Ecological effects of *Undaria pinnatifida* (Harvey) Suringar and nutrient-enrichment on intertidal assemblages in the Wellington region of New Zealand

by

Bionda Morelissen

A thesis
submitted to the Victoria University of Wellington
in fulfilment of the requirements for the degree of
Doctor of Philosophy
in Marine Biology

Victoria University of Wellington

2012

ABSTRACT

The introduction of non-native species and the alteration of seawater nutrient regimes due to anthropogenic impacts are two important threats to marine environments. Moreover, these disturbances may interact in such a way that promotes the success of invasive species in coastal habitats. This thesis contributes to current gaps in knowledge in these areas for low-intertidal communities.

Algal community dynamics and ecological effects of the invasive kelp *Undaria pinnatifida* on low shores in the Wellington region, New Zealand, were examined, using field surveys and experiments. In addition, the role of variability in nutrient concentrations in coastal waters in mediating algal community structure and diversity, and the success of *U. pinnatifida* reproduction were investigated.

Algal surveys were used in two locations thought to differ in nutrient regimes, the Wellington Harbour and the Wellington south coast, to explore the structure and dynamics of algal assemblages. Results showed high variability of low-intertidal algal communities among sites, but no consistent differences in algal community composition were found between the two locations, despite higher *U. pinnatifida* cover in the harbour. Over the duration of the study, nutrient regimes did not differ greatly between the locations.

The response of rocky intertidal algal assemblages to chronic exposure to high nutrient effluent was investigated using two nearshore sewage outfalls in the Wellington region. The Titahi Bay outfall showed a stronger relationship between nutrients and algal community composition. Variation in algal assemblage structure and diversity was best explained by phosphate concentrations. By contrast, at the more wave-exposed Pencarrow outfall, patterns of change in the algal community were less clear and there was a much weaker relationship with seawater nutrients.

Because removal of native algal canopy species may facilitate the establishment of invasive macroalgae, the invasion process of *U. pinnatifida* in disturbed patches in a rocky low-intertidal habitat was investigated. In a site where *U. pinnatifida* had not yet established, patches were scraped clear of native algal cover at two different times of year, and recruitment of *U. pinnatifida* was monitored. While *U. pinnatifida* invaded the site, it recruited in control plots at a similar rate as cleared plots, suggesting that physical disturbance of the native algal assemblage is not a key requirement for this kelp to invade and establish in new areas in the low intertidal zone.

The response of native algal assemblages to removal of *U. pinnatifida* individuals was investigated at intertidal sites in the Wellington Harbour and on the south coast. No significant effect of *U. pinnatifida* on community composition, diversity, and species richness was detected. Removal of this invader did not change native intertidal assemblage structure in either harbour or south coast sites.

Lastly, effects of different nutrient regimes and light intensities on early development and reproduction of *U. pinnatifida* were studied using a laboratory experiment. Under low light conditions *U. pinnatifida* gametophyte growth and reproduction stalled and was not increased by the addition of nutrients. However, at medium and high light levels, gametophyte growth and reproduction, and particularly early stage sporophyte growth rates increased when exposed to higher nutrient concentrations.These effects could have implications for *U. pinnatifida* population dynamics in intertidal habitats where light is not often a limiting resource.

This research contributed to a better understanding of factors that underlie invasion dynamics, distribution, and ecological effects of *U. pinnatifida* and seawater nutrient regimes on low-intertidal assemblages in the Wellington region. The outcomes can assist in setting up strategic environmental protection and conservation plans.

ACKNOWLEDGEMENTS

Firstly, I would like to thank Bruce; I couldn't have finished this PhD without you! Thanks for your endless love, support, understanding, and keeping me sane when I went through stressful research phases.

I am grateful to my supervisor Nicole Phillips for advice, support, and feedback and for telling me I was doing well when I needed it. Thanks to my secondary supervisor Joe Zuccarello for advice and feedback.

I would like to thank Bruce, Shiree, David, Jennifer, Gesine and Duncan for helping me out with fieldwork, which was not always pleasant in Wellington weather and at stinky sewage sites.

Thanks to Alejandra for endless challenging hours in the lab working with the nutrient analyser. Cheers to Jo Davy and Derek Heath for analyser support.

Thanks to Shiree and Jennifer for image analysis of the algal spores.

Thanks to Neill for never-ending seaweed talk and brainstorming about lab experiments, and Bruce for helping out with the spore experiment.

Thanks to the VUCEL crowd for support and feedback and the fun times. Special thanks to Rachel and Erasmo for seaweed-help; Shane, Alejandro, Tim, and Bruce for help with stats issues.

Thanks to the Hutt City Council and the Titahi Bay Waste Water Treatment Plant for access to the sewage outfall roads, MAF Biosecurity and Department of Conservation for research permits.

Thanks to the Victoria Doctoral Assistantship, Victoria PhD Scholarship, Victoria PhD Submission Scholarship, and New Zealand Biosecurity Institute Study Award for funding.

I would like to thank the USDA IPIF for providing me with desk space to finish writing up my thesis in Hawai'i, and Rachel for submitting logistics.

Lastly, I would like to say thank you to my family and friends in the Netherlands and New Zealand for (long-distance) support.

TABLE OF CONTENTS

LIST OF TABLES

Chapter 6

LIST OF FIGURES

Chapter 2

Chapter 3

Chapter 4

Chapter 5

Chapter 6

LIST OF APPENDICES

Chapter 2

CHAPTER 1

GENERAL INTRODUCTION

Biological invasions

Introduction of non-indigenous species in new environments is of huge ecological concern. It may be as detrimental to native species and ecosystems worldwide as loss and degradation of habitats (Vitousek *et al.* 1996). An important research priority in invasion biology is understanding what conditions promote the successful invasion and establishment of non-native species in a new habitat (Byers *et al.* 2002). A lack of predators, competitors, or pathogens in a newly invaded system often allows introduced species to establish successfully, becoming pests, and may eventually lead to the displacement of indigenous species (Trowbridge 1995). Several features of the biology of introduced species may also contribute to the probability of a successful invasion, for example, rapid growth and reproductive rate, ability to reproduce vegetatively or asexually, quick maturation, and high dispersal efficiency (Colautti *et al.* 2006). An introduced species is referred to as invasive when it is demonstrated to cause economic or ecological harm and hence can be considered a pest (Williamson 1996).

The human-mediated introduction of non-native species into marine environments is considered one of the largest threats to marine ecosystems as it may impact biodiversity (Bax *et al.* 2001; Vitousek *et al.* 1996), productivity (Vitousek *et al.* 1996), habitat structure, and fisheries (Carlton 1999). The rates of spread of non-indigenous species have increased enormously worldwide over the last few decades, and continue to climb (Carlton 1989; Ruiz *et al.* 1997, 1999; Cohen and Carlton 1998, Boudouresque and Verlaque 2002). Yet the consequences of these invaders on resident communities still remain largely unknown (Piazzi *et al.* 2001). Compared to terrestrial ecosystems,

relatively less research has been conducted on the ecology of invasive organisms in the marine environment (Carlton 1989; Carlton and Geller 1993; Grosholz 2002; Graham and Bayra 2007). However, non-indigenous species can be extremely common in marine ecosystems (Carlton and Geller 1993; Ruiz *et al.* 1997; Grosholz 2002; Graham and Bayra 2007). A well-known example is San Francisco Bay, probably the most invaded estuary in the world. Cohen and Carlton (1998) reported that over 200 exotic species have established in this ecosystem and dominate many of its biological communities. Furthermore, many marine communities contain species of uncertain origin (cryptogenic species), which may be non-native (Carlton 1996; Cohen and Carlton 1998; Graham and Bayra 2007).

It is often stated that invasions happen more readily in disturbed sites than undisturbed ones (Elton 1958; Hobbs and Huenneke 1992; Burke and Grime 1996; Williamson 1996; Valentine and Johnson 2003). Disturbance may increase susceptibility of communities to invasion due to decreased competition for limiting resources (D'Antonio 1993; Ruiz *et al.* 1999; Davis *et al.* 2000; Sánchez and Fernández 2006; Williams and Smith 2007). Because human actions are responsible for a large degree of disturbance in many habitats (Williamson 1996; GESAMP 2001), it appears that the success of invasions may be mediated by anthropogenic effects (Crooks *et al.* 2011).

Most introductions of non-native species in marine environments have occurred accidentally as a result of ships' ballast water (Carlton 1989; Carlton and Geller 1993; Ruiz *et al.* 1997; Lewis *et al.* 2003). Although most of the species imported this way do not survive in the new habitat, those that do can become a threat to native species and can possibly contribute to 'homogenisation' of marine biodiversity both locally and regionally (Elton 1958; Ruiz *et al.* 1997), and/or can have a substantial impact on commercially important species (Ruiz *et al.* 1997; Cohen and Carlton 1998).

Invasive seaweeds

Invasive algal species can potentially alter benthic habitats and biological assemblages and reduce biodiversity, which could lead to impacts on an ecosystem-level over a broad geographic range (Carlton 1989; Harris and Tyrrell 2001; Piazzi and Cinelli 2003; Piazzi and Ceccherelli 2006; Scheibling and Gagnon 2006; Schmidt and Scheibling 2007). They can possibly alter light availability to other species, change nutrient cycling within the ecosystem, affect food availability to herbivores (Britton-Simmons 2004; Sánchez *et al.* 2005; Henkel and Hoffman 2008), and ultimately displace native species by the development of monocultures (Forrest and Taylor 2002). Well-known examples of invasive seaweeds are e.g., *Caulerpa taxifolia* in the Mediterranean Sea (Meinesz *et al.* 1993; Boudouresque *et al.* 1995), the Japanese *Sargassum muticum* in Europe (Carlton 1989; Walker and Kendrick 1998), and *Undaria pinnatifida* in France (Floc'h *et al.* 1996), Australia (Sanderson 1990; Campbell and Burridge 1998) and New Zealand (Hay and Luckens 1987; Walker and Kendrick 1998). To preserve the marine environment it is of great importance to understand the mechanisms and impacts of biological invasions.

Undaria pinnatifida

New Zealand has an extensive coastline and a vast number of vessels moving around it. This makes New Zealand highly susceptible to invasions of marine pests. The total number of extant non-indigenous marine species in New Zealand was 109 in 1998. 17% of this number consisted of macroalgal species (19 recorded species) (Cranfield *et al.* 1998; Schaffelke *et al.* 2006). *Undaria pinnatifida* and *Caulerpa taxifolia* are the only two marine macroalgae listed as "unwanted organisms" under the Biosecurity Act 1993, based on history of invasiveness overseas, a high likelihood of arrival, potential for significant spread, and the suitability of the environment for establishment in New Zealand.

Undaria pinnatifida (Harvey) Suringar is native along north-western Pacific shores and was first observed in New Zealand in Wellington Harbour in 1987 (Hay and Luckens 1987). It was possibly introduced via fouling on vessels, as this is (together with aquaculture) the most common way non-indigenous seaweeds are introduced to new areas (Williams and Smith 2007). However, Russell *et al.* (2008) suggest that transportation of *U. pinnatifida*'s microscopic gametophytes in ballast water of foreign fishing vessels caused the introduction. Currently it is present in numerous locations around New Zealand in North, South and Stewart Islands (Battershill *et al.* 1998; Forrest *et al.* 2000; Wotton *et al.* 2004). It has been suggested that its distribution is generally restricted to harbours and areas utilised for marine farming. However, it has been observed growing abundantly at Wellington's exposed south coast (Cook Strait) (Battershill *et al.* 1998; personal observation) and off exposed points in Moeraki, Marlborough Sounds, and Banks Peninsula (D. Taylor, *pers. comm.*) too.

Undaria pinnatifida has a complex biphasic life cycle, with microscopic (haploid) gametophytes and macroscopic (diploid) sporophytes (Thornber *et al.* 2004). In its native range, the sporophytes grow during winter (Hay and Luckens 1987; Oh and Koh 1996) and mature in early-mid spring (Forrest 2007). Microscopic spores are typically released in late spring when sea temperatures are higher (Forrest 2007). The sporophytes die off in summer and autumn (Hay and Luckens 1987; Forrest 2007), and the spores settle down to germinate into gametophytes, during late summer/early autumn in *U. pinnatifida*'s native range. When sea temperatures drop, mature gametophytes undergo sexual reproduction to produce new sporophytes (Thornber *et al.* 2004; Forrest 2007). Thus, spores released from a single sporophyte can produce a whole new generation of *U. pinnatifida* (Forrest 2007).

Undaria pinnatifida sporophytes can be found attached to any available solid substratum, including rocks, wood, pebbles, concrete, wharf pilings, ship hulls, and epiphytic on various organisms (Floc'h *et al.* 1996; Wotton *et al.* 2004). The sporophytes can grow in a wide range of habitat types, from below dense multilayered algal canopies to wave-exposed conditions (Russell *et al.* 2008) and can be found from the low intertidal to the

subtidal. Thornber *et al.* (2004) demonstrated in their study in California, USA, that recruitment of *U. pinnatifida* is linked to specific temperature cues. They suggest that cold water temperatures (below ~15 ºC) may increase *U. pinnatifida*'s capacity to develop recruits continuously, which may lead to overlapping generations. This phenomenon has also been observed in New Zealand (Hay and Villouta 1993).

The combination of its rapid growth rate and the ability to reproduce all year round in New Zealand allows it to possibly outcompete many native seaweeds (Thornber *et al.* 2004; Wotton *et al.* 2004). *U. pinnatifida* may have large ecological consequences when it colonises areas without other large canopy species. It is considered a potential fouling nuisance and a threat to natural ecosystems and associated fisheries, e.g. through alteration of the benthic assemblage structure by displacement of native species and the development of monospecific *U. pinnatifida* stands (Battershill *et al.* 1998; Forrest and Taylor 2002), and shading of smaller species, ultimately leading to a possible reduction in biodiversity. However, little is known about effects of invasive macroalgae on native assemblages in New Zealand, particularly on intertidal shores. Studies on the effects of *U. pinnatifida* primarily focus on subtidal communities, e.g., Casas *et al.* 2004 and Battershill *et al.* 1998, who associate the presence of *U. pinnatifida* with shifts in community structure and a decrease in algal species richness and biodiversity in subtidal habitats (in central Patagonia, Argentina, and Wellington Harbour, New Zealand, respectively). Forrest and Taylor (2002), however, recorded little impact of this invader on low shore assemblages in their surveys in Lyttelton Harbour, New Zealand.

Rocky intertidal algal communities

Macroalgae are dominant occupiers of primary space in the mid- to low intertidal zone of temperate rocky shores throughout the world (Adams 1994; Schiel 2004), and are the major habitat-forming organisms in coastal marine environments. They increase spatial complexity and alter environmental conditions, which often promotes diversity of assemblages of plants and animals (Lilley and Schiel 2006).

Light, temperature, salinity, water motion, and nutrient availability are the major environmental factors influencing growth, morphology, and reproduction of macroalgae (Lobban and Harrison 1994). The upper limits of marine macroalgae are largely determined by their ability to withstand desiccation and temperature stress, whereas the lower limits are determined by competition (Mann 2000) for light or space. Among biotic variables, inter- and intraspecific interaction can influence algal community structure in both positive and negative ways, for example, macroalgal canopies can considerably reduce the light that reaches understorey-species. However, the layering of algae at low tide can also be beneficial to the understorey algae because of moisture retention, reduction of temperature stress and protection from solar radiation (Bertness *et al.* 1999; Lilley and Schiel 2006). Interactions with herbivores can likewise have important impacts on algal community structure. For example, herbivores can have a negative impact on algal recruitment and can contribute to reduction of algal diversity by having preference for certain algal species. However, grazing can also contribute to a reduction of competition for light, space, and nutrients within the algal community (Bruno *et al.* 2003; Jaschinski and Sommer 2010).

New Zealand's coastline offers a wide range of habitats, varying from extremely exposed rocky shores to extensive sheltered waterways of fiords or sounds, and lagoons and mangrove swamps, with each of these habitats having typical associations of species which composition may vary with latitude (Adams 1994). Exposed reefs with distinct rock features that provide some degree of shelter (e.g., pools, channels) have the highest diversity of species (Adams 1994). Abundant endemic macroalgae on the intertidal rocky shores of New Zealand are *Carpohyllum maschalocarpum, Carpophyllum angustifolium, Cystophora torulosa* and *Hormosira banksii*, the latter being the most common intertidal fucoid in New Zealand (Schiel 2004). In the more exposed waters, Cook Strait and further south, the giant bull kelp *Durvilleae antarctica* is abundant (Morton and Miller 1968; Schiel 2004).

Disturbance and invasions

The effect of natural disturbance on marine intertidal community structure, recruitment and competition has been investigated in numerous studies (e.g. Dayton 1971; Levin and Paine 1974; Paine and Levin 1981; Sousa 1984a). But disturbance can also play an important role in invasion by non-native species. A habitat's susceptibility to invasions may increase when environmental changes cause an alteration of ecological, biological, chemical, or physical conditions (Carlton 1996). This disturbance may result in an increased availability of limiting resources, e.g. space, light, and nutrients, which can affect species composition and abundance (Airoldi 1998; Araújo et al. 2009). For instance, physical disturbance (e.g. wave action) and biological disturbance (e.g. herbivory, predation) can create open patches which may be invaded by new species (Paine and Levin 1981), and chemical disturbance (e.g. reduced water quality) can promote the invasion of pollution-tolerant species (Carlton 1996).

Disturbance is generally more prevalent in intertidal habitats compared to subtidal environments, due to the large hydrodynamic forces as a result of wave action in intertidal habitats (Denny 1985; Denny and Gaines 1990). These wave forces can influence intertidal community structure and dynamics by controlling the supply of food or propagules, and through damaging or dislodge of organisms (Lubchenco and Menge 1978; Paine and Levin 1981; Sousa 1984a; Bustamante and Branch 1996; Zardi *et al.* 2006). Due to the higher levels of disturbance, resources (space in particular) are freed more frequently on intertidal shores, which can facilitate invasions. Yet, early colonists can rapidly fill openings in intertidal communities, and in this way inhibit, rather than promote subsequent invasion (Lubchenco and Menge 1978; Sousa 1979). The speed at which this re-colonisation occurs is dependent on the life-history characteristics of individual species in the community, e.g. seasonality, quantity of propagule production, dispersal dynamics, recruitment and growth rate, ability of vegetative propagation (Sousa 1980).

Coastal waters like harbours, bays, estuaries, and nearshore waters, belong to the most invaded systems in the world (Carlton 1989; Carlton and Geller 1993; Cohen and Carlton 1998; Grosholz 2002). They are particularly susceptible to invasions because, in addition to 'natural' disturbance, they are often affected by frequent, anthropogenic disturbances, which may increase the availability of limited resources like space and nutrients (Carlton 1989; Carlton and Geller 1993; Cohen and Carlton 1998). In addition, these coastal ecosystems are often regularly exposed to common vectors of marine introduced species, i.e. ships' ballast water (Carlton 1989; Carlton and Geller 1993; Ruiz *et al.* 1997; Lewis *et al.* 2003), fouling (Carlton 1989; Ruiz *et al.* 1997; Lewis *et al.* 2003), and aquaculture and fisheries (Ruiz *et al.* 1997). When high numbers of propagules are introduced through those vectors (high propagule pressure) at these often semi-enclosed or less exposed waters, the chances of success of invasion increase. In addition, conditions in these ecosystems with high human impact are often not ideal for native species, e.g. due to pollution or enriched nutrient regimes which could lead to increased competition for light in algal communities due to phytoplankton blooms (Menge *et al.* 1997; Valiela *et al.* 1997b; Kavanaugh *et al.* 2009). This combination of stressors suggests that coastal habitats have a higher invasibility and, simultaneously, are more susceptible to high frequency, low magnitude disturbance, which can further facilitate invasion success and range expansion (Altman and Whitlatch 2007). Moreover, habitat alteration or expansion, for example wharfs, jetties, marinas, etc., could further promote successful invasions by providing suitable substrata for invasive species (Carlton 1996).

Effects of nutrient-enrichment on coastal algal communities

Worldwide about 60% of the human population lives within 100 km of the coast, hence the ocean's coastal margins are strongly affected by people (Vitousek *et al.* 1997). These anthropogenic impacts include the alteration and destruction of coastal habitats and ecosystems, overexploitation of fish stocks, pollution, changes in sediment flows, and eutrophication (Vitousek *et al.* 1997; GESAMP 2001). Terrestrial sources such as sewage

effluent and agricultural run-off are major contributors to altered nutrient regimes in coastal environments (Vitousek *et al.* 1997).

Nutrients can be limiting resources for macroalgae and therefore nutrient availability plays an important role in determining algal abundance and community composition in coastal habitats (Valiela *et al.* 1997b; Nielsen 2003). Small increases in nutrient supply to nutrient poor coastal ecosystems can stimulate growth rates of ephemeral algae on rocky shores (Bokn *et al.* 2002) and therefore also the total productivity of the ecosystem (Bokn *et al.* 2002). However, macroalgal diversity may decrease due to increases of fast-growing, structurally simple and opportunistic functional groups (Worm *et al.* 2002). In nutrient-rich environments fast-growing species will have an advantage over slow-growing species because of lower competition for nutrients and increased competition for light (Valiela *et al.* 1992; Borum and Sand-Jensen 1996; Valiela *et al.* 1997b; Bokn *et al.* 2002; Worm *et al.* 2002). Furthermore, exposure to sewage effluent can affect algal communities. Kevekordes and Clayton (2000), for instance, showed a significant negative effect on growth and survivorship of propagules of the fucoid alga *Hormosira banksii* when exposed to high ammonium concentrations and freshwater.

Macroalgae play an important role in habitat provision for many marine species and provide food for higher trophic levels. They account for a significant portion of primary production on continental shelves (Smith 1981). Changing nutrient regimes in coastal waters may impact native algal assemblages, but could also affect how introduced algal species behave in new systems. Investigation of the effects of increasing nutrient concentrations will give insight to the consequences of anthropogenic impacts in coastal habitats and help inform appropriate environmental management and conservation strategies (Benedetti-Cecchi *et al.* 2001).

