urchin barren relates to supply of algal propagules. Since dispersal of large brown algae is generally thought to be limited, with most recruits occurring within a few metres of the parent plants (Anderson and North, 1966; Ambrose and Nelson, 1982; Dayton, 1985; Andrew and Viejo, 1998), recovery of native canopy-forming species may be restricted by their poor dispersal characteristics. A number of observations indicate that this is unlikely to account for the observed lack of recruitment. Firstly, on several occasions throughout the study large quantities of drift plants (predominately *Phyllospora comosa* and *Ecklonia radiata)* were evident, often bearing fertile tissue. In addition, dispersal via spores should have occurred from plants in shallower water at the study site where a dense cover of native species was evident. Dispersal from a shallow algal fringe where macroalgae have refuge from sea urchin grazing has been attributed to the rapid recovery of kelp beds on barren grounds in the northwest Atlantic following mortality of sea urchins (Scheibling, 1986; Johnson and Mann, 1988, 1993).

It is notable that the brown turf algal guild recruited onto pavers deployed at the time of transplant in both the barren and algal bed (i.e. BT and NT). The fact that pavers in these two treatments were separated by up to 200 m indicates that this guild is

capable of long distance dispersal, as demonstrated previously for filamentous brown algae in North America (Reed *et al.*, 1988). It is also notable that the relatively high cover of brown turf algae present on the BT treatment was not found on un-manipulated pavers initially deployed in the barren habitat (i.e. BB), despite the fact that these pavers possessed low algal cover. This indicates that the settlement substrate during the period of brown turf algal recruitment on BB pavers was significantly different to that on BT pavers. A possible explanation is that sediment levels on newly deployed BT pavers remained low enough for algal recruitment, while on BB pavers more accumulated sediment was present due to the longer period of deployment, resulting in inhibition of brown turf algal recruitment.

5.5.3 Patterns of sediment accumulation

While there were high sediment loads recorded on some pavers in the algal bed (see below), it is clear that in general, sediment loads were higher on the urchin barren than on the benthos beneath dense macroalgal cover. This observation is consistent with our observations from other experiments showing an immediate and significant increase in sediment cover following artificial removal of the canopy (Chapter 2) and following natural canopy dieback (Chapter 3). Notably, in the present experiment, the greatest accumulation of sediment on pavers located in the algal bed were associated with patches of significant canopy decline as a result of dieback of dense patches of *Phyllospora comosa*. The loss of canopy algae and associated higher sediment levels may partially explain the lower recruitment of native algae to pavers deployed in the algal zone after transplantation (i.e. NT).

Why does reduced canopy cover result in increased sediment accumulation on the benthos? There are several possible explanations. The most compelling is that sweeping of the seafloor by macroalgal fronds in dense beds prevents accumulation on exposed horizontal surfaces of reef (Kennelly, 1989). While it is possible that rates of sediment deposition were locally greater on the barren habitat than in the algal bed, reflecting small-scale variability in sediment deposition (Airoldi and Virigilo, 1998), we did not quantify spatial variability in sedimentation. In our study area sediment dynamics are poorly understood, so further research should address both the rates of sediment deposition and accumulation at a range of spatial and temporal scales.

Although our data show a clear negative relationship between sediment load and foliose algal cover, the relationship is correlative and does not infer causality. Further experiments are required to determine whether sediment controls algal abundance, whether algal abundance controls sediment accumulation, or whether a combination of both mechanisms occurs. While our data are correlative, we argue that the combined evidence indicates that sediment is an important factor shaping algal community structure. Our canopy removal experiments showing an increase in sediment cover on the reef surface relative to areas where the canopy was left intact clearly indicates that the presence of a canopy inhibits sediment accumulation, as has been demonstrated elsewhere (Kennelly, 1987; Kennelly and Underwood, 1993; Melville and Connell, 2001). We measured sediment cover on the urchin barren habitat over a 30-month period and it was consistently high (average > 50 %) (Chapter 4). We interpret this persistent sediment cover to reflect the lack of canopy-forming algal cover.

5.5.4 General Conclusions

We suggest that urchins are playing a minor role in preventing recovery of canopy-forming species in the Mercury passage. However, it is clear that destructive grazing of seaweed beds by sea urchins can indirectly lead to sediment accumulation through removal of the canopy in the first place, with subsequent inhibition of algal recruitment. This indirect link between sea urchins and sediment levels, whereby sea urchins mediate sediment dynamics through their grazing activities on kelp plants, has been suggested previously (Estes and Palmisano, 1974). Interestingly, our urchin removal experiments in the barren habitat have shown lower levels of sediment accumulation in the presence of sea urchins (Chapter 4), indicating that urchins can have both positive and negative indirect effects on sediment accumulation. The lack of evidence to indicate that urchin grazing affects recruitment to the urchin barren probably reflects that urchins were observed to feed largely on drift algae. If the supply of drift were to reduce dramatically, it may be that urchins would play a greater role in preventing recruitment to this barren (Harrold and Reed, 1985).