Thesis research

There are important gaps in our knowledge about how nutrients mediate algal dynamics in New Zealand coastal habitats, and the ecological effects of what is considered globally to be an important marine pest, the invasive kelp *U. pinnatifida.* Almost all work done on this species in any system has been subtidally, very little is known about its effects in the intertidal, or how it responds to variability in nutrients.

In this PhD research I investigated algal community dynamics and the ecological effects of the invasive kelp *U. pinnatifida* on low intertidal shores of the Wellington Harbour and the Wellington south coast, using field surveys and experiments. In addition, I examined the role of variability in nutrient availability in mediating algal community structure and diversity, and the success of *U. pinnatifida* reproduction.

Wellington Harbour experiences more sheltered conditions compared with the wave-exposed Wellington south coast that faces Cook Strait. Despite the short distance apart (~4 km), these locations differ greatly in intertidal communities. Mid-intertidal shores in the harbour are primarily dominated by barnacles and extensive mussel beds, while these are mostly absent on the south coast, where the mid-high intertidal zone mainly consists of bare rock (Morton and Miller 1968; Gardner 2000; Helson and Gardner 2004). Assemblages of mobile grazing invertebrates, on the contrary, appear to be relatively similar between the two locations (Morton and Miller 1968). Macroalgal communities may be different between these two coasts, mirroring the different conditions they experience. However, studies investigating algal assemblages in the Wellington region are scarce.

To be able to investigate the possible ecological effects of invasive macroalgae on native communities, it is essential to know the structure and dynamics of the native algal community. In Chapter 2, I used surveys to determine algal community structure in the low intertidal zone in Wellington Harbour and on the Wellington south coast, two locations where intertidal animal communities are very different, but little is known about

the algal communities. It has been suggested that low nutrients on the south coast contribute to these community differences (Gardner 2000; Helson *et al.* 2007); therefore nutrient concentrations in the water were measured to be able to possibly link algal patterns to nutrient regimes. I hypothesised that nutrient concentrations would be higher, and that opportunistic, fast-growing algal species (mainly filamentous and foliose algae) would dominate in the harbour. Hence, I hypothesized that algal community composition would be different between the harbour and south coast. In addition, I hypothesized that the invasive *U. pinnatifida* would be more abundant in the harbour, as this is the location where it was first introduced/ observed.

Sewage outfalls can have major effects on coastal communities through the point source introduction of locally high levels of nutrients. In Chapter 3, I used two sewage outfalls in the Wellington region to investigate the effect of sewage effluent on algal community composition and abundance on adjacent rocky intertidal shores. I hypothesised that closest to the outfalls nutrient supply would be highest and algal diversity would be lowest. With distance from the outfalls nutrient levels would decrease and algal diversity would increase. Further I expected opportunistic filamentous algae and foliose algae to be dominant close to the outfalls, switching to more structurally complex functional groups with increasing distance from the point source.

Chapter 4 discusses the effects of physical disturbance and the availability of bare space on the invasion capability of *U. pinnatifida* in the low intertidal zone. Three different clearing treatments (total clearings, partial clearings, and controls) were employed at a site where *U. pinnatifida* had not established yet at the time of experimental set-up, but where established populations were present at adjacent sites. This experiment was conducted twice, in summer and in winter, to investigate the effect of timing of clearing and native algal seasonality on *U. pinnatifida* recruitment. I hypothesised that *U. pinnatifida* recruitment would depend on clearing treatment, and that *U. pinnatifida* would recruit in both summer and winter as it is capable of reproducing year-round in New Zealand.

The response of the algal community to the removal of established *U. pinnatifida* plants and the restoration capacity of the natives were investigated in Chapter 5 by means of a removal experiment, where *U. pinnatifida* was removed from some quadrats, but left in place in others. Algal communities were examined before manipulation and after four and six months. Wellington Harbour and south coast sites were compared in this experiment. I hypothesised that removal would increase space and light resources resulting in a higher abundance of (opportunistic) algal species. Algal community composition may differ between the Wellington Harbour and the south coast, which could result in a different response of the native algal assemblage to the removal of the invader.

In Chapter 6 I examined *U. pinnatifida* reproduction in response to nutrients and light with a laboratory experiment. I exposed *U. pinnatifida* spores to three nutrient regimes and three light levels in a factorial design. Spore settlement, germination, gametophyte development, reproduction, and sporophyte development were measured under the different treatments. I hypothesised that spores exposed to high nutrient and light levels would grow and develop more rapidly than spores exposed to lower levels, and that more spores would develop into sporophytes when exposed to excess amounts of these resources. Further, I hypothesised that excess nutrients would aid in growth and development of light limited germlings.

CHAPTER 2

A COMPARISON OF ALGAL COMPOSITION AND DIVERISTY, AND THE EFFECT OF DIFFERENT NUTRIENT REGIMES ON ALGAL PATTERNS IN THE WELLINGTON REGION

ABSTRACT

Low-intertidal algal assemblages at three sites in the harbour in the Wellington Harbour and three sites on the Wellington south coast were surveyed every 2-3 months for one year to explore their composition and dynamics, and to investigate the distribution of the invasive Japanese kelp *Undaria pinnatifida* in the region. In addition, water samples were taken at each site throughout the year to measure nutrient concentrations in coastal water to investigate whether algal community patterns could be related to nutrient regimes. The harbour and the south coast are thought to differ in nutrient regimes, with the harbour having increased nutrient levels due to higher anthropogenic input. Hence, algal communities could be different between these coasts to reflect the conditions they are exposed to. In this study, however, no significant differences in total inorganic nitrogen (TIN) and phosphate levels were found between the harbour and the south coast and among sites nested within coasts. The hypothesis that algal communities on the south coast would be more diverse compared to the harbour, and that opportunistic, fast-growing algae would dominate in the harbour due to higher nutrient levels, was not supported in this study. Only a very weak correlation was found between TIN levels and algal community composition, suggesting that other factors (e.g. recruitment, grazing, competition) are more likely to play a role in structuring algal assemblages at these locations. Spatial variability of algal communities was very high on smaller scale (among sites), but no difference on larger scale (between the harbour and south coast) was detected. However, Shannon diversity index and Pielou's species evenness were higher in

the harbour. As predicted, *Undaria pinnatifida* was more abundant in the harbour where its introduction was first observed.

INTRODUCTION

Recent studies investigating changes in rocky shore assemblage composition have shown that variability is scale-dependent suggesting that variance at small scales (from centimeters to hundreds of meters) is at least as high as that at larger scales (several kilometers) (Coleman 2002; Fraschetti *et al.* 2005; Reichert *et al.* 2008), as a result of pervasive small-scale biological interactions and local physical processes (e.g. Benedetti-Cecchi 2001; Coleman 2002). In macroalgal communities spatial variation in patterns of distribution and abundance over a variety of scales (e.g. among quadrats within sites, among sites on a shore, among shores) is evident (Underwood and Chapman 1998a; Coleman 2002). Small-scale (local) variation arises from processes such as dispersal and recruitment, or from disturbances acting on post-recruitment stages, e.g. grazing by herbivores, competitive interactions, or physical stresses (e.g. sediment movement [Kendrick 1991], desiccation) (Menge and Olsen 1990; Coleman 2002). Examples of larger-scale (regional) processes are light and nutrient levels, and availability of algal propagules (Menge and Olsen 1990; Coleman 2002). In addition to spatial variation, algal assemblages are also known to vary temporally, e.g. as a result of factors affecting patterns of recruitment over time. Algal reproduction is often seasonal (Hoffmann and Ugarte 1985) and many species are only present (in macroscopic form) during short, specific times a year. Peak seasonal algal growth is generally limited by the availability of nitrogen in temperate coastal waters (Smith 1984).

In this study I investigated spatial and temporal variation in algal communities on the low-intertidal rocky shores in the Wellington Harbour and on the Wellington south coast on the lower North Island of New Zealand. Despite their relative proximity (only ~ 4 km apart), these coasts are exposed to different conditions and are well known for having vastly different intertidal animal communities (Morton and Miller 1968). The harbour has

extensive mussel beds in the intertidal zone, while mussels are mostly absent on the south coast (Gardner 2000; Helson and Gardner 2004; Helson *et al.* 2007).

Cook Strait separates the North and South Islands of New Zealand and has some of the strongest tidal currents in the world (Bowman *et al.* 1983). Waters of both subtropical and subantarctic origins come together in the Strait (Bowman *et al.* 1983). The Wellington south coast faces Cook Strait and is a high energy, very exposed coastline which frequently experiences fierce southerly winds which are characteristic for this region. Significant wave height (the highest one-third of the waves) can exceed 8m during large storm events (Carter *et al.* 2002). Primary productivity of the coastal water column is generally low along the Wellington south coast, supposedly due to lack of significant input of particulate organic matter and nutrients from watershed run-off (Helson and Gardner 2004). The semi-enclosed Wellington Harbour is more protected, and is likely more impacted by human activity because of the adjacent high populations, industries, a major port and many marinas. The Hutt river flows into the harbour on the northern end, which could, besides affecting factors such as salinity and dissolved matter, influence nutrient dynamics in the water, especially after heavy rainfall. The Hutt river estuary receives high inputs of nutrients and sediment from its large catchment (Robertson and Stevens 2010) and is currently a eutrophic estuary (Fry *et al.* 2011). The floodplain has been highly modified through extensive reclamations and channelization (Robertson and Stevens 2010) and is now occupied by residential, commercial and industrial developments (Fry *et al.* 2011).

Previous research suggests an east-west gradient of nutrient and particulate matter concentrations in Cook Strait with highest concentrations at the Wellington Harbour entrance and lowest concentrations at the entrance of Cook Strait in the west (Bowman *et al.* 1983; Gardner 2000; Helson *et al.* 2007). Macroalgal communities may differ between these locations to reflect these different conditions they are exposed to, but they have rarely been examined, previous studies have focused on the sessile animals (but see Phillips and Hutchinson 2008). For example, in more nutrient enriched locations, one would expect a higher abundance of fast growing opportunistic species (Pedersen and

Borum 1996; Bokn *et al*. 2003), which are able to take advantage of increased nutrient concentrations in the water because of their high nutrient uptake kinetics (e.g. *Ulva* spp.).

Another goal of this study was to investigate the distribution of the invasive Japanese kelp *Undaria pinnatifida* in the Wellington region. *U. pinnatifida* was first observed in New Zealand in the Wellington Harbour in 1987 (Hay and Luckens 1987). Currently, it is present in numerous locations around New Zealand and abundant along Wellington Harbour shores as well as on the Wellington south coast. By using algal surveys at multiple sites in the harbour and on the south coast, I investigated whether the distribution of *U. pinnatifida* differed between locations across the region. To be able to study possible ecological effects of *U. pinnatifida* on native macroalgal communities, and the effect of different nutrient regimes on algal assemblages and the success of *U. pinnatifida*, it is essential to know the structure and dynamics of the native algal communities and the scales over which they vary. I hypothesised that algal communities on the south coast would be more diverse compared to the harbour, and that opportunistic, fast-growing algae (mainly filamentous and foliose algae) would dominate more structurally complex, slower-growing algae in the harbour, where nutrient levels would generally be higher. Finally, I hypothesised that *U. pinnatifida* would be more abundant in the harbour (where it was likely introduced and was first seen) than on the south coast.

MATERIALS AND METHODS

Study sites

Surveys were conducted at six sites on intertidal rocky shores within the Wellington region: three sites were located in the Wellington Harbour (Point Halswell (PH) [41º17`S; 174º49`E], Kau Point (KP) [41º17`S; 174º50`E], Worser Bay (WB) [41º18`S; 174º50`E]), and three on the south coast (Moa Point (MP) [41º20`S; 174º48`E], Island Bay (IB) [41º21`S; 174º46`E], Owhiro Bay (OB) [41º21`S; 174º45`E]) (Figure 2.1).

The rocky shores of the south coast are generally more wave exposed than the shores in the harbour. However, sites on the south coast were selected where there was sufficient shelter by off shore rocks to minimize wave exposure effect between different locations. The rocky substratum both in the Wellington Harbour and on the south coast consists of sedimentary greywacke, with a high vertical relief.

At each site 10 permanent 20 × 20 cm quadrats were randomly selected along a 60 m transect in the low intertidal zone (0.4 to 0.6 m above the lowest astronomical tide). Corners of the selected quadrats were marked with buttons of marine epoxy (Z-spar brand, Splash Zone 788, Kop-Coat Inc., United States). I recorded the identity and percentage cover of each algal species/taxomomic group in each quadrat, visually in the field and using digital photographs. Surveys were carried out in December 2007, January/February 2008, April 2008 (Island Bay and Point Halswell only), May/June 2008, August 2008, and January 2009. I classified species into functional groups according to Appendix 2.1.

I took water samples at each sample time, and at several additional times, to quantify nutrient concentrations in the surrounding water. Water samples were collected in sterile polyethylene tubes (50 ml) and rinsed with sample water before filling with sample. At each site (at least) two separate sample tubes were filled, taken no less than 20 m distance from each other, and always on an incoming tide. After collection I placed the sample tubes on ice and in darkness and transported back to the laboratory where they were stored at -20 ºC, within 1 h of collection, for subsequent analysis. Nitrate, nitrate, ammonia and phosphate concentrations in the seawater samples were measured using a SAN^{PLUS} continuous flow analyser (SKALAR, Breda, The Netherlands). Samples were always measured in duplicate to reduce handling error.

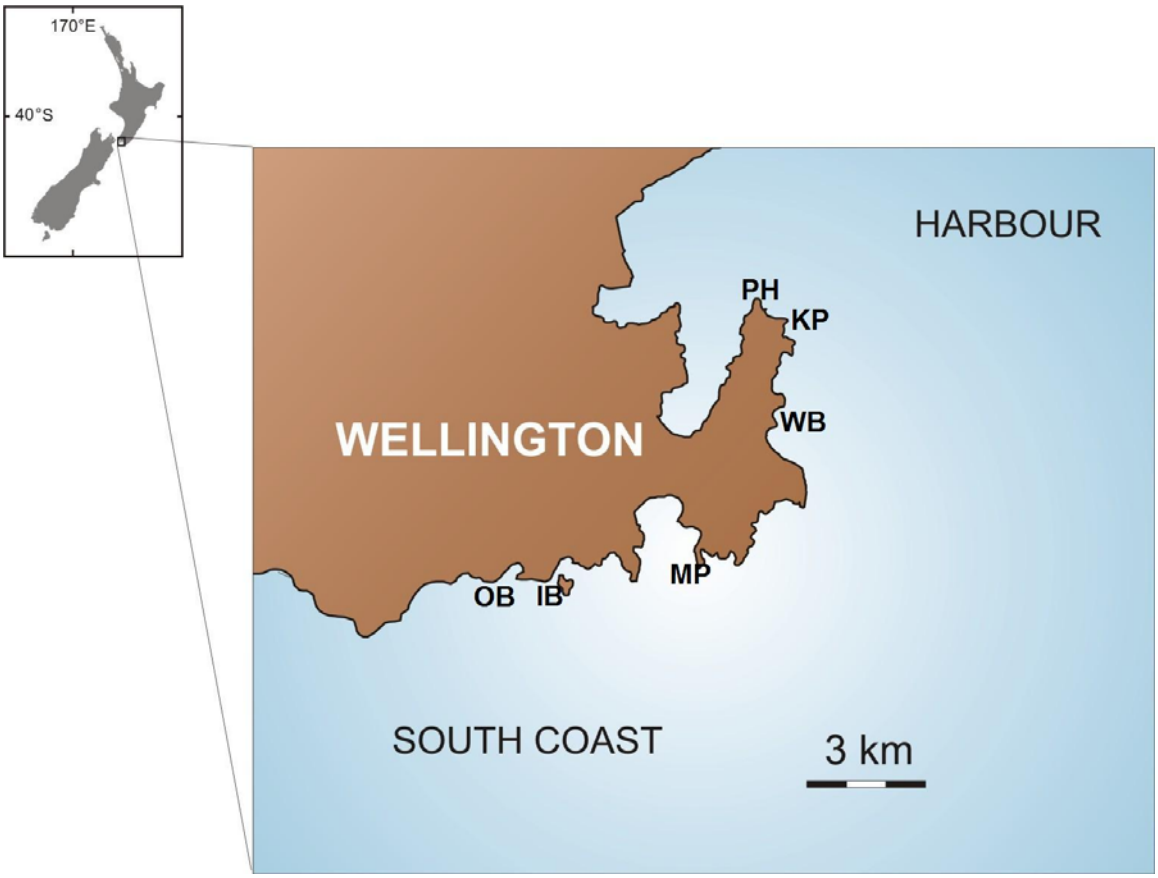


Figure 2.1: Map of Wellington Harbour and south coast showing the survey sites (OB: Owhiro Bay; IB: Island Bay, MP: Moa point; WB: Worser Bay; KP: Kau Point; PH: Point Halswell)

Data analysis

Algal communities

To test for differences in algal community composition between Wellington Harbour and south coast sites two-way nested analyses of similarity (ANOSIM) (Clarke 1993) were conducted for each sampling time separately, using sites as a nested factor within coast (harbour vs. south coast) and quadrats as replicates. ANOSIMs (using 9999 permutations) were conducted using algal species data and algal functional groups data (classification according to Appendix 2.1). Analysis was based on Bray-Curtis similarity matrices and data were fourth root transformed before analysis to reduce the influence of dominant

species (Clarke and Gorley 2006). Pairwise tests, using one-way ANOSIM, were carried out to determine similarity and dissimilarity between the six study sites at different times of year. Non-metric multidimensional scaling (nMDS) was used to describe the algal assemblages at the different sites and locations. To investigate the temporal variability within sites two-way crossed ANOSIM with 'site' and 'time' as factors was conducted (January/February 2008, May/June 2008, August 2008, and January 2009 data) and pairwise tests of one-way ANOSIM (using all available data for each site) were used to examine the difference among different sampling times.

The two-way (crossed) SIMPER routine (based on square root transformed algal species abundance data and the Bray-Curtis similiarity matrix), with 'site' and 'sampling time' as factors was used to test which algal species were responsible for differences found in species composition between sites and between different sampling times. For this procedure sampling events of January/February 2008, May/June 2008, August 2008, and January 2009 were used.

Algal species richness (number of species), algal diversity, and species evenness were determined for every quadrat. Algal diversity was calculated using the Shannon diversity index (H') using the following equation:

$$H' = -\sum p_i (\ln p_i)$$

where p_i is the relative abundance of each macroalgal species, calculated as the cover of species i divided by the total macroalgal cover.

Species evenness was calculated using Pielou's evenness with the following equation:

$$J' = H' / \log_e S$$

where H' is the Shannon diversity index, and S is the number of species (species richness).

Two-way nested ANOVAs (site nested within coast) were used to test for differences in these indices between sites and coasts in January/February 2008, May/June 2008, August

2008, and January 2009. Assumptions of normality (Q-Q plots) and homogeneity of variances were met (Bartlett's test; $p > 0.05$) for all indices.

To test the effects of coast (harbour vs. south coast) and time of sampling (Jan/Feb 08, May/Jun 08, Aug 08, and Jan 09) on *Undaria pinnatifida* abundance, GLM analysis of deviance was conducted using a quasi-Poisson distribution to account for overdispersion (residual deviance = 1727.9, residual *df* = 234). The reduced model was used as no interaction was found between effects ($\chi^2 = 32.82$, *df* = 3, $p = 0.5467$).

Because poor conditions prevented sampling in Owhiro Bay in January/February 2008, algal assemblage data collected in March 2008 were used instead for this site in statistical analyses.

The occupancy (number of quadrats out of ten) of the different algal species or taxonomic units at each sampling site in January/February 2008, May/June 2008, August 2008, and January 2009 is shown in Appendix 2.2.

Nutrients

Ammonium is generally the preferred nitrogen source for seaweeds as it is energetically cheaper to assimilate (Vergara *et al.* 1995; Barr 2007), and nitrate uptake rates may be reduced when both ammonium and nitrate are available (Thomas and Harrison 1987). However, this preferential uptake may not occur in locations with limiting nitrogen concentrations in the water (Thomas and Harrison 1985, 1987; Corzo and Niell 1992). Nitrite typically only makes up a very low proportion of the total available nitrogen in seawater. Hence Total Inorganic Nitrogen concentrations were used in the analyses rather than ammonia, nitrate, and nitrite concentrations separately. To test whether nutrient regimes differed between the harbour sites and south coast sites, nested ANOVAs (site nested within coast) were conducted for TIN and phosphate concentrations. TIN concentrations were ln transformed to increase normality.

Multiple regression was used to test if variation in species richness, Shannon diversity and Pielou's evenness could be explained by TIN and/or P concentrations in the water. Data were pooled for January/February 2008, May/June 2008, August 2008, and January 2009 sampling events. Nutrient concentration data were ln transformed before analysis.

Linking algal community composition and nutrient regimes

Several multivariate statistical procedures were conducted to investigate the relationship between nutrient conditions in the seawater and algal community composition. For these analysis data from January/February 2008, May/June 2008, August 2008, and January 2009 were used.

To reduce the dominance of abundant species, percent cover data of the algal communities were square-root transformed before analysis. Bray-Curtis resemblance matrices were created based on the transformed algal data. Examination of the Draftsman plot suggested that transformation of the nutrient concentration (TIN and PO_4^{3-}) data (to approach normality) was not necessary, and thus Euclidean distance based resemblance matrices were created of untransformed nutrient data for subsequent analysis.

The RELATE procedure tested the relative strength of rank based relations between algal assemblage structure and nutrient conditions in the water. The analysis performs a multivariate regression on two independently derived resemblance matrices and tests the hypothesis that there is no relation between the resemblance matrix of the algal assemblage dataset (biotic data) and the nutrient dataset (environmental data) (Clarke and Ainsworth 1993; Clarke and Warwick 2001).

The BEST (BV-Step) procedure was conducted (using Spearman rank correlations) to test which nutrient (Total Inorganic Nitrogen or Phosphate) best 'explained' the algal community composition. This procedure identifies the 'best' match between the multivariate patterns of an assemblage and that from environmental variables associated with those samples (Clarke and Gorley 2006), by searching for high rank correlations

between the Bray-Curtis similarity matrix of the algal assemblage data and the Euclidian distance matrix of the nutrient data.

Multivariate statistical tests were conducted using PRIMER v6 (Plymouth Marine Laboratory, Plymouth, UK). The R statistical package, version 2.9.2 (R development Core Team 2009) was used for univariate statistics.

RESULTS

Algal spatial and temporal variability

Multivariate two-way nested ANOSIM showed that algal species composition (Table 2.1) and algal functional group composition (Table 2.2) was significantly different between sites within each coast at all times. However, no differences between harbour and south coast assemblages could be detected.

Table 2.1: Two-way nested ANOSIM for differences in algal species composition between sites (averaged between coasts) and between coasts (using sites as samples). Analysis was based on Bray-Curtis similarities on fourth root transformed data and 9999 permutations.

	Jan/Feb 2008		*May/Jun 2008*		*Aug 2008*		*Jan 2009*	
	R	p	R	p	R	p	R	p
Site	0.63	<0.001	0.53	<0.001	0.58	<0.001	0.57	<0.001
Coast	0.07	0.40	-0.33	1	0.19	0.40	0.33	0.30

Table 2.2: Two-way nested ANOSIM for differences in algal functional group composition between sites (averaged between coasts) and between coasts (using sites as samples). Analysis was based on Bray-Curtis similarities on fourth root transformed data and 9999 permutations.

	Jan/Feb 2008		*May/Jun 2008*		*Aug 2008*		*Jan 2009*	
	R	p	R	p	R	p	R	p
Site	0.47	<0.001	0.44	<0.001	0.35	<0.001	0.36	<0.001
Coast	0.	0.70	-0.15	0.70	-0.44	1	-0.04	0.60

Two-way crossed ANOSIM ('site' and 'time' as factors) showed that algal community composition was significantly different at each site (Global R: 0.653, p = 0.001; pairwise tests: all < 0.05) and at each sampling time (Global R: 0.226, p = 0.001; pairwise test: all < 0.05).

Pairwise tests of one-way ANOSIM revealed, however, that especially in the winter months (May/June – August 2008), no significant difference was found between some sampling times (Table 2.3) at the majority of the study sites. At Kau point, the algal assemblage was significantly different between all sampling events (Table 2.3).

Table 2.3: One-way ANOSIM for temporal variability within each study site.

Coast	*Site*	*Global R*	*p*	*Sampling times at which difference was **not** significant (at 0.05 level) (pairwise tests).* *p values are shown between brackets*
Harbour	Kau Point	0.269	0.001	--
Harbour	Point Halswell	0.343	0.001	Jun 08 and Aug 08 (0.248); Jun 08 and Jan 09 (0.073)
Harbour	Worser Bay	0.102	0.070	Dec 07 and Feb 08 (0.732); Feb 08 and May 08 (0.592); Feb 08 and Aug 08 (0.084); Feb 08 and Jan 09 (0.096); May 08 and Aug 08 (0.775)
South coast	Island Bay	0.534	0.001	May 08 and Aug 08 (0.522)
South coast	Moa Point	0.245	0.001	May 08 and Aug 08 (0.239)
South coast	Owhiro Bay	0.196	0.001	Dec 07 and Jan 09 (0.219); Mar 08 and Jun 08 (0.231); Mar 08 and Aug 08 (0.101); Jun 08 and Aug 08 (0.851)

The results of the two-way SIMPER procedure are shown in Appendix 2.4, which displays the percentage contribution of each algal species to measures of dissimilarity in species composition between sites (Appendix 2.4 A) and between different sampling times (Appendix 2.4 B). Algal species contributing most to the dissimilarity among harbour sites were *Hormosira banksii*, *Carpophyllum maschalocarpum*, and erect coralline algae. Percentage cover of *H. banksii*, *Zonaria turneriana*, and erect coralline algae contributed most to the dissimilarity among south coast sites. Cover of bare substratum and erect coralline algae were the main contributors to dissimilarity among all sampling times.

nMDS ordination plots (Figure 2.2) show the difference in algal assemblage structure among the sites at each sampling time, and indicate no clear dissimilarity between the harbour and the south coast.

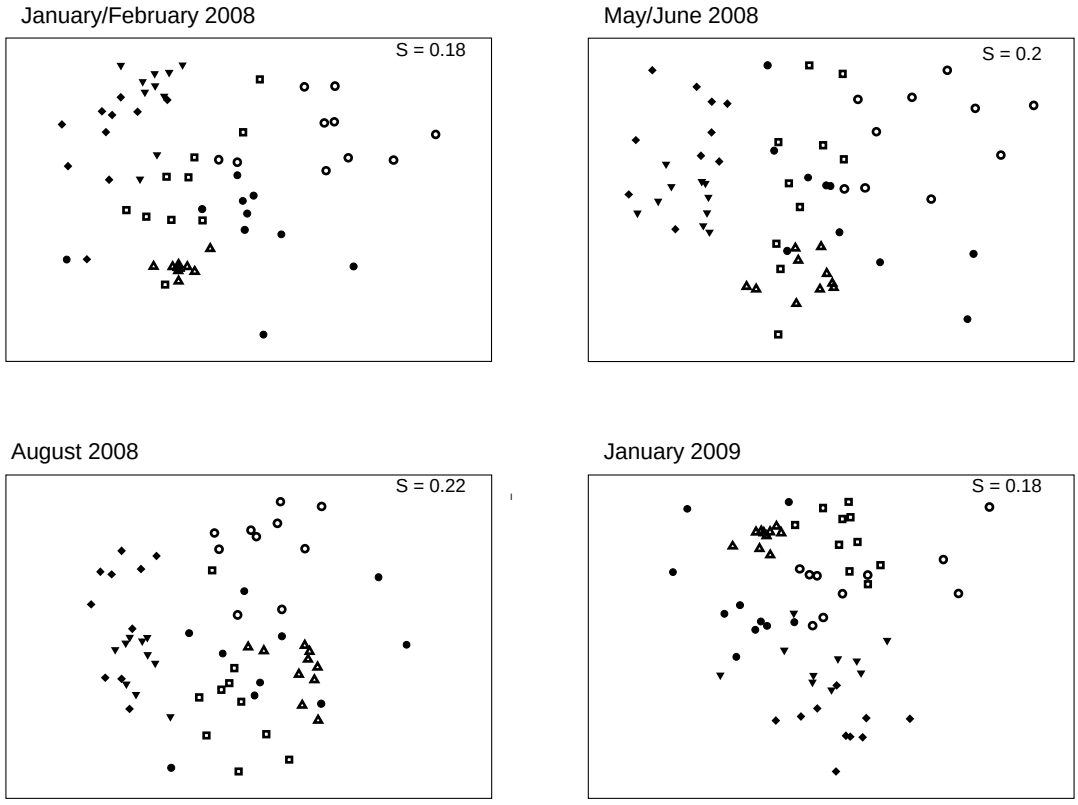


Figure 2.2: nMDS ordinations for algal species abundance data for each sampling time show difference in algal community composition among sites but no clear dissimilarity between harbour and south coast. Data was fourth root transformed. Open symbols represent south coast sites (Δ Island Bay; □ Moa Point; ○ Owhiro Bay); closed symbols represent harbour sites (▾ Kau Point; ♦ Point Halswell; ● Worser Bay). S indicates stress value.

Algal abundance patterns

In the harbour, the leathery macrophyte *Carpophyllum maschalocarpum* comprised the highest mean percent cover (19.1% ± 2.2 SE) of all recorded species at Point Halswell. At Worser Bay, *Hormosira banksii* had the greatest percentage cover (18.4% ± 2.2 SE),

and erect coralline algae were the most common algae at Kau Point (23.0% ± 2.8 SE). On the south coast, erect coralline species had the highest percentage cover in the low-intertidal at Island Bay (56.1% ± 2.8 SE) and Moa Point (37.0% ± 3.7 SE), but at Owhiro Bay the most dominant species was *Zonaria turneria*. This corticated foliose alga occupied on average 31.9% ± 4.4 SE of the quadrats, compared to 13.0% ± 3.0 SE of erect coralline algae.

The functional group 'erect coralline algae' comprised the highest mean percent cover of all groups on the south coast (36.7% ± 2.3 SE). The harbour sites contained the highest cover of bare substratum (27.2% ± 1.6 SE) and corticated macrophytes (25.8% ± 1.5 SE). However, not all sites within the two coasts showed similar patterns in algal functional group abundance throughout the year (Figure 2.3A to 2.3I).

The filamentous algae were the functional group with the lowest percentage cover at all sites. Mean percentage cover of this group was very variable throughout the year (Figure 2.3A). *Ceramium* spp. was the most common alga in this group. Abundance of foliose algae was also fairly changeable during the study period, but the south coast sites Island Bay and Moa Point contained a higher mean percentage cover of this functional group (Figure 2.3B). Differences in cover were mainly caused by the abundance of the opportunistic green alga *Ulva* spp., which dominated the foliose algae at all sites (average across harbour sites: 0.1% ± 0.0 SE; average across south coast sites 5.0% ± 1.0 SE). The high percent cover of corticated foliose algae at Owhiro Bay (south coast) (Figure 2.3C) was caused by the brown alga *Z. turneriana,* which was highly abundant at this site. At all harbour sites, *Dictyota kunthii* was the most abundant corticated foliose algae (average across sites: 2.7% ± 0.6 SE). At south coast sites *Z. turneriana* dominated this group (average across sites: 10.1% ± 1.8 SE). The total cover of the corticated macrophytes was comprised of a large number of species (Appendix 2.1). Different algal species dominated in the corticated macrophyte group at each site. In the harbour, the most common corticated macrophyte was *Champia novae-zelandiae* at Kau Point (9.2% ± 1.9 SE), *Chondria macrocarpa* at Point Halswell (8.6% ± 1.4 SE), and *Codium convolutum* at Worser Bay (11.1% ± 3.0 SE). On the south coast *Colpomenia sinuosa* (3.3% ± 0.6

SE) and *Leathesia* spp. (3.4% ± 0.7 SE) were the dominant corticated macrophytes in Island Bay, *C. convolutum* was most common in Moa Point (7.9% ± 2.2 SE), and *C. novae-zelandiae* in Owhiro Bay (13.1% ± 2.9 SE). Island Bay contained the lowest mean percentage cover of corticated macrophytes of all sites throughout the year (Figure 2.3D). *H. banksii* was responsible for the high percentage cover of leathery macrophytes (23.8% ± 2.1 SE) at Island Bay (Figure 2.3E). *Cystophora torulosa* was most abundant in Moa Point (8.0% ± 1.7 SE) and Owhiro Bay (9.3% ± 2.0 SE). *Carpophyllum maschalocarpum* was the most abundant leathery macrophyte at the harbour sites Kau Point (15.2% ± 2.5 SE) and Point Halswell (19.1% ± 2.2 SE), but *H. banksii* was more common at Worser Bay (18.4% ± 2.2 SE). At harbour sites, cover of leathery macrophytes steadily increased from the start of sampling (summer 07/08) until August (winter) 2008, after which cover decreased. This pattern was not observed on the south coast (Figure 2.3E). Crustose coralline algae (CCA) were the most common crustose algae at all sites on both coasts. There was a significant effect of coast on *Undaria pinnatifida* abundance (GLM, $p = 0.003$) with the invasive kelp being more abundant in the harbour. Abundance was higher at the last sampling event in January 2009 (GLM, $p = 0.040$), when percent cover peaked at 17.3% ± 7.5 SE at Point Halswell (Figure 2.3F). Erect coralline algae were more common on south coast sites, especially at Island Bay and Moa Point (Figure 2.3G). High percentage cover of crustose algae in Worser Bay (harbour) (Figure 2.3H) was caused by CCA (7.3% ± 1.5 SE). At Owhiro Bay (south coast) CCA cover peaked in March 2008 (Figure 2.3H) when a mean cover of 25.0% ± 5.6 SE was recorded. Lastly, Figure 2.3I shows that more bare substratum was found at harbour sites compared to south coast sites.

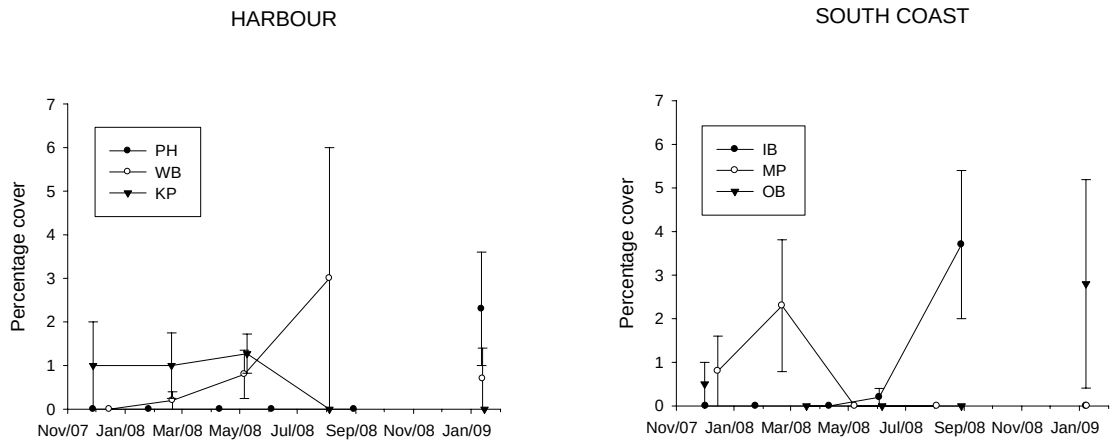


*Figure 2.3A: Average percentage cover of **filamentous algae** at each of the study sites in the harbour and on the south coast from summer 2007/2008 until summer 2008/2009 (mean ± SE, n = 10)*

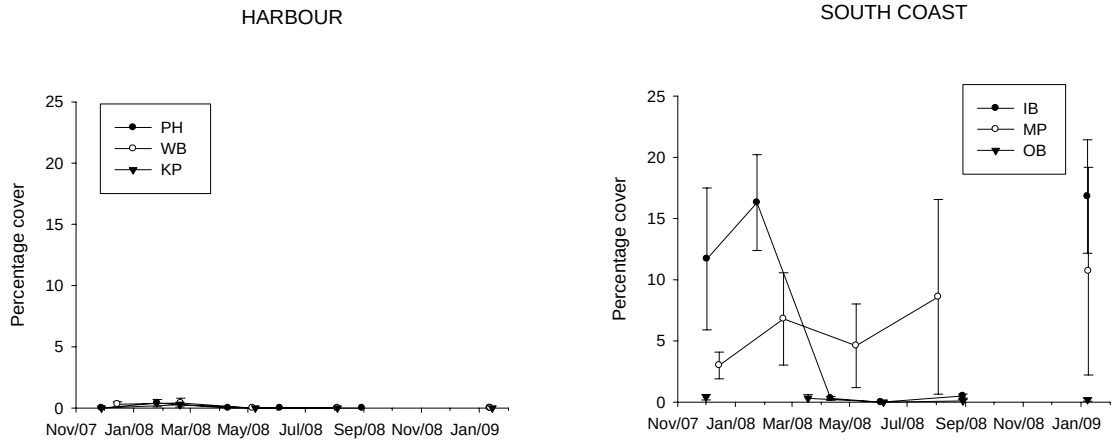


*Figure 2.3B: Average percentage cover of **foliose algae** at each of the study sites in the harbour and on the south coast from summer 2007/2008 until summer 2008/2009 (mean ± SE, n = 10)*

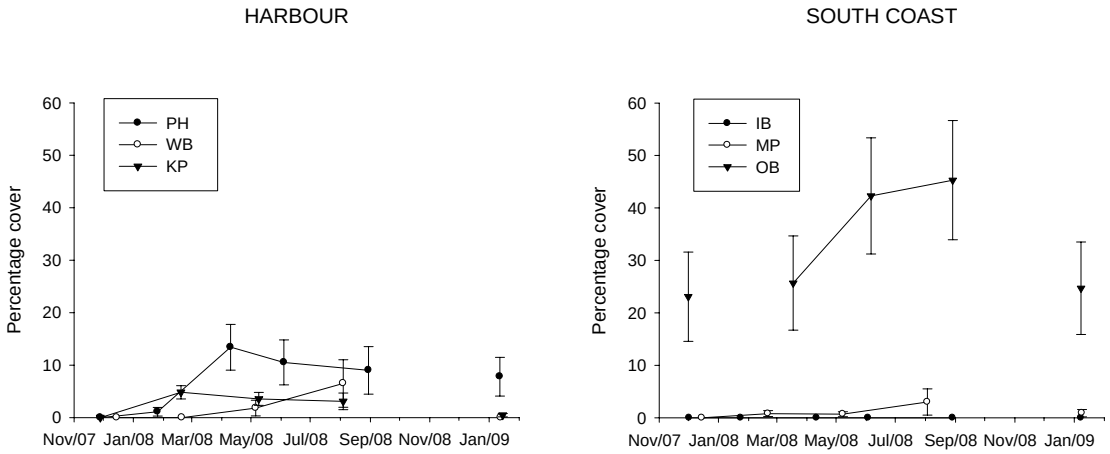


Figure 2.3C: Average percentage cover of ***corticated foliose algae*** *at each of the study sites in the harbour and on the south coast from summer 2007/2008 until summer 2008/2009 (mean ± SE, n = 10)*

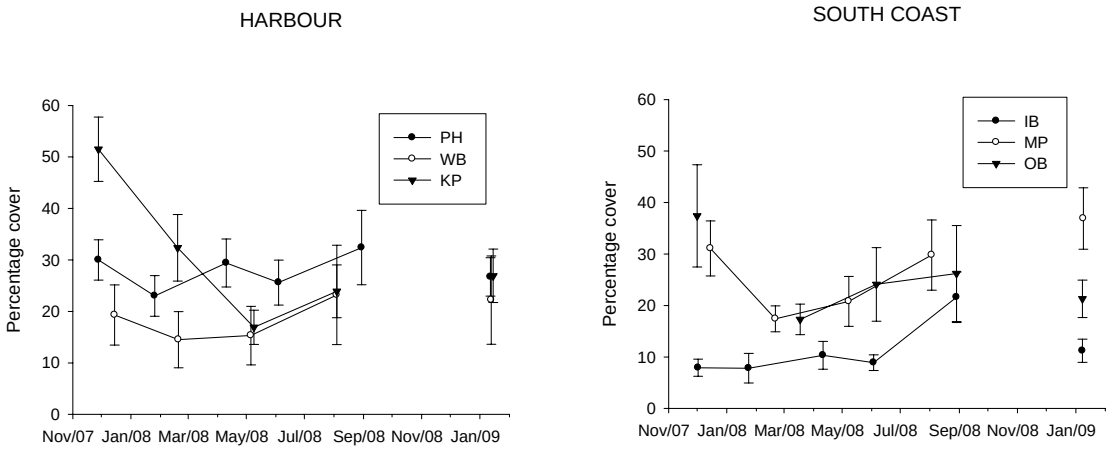


Figure 2.3D: Average percentage cover of ***corticated macrophytes*** *at each of the study sites in the harbour and on the south coast from summer 2007/2008 until summer 2008/2009 (mean ± SE, n = 10)*

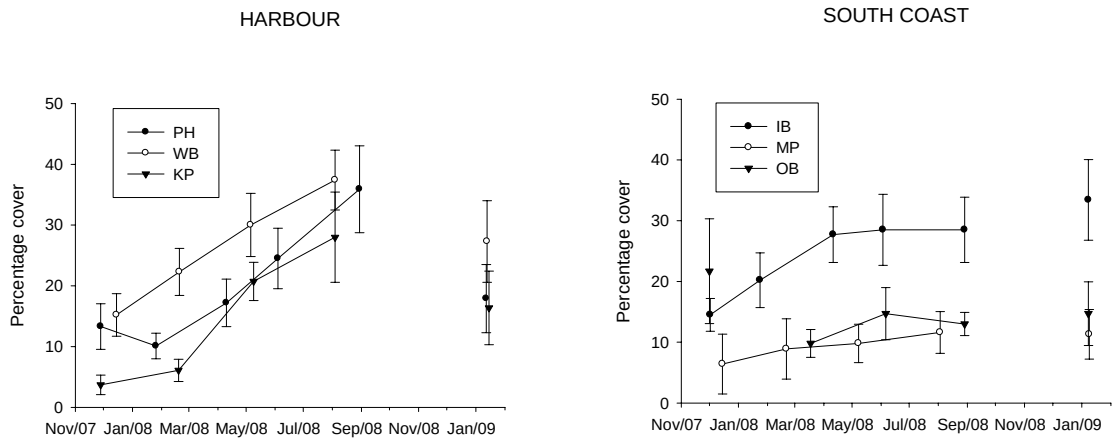


Figure 2.3E: Average percentage cover of ***leathery macrophytes*** *at each of the study sites in the harbour and on the south coast from summer 2007/2008 until summer 2008/2009 (mean ± SE, n = 10)*