Our overall conclusion is that sediment plays an important role in maintaining the urchin barren state by inhibiting early developmental stages of canopy-forming algae. If this is true, then identifying the source of sediment becomes an important issue. While sedimentation is a natural process on rocky reefs, various anthropogenic activities such as deforestation, dredging, industrial and domestic discharges, construction activities and land reclamation can lead to increased sedimentation rates (Airoldi, 2003). A critical question from a management perspective will be to determine whether sediment accumulation in our study area is being influenced by human activities. If sediment deposition can be linked to human activity, then

recovery of native species may require management to control sedimentation. If the sediments at this site are derived from natural sources, then recovery of canopy species is problematic since removal of sea urchins and *U. pinnatifida* from the barren is insufficient to promote regrowth of canopy-species (Chapter 4). Clearly prevention of loss of canopy species in the first place is the preferred management option.

Chapter 6

General Discussion

During the past two decades there has been a rapid increase in the worldwide spread of non-indigenous marine organisms (Bax *et al.*, 2001) providing a major challenge for managers of the coastal zone. Since resources to control or eliminate introduced species are always limiting, it is important to prioritise non-indigenous species in terms of the threat they pose to native systems (Byers *et al.*, 2002). Understanding the role of disturbance in the invasion process is an important stage in prioritising species for management purposes (Hiebert, 1997). If an introduced species can establish, maintain persistent populations and expand its distribution in the absence of disturbance, it represents a major threat to the integrity of native communities. Conversely, if an introduced species requires disturbance for successful invasion, the key threatening process to native assemblages may be the disturbance rather than the exotic species itself.

6.1 Disturbance and establishment of dense stands of *Undaria pinnatifida*

Disturbance plays an important role in the invasion process for *U. pinnatifida*, particularly in the establishment phase. A reduction in cover of native algae, either by experimental removal (Chapter 2) or natural dieback of the canopy (Chapter 3), facilitated establishment of *U. pinnatifida* sporophytes at high densities, while the presence of a stable native canopy inhibited sporophyte development. Removing native algal canopies in different seasons demonstrated that the presence of the native algal canopy does not prevent *U. pinnatifida* propagules from reaching the reef, but inhibits sporophyte development, most likely via competition for light. The

role of disturbance in facilitating establishment of *U. pinnatifida* appears similar to other introduced macroalgae such as *Sargassum muticum* (Ambrose and Nelson, 1982; Deysher and Norton, 1982; Andrew and Viejo, 1998) and *Codium fragile* ssp. *tomentosoides* (Chapman *et al.*, 2002; Levin *et al.*, 2002), which also require disturbance to reduce cover of native algae to establish. This mechanism is in stark contrast to the invasive alga *Caulerpa taxifolia*, which has flourished following its introduction to the Mediterranean and is able to establish and smother native seagrasses in the absence of disturbance (de Villele and Verlaque, 1995; Sant *et al.*, 1996).

6.2 Disturbance and persistence of dense stands of *Undaria pinnatifida*

While disturbance may be required for the establishment of an introduced species, it does not necessarily follow that continued disturbance is required for its persistence. For example, establishment of *Sargassum muticum* depends on disturbance, but once established the plant can prevent settlement and development of other algae by shading (Ambrose and Nelson, 1982; Critchley *et al.*, 1990). Similarly, establishment of *Codium fragile* in the northwest Atlantic depends on disturbance, however, established populations show high levels of persistence stability (*sensu* Johnson and Mann, 1988) in the absence of continued disturbance by inhibiting recruitment of native kelps (Chapman *et al.*, 2002). The present study provides conflicting evidence as to the role of disturbance in the persistence of dense stands of *U. pinnatifida*. In the second year of sporophyte development following artificial removal of native algal canopies, *U. pinnatifida* declined substantially, associated with increased abundance of native canopy-forming species (Chapter 2). This result is consistent with the hypothesis that continued disturbance is required for dense stands of *U.*

pinnatifida to persist. In contrast, experiments on sea urchin barrens to assess persistence of *U. pinnatifida* showed that disturbance in the form of grazing by urchins was not required for *U. pinnatifida* to persist (Chapter 4). In this situation, other mechanisms, most likely accumulation of a sediment matrix on the reef surface, inhibited the development of native algae.

6.3 What factors influence invasion success of *Undaria pinnatifida*?

The results from this study highlight some important ecological principles for invasion biology. In particular, the life history characteristics of the invading species and the invasibility of the recipient environment are identified as being critical in determining invasion success.

While there are exceptions (see Mack *et al.*, 2000), a broad list of qualitative descriptions have been proposed as characteristic of invading species. These include possession of *r*-selected traits, high dispersal rates, vegetative reproduction, high genetic variability, phenotypic plasticity, a large native range, eurytopy and polyphagy (Lodge, 1993). *Undaria pinnatifida* clearly possesses a number of *r*-selected traits including 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). Other well-studied exotic marine plants possess adaptations that confer invasiveness. For example *Sargassum muticum* is also highly fecund, possessing vesicles that allow the reproductive fronds to drift with currents and inoculate new locations (Andrew and Viejo, 1998). Similarly, the invasive alga *Codium fragile* exhibits rapid growth (up to 7 cm month^{-}

^{1}) and high dispersal (65-70 km year^{-1}), as well as the capacity to regenerate from utricles, medullary filaments or branches (Trowbridge, 1998).

The annual life history exhibited by *U. pinnatifida* has important ramifications for its ability to maintain persistent populations. Given that *U. pinnatifida* overwinters as a microscopic gametophyte, it is unlikely to compete effectively with perennial native species for resources such as suitable substratum for attachment and light. This is consistent with the results from Chapter 2 that demonstrated a substantial recovery of native species and a reduction in cover of *U. pinnatifida* in the second year following disturbance. The results contrast with the perennial species *Codium fragile*, which requires a single disturbance event to establish and maintain persistent populations (Chapman *et al.*, 2002).

The characteristics of the recipient community are also believed to be critical in determining invasion success (Lodge, 1993; Carlton, 1996; Davis *et al.*, 2000; Mack *et al.*, 2000; Sakai *et al.*, 2000). The results from the present study clearly indicate that disturbance is a critical factor in determining invasion success for *U. pinnatifida*. Another generalization proposed for community invasibility is the existence of vacant or under-utilised niches. Whilst it is difficult to define a vacant niche until it is occupied (Trowbridge, 1999), observations of *U. pinnatifida* occurring abundantly on 'urchin barrens' also suggest that this generality can be applied to *U. pinnatifida*.

Yet another generalization proposed by invasion ecologists is that stable communities resist invasion (Mack *et al.*, 2000), clearly demonstrated in Chapter 2 where stable canopies of native algal species resisted invasion by *U. pinnatifida*.

Although the cause of invasion resistance is not well understood, communities and geographic regions with low species diversity are thought to be less stable (and hence more invasible), than high diversity areas (Ribera and Boudouresque, 1995; Trowbridge, 1999), but there are notable exceptions (see Levine and D'Antonio, 1999; Shea and Chesson, 2002). It should be emphasised that the factors influencing community stability for macroalgal communities in temperate Australian waters remain poorly understood and should be the focus of future work.

Of particular relevance to macroalgal communities is the observation that for plant communities on land resistance to plant invasion may correlate more strongly with the architecture of the plant community rather than the species diversity (Mack *et al.*, 2000). For example, forest communities have remained resistant to plant invaders as long as the canopy remained intact (Corlett, 1992). While this also seems likely to be true for macroalgal communities, experiments are required to verify the theory.

The stage of ecological succession of a native algal community is also likely to be important in determining invasion success. The experiments presented in Chapter 2 indicate that invasion success of *U. pinnatifida* was reduced when the native algal community was in a more advanced stage of succession. For disturbances initiated several months prior to the sporophyte growth season, native algal succession occurred prior to sporophyte development. This resulted in lower *U. pinnatifida* sporophyte densities compared to disturbances initiated immediately prior to the sporophyte growth season, where there was limited opportunity for native algal succession.

While both the life history characteristics of *U. pinnatifida* and the characteristics of the recipient environment are important in determining invasion success, it should be emphasised that it is a complex process. If disturbance occurs in the absence of a source of propagules, then clearly invasion will not occur. Conversely, if there are propagules present but no disturbance, again invasion will not succeed. These predictions are consistent with a general theory of community invasibility recently proposed by Davis *et al.* (2000). These authors suggest that the variable nature of invasion success is determined by conditions of resource enrichment or release, which occur intermittingly. For invasion to occur, the resource enrichment or release must coincide with the availability of invading propagules (Davis *et al.*, 2000).