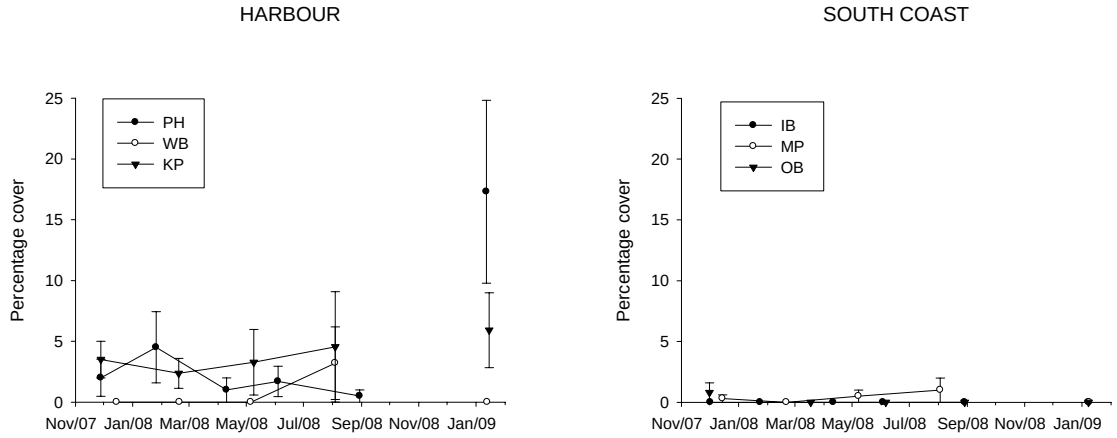


Figure 2.3F: Average percentage cover of **Undaria pinnatifida** *at each of the study sites in the harbour and on the south coast from summer 2007/2008 until summer 2008/2009 (mean ± SE, n = 10)*

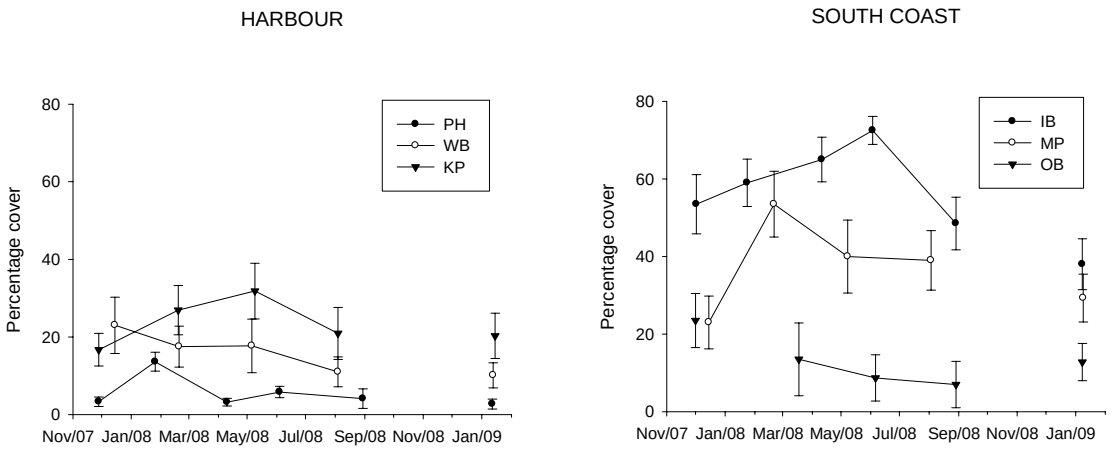


Figure 2.3G: Average percentage cover of ***erect coralline algae*** *at each of the study sites in the harbour and on the south coast from summer 2007/2008 until summer 2008/2009 (mean ± SE, n = 10)*

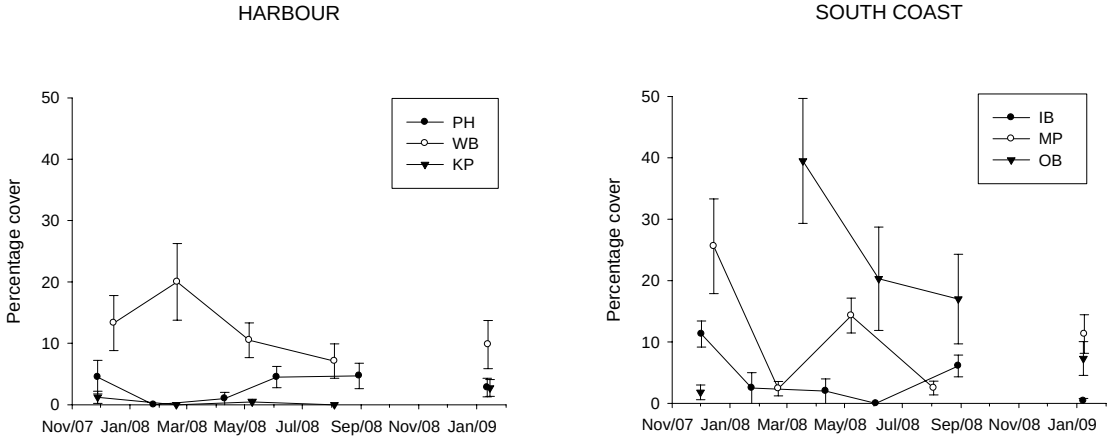


Figure 2.3H: Average percentage cover of ***crustose algae*** *at each of the study sites in the harbour and on the south coast from summer 2007/2008 until summer 2008/2009 (mean ± SE, n = 10)*

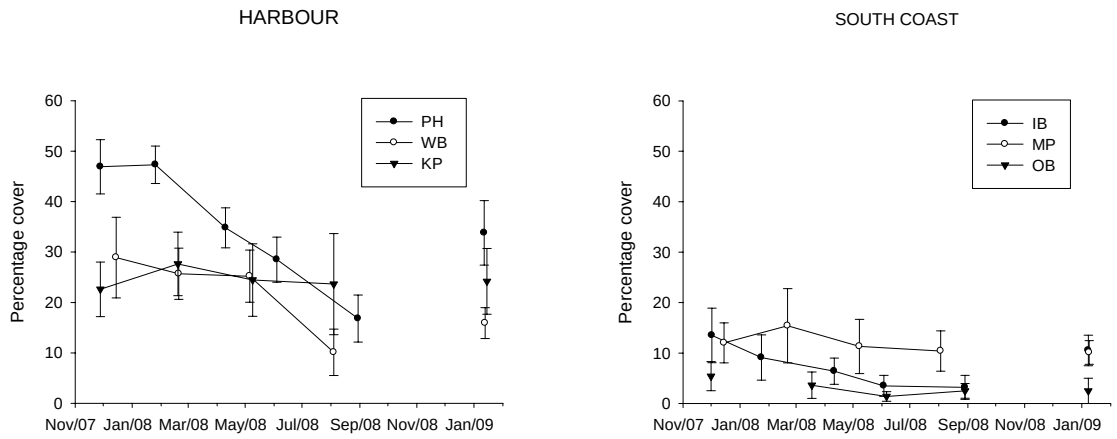


Figure 2.3I: Average percentage cover of ***bare substratum*** *at each of the study sites in the harbour and on the south coast from summer 2007/2008 until summer 2008/2009 (mean ± SE, n = 10)*

NB: PH - Point Halswell; IB - Island Bay;
WB - Worser Bay; MP - Moa Point;
KP - Kau Point; OB - Owhiro Bay

Algal diversity

Univariate two-way nested ANOVA (using 'sites nested within coast' and 'time of year' as factors) conducted on survey data of summer (Jan/Feb) 2008, autumn (May/Jun) 2008, winter (Aug) 2008, and summer (Jan) 2009, showed that species richness S was significantly different among sites nested within coasts ($p = 0.013$) (Table 2.4A, Figure 2.4 A,B). Shannon species diversity index H' was significantly higher in the harbour than on the south coast ($p = 0.08$) during the study period (Table 2.4B; Figure 2.4C,D). Pielou's evenness J' was also significantly higher in the harbour ($p < 0.01$) (Table 2.4C, Figure 2.4E,F). Species richness S, Shannon species diversity index H', and Pielou's evenness J' were very variable at all the sites throughout the year in which this survey was conducted. No site showed a consistent higher or lower S, H' or J' than other sites throughout the year (Figure 2.4). It appeared that Island Bay had a lower species richness compared to the other south coast sites (Moa Point and Owhiro Bay) in the summer months but this pattern reversed in winter (August 2008) when the highest richness and

diversity were recorded at this site (Figure 2.4B). In the harbour, Worser Bay had a lower species richness (Figure 2.4A) and diversity (Figure 2.4C) than Kau Point in January/February 2008, and Point Halswell had a higher S and H' than Worser Bay in January 2009 (Figure 2.4A,B).

Table 2.4: Two-way nested ANOVAs for diversity indices ('sites nested within coast' and 'time of year' as factors). Data of summer (Jan/Feb) 2008, autumn (May/Jun) 2008, winter (Aug) 2008, and summer (Jan) 2009 were used for the analysis.

A Species richness

	df	*Sum Sq*	*Mean Sq*	*F value*	*p*
Coast	1	2.02	2.02	0.695	0.405
Time of year	3	2.88	0.96	0.331	0.803
Coast:Site	4	37.63	9.41	3.243	**0.013**
Residuals	231	670.12	2.90		

B Shannon diversity

	df	*Sum Sq*	*Mean Sq*	*F value*	*p*
Coast	1	0.867	0.867	7.258	**0.008**
Time of year	3	0.184	0.062	0.515	0.673
Coast:Site	4	1.056	0.264	2.209	0.069
Residuals	231	27.594	0.120		

C Pielou's evenness

	df	*Sum Sq*	*Mean Sq*	*F value*	*p*
Coast	1	0.395	0.395	22.057	**<0.01**
Time of year	3	0.061	0.020	1.140	0.333
Coast:Site	4	0.023	0.006	0.326	0.860
Residuals	231	4.137	0.018		

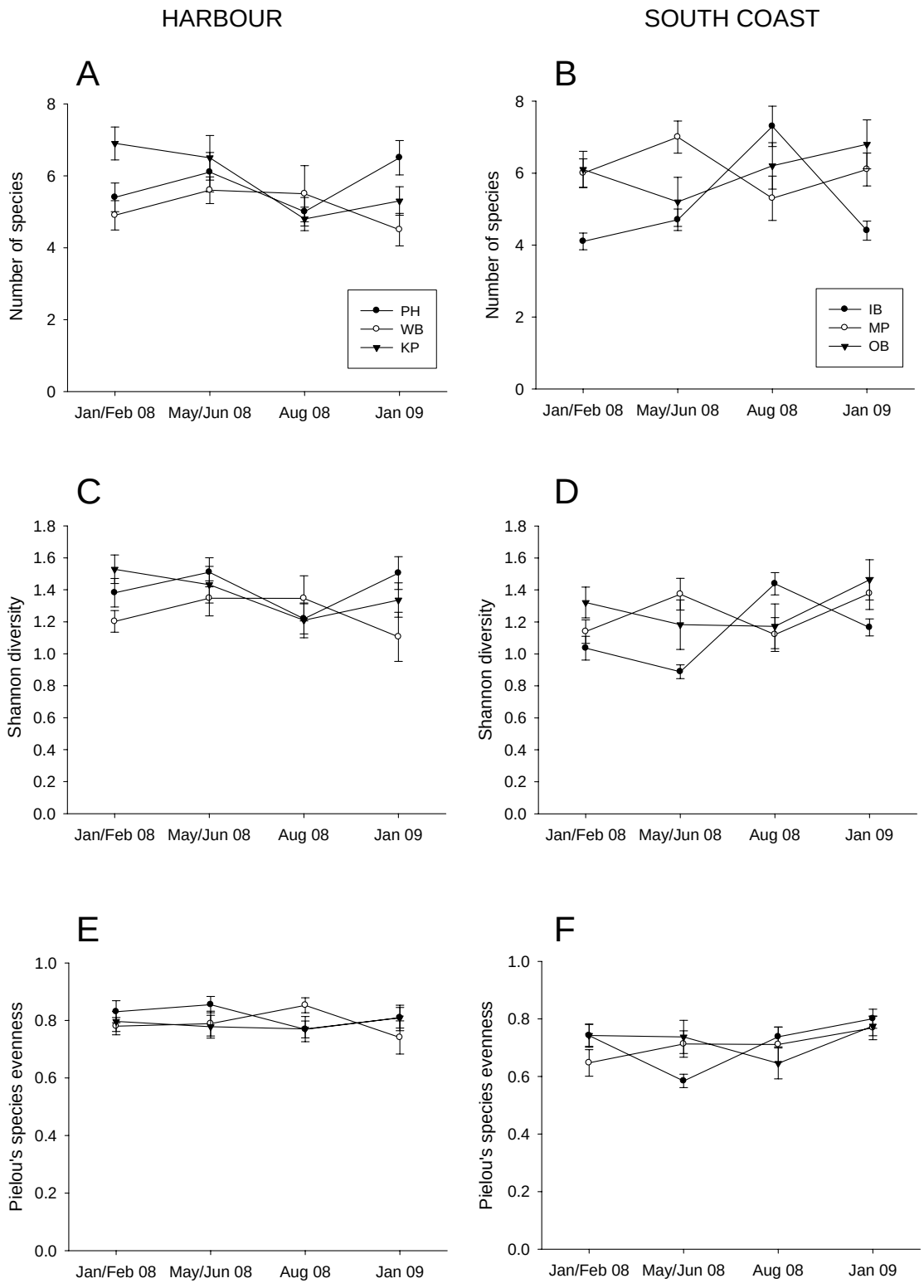


Figure 2.4: Species richness (A, B), Shannon diversity (C, D), and Pielou's species evenness (E, F) at the three study sites in the harbour and the three study sites on the south coast from January/February 2008 to January 2009 (mean ± SE, n = 10).

At both coasts, TIN concentrations showed an increase over the study period (Figure 2.5A), due to the large contribution of ammonia, which showed a similar trend (Appendix 2.5, panel C). Phosphate concentrations were very low and remained relatively constant at all sites and both coasts over the year in which this study was conducted (Figure 2.5B). (Nitrate, nitrite, and ammonia concentrations over the study period are shown in Appendix 2.5.)

Even though nutrient concentrations varied throughout the year at all sites (Figure 2.5), nested ANOVAs for TIN and phosphate concentrations showed that there was no significant difference in nutrient concentrations between coasts and among sites nested within coasts (Table 2.5).

Table 2.5: Nested ANOVA (Site nested within Coast) for TIN and P concentrations for sites in the Wellington Harbour and sites on the south coast from December 2007 until January 2009. TIN concentrations were ln transformed.

	Df	*Sum Sq*	*Mean Sq*	*F value*	*Pr(>F)*
TIN					
Coast	1	0.096	0.096	0.488	0.490
Coast : Site	5	0.796	0.159	0.807	0.553
Residuals	35	6.909	0.197		
P					
Coast	1	0.002	0.002	0.943	0.338
Coast : Site	5	0.007	0.001	0.603	0.698
Residuals	35	0.080	0.002		

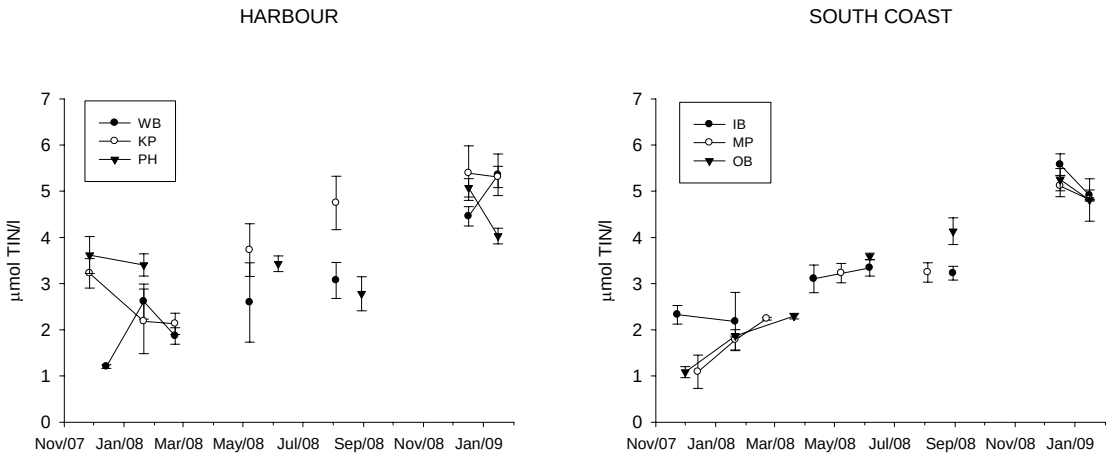


Figure 2.5A: Total Inorganic Nitrogen (TIN) concentrations at Wellington Harbour sites and at the Wellington south coast from December 2007 until January 2009. Harbour sites: Worser Bay (WB), Kau Point (KP), Point Halswell (PH). South coast sites: Island Bay (IB), Moa Point (MP), Owhiro Bay (OB)

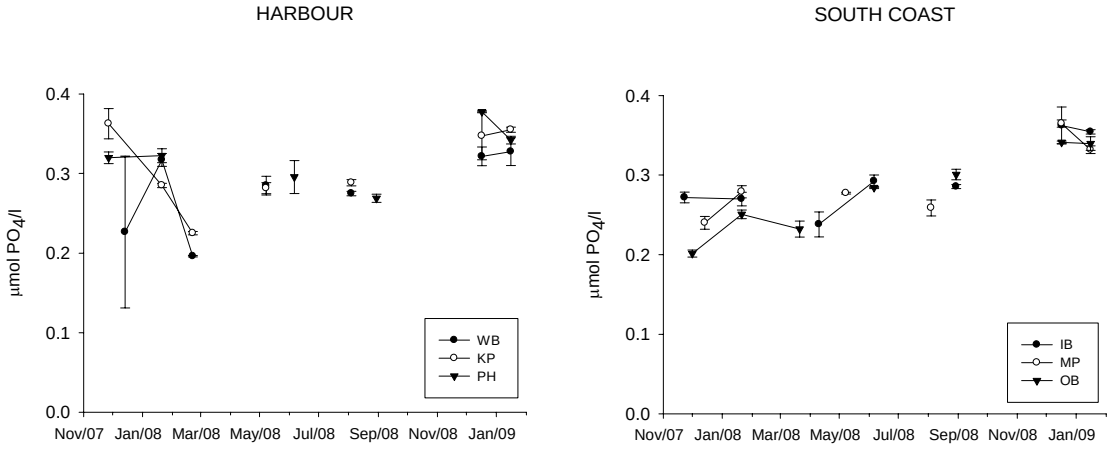


Figure 2.5B: Phosphate concentrations at Wellington Harbour sites and at the Wellington south coast from December 2007 until January 2009.

Linking algal assemblage composition and nutrient dynamics

The results of the RELATE analysis suggest that there was a relation between nutrient concentration in the water and algal assemblage structure, but this relation was very weak (Sample statistic $\rho = 0.043$, significance level of $\rho = 0.011$). The sample statistic ρ (rho) of the RELATE procedure is almost equal to zero or negative when there is no relation between the environmental and biological datasets.

Results of the BEST procedure indicated that, between phosphate and total inorganic nitrogen, TIN 'best' explained the variation in the algal assemblage structure. However, the correlation was very weak (corr. = 0.043).

Results of multiple regression analysis showed no significant correlation of neither TIN nor P concentrations with algal species richness, Pielou's evenness or Shannon diversity ($p > 0.22$ for all), indicating that the variation in these diversity indices could not be explained by the TIN and phosphate concentrations in the water.

DISCUSSION

Algal communities

Spatial variability

Results of this study showed high spatial variability of low-intertidal algal communities among sites throughout the study period, but no consistent differences between Wellington Harbour and the south coast. Phillips and Hutchison (2008) also found similar results for mid-intertidal algal assemblages in response to grazer exclusion (dominated by *Ulva* spp., *Scytothamnus australis*, non-calcareous crust and microalgae) which also had high variability between sites within coasts.

However, algal abundance and percentage cover were highly variable among sites and not all three sites within each coast showed the same patterns. In the harbour, algal assemblages at Point Halswell were dominated by *C. maschalocarpum*, at Worser Bay *H. banksii* was most abundant and erect coralline algae had the highest cover at Kau Point. On the south coast erect coralline algae were dominant at Island Bay and Moa Point, but *Z. turneriana* was most abundant at Owhiro Bay. This variance in algal community composition among sites within each coast was so great that it overwhelmed any differences between the two coasts. However, there were some distinct differences between the two coasts. For example, erect coralline algae and foliose algae were on average more abundant on the south coast, whereas there tended to be a greater percentage of bare substratum, cover of corticated macrophytes and the invasive *Undaria pinnatifida* in the harbour throughout most of the year.

Despite a lack of significant difference in algal assemblage structure between the harbour and south coast, diversity and evenness indices were higher in the harbour. Species richness (number of species) was not significantly different between the two coasts but was different among sites, with Island Bay having a lower richness than the other two south coast sites (except in August 2008), and Kau Point having the highest richness of the harbour sites (except in August 2008). These results do not support the hypothesis of south coast algal communities being more diverse compared to the harbour. However, they do support the findings of other studies (e.g. in NSW, Australia [Kennelly and Underwood 1992; Underwood and Chapman 1998b]) in that assemblage composition shows great natural variability among sites within shores. In addition, the results of this study are consistent with results from previous research on spatial patterns in algal communities e.g., in intertidal and subtidal habitats in NSW, Australia (Coleman 2002), and on rocky shores of the Mediterranean Sea (Benedetti-Cecchi *et al.* 2003; Fraschetti *et al.* 2005), and suggest that the greatest proportion of variation in species distribution, abundance and composition could be explained by processes occurring on relatively smaller scale, while little additional variation is explained by large-scale processes (Coleman 2002). These patterns were temporally consistent, which is coherent with other studies (e.g. Coleman 2002).

Temporal variability

In this study, temporal variability throughout the year was high at all sites, but no significant difference in algal species composition was found between May/June 2008 and August 2008 at all sites (except Kau Point where each sampling time was significantly different from the others). This implies that algal assemblage structure may not change as much during the winter months, suggesting a more static community state, with lower biotic dynamics, likely caused by reduced algal growth and competition in this time of year.

Abundance of opportunistic and ephemeral algae showed a more stochastic pattern throughout the study period than long-lived larger algae, like the leathery macrophytes, which exhibited a more gradual course. Underwood and Chapman (1998b) showed similar results for their study on sheltered shores in New South Wales, in which they found foliose algae to vary significantly from month to month among shores while the leathery macrophyte *H. banksii* did not change significantly in cover through time. Further, they found that components of assemblages that contributed most to spatial dissimilarity were not the same at every sampling event. This contrasts with the results of this study, where bare substratum and erect coralline algae where the main contributors to dissimilarity between all sampling events.