6.4 A distinctive 'sea urchin-macroalgal' dynamic

While the existence of two alternative stable states is usually recognised for urchin barren/seaweed communities (eg. Harrold and Reed, 1985; Johnson and Mann 1988; Shears and Babcock, 2003), we recognise four community states on the east coast of Tasmania (Figure 6.1). Two of the states are common to the established view of dynamics of kelp beds-urchin barrens, *viz.* the extremes of dense stands of macroalgae (state 1) and urchin barrens devoid of fleshy macroalgae (state 3). The remaining two states are unique. The state characterised by urchin 'barrens' supporting seasonally dense stands of *U. pinnatifida* (state 2), exists only at intermediate grazing intensity and characterises the many urchin barrens in the Mercury Passage. *U. pinnatifida* is believed to survive grazing pressure that other native macroalgae cannot because of its high reproductive capacity and very rapid growth rate that exceeds the grazing capabilities of *H. erythrogramma.* The remaining state is comprised of an understorey of ephemeral filamentous and foliose

species beneath a seasonal *U. pinnatifida* canopy (state 4). This state occurred only in our experimental manipulations, but could theoretically arise with a reduction in urchin grazing intensity caused by any of a number of possible mechanisms.

With the possible exception of the '*Undaria*/native understorey' state (state 4), the different community configurations show persistence stability over time scales of at least decades. Monitoring of several native algal stands and an urchin barren habitat in Mercury Passage indicates they are persistent for at least 10-12 years (Edgar and Barrett, unpublished). Admiralty charts published in the 1800s show kelp beds in areas that still support rich macroalgal cover, while anecdotal evidence suggests that formation of urchin barrens (by destructive grazing) at Lords Bluff occurred in the 1970s (C. Sanderson, pers. comm.). While persistence of monospecific *U. pinnatifida* stands on urchin barrens (state 2) has not been examined specifically, they also appear persistent over time scales of decades, having been recorded from 1989 through to the present (Sanderson and Barrett, 1989; Sanderson, 1997; Chapter 4). Notably, destructive grazing of *U. pinnatifida* in experimental plots by urchins in 2001 (i.e. state 3) was the first observation of such an event.

While highlighting the distinction between the well recognised two phase system (urchin barrens⇄ macroalgal bed) and the unique 'barrens' of the Mercury Passage, the model highlights the general lack of understanding of the dynamics of the system. There is limited understanding of the factors leading to formation of *H. erythrogramma* dominated barrens. Anecdotal evidence suggests that sea urchins destructively grazed native algae to form these barren grounds (W. James, pers. observation), however, the circumstances leading to this event are unknown. It is

reasonable to assume that a change in urchin density and/or behaviour resulted in barren formation, as reported from other temperate regions (Lawrence, 1975; Mann, 1977; Harrold and Reed, 1985; Chapman and Johnson, 1990; Watanabe and Harrold, 1991; Hagen, 1995; Scheibling *et al.*, 1997; Sivertson, 1997).