Undaria pinnatifida

Percentage cover of the invasive kelp *U. pinnatifida* was higher in the harbour (except Worser Bay) than on the south coast. Especially at the last sampling event in January 2009, *U. pinnatifida* was highly abundant at Point Halswell where a mean percent cover of 17.3% ± 7.5 (S.E.) was observed. This result supported the hypothesis that this invader would be more abundant in the harbour, possibly because the kelp was first observed here (Hay and Luckens 1987) and had a head-start in establishing and expanding its populations here compared with south coast sites. In addition, the patterns found in *U. pinnatifida* abundance show that around the Wellington region this invader is not a strict winter annual but also abundantly present (at harbour sites) in the warmer months.

Nutrient dynamics

Spatial variability

Wellington harbour has a higher human population, more industry, and a river flowing into it, which all could potentially act in concert to increase nutrient levels in this body of water compared to the open coast. In contrast to suggestions by other studies, however, there was no significant difference in TIN and phosphate concentrations between the harbour and the south coast and among sites nested within coasts. Previous research suggested a gradual increase in nutrient levels from the Cook Strait entrance in the west to the Wellington Harbour entrance (Bowman *et al.* 1983; Gardner 2000; Helson *et al.* 2007). In this study, Owhiro Bay was located closest to the Cook Strait entrance, although still ~15 km distance away. However, no gradient in nutrient concentrations was found from Owhiro Bay (closest to the Cook Strait entrance) to Moa Point (closest to the harbour entrance), or to the harbour sites.

Temporal variability

Over the study period, Total Inorganic Nitrogen concentrations increased, due to the large contribution of ammonia to TIN. In December2008/January 2009 TIN concentrations were up to 5 times higher than in December2007/January 2008, both in the harbour and on the south coast.

Little work has been done on nutrient regimes in the Wellington Region. Barr (2007) also found higher nitrate concentrations in winter compared to summer at (semi-)exposed 'urban' sites around New Zealand, however, the difference between summer and winter in his study (0.3 μM in summer vs. 0.6 μM in winter) was not as great as in this study. Nonetheless, in his work sites were only sampled once during summer and winter season and thus were snapshots of nutrient levels at the different sites. On the Oregon coast (USA), Fujita *et al.* (1989) and Menge *et al.* (1997) found maximum nitrate levels in late summer and autumn. This area experiences strong upwelling resulting in pulses of very high nitrate concentrations (up to 28 μM; Fujita *et al.* 1989) during the upwelling season (May – September). In the winter season nitrate levels were still variable but much lower

(~ 0.5 – 10 μM). However, this is still considerably higher than concentrations found in the Wellington Region. In addition, Menge *et al.* (1997) found that nutrient concentrations along the Oregon coast differed between sites at mesoscale (100s of m) and large scale (~80 km separated) levels.

Phosphate concentrations remained low and fairly constant throughout the year, unlike nitrogen concentration patterns. Concentrations found in this study are comparable to those found for (semi-)exposed urban sites around New Zealand by Barr (2007). Yet, unlike the study by Menge *et al.* (1997), no seasonal pattern (peak in late summer and autumn) in phosphate levels could be detected. Phosphate concentrations measured on the Oregon coast were up 6 times higher than in this study (Fujita *et al.* 1989; Menge *et al.* 1997), due to the strong upwelling regime in that region.

Precipitation can be an important direct source of nitrogen to coastal waters (Correll and Ford 1982). Indirectly rainfall can prompt increased land run-off resulting in additional nitrogen supplement due to fertilizer use in the coastal watershed (Correll and Ford 1982; Valiela *et al.* 1997a). However, even though, total monthly rainfall peaked in winter (maximum in July 2008) in Wellington (CliFlo database, NIWA), climate data showed that September to November 2008 were relatively dry with total rainfall below the average of the study period (Appendix 2.3), and thus it is doubtful that increases in TIN levels were caused by excessive rainfall only. Also, the seasonal nitrate, nitrite, and ammonia patterns did not correspond to the monthly rainfall data for the study period (Appendix 2.3; Appendix 2.5), indicating that different factors are contributing to the nutrient dynamics in this region.

The nutrient concentration patterns observed in this study are likely to be a combination of biological productivity, upwelling and rainfall. Because the nitrate and nitrite seasonality appeared to have a smooth transition, it seems likely that primary productivity was the main driver for the observed patterns as upwelling and rainfall tend to have a more stochastic effect on nutrient concentrations.

Linking algal assemblage structure and nutrient regimes

The patterns in TIN levels in this region may reflect primary productivity in the coastal fringe. During the winter season, primary production decreases resulting in reduced uptake of nitrogen, and hence nitrogen levels in the water increase as this nutrient is not taken up as much by primary producers as during the summer months. Abundance data of the algal functional groups show that filamentous and foliose algae, which often are fast-growing opportunistic ephemeral algae, have a higher cover in the summer months, contributing to increased primary production in the warmer months. The high nutrient uptake ability of these algae may be linked to the reduced nitrate and nitrite concentrations in the seawater in the summer months when these algae are most abundant. Nonetheless, only a very low (although significant) correlation was found between TIN concentration and the variation in algal assemblage structure. A weak correlation between nutrients and between-site ecological differences was also found by Menge *et al.* (1997). However, the weak correlation suggests that other factors are more likely to be important in determining the algal community composition at these sites and coasts. In addition, no significant correlation was found between phosphate levels in the water and algal assemblage structure. No relationship was found between nutrient concentrations in the water and species richness, diversity, and evenness. In addition, because nutrient regimes were not significantly different between the two coasts and because the *U. pinnatifida* abundance at the different sites does not correspond to measured nutrient concentrations in the water, it is unlikely that there is a correlation between nutrient availability and *U. pinnatifida* abundance in this region.

In summary, I found high spatial and temporal variability in algal community structure on shores in the Wellington Harbour and on the south coast in this year-long survey. Algal assemblage structure was significantly different among study sites within the two coasts indicating that there was large variability on smaller scale, but no difference on larger scale (between the two coasts) was detected. Yet, higher average cover of *Undaria pinnatifida* was recorded at harbour sites, indicating that the invasive kelp is more abundant in the Wellington Harbour, which could be due to the fact that its introduction

was first observed in this bay about 24 years ago. I found no significant difference in nitrogen and phosphate regimes between the harbour and south coast. Consequently, the hypothesis that opportunistic, fast-growing algae (mainly filamentous and foliose algae) would be more abundant in the harbour due to expected higher nutrient concentrations was not supported. Only a very low correlation was found between variation in algal community composition and TIN concentration in the seawater and no significant correlation was found between phosphate concentration and algal assemblage structure. In addition, no relationship was found between seawater nutrient patterns and algal diversity. This suggests that other factors (e.g. recruitment, grazing by herbivores, competition, physical stresses [Coleman 2002]) are more important than nutrient regimes in determining the algal community structure in the low-intertidal zone in these sites.

Appendix 2.1: *Algal species or taxonomic units and the functional group to which they were classified (modified from Steneck and Dethier 1994, Guerry* et al. *2009, and M. Dethier, pers. comm.)*

Species	Functional group	Division
Bryopsis plumosa	Filamentous	Chlorophyta
Ceramium spp.	Filamentous	Rhodophyta
Unid. brown filamentous alga	Filamentous	Phaeophyta
Unid. red epiphyte	Filamentous	Rhodophyta
Unid. red filamentous alga	Filamentous	Rhodophyta
Ulva spp.	Foliose	Chlorophyta
Cladhymenia oblongifolia	Corticated foliose	Rhodophyta
Dictyota kunthii	Corticated foliose	Phaeophyta
Gigartina atropurpurea	Corticated foliose	Rhodophyta
Hymenena spp.	Corticated foliose	Rhodophyta
Zonaria turneriana	Corticated foliose	Phaeophyta
Caulacanthus ustulatus	Corticated macrophytes	Rhodophyta
Caulerpa geminata	Corticated macrophytes	Chlorophyta
Champia novae-zelandiae	Corticated macrophytes	Rhodophyta
Champia laingii	Corticated macrophytes	Rhodophyta
Chondria macrocarpa	Corticated macrophytes	Rhodophyta
Codium convolutum	Corticated macrophytes	Chlorophyta
Colpomenia bullosa	Corticated macrophytes	Phaeophyta
Colpomenia sinuosa	Corticated macrophytes	Phaeophyta
Gelidium caulacantheum	Corticated macrophytes	Rhodophyta
Halopteris spp.	Corticated macrophytes	Phaeophyta
Heterosiphonia spp.	Corticated macrophytes	Rhodophyta
Laurencia thyrsifera	Corticated macrophytes	Rhodophyta
Leathesia spp.	Corticated macrophytes	Phaeophyta
Lomentaria umbellata	Corticated macrophytes	Rhodophyta
Lophurella caespitosea	Corticated macrophytes	Rhodophyta
Lophurella persiclados	Corticated macrophytes	Rhodophyta
Scytothamnus australis	Corticated macrophytes	Phaeophyta
Splachinidium rugosum	Corticated macrophytes	Phaeophyta
*Strebloclad*ia *glomerulata*	Corticated macrophytes	Rhodophyta
Unid. brown turfing alga	Corticated macrophytes	Phaeophyta
Unid. red corticated alga	Corticated macrophytes	Rhodophyta
Carpophyllum maschalocarpum	Leathery macrophytes	Phaeophyta
Cystophora torulosa	Leathery macrophytes	Phaeophyta
Hormosira banksii	Leathery macrophytes	Phaeophyta
Macrocystis pyrifera	Leathery macrophytes	Phaeophyta
Xiphophora gladiata	Leathery macrophytes	Phaeophyta
Undaria pinnatifida	*Undaria pinnatifida*	Phaeophyta
Coralline algae	Erect coralline algae	Rhodophyta
Crustose Coralline Algae	Crustose algae	Rhodophyta
Ralfsia verrucosa	Crustose algae	Phaeophyta
Unid. brown crustose alga	Crustose algae	Phaeophyta

Appendix 2.2: *Occupancy (number of quadrats out of 10) of algal species or taxonomic units at each sampling site in January/February 2008 (A), May/June 2008 (B), August 2008 (C), and January 2009 (D).*

A January/February 2008

Species	***Harbour***			***South coast***		
	KP	**PH**	**WB**	**IB**	**MP**	**OB**
Ceramium spp.	1	-	1	-	-	-
Unid. red epiphyte	-	-	-	-	1	-
Ulva spp.	2	2	1	10	8	1
Dictyota kunthii	6	-	-	-	-	-
Gigartina atropurpurea	6	1	-	-	1	-
Hymenena spp.	-	1	-	-	-	-
Zonaria turneriana	-	-	-	-	1	8
Caulacanthus ustulatus	-	-	-	-	-	1
Caulerpa geminata	-	-	-	-	-	1
Champia novae-zelandiae	8	5	-	-	2	7
Chondria macrocarpa	7	3	-	-	-	-
Codium convolutum	2	2	3	-	2	1
Colpomenia sinuosa	10	6	4	-	8	8
Gelidium caulacantheum	-	7	1	1	-	-
Halopteris spp.	-	-	-	-	-	1
Laurencia thyrsifera	1	-	1	-	1	2
Leathesia spp.	2	4	4	8	5	-
Lophurella caespitosea	4	-	-	-	1	-
Scytothamnus australis	-	-	-	1	2	-
Splachinidium rugosum	-	-	-	-	4	-
Unid. brown turfing alga	-	-	-	-	2	-
Unid. red corticated alga	1	-	-	-	-	-
Carpophyllum maschalocarpum	7	9	3	-	1	1
Cystophora torulosa	-	-	5	1	6	9
Hormosira banksii	-	-	9	9	1	5
Undaria pinnatifida	2	4	-	-	-	-
Coralline algae	-	10	8	10	10	2
Crustose Coralline Algae	10	-	5	-	-	8
Unid. brown crustose alga	-	-	4	1	4	6

B May/June 2008

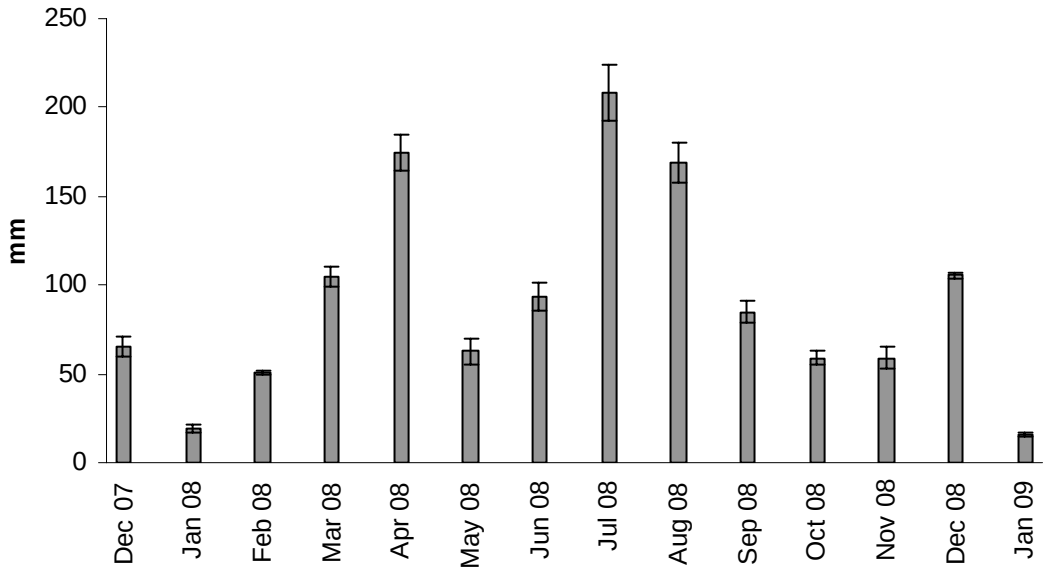
Species	*Harbour*			*South coast*		
	KP	**PH**	**WB**	**IB**	**MP**	**OB**
Ceramium spp.	5	-	2	-	-	-
Unid. red filam. alga	-	-	-	1	-	-
Ulva spp.	-	-	-	-	6	-
Cladhymenia oblongifolia	-	2	-	-	-	-
Dictyota kunthii	6	5	2	-	1	-
Zonaria turneriana	-	-	-	-	1	10
Caulerpa geminata	-	-	-	-	-	1
Champia novae-zelandiae	5	3	4	1	3	6
Chondria macrocarpa	9	9	1	2	1	-
Codium convolutum	2	4	3	-	4	1
Colpomenia bullosa	-	-	1	-	-	-
Colpomenia sinuosa	8	5	4	10	8	4
Gelidium caulacantheum	-	2	1	-	1	-
Halopteris spp.	-	-	-	1	2	3
Heterosiphonia spp.	2	2	-	-	-	-
Laurencia thyrsifera	-	1	1	-	1	-
Leathesia spp.	-	-	-	-	2	-
Lomentaria umbellata	-	-	-	3	-	-
Lophurella caespitosea	4	-	-	-	1	-
Scytothamnus australis	-	-	-	-	1	-
Splachinidium rugosum	-	-	-	-	1	-
Unid. red corticated alga	-	-	-	1	-	-
Carpophyllum maschalocarpum	10	10	5	2	5	3
Cystophora torulosa	-	1	7	7	9	8
Hormosira banksii	-	-	8	9	1	5
Macrocystis pyrifera	-	2	-	-	-	-
Undaria pinnatifida	3	2	-	-	1	-
Coralline algae	10	8	8	10	10	3
Crustose Coralline Algae	-	5	6	-	7	6
Unid. brown crustose alga	1	-	3	-	4	2

C August 2008

Species	*Harbour*			*South coast*		
	KP	**PH**	**WB**	**IB**	**MP**	**OB**
Ceramium spp.	-	-	1	3	-	-
Unid. red filam. alga	-	-	-	2	-	-
Ulva spp.	-	-	-	5	3	1
Cladhymenia oblongifolia	2	1	-	-	-	-
Dictyota kunthii	2	1	3	-	1	2
Gigartina atropurpurea	-	2	1	-	-	-
Zonaria turneriana	-	-	-	-	1	10
Caulerpa geminata	-	-	-	-	-	1
Champia novae-zelandiae	7	5	3	2	4	6
Champia laingii	-	-	-	-	-	1
Chondria macrocarpa	8	9	1	1	1	-
Codium convolutum	2	3	3	-	5	2
Colpomenia bullosa	-	3	1	8	-	-
Colpomenia sinuosa	2	1	4	8	4	3
Gelidium caulacantheum	-	4	-	2	-	-
Halopteris spp.	-	-	-	-	2	5
Heterosiphonia spp.	-	-	2	-	-	-
Laurencia thyrsifera	-	-	-	1	-	-
Leathesia spp.	-	-	-	-	1	-
Lomentaria umbellata	-	-	-	2	-	-
Lophurella caespitosea	3	-	-	-	1	-
Lophurella persiclados	-	-	-	-	1	-
Unid. red corticated alga	1	-	1	-	-	-
Carpophyllum maschalocarpum	10	10	6	2	4	5
Cystophora torulosa	-	-	7	7	9	8
Hormosira banksii	-	-	8	10	1	4
Macrocystis pyrifera	-	1	-	-	-	-
Undaria pinnatifida	1	1	2	-	1	-
Coralline algae	10	4	7	10	10	2
Crustose Coralline Algae	-	5	2	8	-	9
Unid. brown crustose alga	-	-	3	-	4	3

D January 2009

Species	*Harbour*			*South coast*		
	KP	**PH**	**WB**	**IB**	**MP**	**OB**
Bryopsis plumosa	-	-	-	-	-	1
Unid. brown filam. alga	-	1	1	-	-	1
Unid. red epiphyte	-	2	-	-	-	1
Ulva spp.	-	-	-	10	4	2
Cladhymenia oblongifolia	-	1	-	-	-	-
Dictyota kunthii	1	4	-	-	-	-
Gigartina atropurpurea	-	4	-	-	1	-
Zonaria turneriana	-	-	-	-	1	8
Caulerpa geminata	-	-	-	-	-	1
Champia novae-zelandiae	7	6	2	-	5	8
Chondria macrocarpa	6	10	-	1	-	-
Codium convolutum	3	2	3	1	5	1
Colpomenia sinuosa	7	9	7	-	-	2
Gelidium caulacantheum	1	5	1	-	-	-
Halopteris spp.	-	-	-	-	3	3
Laurencia thyrsifera	1	-	1	-	-	2
Leathesia spp.	1	-	1	9	10	5
Lophurella caespitosea	-	-	-	-	2	-
Unid. brown turfing alga	-	-	-	-	-	1
Carpophyllum maschalocarpum	8	8	2	-	2	3
Cystophora torulosa	-	-	2	2	8	8
Hormosira banksii	-	-	9	10	1	7
Undaria pinnatifida	4	5	-	-	-	-
Coralline algae	10	4	8	10	10	7
Crustose Coralline Algae	-	4	3	-	2	1
Ralfsia verrucosa	4	-	5	1	-	6
Unid. brown crustose alga	-	-	-	-	7	-



Appendix 2.3: *Total monthly rainfall over the study period (December 2007 – January 2009). Averaged data for stations Wellington Aero and Wellington Rongotai (41°32`S; 174°80`E). Error bars represent SE. Data from CliFlo, National Institute of Water and Atmospheric research, New Zealand.*

Appendix 2.4 A: *Two-way SIMPER results displaying the contribution of each algal species to measures of dissimilarity in species composition between sites. Only species contributing ≥ 5% to the dissimilarity were included.*

Groups IB and KP
Average dissimilarity = 69.40

Species	Group IB Av.Abund	Group KP Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
H. banksii	4.68	0	10.55	2.36	15.2	15.2
C. maschalocarpum	0.18	3.82	8.23	1.59	11.86	27.06
Bare substrate	1.58	3.66	6.72	1.27	9.68	36.74
Erect coralline algae	7.21	4.85	6.24	1.68	8.99	45.73
C. sinuosa	1.13	1.69	4.69	1.43	6.76	52.48
C. novae-zelandiae	0.16	2.08	4.54	1.21	6.54	59.03
Ulva spp.	2.01	0.06	4.35	0.95	6.26	65.29
C. macrocarpa	0.24	1.99	4.17	1.45	6.01	71.3

Groups IB and MP
Average dissimilarity = 58.07

Species	Group IB Av.Abund	Group MP Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
H. banksii	4.68	0.25	10.05	2.21	17.3	17.3
Bare substrate	1.58	2.5	5.38	1.08	9.27	26.57
Erect coralline algae	7.21	5.97	5.06	1.28	8.72	35.29
Ulva spp.	2.01	1.51	4.71	1.03	8.1	43.39
C. torulosa	0.84	2.28	4.03	1.09	6.94	50.33
C. convolutum	0.05	1.66	3.7	0.68	6.37	56.7
Unid. brown crustose	0.16	1.29	3.15	0.91	5.43	62.13
CCA	0.51	0.91	3.15	0.76	5.43	67.56
C. sinuosa	1.13	1.17	3.1	0.9	5.34	72.9
C. novae-zelandiae	0.16	1.35	3.04	0.69	5.23	78.13

Groups KP and MP
Average dissimilarity = 63.37

Species	Group KP Av.Abund	Group MP Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
C. maschalocarpum	3.82	0.6	7.29	1.44	11.5	11.5
Bare substrate	3.66	2.5	6.47	1.31	10.22	21.72
Erect coralline algae	4.85	5.97	5.54	1.46	8.74	30.47
C. torulosa	0	2.28	4.94	1.29	7.79	38.26
C. novae-zelandiae	2.08	1.35	4.68	1.16	7.38	45.63
C. convolutum	1.05	1.66	4.64	0.81	7.32	52.95
C. macrocarpa	1.99	0.1	4.18	1.45	6.59	59.55

Groups IB and PH
Average dissimilarity = 79.13

Species	Group IB Av.Abund	Group PH Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Erect coralline algae	7.21	1.94	11.81	2.5	14.93	14.93
H. banksii	4.68	0	10.43	2.41	13.18	28.1
C. maschalocarpum	0.18	4.09	8.89	1.76	11.24	39.35
Bare substrate	1.58	5.13	8.82	1.59	11.15	50.49
C. macrocarpa	0.24	2.84	5.86	1.34	7.41	57.9
Ulva spp.	2.01	0.07	4.32	0.95	5.46	63.36

Groups KP and PH
Average dissimilarity = 51.51

Species	Group KP Av.Abund	Group PH Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Erect coralline algae	4.85	1.94	6.92	1.38	13.43	13.43
Bare substrate	3.66	5.13	6.24	1.23	12.11	25.54
C. maschalocarpum	3.82	4.09	4.66	1.21	9.04	34.58
C. macrocarpa	1.99	2.84	4.24	1.25	8.23	42.81
C. novae-zelandiae	2.08	0.99	3.93	1.2	7.63	50.44
C. convolutum	1.05	1.14	3.88	0.72	7.53	57.97
U. pinnatifida	0.93	1.2	3.36	0.73	6.52	64.48
D. kunthii	0.84	0.9	2.8	0.83	5.43	69.91
C. sinuosa	1.69	1.1	2.73	1	5.31	75.22

Groups MP and PH
Average dissimilarity = 73.23

Species	Group MP Av.Abund	Group PH Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Erect coralline algae	5.97	1.94	9.15	1.74	12.49	12.49
C. maschalocarpum	0.6	4.09	7.93	1.57	10.83	23.33
Bare substrate	2.5	5.13	7.65	1.46	10.45	33.77
C. macrocarpa	0.1	2.84	5.97	1.39	8.15	41.92
C. torulosa	2.28	0.08	4.84	1.27	6.61	48.53
C. convolutum	1.66	1.14	4.69	0.84	6.41	54.93

Groups IB and WB
Average dissimilarity = 59.70

Species	Group IB Av.Abund	Group WB Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Erect coralline algae	7.21	3.06	9.98	1.64	16.71	16.71
Bare substrate	1.58	3.7	6.83	1.29	11.45	28.16
H. banksii	4.68	3.91	5.45	1.3	9.13	37.3
Ulva spp.	2.01	0.05	4.66	0.94	7.81	45.1
CCA	0.51	1.68	4.48	0.95	7.5	52.6
C. convolutum	0.05	1.74	4.17	0.6	6.99	59.59
C. sinuosa	1.13	0.87	3.59	1.25	6.01	65.6
C. torulosa	0.84	1.69	3.34	0.99	5.59	71.2

Groups KP and WB
Average dissimilarity = 67.01

Species	Group KP Av.Abund	Group WB Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
H. banksii	0	3.91	9.03	1.67	13.47	13.47
C. maschalocarpum	3.82	1.01	7	1.31	10.45	23.92
Erect coralline algae	4.85	3.06	6.04	1.16	9.02	32.94
Bare substrate	3.66	3.7	5.86	1.14	8.75	41.69
C. convolutum	1.05	1.74	5.18	0.74	7.73	49.41
C. novae-zelandiae	2.08	0.61	4.65	1.21	6.95	56.36
C. macrocarpa	1.99	0.2	4.41	1.46	6.57	62.93
C. torulosa	0	1.69	3.66	0.88	5.46	68.39
CCA	0	1.68	3.61	0.76	5.38	73.77
C. sinuosa	1.69	0.87	3.42	1.13	5.11	78.88

Groups MP and WB

Average dissimilarity = 66.15

Species	Group MP Av.Abund	Group WB Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
H. banksii	0.25	3.91	8.63	1.63	13.05	13.05
Erect coralline algae	5.97	3.06	8	1.39	12.1	25.14
Bare substrate	2.5	3.7	6.37	1.3	9.64	34.78
C. convolutum	1.66	1.74	5.78	0.87	8.73	43.51
C. torulosa	2.28	1.69	4.69	1.25	7.09	50.6
CCA	0.91	1.68	4.01	0.82	6.06	56.66
Unid. brown crustose	1.29	0.81	3.76	0.99	5.69	62.35
C. novae-zelandiae	1.35	0.61	3.43	0.77	5.18	67.54
C. sinuosa	1.17	0.87	3.42	1.16	5.17	72.7

Groups PH and WB

Average dissimilarity = 68.37

Species	Group PH Av.Abund	Group WB Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
H. banksii	0	3.91	8.92	1.69	13.05	13.05
C. maschalocarpum	4.09	1.01	7.5	1.4	10.97	24.02
C. macrocarpa	2.84	0.2	6.22	1.34	9.1	33.11
Bare substrate	5.13	3.7	5.75	1.18	8.4	41.52
C. convolutum	1.14	1.74	5.14	0.77	7.52	49.04
Erect coralline algae	1.94	3.06	5.03	1.25	7.36	56.4
CCA	0.99	1.68	4.33	0.99	6.34	62.74
C. torulosa	0.08	1.69	3.61	0.89	5.28	68.03

Groups IB and OB

Average dissimilarity = 78.31

Species	Group IB Av.Abund	Group OB Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Erect coralline algae	7.21	1.75	13.36	1.91	17.06	17.06
Z. turneriana	0	4.97	11.79	1.47	15.05	32.11
H. banksii	4.68	1.12	8.62	1.79	11.01	43.12
C. novae-zelandiae	0.16	2.6	5.78	1.14	7.39	50.5
CCA	0.51	2.72	5.46	0.9	6.97	57.47
C. torulosa	0.84	2.38	4.52	1.18	5.77	63.24
Ulva spp.	2.01	0.12	4.42	0.94	5.65	68.89
Bare substrate	1.58	0.7	4.15	0.93	5.3	74.19

Groups KP and OB

Average dissimilarity = 80.23

Species	Group KP Av.Abund	Group OB Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Z. turneriana	0	4.97	11.47	1.46	14.3	14.3
Erect coralline algae	4.85	1.75	8.97	1.63	11.18	25.48
Bare substrate	3.66	0.7	7.61	1.35	9.49	34.97
C. maschalocarpum	3.82	0.68	7.42	1.4	9.25	44.22
CCA	0	2.72	5.88	1.02	7.33	51.55
C. torulosa	0	2.38	5.32	1.34	6.64	58.18
C. novae-zelandiae	2.08	2.6	5.08	1.13	6.33	64.52
C. macrocarpa	1.99	0	4.43	1.5	5.52	70.03

Groups MP and OB

Average dissimilarity = 73.31

Species	Group MP Av.Abund	Group OB Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Z. turneriana	0.3	4.97	11.01	1.43	15.02	15.02
Erect coralline algae	5.97	1.75	10.94	1.7	14.93	29.94
CCA	0.91	2.72	6.41	1.16	8.75	38.69
Bare substrate	2.5	0.7	5.62	1.14	7.67	46.36
C. novae-zelandiae	1.35	2.6	5.58	1.12	7.62	53.98
C. torulosa	2.28	2.38	4.35	1.25	5.93	59.91
Unid. brown crustose	1.29	1.04	4.11	1	5.61	65.52
C. convolutum	1.66	0.34	3.92	0.73	5.35	70.87

Groups PH and OB

Average dissimilarity = 84.84

Species	Group PH Av.Abund	Group OB Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Z. turneriana	0	4.97	11.35	1.47	13.38	13.38
Bare substrate	5.13	0.7	10.3	1.88	12.14	25.53
C. maschalocarpum	4.09	0.68	8.02	1.54	9.45	34.98
C. macrocarpa	2.84	0	6.35	1.41	7.48	42.46
CCA	0.99	2.72	5.84	1.1	6.88	49.34
Erect coralline algae	1.94	1.75	5.69	1.31	6.71	56.05
C. torulosa	0.08	2.38	5.21	1.35	6.14	62.19
C. novae-zelandiae	0.99	2.6	5	1.1	5.89	68.08

Groups WB and OB

Average dissimilarity = 74.49

Species	Group WB Av.Abund	Group OB Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Z. turneriana	0	4.97	11.81	1.47	15.85	15.85
Bare substrate	3.7	0.7	7.98	1.52	10.71	26.56
H. banksii	3.91	1.12	7.5	1.49	10.07	36.63
Erect coralline algae	3.06	1.75	7.01	1.32	9.41	46.05
CCA	1.68	2.72	5.86	1.11	7.86	53.91
C. novae-zelandiae	0.61	2.6	5.66	1.16	7.59	61.5
C. torulosa	1.69	2.38	4.85	1.19	6.51	68.01
C. convolutum	1.74	0.34	4.43	0.64	5.95	73.95

Appendix 2.3 B: *Two-way SIMPER results displaying the contribution of each algal species to measures of dissimilarity in species composition between sampling times. Only species contributing ≥ 5% to the dissimilarity were included.*

Groups Jan/Feb 08 and May/Jun 08
Average dissimilarity = 50.18

Species	Group Jan/Feb 08 Av.Abund	Group May/Jun 08 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Bare substrate	3.52	2.79	4.95	1	9.86	9.86
Erect coralline algae	4.73	4.49	4.82	1	9.61	19.46
CCA	1.12	1.53	3.67	0.79	7.32	26.78
C. sinuosa	1.66	1.18	3.56	1.32	7.09	33.87
C. novae-zelandiae	0.93	1.27	2.97	0.84	5.92	39.79
C. convolutum	0.8	0.94	2.96	0.63	5.91	45.7
C. maschalocarpum	1	2.08	2.93	0.9	5.83	51.53
C. torulosa	0.85	1.46	2.81	0.83	5.61	57.14
Ulva spp.	1.11	0.21	2.56	0.64	5.1	62.24
Unid. brown crustose	0.94	0.51	2.51	0.57	5	67.24

Groups Jan/Feb 08 and Aug 08
Average dissimilarity = 56.68

Species	Group Jan/Feb 08 Av.Abund	Group Aug 08 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Bare substrate	3.52	2.02	6.28	1.15	11.09	11.09
Erect coralline algae	4.73	3.68	5.22	1.08	9.21	20.3
C. sinuosa	1.66	0.81	4.37	1.29	7.71	28.01
C. maschalocarpum	1	2.47	3.89	0.88	6.87	34.88
C. novae-zelandiae	0.93	1.75	3.74	0.82	6.6	41.47
C. convolutum	0.8	1.14	3.52	0.61	6.22	47.69
CCA	1.12	1.29	3.31	0.78	5.84	53.53
C. torulosa	0.85	1.5	2.85	0.83	5.02	58.55

Groups May/Jun 08 and Aug 08
Average dissimilarity = 50.08

Species	Group May/Jun 08 Av.Abund	Group Aug 08 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Bare substrate	2.79	2.02	5.37	1.05	10.73	10.73
Erect coralline algae	4.49	3.68	4.93	1.12	9.85	20.58
C. novae-zelandiae	1.27	1.75	4.34	0.9	8.66	29.24
CCA	1.53	1.29	4.27	0.99	8.53	37.77
C. convolutum	0.94	1.14	3.42	0.65	6.83	44.6
C. maschalocarpum	2.08	2.47	3.36	1.05	6.71	51.31
C. torulosa	1.46	1.5	2.74	0.8	5.47	56.78

Groups Jan/Feb 08 and Jan 09

Average dissimilarity = 51.56

Species	Group Jan/Feb 08 Av.Abund	Group Jan 09 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Erect coralline algae	4.73	3.63	5.82	1.31	11.29	11.29
Bare substrate	3.52	3.18	5.02	1.14	9.74	21.04
C. convolutum	0.8	1.12	3.52	0.61	6.83	27.86
C. sinuosa	1.66	0.95	3.44	1.06	6.67	34.54
CCA	1.12	0.6	3.27	0.64	6.34	40.88
Leathesia spp.	0.78	1.42	3.12	0.85	6.05	46.93
H. banksii	1.56	1.89	2.59	0.68	5.03	51.96

Groups May/Jun 08 and Jan 09

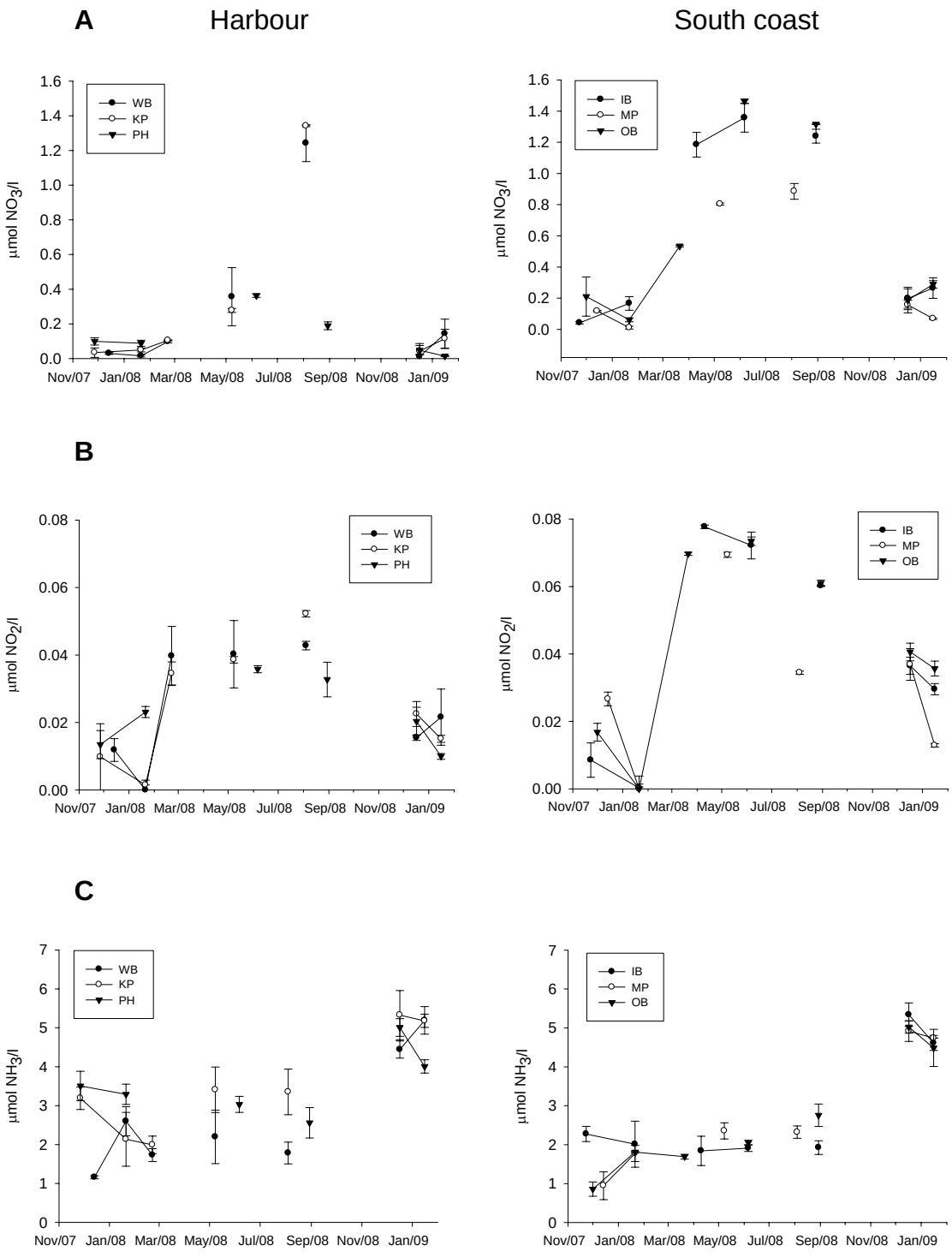
Average dissimilarity = 52.76

Species	Group May/Jun 08 Av.Abund	Group Jan 09 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Erect coralline algae	4.49	3.63	5.44	1.23	10.3	10.3
Bare substrate	2.79	3.18	4.92	1.13	9.33	19.64
C. convolutum	0.94	1.12	3.5	0.65	6.63	26.27
CCA	1.53	0.6	3.42	0.74	6.48	32.75
C. novae-zelandiae	1.27	1.24	3.3	0.94	6.26	39.01
C. sinuosa	1.18	0.95	3.17	1.4	6	45.01
C. maschalocarpum	2.08	1.38	3.15	0.97	5.97	50.97
Leathesia spp.	0.07	1.42	3.09	0.73	5.86	56.83
C. torulosa	1.46	1.03	2.99	0.8	5.66	62.49

Groups Aug 08 and Jan 09

Average dissimilarity = 56.35

Species	Group Aug 08 Av.Abund	Group Jan 09 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Bare substrate	2.02	3.18	5.68	1.2	10.07	10.07
Erect coralline algae	3.68	3.63	4.75	1.14	8.42	18.49
C. convolutum	1.14	1.12	3.94	0.63	6.99	25.48
C. novae-zelandiae	1.75	1.24	3.88	0.89	6.88	32.36
C. maschalocarpum	2.47	1.38	3.87	0.9	6.87	39.23
CCA	1.29	0.6	3.51	0.8	6.23	45.46
C. sinuosa	0.81	0.95	3.31	1.19	5.87	51.33
Leathesia spp.	0.06	1.42	3.08	0.74	5.46	56.79
C. torulosa	1.5	1.03	2.98	0.8	5.3	62.09



Appendix 2.5: *Nitrate (A), nitrite (B), and ammonia (C) concentrations at Wellington Harbour sites and at Wellington south coast sites from December 2007 until January 2009 (mean ± SE, n = 10). Harbour sites: Worser Bay (WB), Kau Point (KP), Point Halswell (PH). South coast sites: Island Bay (IB), Moa Point (MP), Owhiro Bay (OB)*

CHAPTER 3

THE EFFECT OF HIGH NUTRIENT LEVELS ON LOW INTERTIDAL ALGAL ASSEMBLAGES - USING SEWAGE EFFLUENT AS A PROXY FOR NUTIENT ENRICHED SEAWATER CONDITIONS

ABSTRACT

One of the repercussions of rising human populations in coastal regions is increased nutrient levels in coastal waters, which can promote algal growth and productivity and result in a reduction in macroalgal diversity. One source of long-term nutrient addition to coastal waters is via nearshore sewage outfalls. In this study two sewage outfall sites in the Wellington region, Titahi Bay and Pencarrow, were used to investigate the response of rocky intertidal algal assemblages to chronic exposure to high nutrient levels. At both locations, low-intertidal algal communities were surveyed and water samples were taken every two to three months over 18 months at sites along a gradient away from the outfall. It was hypothesised that nutrient limitation would be reduced close to the point sources resulting in low algal diversity and high abundance of fast-growing, opportunistic algal species as these species would outcompete slower-growing algae. A gradual increase of algal diversity and a change in algal community composition was expected with distance from the outfall with more structurally complex species dominating sites further away from the point source. Results showed that Titahi Bay had higher nutrient concentrations closest to the outfall but both locations showed steep gradients in nutrient levels in nearshore waters with distance from the outfall. Relationships were found between algal community composition and nutrient levels at both sewage discharge locations, but the relationship was stronger at Titahi Bay and best explained by phosphate concentrations. Algal species richness and Shannon diversity (H') were negatively related with phosphate levels at this location. At Pencarrow, a very wave-exposed location, total inorganic

nitrogen and phosphate together contributed to algal assemblage structure, but no relationship was found between nutrient levels and algal diversity. Results of this study indicate that care needs to be taken when drawing general conclusions about the effects of sewage effluent on marine communities as these can vary between different sewage outfall locations, even within the same region. The effects are likely mediated by several interacting factors (e.g. degree of nutrient-enrichment, wave-exposure, and sedimentation) and may be location-specific and not unequivocal.

INTRODUCTION

Rising human populations along coasts leads to increased pressure on coastal ecosystems from anthropogenic activities (Vitousek *et al.* 1997). One consequence is altered nutrient regimes in aquatic environments (Nielsen 2003), particularly the addition of fixed nitrogen and biologically available phosphorous. Even small increases in nutrient supply in coastal waters can promote algal growth rates and hence the productivity of coastal ecosystems (Bokn *et al.* 2002). With increasing nutrient concentrations in seawater, macroalgal diversity is likely to decrease as opportunistic functional groups, often fast-growing and structurally simple, take advantage of the reduced nutrient limitation (Bokn *et al.* 2002). When competition for nutrients is reduced, these fast-growing opportunistic species have an advantage over slower-growing species and can eventually outcompete them as competition for light increases (Borum and Sand-Jensen 1996; Valiela *et al.* 1997b; Bokn *et al.* 2002), and larger canopy-forming algae may be replaced by smaller opportunistic species (Duarte 1995; Pedersen and Borum 1996).

By shifting community composition, nutrient enrichment in coastal waters may also increase the invasibility of a community. When availability of key resources is not limiting, e.g. when nutrients are available in excess, competition with native species for these resources is low. Invasive species are likely to be more successful in these conditions (Fluctuating Resource Availability Theory, Davis *et al.* 2000) and may

possibly outcompete native species. Hence, changing nutrient regimes may affect how these invaders behave in new habitats.

Previous research on nutrient enrichment suggests that ephemeral algae are able to take up nitrogen rapidly and thus can respond quickly to increased nutrient concentrations by enhanced growth and performance (Worm and Sommer 2000; Guerry *et al.* 2009). However, they have limited nutrient storage capacity, while perennial species have larger nutrient storage capacities but are less responsive to sudden nutrient increases (Fujita 1985). Kraufvelin *et al.* (2006) reported only minor effects of nutrient enrichment on algal communities in a mesocosm experiment in the first 3 years, but large changes in the following years, suggesting that time of exposure to enriched conditions may be an important factor in determining algal community structure.