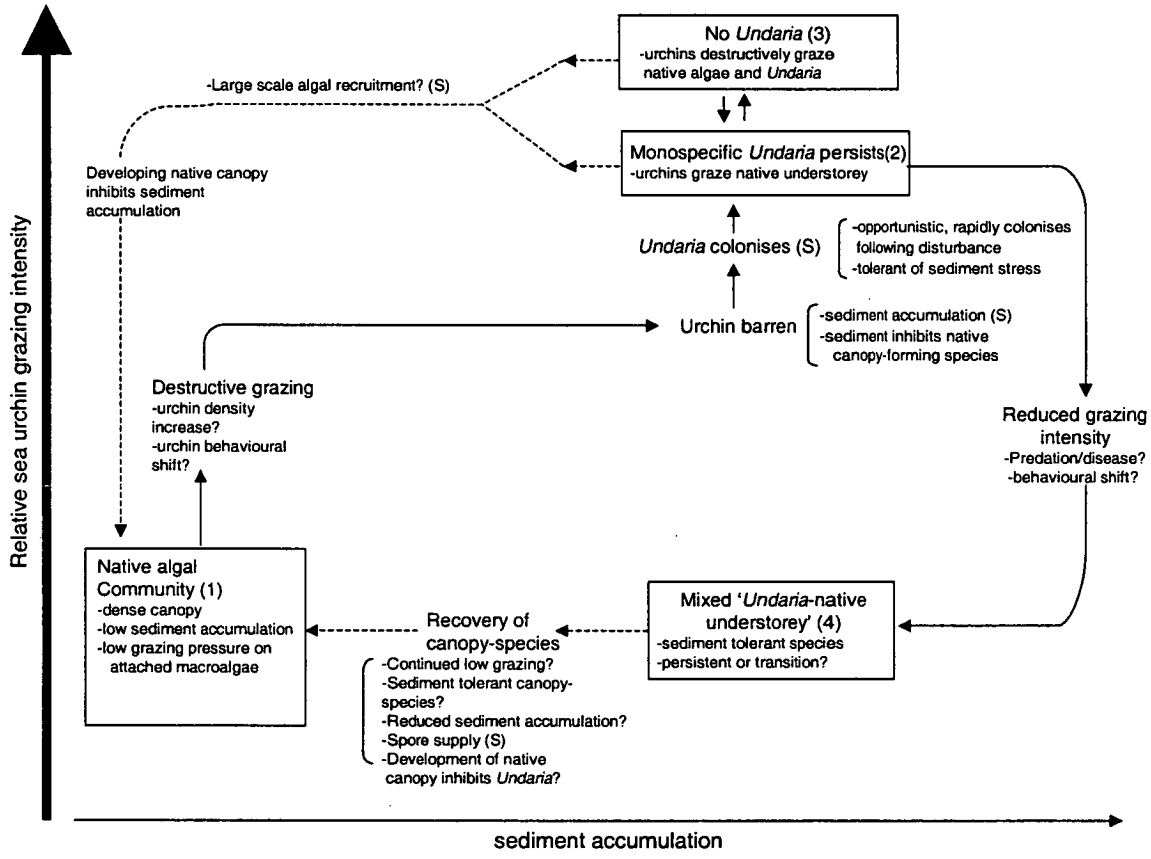


Figure 6.1. Qualitative model of algal dynamics in the Mercury Passage. Four different community states are recognized. The degree of persistence of native canopy-forming algae and *Undaria pinnatifida* is regulated primarily by relative sea urchin grazing intensity. It is important to note that sediment accumulation does not drive system dynamics but occurs as an indirect result of canopy removal by sea urchins. The parentheses '(S)' denotes factors that may be affected by the spatial scale of the initial destructive grazing event. Transition processes in the model that remain poorly understood are indicated by dashed lines. Note that relative sea urchin grazing intensity can be mediated by algal recruitment success. For example, the transition from the persistent *U. pinnatifida* community state (2) to the community devoid of all macroalgae (3) can occur through increased sea urchin grazing intensity, decreased recruitment success of *U. pinnatifida*, or a combination of both factors. See text for detailed discussion of the attributes of the model.

6.5 The effects of accumulated sediment

The major gap that remains in our understanding of the dynamics of the system is the transition from either of the 'urchin barren/*U. pinnatifida*' community states (i.e. states 2, 3) to a community dominated by native canopy-forming algae (state 1). Typically, native canopy species recover rapidly (usually within 12 months) following a reduction in urchin grazing pressure (Duggins, 1980; Chapman, 1981; Andrew and Choat, 1982; Himmelman *et al.*, 1983; Dayton *et al.*, 1984; Scheibling, 1986; Keats *et al.*, 1990; Leinnas and Christie, 1996; Agatsuma *et al.*, 1997; Shears and Babcock, 2002), however, on the barren at Lords Bluff meaningful recovery was not observed following 30 months of sea urchin removals (Chapter 4). Given recovery rates observed in similar experiments elsewhere, it is unlikely urchin removal plots were maintained for an insufficient period. It is apparent that other factors may influence recovery of native canopy-forming species.

The experiments in this study have clearly identified accumulation of sediment as a possible factor influencing maintenance of the *U. pinnatifida* dominated state in the absence of sea urchins. The urchin barren area displayed a consistently high sediment load on a large spatial scale and it is likely that it plays a key role in maintaining dense *U. pinnatifida* stands by inhibiting early developmental stages of native canopy-forming species (Chapter 5).

Further research is required to investigate sediment dynamics in the study area, particularly in relation to spatial and temporal variation in deposition rates and the source of the accumulated sediment. It should be emphasised that the high sediment cover present on *H. erythrogramma* barrens in the Mercury Passage represents a

clear difference to urchin barrens described elsewhere, which are characterised by low cover of sediment and high cover of encrusting coralline algae (eg. Ayling, 1981; Chapman, 1981; Harrold and Reed, 1985; Chapman and Johnson, 1990; Keats *et al.*, 1990; Andrew, 1993; Leinnas and Christie, 1996; Agatsuma *et al.*, 1997).

While it is likely that sediment accumulation represents a potentially significant source of stress and mortality for macroalgae on the urchin barren, clearly *U. pinnatifida* is capable of surviving these conditions. Although a range of physiological, reproductive and morphological adaptations may be advantageous in habitats subject to sediment accumulation (see Airoldi, 2003), the life history characteristics that enable *U. pinnatifida* to cope with the effects of sediment remain unknown. The opportunistic nature of *U. pinnatifida*, evidenced by its rapid colonisation of disturbed patches (Chapter 2; Chapter 3), and its abundance on unstable substrata such as rock and shell fragments, remains the most likely explanation for the success of *U. pinnatifida* in areas subject to sediment accumulation. It is notable that opportunistic species that rapidly recolonise the substratum following mortality caused by burial and scour are characteristic of habitats prone to sediment accumulation (Littler *et al.*, 1983).