One source of chronic nutrient enrichment to coastal waters is through sewage outfalls. Sewage outfalls are point sources of nutrients that are pulsed, but over a long period of time. Considerable research on marine communities close to sewage outfalls has been conducted in Australia, focussing on e.g. algal diversity and composition (Borowitzka 1972; Archambault *et al.* 2001), spatial variability of algal assemblages (Chapman *et al.* 1995; Bishop *et al.* 2002), and the effects of sewage on algal recruitment processes (Bellgrove *et al.* 1997). In other parts of the world, studies have been conducted on the impact of sewage on the structure of intertidal communities (e.g. Littler and Murray 1975, USA), and subtidal macroalgal communities (e.g. Arévalo *et al.* 2007, Mediterranean). Littler and Murray (1978) focussed on calorific contents of algae exposed to sewage effluent. However, little is known of the effects of sewage effluent on intertidal algal community composition in New Zealand. In this study, I investigated patterns of rocky intertidal algal assemblages at varying distances from two nearshore sewage outfalls within the same region (~30 km apart).

I hypothesised that, due to reduced nutrient limitation close to the sewage point sources, abundance of fast-growing opportunistic algal species would be greater resulting in decreased algal diversity. With distance from the outfalls nutrient levels in the water

would decrease and algal diversity would gradually increase. This would indicate that biodiversity decreases when eutrophication occurs in coastal waters. In addition, I hypothesised that fast-growing opportunistic and ephemeral species would dominate at sites near the outfalls, and that with increasing distance from the outfalls, the algal assemblage composition would change to a more diverse assemblage with more structurally complex species.

MATERIAL AND METHODS

Study sites

To investigate the effect of sewage discharge on adjacent rocky intertidal algal communities, two study sites with (tertiary treated) sewage outfalls discharging near shore were selected in the Wellington Region: Titahi Bay (41º06`S; 174º49`E) (Titahi Bay Waste Water Treatment Plant), located on the West coast, and Pencarrow Head (41º21`S; 174º51`E) (Hutt Valley Waste Water Treatment Plant), in Fitzroy Bay, on the East-side of the Wellington Harbour entrance (Figure 3.1). Both outfalls discharge directly from the shore and have been operational for several decades.

At both locations, six permanent sites were identified along a distance gradient away from the outfall on low-intertidal rocky substrate (0.4 to 0.6 m above the lowest astronomical tides, LAT). Sites (1 to 6) at Titahi Bay were selected south-west of the outfall at 53, 95, 165, 270, 338, 403 m distance from the point source. Selection of the sites at Titahi Bay was based on the availability of sufficient intertidal rocky substratum and on information that the predominant flow direction around the waste water outfall is westward (Dudley and Shima 2010). Sites (1 to 6) at Pencarrow were selected north of the outfall at 51, 61, 74, 95, 176, 247 m distance (resp.). Selection of these sites was based on limited availability of intertidal rock south of the point source. The identified sites consisted of intertidal rock with sufficient surface area to allow random quadrat selection at every sampling event.

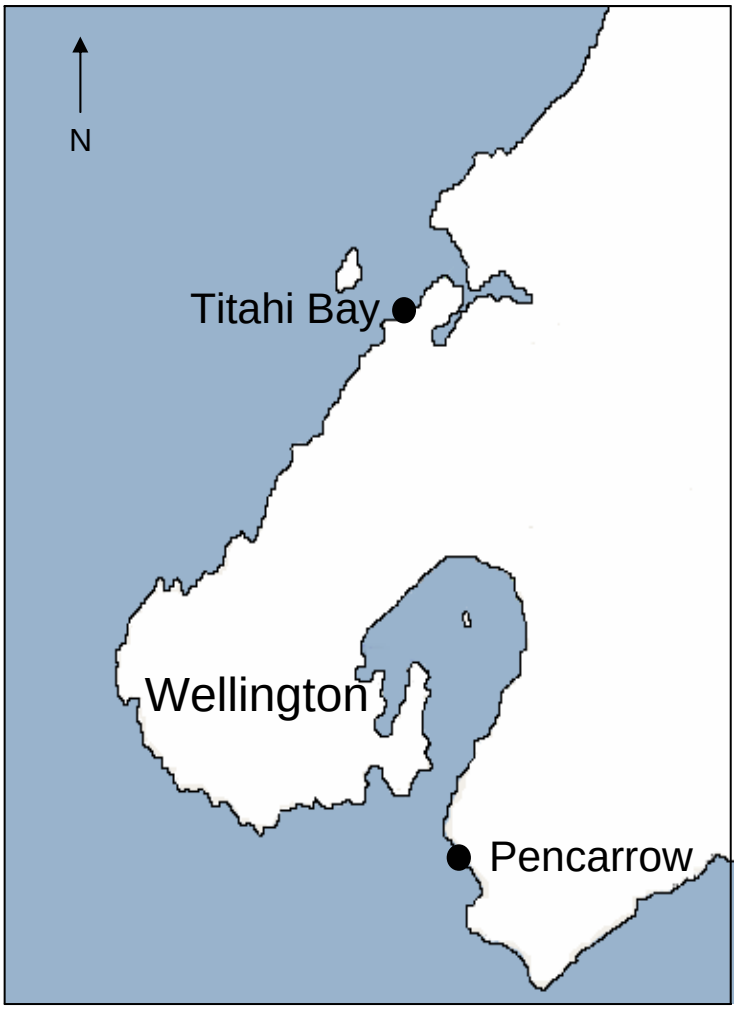


Figure 3.1: Map of the Wellington region with locations of the study sites Titahi Bay and Pencarrow.

The intertidal rocky substratum at both locations consists of sedimentary greywacke (grey sandstone-mudstone sequences and poorly bedded sandstone). The beach at Pencarrow consists of poorly sorted floodplain gravels (Begg and Johnstone 2000), which dynamically interrupts the rocky intertidal shore. Because of the discontinuous nature of the rocky substrata at Pencarrow, I was only able to establish a ~250 m transect away from the outfall. Whereas at Titahi Bay, the rocky shore is continuous and allowed a distance of ~400 m away from the point source.

At every sampling event, three 20 x 20 cm quadrats were randomly placed within each of these six sites event to monitor macroalgal abundance and diversity every 2 – 3 months, when conditions allowed. Pencarrow sites were sampled six times between August 2007 and January 2009 and Titahi Bay sites seven times between September 2007 and January 2009. Algal abundance and percentage cover within the quadrats were recorded during observations in the field when possible, and digital photographs were taken of the individual quadrats to allow analysis of algal communities from images. Recorded algal species in quadrats were later classified into algal functional groups (Appendix 3.1).

The Shannon diversity index (H') was determined for every quadrat using the following equation:

$$H' = -\sum p_i (\ln p_i)$$

where p_i is the relative abundance of each macroalgal species, calculated as the cover of species *i* divided by the total macroalgal cover.

Seawater samples were taken at all of the six sites at every monitoring event plus one extra time at each location. Water samples were collected in sterile polyethylene tubes (50 ml) (in duplicates) and rinsed with sample water before filling with sample. After collection they were directly put on ice and in darkness and transported back to the laboratory where they were stored at -20 ºC, within 1.5 h of collection, for subsequent analysis. Nitrate (NO_3), nitrite (NO_2), ammonia (NH_3) and phosphate (PO_4) concentrations in the seawater samples were measured using a SAN^{PLUS} segmented flow analyser (SKALAR, Breda, The Netherlands).

Data analysis

To investigate the relationship between nutrient conditions in the seawater and the algal community composition, the following multivariate statistical approaches were conducted using PRIMER v6 (Plymouth Marine Laboratory, Plymouth, UK).

The relative strength of rank-based relations between the algal community composition and the nutrient conditions in the surrounding water was tested using the RELATE

analysis, in which a multivariate regression is conducted on two independently derived resemblance matrices (Clarke and Ainsworth 1993, Clarke and Warwick 2001). The procedure tests the hypothesis that no relation exists between the resemblance matrix of the biotic dataset and the environmental dataset. Square root transformation of the percentage cover data achieved the lowest stress in nMDS ordination, and was used to create the Bray-Curtis resemblance matrices for the biological data at both Pencarrow and at Titahi Bay. Examination of Draftsman plots suggested square root transformation for nutrient concentration (TIN and PO_4^{3-}) data to approach normality, and Euclidean distance based resemblance matrices were created from square root transformed nutrient data for subsequent analysis.

To test which nutrient (Total Inorganic Nitrogen [TIN] or Phosphate [PO_4]) best 'explained' the algal community composition, the BEST (BV-Step) procedure was conducted for both study locations separately, using Spearman rank correlations. The procedure identifies the best match between the multivariate patterns of an assemblage and that from environmental variables associated with those samples (Clarke and Gorley 2006). The BEST procedure searches for high rank correlations between (in this case) the Bray-Curtis similarity matrix of square root transformed algal species assemblage (the secondary fixed sample matrix) and the Euclidian distance matrix of square root transformed nutrient concentration data (the primary matrix).

Two-way crossed ANOSIM was used to test if the sites along a gradient away from the outfall differed amongst each other in terms of algal species composition. The analysis was conducted for both locations separately and based on Bray-Curtis similarity matrices. 'Date' and 'Site (distance from outfall)' were used as factors in the ANOSIM procedure. Here, two-way crossed ANOSIM (symmetrically) tests the null hypothesis of 'no site effect' (with site [distance from sewage outfall] being a proxy for nutrient condition), allowing for the fact that there may be differences in algal community composition between sampling events (dates), and also for no 'date effect', allowing for the fact that there may be a 'site effect'. The SIMPER procedure (based on square root transformed species abundance data and the Bray-Curtis similarity matrix) was used to test which

algal species were responsible for differences found in species composition between sites. Non-metric multidimensional scaling (nMDS) was used to describe algal community composition at both locations over the study period.

Multiple regression was used to detect which nutrient, TIN or PO_4, explained the variation in species richness and Shannon diversity best at Titahi Bay and Pencarrow. Nutrient concentration data was ln transformed before analysis to improve homogeneity of variances. To test if algal species richness (number of species), and Shannon diversity changed with distance from the outfall one-way ANOVA was conducted. Normal Q-Q plots were created to examine the distribution of the species richness data. Normality was obtained at both Titahi Bay and Pencarrow and transformation of the data was not required.

Multiple regression and ANOVA were conducted using the R statistical package, version 2.9.2 (R development Core Team 2009).

RESULTS

Concentrations of TIN and phosphate were highest at the site closest to the outfalls and dropped quickly with distance away at both sites (Fig 3.2, 3.3). By 100 m from the outfall concentrations of TIN were two times lower at Titahi Bay and 4 times lower at Pencarrow, whereas phosphate concentrations were 1.5 times lower at Titahi Bay and nearly five times lower at Pencarrow. Peaks in concentrations of both nutrients were up to two times higher at Pencarrow compared to Titahi Bay.

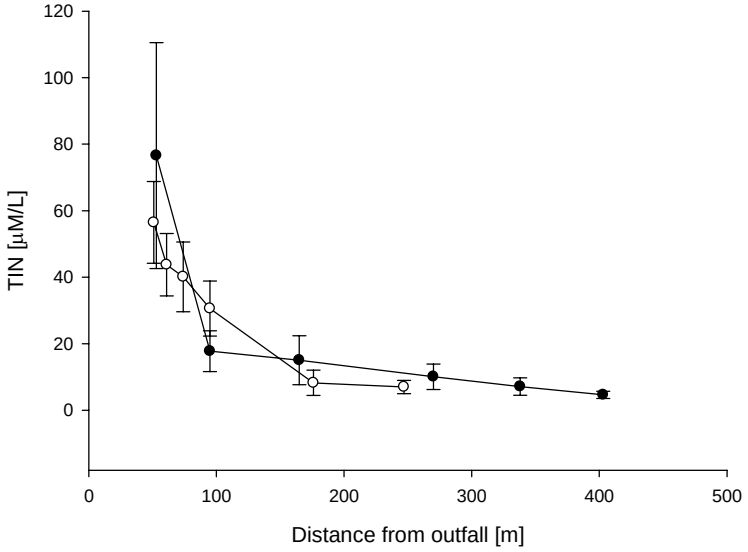


Figure 3.2: Mean total inorganic nitrogen (TIN) concentrations (± S.E.) with distance from the sewage outfall (per site) over the study period. Open symbols: Pencarrow (n = 7 per data point); closed symbols: Titahi Bay (n = 8 per data point)

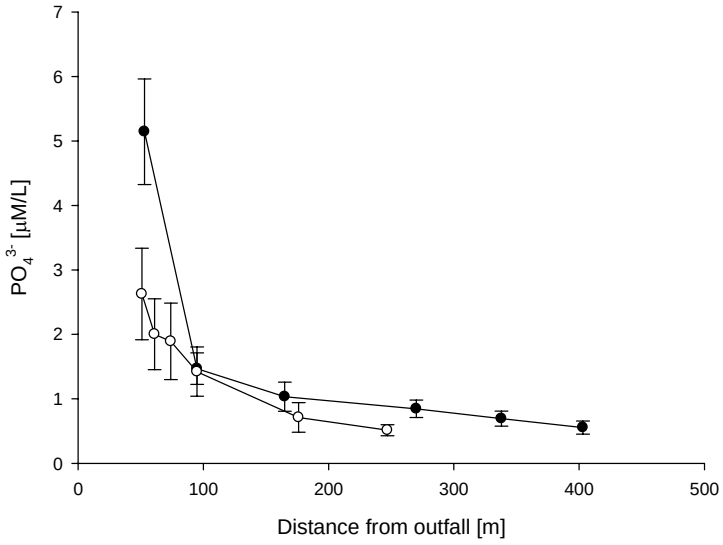


Figure 3.3: Mean phosphate concentrations (± S.E.) with distance from the sewage outfall (per site) over the study period. Open symbols: Pencarrow (n = 7 per data point); closed symbols: Titahi Bay (n = 8 per data point)

Mean concentrations of nitrate (NO_3), nitrite (NO_2), and ammonia (NH_3) separately are shown in Appendix 3.2. Nutrient concentrations measured at sites at each sampling event can be seen in Appendix 3.3 (N) and 3.4 (P).

Algal species composition differed between Titahi Bay and Pencarrow (Figure 3.4A,B). The site closest to the outfall at Titahi bay contained mostly corticated macrophytes and small amounts of foliose algae (Figure 3.4A; Appendix 3.1). The site closest to the outfall at Pencarrow was more diverse (filamentous algae, corticated macrophytes, foliose, and erect coralline algae; Figure 3.4B; Appendix 3.1) than sites further away from out point source, and also more diverse than site 1 at Titahi Bay. By contrast, species richness/diversity generally increased with distance from the outfall at Titahi Bay.

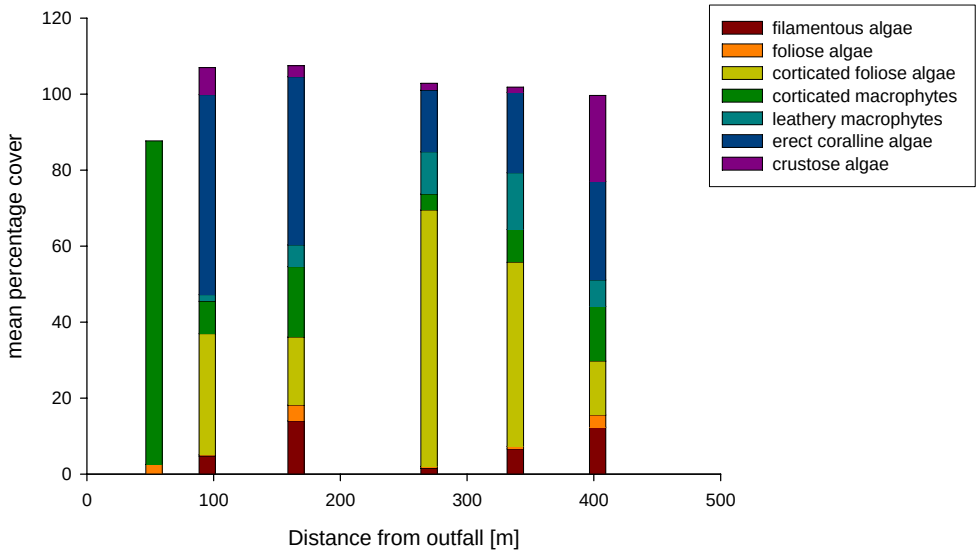


Figure 3.4A: Mean percentage cover of algal functional groups with distance from the outfall at Titahi Bay, from September 2007 until January 2009 (n = 7). Percentage cover can add up to >100% because of layering of algae (understory and overstory).

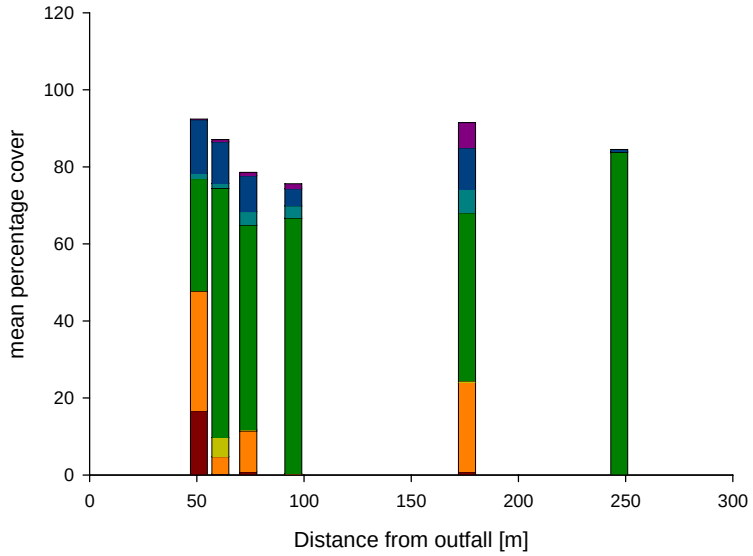


Figure 3.4B: Mean percentage cover of algal functional groups with distance from the outfall at Pencarrow, from August 2007 until January 2009 (n = 6).

When using the RELATE procedure to examine relationships between environmental and ecological datasets, the sample statistic ρ (rho) is almost equal to zero or negative when the null hypothesis (no relation between environmental and ecological datasets) is true. The RELATE results showed a significant relationship between algal community composition and nutrient (TIN and PO_4) concentrations in the water at both study locations, (Titahi Bay: $\rho = 0.309$, $p < 0.0001$; Pencarrow: $\rho = 0.116$, $p < 0.0001$) but a stronger relationship at Titahi Bay.

I used the BEST (BV-Step) procedure to test which nutrient best explained the algal community composition at both locations. Phosphate concentrations explain the algal community composition best at Titahi Bay (corr.: 0.457; Table 3.1). Total inorganic nitrogen and phosphate concentrations together explain the variation in the algal community composition best at Pencarrow, though, the correlation is comparatively weak (corr.: 0.116; Table 3.1).

Table 3.1: BEST (BV-Step) test for identification of which nutrient 'explained' the algal community composition best at Titahi Bay and Pencarrow

Titahi Bay		**Pencarrow**	
Global test		*Global test*	
ρ	0.457	ρ	0.116
Significance level of ρ	0.001	Significance level of ρ	0.002
Best results		*Best results*	
Correlation	0.457	Correlation	0.116
Variable	PO_4	Variables	TIN and PO_4

Two-way crossed ANOSIM (using 9999 permutations) showed that at Titahi Bay no significant difference was detected between site 4 and 5, but all other sites were significantly different from each other (Table 3.2A). Site 1 differed most from the other sites in terms of algal species composition (Figure 3.5). At Pencarrow the difference between site 2 and 4 was insignificant, but all other sites were significantly different from each other (Table 3.2B, Figure 3.6).

Table 3.2: Two-way crossed ANOSIM for differences in algal community structure between sites and between sampling dates for Titahi Bay (A) and Pencarrow (B)

A Titahi Bay

Test for difference between 'sites'		*Pairwise tests between 'sites'*
(Global) R	0.603	No sign. diff. between site 4 and 5 (270 m and 338 m from outfall) ($p = 0.922$). All other sites $p \leq 0.003$
Significance level p	0.001	
Test for difference between 'dates'		*Pairwise tests between 'dates'*
(Global) R	0.307	No sign. diff. at the 0.05 level between: Sep 07 – Oct 07 ($p = 0.739$); Oct 07 – Dec 07 ($p = 0.103$); Feb 08 – Jun 08 ($p = 0.120$); Sep 07 – Dec 07 ($p = 0.089$); Dec 07 – Aug 08 ($p = 0.051$)
Significance level p	0.001	

B Pencarrow

Test for difference between 'sites'		*Pairwise tests between 'sites'*
(Global) R	0.61	No sign. diff. at the 0.05 level between site 2 and 4 (61 m and 95 m from outfall) ($p = 0.085$). All other sites $p \leq 0.016$.
Significance level p	0.001	
Test for difference between 'dates'		*Pairwise tests between 'dates'*
(Global) R	0.445	All sign. diff. ($p \leq 0.038$), except Jan 08 and May 08 ($p = 0.120$)
Significance level p	0.001	

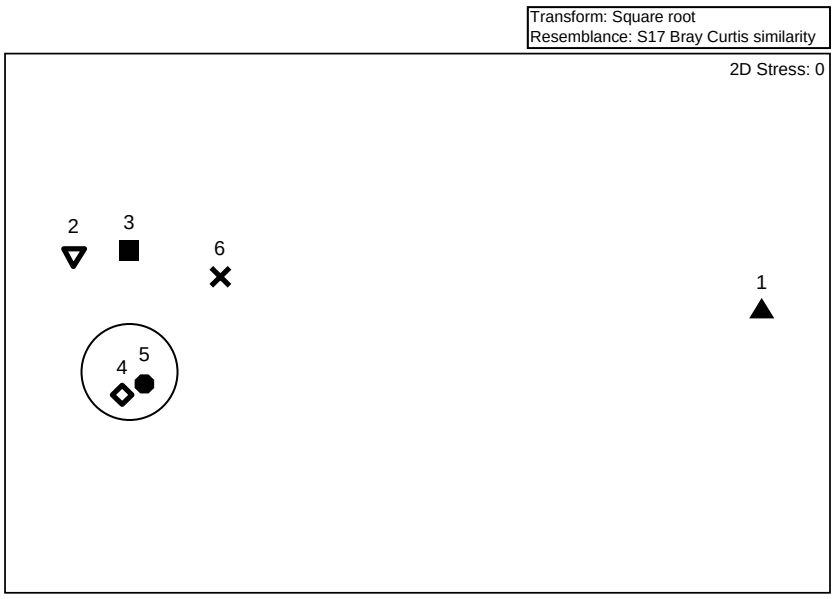


Figure 3.5: nMDS ordination of algal community composition at Titahi Bay over the study period. Algal species data (percentage cover) were averaged per site (1-6) and sampling dates over the study period were pooled. Circle indicates no significant difference between sites at the 0.05 level (p = 0.922).