6.6 Scaling effects

The spatial scale of disturbance should also be considered in relation to recovery of native canopy-forming species and persistence of *U. pinnatifida*. The disturbances created in the canopy removal experiment, where recovery of native algal species was observed (Chapter 2), were significantly smaller (16 m^2) than the disturbance attributed to destructive urchin grazing (approx. 1.2 x 10^4 m^2). These differences in

the spatial extent of disturbance could affect persistence via a range of mechanisms. For example, higher supply of native algal spores would be expected in the smaller patches given the close proximity to reproductive individuals and their limited dispersal range (Sousa, 2001). The spatial scale of disturbance could also affect sediment load on the urchin barren. Canopy removal experiments have shown that sediment accumulation is greatest in the centre than on the edges of 4 m^2 clearings (Kennelly and Underwood, 1993). Although sediment accumulation has not been examined previously on a scale as large as an urchin barren, it is possible that the high sediment load is related to the large scale of the disturbance. Consequently inhibitory effects of sediment on macroalgal recovery may be greater on the urchin barren.

6.7 Sea urchin grazing intensity and native algal recruitment

While sea urchins may be important in maintaining the barren state, particularly in the absence of significant sediment accumulation, the conditions leading to lowered grazing intensity remains uncertain. In the northwest Atlantic, sea urchins have been decimated by a pathogen, allowing kelps to recover (Jones and Scheibling, 1985; Scheibling and Hennigar, 1997). Mass mortality due to disease has not been reported for *Heliocidaris erythrogramma* (Keesing, 2001) so it is unlikely that this is a potential mechanism to stimulate recovery of native canopy-forming species. In other regions recovery of seaweeds has been linked to recovery of predators that prey on urchins (Estes and Duggins, 1995; Shears and Babcock, 2003). This is a possible mechanism to facilitate recovery of native algae in Tasmania. Recent work has identified that rock lobster (*Jasus edwardsii*), a heavily fished species on the east coast of Tasmania, is a significant predator of *H. erythrogramma* (Pederson and

Johnson, unpublished). Sea urchin population modelling indicates that the reduction in the population of legal-sized rock lobster, as a direct result of fishing, is sufficient to account for increases in urchin density to the point of urchin barren formation (Pederson and Johnson, unpublished).

Another possibility is that hydrographic conditions during the study were not conducive for large-scale algal recruitment. It has been suggested that favourable environmental conditions for large-scale recruitment can overwhelm the effects of urchin grazing leading to establishment of kelps, an increased supply of drift algae, and a switch in urchin feeding mode from active grazing to reliance on drift algae (Harrold and Reed, 1985). This mechanism is unlikely to account for the lack of recovery of canopy-species, however, given that recovery of native canopy-forming species occurred in canopy-removal areas on adjacent algal beds (Chapter 2).

6.8 Options for *Undaria pinnatifida* control – a system management approach

Although the relationship between disturbance and persistence of *U. pinnatifida* appears variable, disturbance is clearly critical in enabling dense stands of *U. pinnatifida* to establish in the first place. Consequently, management strategies that target *U. pinnatifida* sporophytes using physical removal while ignoring disturbance are not only expensive but are unlikely to succeed in the long term. The present work suggests that microscopic gametophytes and/or sporophytes are widely spread and to control invasion it is necessary to identify potential sources of disturbance that lead to a reduction in cover of native canopy species. Where disturbance can be linked to human activity, indirect control options for *U. pinnatifida* may exist by focusing efforts to minimise anthropogenic disturbances.

On temperate subtidal rocky reefs, a range of disturbances or physiological stresses can lead to a reduction in cover of the native canopy, including physical damage by storms (Kennelly, 1987a; Kennelly, 1987b; Dayton *et al.*, 1992), high water temperatures (Tegner and Dayton, 1987), burial or abrasion by sediments (Airoldi *et al.*, 1996; Airoldi and Virgilio, 1998), sea urchin grazing (Lawrence, 1975; Mann, 1977; Ayling, 1981; Himmelman *et al.*, 1983; Harrold and Reed, 1985; Johnson and Mann, 1988; Keats *et al.*, 1990; Watanabe and Harrold, 1991; Andrew, 1993; Bulleri *et al.*, 1999; Scheibling *et al.*, 1999; Villouta *et al.*, 2001) and pollution (Hardy *et al.*, 1993). Many of these disturbances can be influenced by human activities. For example, sedimentation is increasing on rocky coasts around the world as a direct result of activities such as industrial and domestic discharges and as an indirect result of modifying coastlines and river catchments (reviewed by Airoldi, 2003). Similarly, the predicted effects of global warming include not only increased water temperatures, but also increased frequency and intensity of storms, both of which can lead to reductions in cover of canopy-forming species (Coelho *et al.*, 2000). Another effect of global change that could lead to reduced cover of canopy-forming species, particularly in the shallow subtidal and intertidal habitats is increased ultraviolet radiation due to ozone depletion (Coelho, 2000). There is significant evidence to suggest that human activities have resulted in the world-wide decline of canopy forming species observed in the last 30 years (Benedetti-Cecchi *et al.*, 2001).

In our study area, destructive grazing by sea urchins is the most obvious source of disturbance to native algal communities. 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; 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 possible that overfishing of sea urchin predators is the ultimate cause of reduced native algal cover in the Mercury Passage which has facilitated establishment of dense *U. pinnatifida* stands. Managing populations of *J. edwardsii* to maintain urchin numbers at low levels, therefore, provides a potential option for control of *U. pinnatifida*. It should be emphasised that the time frame for recovery of the native algal canopy on barren grounds using a system management approach may require several decades. For example, the transition from urchin barren to kelp on New Zealand reefs occurred over a 20-year period following reduced fishing pressure after declaration of a marine reserve (Babcock *et al.*, 1999).

6.9 Ecological impacts of *Undaria pinnatifida*

The ecological impact of *U. pinnatifida* on native communities has received little attention to date. Even if a 'system management' approach is adopted to successfully control *U. pinnatifida*, natural disturbances that cannot be controlled by humans will continue to be exploited opportunistically by *U. pinnatifida*. Under the least threatening scenario, *U. pinnatifida* would establish following disturbance, but then be inhibited as native canopy-forming species gradually recover, as observed in the canopy removal experiment (Chapter 2). What are the potential impacts of *U. pinnatifida* on native communities under this scenario? In terms of the effects on algal community structure, the impact will be largely dependent on seasonality of

recruitment for native algal species and the timing of disturbance (see Chapter 2). Unfortunately, there is limited understanding of the phenology of native canopy-forming species in Tasmania so it is difficult to predict these impacts. If recruitment windows for native algae coincide with peaks in *U. pinnatifida* abundance, the rate of recovery of native canopy species may be slowed significantly. For species with narrow recruitment windows, inhibition of recruitment could occur. For example, peaks in abundance of the introduced algae *Sargassum muticum* in North America occurred during a critical period in the life cycle of the native kelp *Macrocystis pyrifera*, resulting in complete inhibition of recruitment (Ambrose and Nelson, 1982).

The impact of *U. pinnatifida* on *Macrocystis pyrifera* in Tasmanian waters is a particular concern, since both species occupy a similar ecological niche (Sanderson and Barrett, 1989). The present distributions of *U. pinnatifida* and *M. pyrifera* have only recently overlapped and it is vital that further research examines the outcome of competition between the two species. Interestingly, the Mercury Passage area once contained dense stands of *M. pyrifera* (Olsen, 1965), but the plant has now been largely absent from the area for more than 30 years. The cause of the decline remains speculative, although low nutrient conditions associated with warmer surface waters off the Tasmanian coast is the most likely candidate (Edgar, 1997).

Invasion by *U. pinnatifida* may have implications for secondary production. The number, biomass and diversity of epifaunal invertebrates has been shown to be significantly lower in *U. pinnatifida* dominated communities compared to those dominated by native canopy-forming species in the same area (Innes and Johnson,

unpublished). Since these animals are potential prey of secondary consumers and provide links to higher trophic levels (Stoner, 1980; Virnstein and Curran, 1986), secondary production may be reduced significantly if *U. pinnatifida* becomes locally abundant.

U. pinnatifida invasion may also have significant implications for nutrient cycling through inputs of detritus, which is an important source of organic matter for heterotrophs (Yoshikawa *et al.*, 2001). Production of detritus by *U. pinnatifida* during sporophyte growth and senescence is likely to be significantly different to detrital production derived from native canopy-forming species. The impact of a change in detrital production on near-shore food webs remains unknown.

6.10 General conclusions

This study has provided valuable insights into the invasion process for *U. pinnatifida*, identifying disturbance as a key mechanism facilitating establishment of high densities of sporophytes. While destructive grazing by sea urchins is the most likely disturbance leading to *U. pinnatifida* establishing in dense stands in the Mercury Passage, several unanswered questions remain in relation to the processes leading to urchin barren formation and the reverse transition of recovery by native canopy-forming species. It is particularly important that further research examines the processes of recovery of native canopy-species, since *U. pinnatifida* is affected negatively by their presence.

Given that the underlying cause of *U. pinnatifida* invasion is disturbance to reduce cover of native algae, controlling disturbance using a system management approach (eg. by managing sea urchin predator populations) may prove an effective long-term

strategy for reducing *U. pinnatifida* abundance. Such an approach is unlikely to result in complete elimination of *U. pinnatifida*, however, because the plant is also well adapted to exploiting natural disturbance regimes that cannot be controlled by human intervention. For example, in the Mercury Passage the plant is often locally abundant on unstable substrata, in the sand scour zone at the base of reefs and on reefs subjected to storm swells. Although the ecological impacts of *U. pinnatifida* incursions remain largely speculative, there are certainly potential negative effects of even brief periods of invasion following natural disturbance. Consequently, efforts to prevent further spread on a local scale through public awareness programs (eg. Dextrase, 2002) and on an international scale via ballast water management (IMO, 1997) should continue. Preventing introduction in the first place is the only way to ensure complete protection of the integrity of native communities.

Appendix I.

Taxa	Flensers Point	Lords Bluff
Canopy-forming algae		
Carpoglossum confluens	Y	Y
Caulocystis cephalornithos	Y	Y
Cystophora monoliformis	Y	Y
Cystophora platylobium	N	Y
Cystophora retroflexa	Y	Y
Cystophora siliquosa	N	Y
Ecklonia radiata	Y	Y
Phyllospora comosa	Y	Y
Sargassum decipiens	Y	N
Sargassum fallax	Y	Y
Sargassum spp.	Y	Y
Sargassum verruculosum	Y	Y
Sargassum vestitum	Y	Y
Seirococcus axillaris	Y	Y
Undaria pinnatifida	Y	Y
Brown turf algae		
Sporochnus spp.	Y	Y
Scytosiphon sp.	Y	Y
Colpomenia sp.	Y	Y
Halopteris spp.	Y	Y
Dictyopteris muelleri	Y	Y
Dictyota dichotoma	Y	Y
Unidentified filamentous brown algae	Y	Y
Zonaria/Lobophora complex		
Zonaria angustata	Y	Y
Zonaria turneriana	Y	Y
Lobophora variegata	Y	Y
Homeostrichus olsenii	Y	Y
Foliose Red Algae		
Jeanneretia lobata		
Echinothamnion		
Dasya ceramiodes		
Dictymenia harveyii	Y	Y
Sonderopelta coriacea	Y	Y
Plocamium angustatum	Y	Y
Unidentified filamentous red algae	Y	Y
Encrusting Red Algae		
Encrusting coralline algae	Y	Y
Peyssionella spp.	Y	Y
Green algae		
Caulerpa flexilis	Y	Y
Caulerpa trifarium	Y	N
Caulerpa germinata	N	Y
Codium fragile	Y	Y
Ulva sp.	Y	Y
Cladophora spp.	N	Y

Appendix I. Algal taxa and associated guilds recorded at Flensers Point and Lords Bluff, November 1999-November 2001 (Y=recorded, N=Not recorded).

Appendix II.

Taxa	Algal Guild	Relative abundance (%)
Dasya ceramiodes	Foliose red	50.31
Cystophora retroflexa	Canopy-forming brown	8.65
Echinothamnion sp.	Foliose red	7.02
*Seirococcus axillaris**	Canopy-forming brown	6.62
Zonaria angustata	Brown turf	6.10
Dictymenia harveyii	Foliose red	4.45
Dictyopteris muellerii	Brown turf	3.67
Sargassum verruculosum	Canopy-forming brown	2.38
Cystophora monoliformis	Canopy-forming brown	2.16
Heterosiphonia gunniana	Foliose red	1.70
Hemineura sp.	Foliose red	0.94
Sargassum decipiens	Canopy-forming brown	0.81
Caulerpa flexilis	Green algae	0.78
Plocamium angustatum	Foliose red	0.73
Sargassum fallax	Canopy-forming brown	0.57
Zonaria turneriana	Brown turf	0.48
Carpoglossum confluens	Canopy-forming brown	0.44
Laurencia filiformis	Foliose red	0.38
Sporochnus sp1.	Brown turf	0.33
Acrocarpia paniculata	Canopy-forming brown	0.23
Sargassum spp. recruit	Canopy-forming brown	0.19
Filamentous brown sp1.	Brown turf	0.19
Caulocystis cephalornithos	Canopy-forming brown	0.16
Craspedocarpus ramentaceus	Foliose red	0.14
Dictyota dichotoma	Brown turf	0.13
Cladophora sp.	Green algae	0.10
Gelidium sp.	Foliose red	0.07
Wrangelia sp.	Foliose red	0.06
Halopteris paniculata	Brown turf	0.06
Ballia sp.	Foliose red	0.06
Polysiphonia sp.	Foliose red	0.04
Codium sp.	Green algae	0.02
Sporochnus sp2.	Brown turf	0.01
Filamentous brown sp2.	Brown turf	0.01

Appendix II. Relative abundance of dominant native algal taxa recorded in sea urchin removal plots following destructive sampling (biomass data pooled across all sea urchin removal plots). Taxa are presented in decreasing order of abundance. Note that the value for *Seirococcus axillaris* was dominated by a single large plant that was present in one of the plots at the beginning of the experiment and persisted throughout the study period.

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