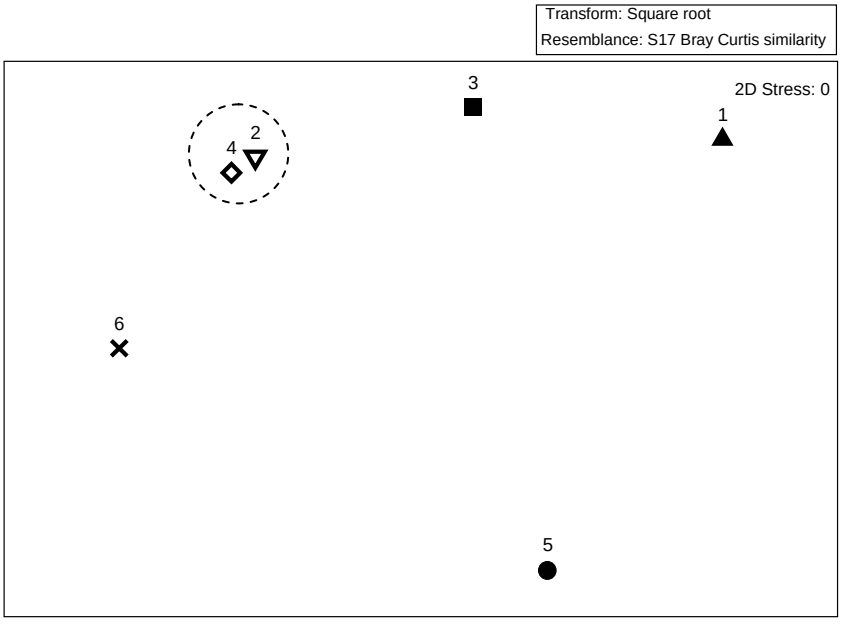


Figure 3.6: nMDS ordination of algal community composition at Pencarrow over the study period. Algal species data (percentage cover) were averaged per site (1-6) and sampling dates over the study period were pooled. Circle indicates no significant difference between sites at the 0.05 level (p = 0.085).

SIMPER results (see Appendix 3.5) show that at Titahi Bay the large dissimilarity between the site closest to the sewage outfall and the other sites (average dissimilarity > 95) was caused by the low diversity at this site, where the assemblage mainly consisted of the red corticated macrophyte *Gigartina* spp. The dissimilarities between the other five sites were predominantly caused by the difference in abundance of *Zonaria turneriana*, (erect) coralline algae, *Dictyota kunthii*, *Carpophyllum maschalocarpum*, and *Leathesia* spp. between sites. Erect coralline was relatively abundant at site 2, 3, 5 and 6 (ranging from 21.2% ± 4.2 [mean ± S.E.] at site 5 to 52.6% ± 5.4 at site 2). *Z. turneriana* was the main species at site 4 and 5 (49.5% ± 7.5 and 42.6 ± 5.7 respectively). In addition, the relatively high abundance of crustose coralline algae at the site furthest away from the outfall (site 6) (19.8% ± 6.5) contributed considerably to the dissimilarity to the other sites.

At Pencarrow, site 2, 4, and 6 had high percent cover of *Gigartina decipiens* (ranging from 52.8% ± 6.9 at site 6 to 64.6% ± 8.4 at site 2). *Gigartina decipiens* was the main contributor to the dissimilarity between all sites except between site 1 and 5, where *Champia novae-zelandiae* was mainly responsible for the difference. The higher abundance of *C. novae-zelandiae* at site 5 and 6 (38.1% ± 7.1 and 30.8 ± 8.0 respectively) added substantially to the dissimilarity with the sites closer to the outfall. The site closest to the outfall (1) contained a relatively high abundance of the green foliose *Ulva* spp. (31.1% ± 8.7), and site 1 and 3 had a relatively high abundance of *Streblocladia glomerulata* (20.6% ± 7.1 and 16.7% ± 6.9 respectively). Relatively large areas of site 3 and 4 contained no algal cover (bare substratum) (21.9% ± 4.7 and 24.4% ± 4.2 respectively). *Ulva* spp., *Streblocladia glomerulata*, erect coralline algae, and the amount of bare rock were important contributors to the dissimilarities between sites at Pencarrow.

Multiple regression showed that species richness ($p < 0.01$) and Shannon diversity ($p < 0.01$) were significantly correlated with phosphate concentration but no correlation of the diversity indices with TIN concentration was found ($p = 0.696$ and $p = 0.306$ for richness and diversity respectively) at Titahi Bay. TIN and phosphate together explained ~45%

($r^2 = 0.446$) of the variability in species richness and ~35% ($r^2 = 0.353$) of the variability of the Shannon diversity at Titahi Bay.

At Pencarrow, no significant correlation was found between algal species richness and nutrients concentrations in the water (TIN: $p = 0.345$; Phosphate: $p = 0.681$), nor between the Shannon diversity and nutrient conditions (TIN: $p = 0.103$; Phosphate: $p = 0.399$).

Algal species richness (number of species) was significantly different between sites at Titahi Bay (one-way ANOVA; $F_{5,120} = 32.387$; $p = <<0.01$) and Pencarrow (one-way ANOVA; $F_{5,102} = 16.027$; $p = <<0.01$). Post-hoc Tukey's test show that at Titahi Bay the site closest to the outfall has significantly lower species richness than the other sites (Figure 3.7). This pattern was not shown at Pencarrow (Figure 3.8), and species richness overall appears lower at this location compared to Titahi Bay. Significant differences ($p_{adj.} < 0.05$; post-hoc Tukey's test) in algal species richness between sites are indicated with A, B, C, D in Figure 3.7 and 3.8.

At Titahi Bay, the Shannon diversity index H' was significantly different between sites (one way ANOVA; $F_{5,120} = 31.863$; $p = <<0.01$). Post-hoc Tukey's test showed that this difference was caused by the site closest to the outfall, having a far smaller diversity than the other sites.

At Pencarrow, one-way ANOVA also showed a significant difference in Shannon diversity between sites ($F_{5,102} = 13.134$; $p = <<0.01$). Post-hoc Tukey's test indicated that site 5 (176 m from the outfall) had a significantly higher diversity than the other sites. In addition, site 2 and 3 (61 and 74 m from the outfall, respectively) were significantly different from each other, with site 2 having a lower Shannon diversity ($p_{adj.} <0.05$).

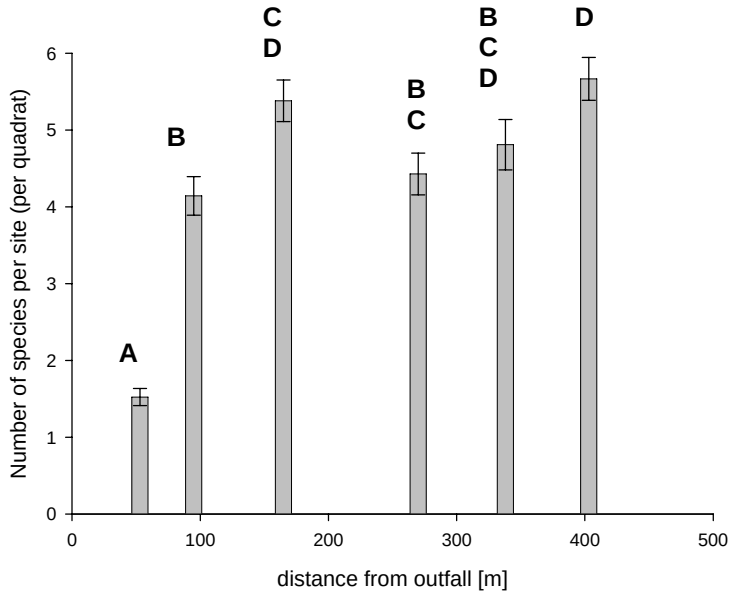


Figure 3.7: Average number of algal species with distance from the sewage outfall at Titahi Bay. Data of all sampling dates (7) are pooled. Error bars represent standard errors. N = 21 for each site/distance from outfall (3 replicates per site per sampling event). Letters (A, B, C, D) indicate results of Tukey's post-hoc test ($p_{adj.} < 0.05$).

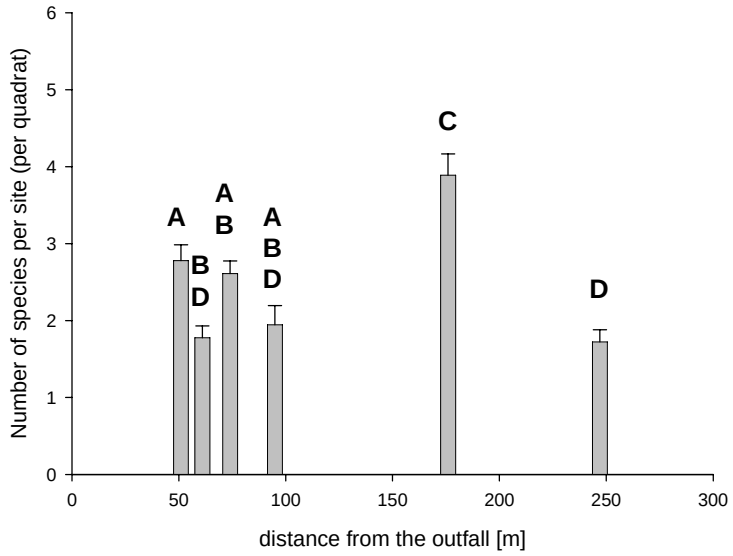


Figure 3.8: Average number of algal species with distance from the sewage outfall at Pencarrow. Data of all sampling dates (6) are pooled. Error bars represent standard errors. N = 18 for each site/distance from outfall (3 replicates per site per sampling event). Letters (A, B, C, D) indicate results of Tukey's post-hoc test ($p_{adj.} < 0.05$).

DISCUSSION

The results of this study show clear increases in nutrient levels close to sewage outfall sites, which rapidly dissipate within 100 m from the outfall. Nutrient concentrations at the site closest to the outfall, especially phosphate, were greater at Titahi Bay. Relationships between algal community structure and nutrient concentrations in the water were found at both sewage discharge locations, but the relationship was stronger at Titahi Bay and best explained by phosphate concentrations. Total inorganic nitrogen and phosphate together contributed to algal community structure at Pencarrow. A similar trend was found for algal diversity indices, where phosphate concentration was negatively related with species richness and Shannon diversity at Titahi Bay. There was no relationship with algal diversity and phosphate at Pencarrow, and at neither site was there a relationship with TIN and algal diversity. These results do not necessarily indicate that phosphate is responsible for the variation in algal community composition but suggest that phosphate concentration can be used as an indicator for sewage presence in seawater; other constituents of sewage effluent which co-vary with phosphate concentration (e.g. pollutants, particulate matter), may contribute to driving changes in algal community structure.

Overall, algal diversity near sewage outfall sites was low, compared to other rocky intertidal communities in the Wellington region. With perhaps the exception of a low percentage cover of unidentified filamentous and turfing algae, all algal species recorded at the two sewage locations were also found at the sites on the shores of the Wellington Harbour and south coast monitored in Chapter 2. Fleshy macrophytes like *Gigartina* spp., *Zonaria turneriana*, and *Champia novae-zelandiae* dominated most sites. In addition, erect coralline algae were abundant at Titahi Bay, and *Ulva* spp. at the Pencarrow outfall.

The average number of species (2.45 ± 0.11 SE) and average Shannon diversity (0.48 ± 0.04 SE) across all sites at Pencarrow was considerably smaller than values found at sites in the Wellington region monitored in the previous chapter (5.68 ± 0.18 SE and 1.28 ± 0.03 SE respectively). At Titahi Bay differences were less dramatic (richness: 4.35 ± 0.16

SE; diversity: 0.92 ± 0.04 SE across all sites), and at the site furthest away from the outfall (403 m), mean species richness (5.67 ± 0.28 SE) and Shannon diversity (1.18 ± 0.07 SE) were comparable to values at other sites in the region.

On some sampling dates some sites only contained a single species, usually the corticated macrophyte *Gigartina* spp. This was the case at the site closest to the outfall (51 m) at Titahi Bay, but at Pencarrow this occurred repeatedly at sites 95 and 247 m away from the outfall. At Titahi Bay the site closest to the outfall had a significantly lower species richness and diversity than the other five sites and also fell far away from the other sites in the nMDS plot on species composition. A decrease in number of species and the absence of large brown algae at sites in proximity to sewage outfalls, has been shown in other studies (e.g. Borowitzka 1972; Littler and Murray 1975; Fairweather 1990), and this was also apparent at Titahi Bay. At Pencarrow, algal species composition, richness and Shannon diversity differed significantly among all sites, but there was no clear pattern with distance from the outfall. The highest diversity was recorded at 176 m from the outfall (site 5), but diversity dropped significantly further away from the outfall (247 m; site 6). The expected pattern of increasing species richness and diversity with increasing distance from the outfall was not detected at Pencarrow.

The site closest to the outfall at Pencarrow showed a fairly diverse assemblage consisting of filamentous algae (*Ceramium* spp.), foliose algae (*Ulva* spp.), corticated macrophytes (turf-forming *Gelidium caulacantheum*) and erect coralline algae, functional groups that are consistent with other studies which investigated the effects of sewage on algal communities (e.g. Littler and Murray 1975; Brown *et al.* 1990). All sites at Pencarrow contained a high percent cover of corticated macrophytes, with *Gigartina decipiens* the main contributor to this functional group at the majority of sites. Algae belonging to the genus *Gigartina* thrive well at exposed conditions (Adams 1994). In Titahi Bay, the site closest to the outfall was dominated by the corticated rhodophyte *Gigartina decipiens,* while the green foliose *Ulva* spp. covered only a small percentage of the quadrats at the majority of the sampling events. This is not consistent with previous studies which found a reduction of Phaeophyceae and Rhodophyceae adjacent to sewage outfalls (e.g.

Borowitzka 1972) and a domination of green ephemeral algae (e.g. Fairweather 1990; Archambault *et al.* 2001).

In addition to high nutrient concentrations, considerable amounts of freshwater are discharged at sewage outfalls during rain events, causing periodic locally reduced salinity. Increased concentrations of pollutants (including pesticides, soluble (industrial) waste products, and heavy metals) can also be expected in proximity to sewage outfalls, which can potentially have dramatic effects on coastal marine communities. However, these pollutants were not measured in this study. Nevertheless, one can expect concentrations of these pollutants to decrease with distance from the outfall in a similar fashion as the nutrient concentrations measured in this study.

The lack of a clear pattern in algal communities away from the point source suggests that other factors than chemical composition of the seawater play a role in the structuring of algal assemblages at the Pencarrow sewage outfall site. One possible factor could be the degree of wave exposure which is higher at Pencarrow and may affect algal settlement success and likelihood of dislodgement of newly settled propagules and removal of adult plants. In addition, there is a lot of gravel at this location interspersed with the rocky outcrops, in contrast to Titahi Bay where the rocky substratum is more continuous. The great volume of gravel at Pencarrow can cause considerable scour and sedimentation of the shore. The rocky substratum is very smooth at most sites at this location, which could inhibit colonization of new settlers (cf., Schiel 2004). The algal community structure at Pencarrow thus could in part be explained by the ability of certain algal species to attach to a smooth rocky surface and ability to withstand high wave energy and scour.

Notably, there were no recordings of the invasive kelp *Undaria pinnatifida* at either outfall location, even though it is abundantly present in the Wellington region. Small populations of *U. pinnatifida* were observed ~3 km north of the Pencarrow study location (personal observation), and it has been recorded in Porirua harbour (Forrest *et al.* 2000; Stuart 2003), an inlet ~ 3 km from the Titahi Bay site. However, no *U. pinnatifida* individuals were observed around the Titahi Bay study location on the (open) west coast

or at Makara Beach (also on the west coast) (B. Morelissen, unpublished data), ~ 16 km southwest of Titahi Bay. The reason for *U. pinnatifida*'s absence in locations adjacent to sewage discharge points is debatable, but it is doubtful that it is related to nutrient regimes at the sites. In fact, a study in Patagonia, Argentina found that *U. pinnatifida* thrived well in sewage-enriched water (Torres *et al.* 2004). Nitrogen is usually the limiting element for primary production in temperate waters and *U. pinnatifida* has been shown to have high nutrient uptake rates (similar to fast-growing ephemeral species, like *Ulva* spp.) (Torres *et al*. 2004; Dean and Hurd 2007), suggesting that increased TIN concentrations in coastal water would benefit *U. pinnatifida* growth. High nutrient environments could potentially give this invader the opportunity to outcompete native seaweeds and form established populations at these locations. However, if no vector exists to distribute spores or sporelings, new populations will not become established at new locations. An explanation for the lack of *U. pinnatifida* at the study locations could simply be that it has not been introduced there (yet).

Most studies investigating consequences of exposure to sewage-enriched seawater only examine communities adjacent to one sewer outfall (but see Fairweather 1990; Archambault *et al.* 2001). This study shows that the effects of sewage effluent can vary between different sewage outfall locations, even within the same region. Caution needs to be taken when drawing general conclusions about effects of effluent on marine communities, as effects on algal community composition and diversity may not be unambiguous and may be location-specific. Here, at the location with higher nutrient concentrations closest to the outfall, there was a stronger effect on algal communities, and the relationships were similar as have been found in other studies. By contrast, at the other site, with lower nutrient concentrations close to the outfall, on a more open coast, with greater wave exposure, and rocky outcrops interspersed with long stretches of sand and pebble beach, patterns were less clear. Thus the effects of nutrient-enrichment from sewage on algal communities are likely mediated by several interacting factors, including distance from the outfall, magnitude of the nutrient enrichment, degree of wave exposure at the site, degree of sedimentation, and the abundance of grazers (Brown *et al.* 1990).

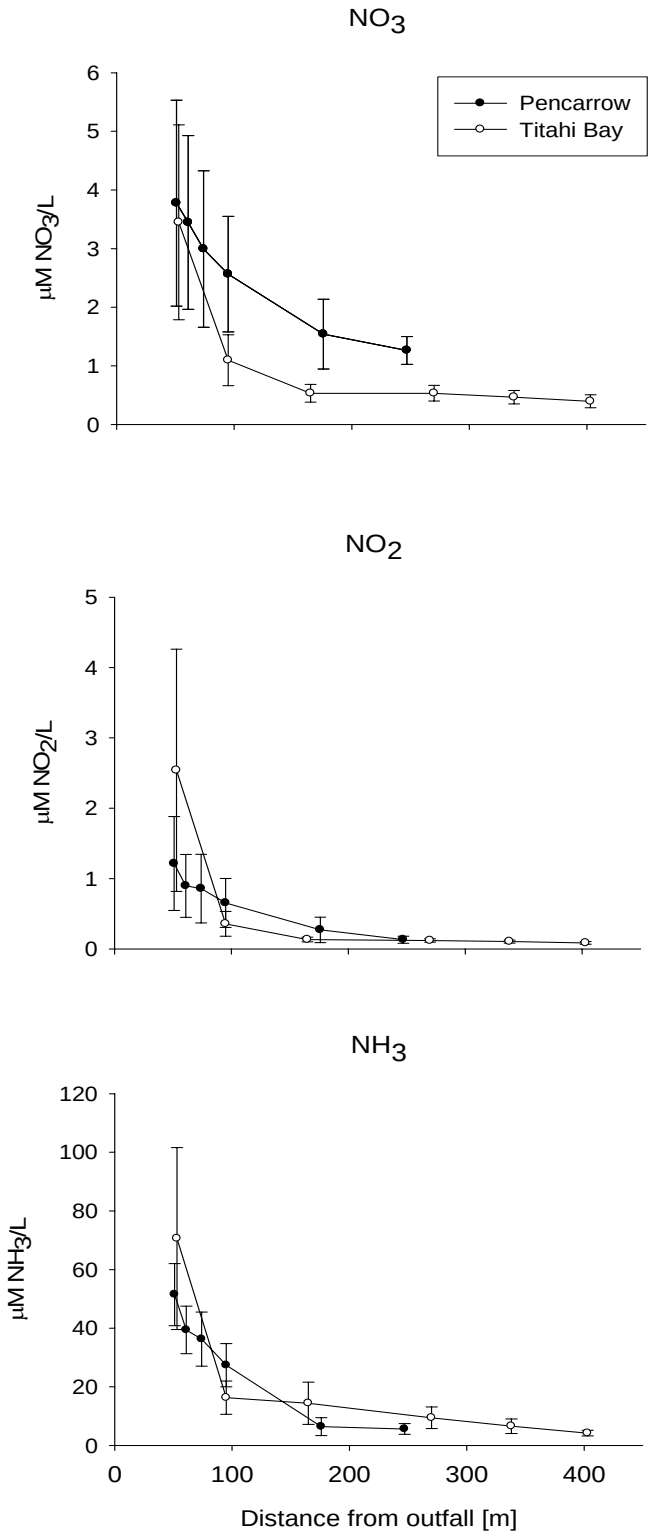
Appendix 3.1: *Algal species or taxonomic units recorded in the quadrats and the functional group to which they were classified (modified from Steneck* and *Dethier 1994, Guerry et al. 2009, and M. Dethier, pers. comm.) at Titahi Bay (A) and at Pencarrow (B). Sites where the algae were recorded are noted with 'x'.*

A Titahi Bay

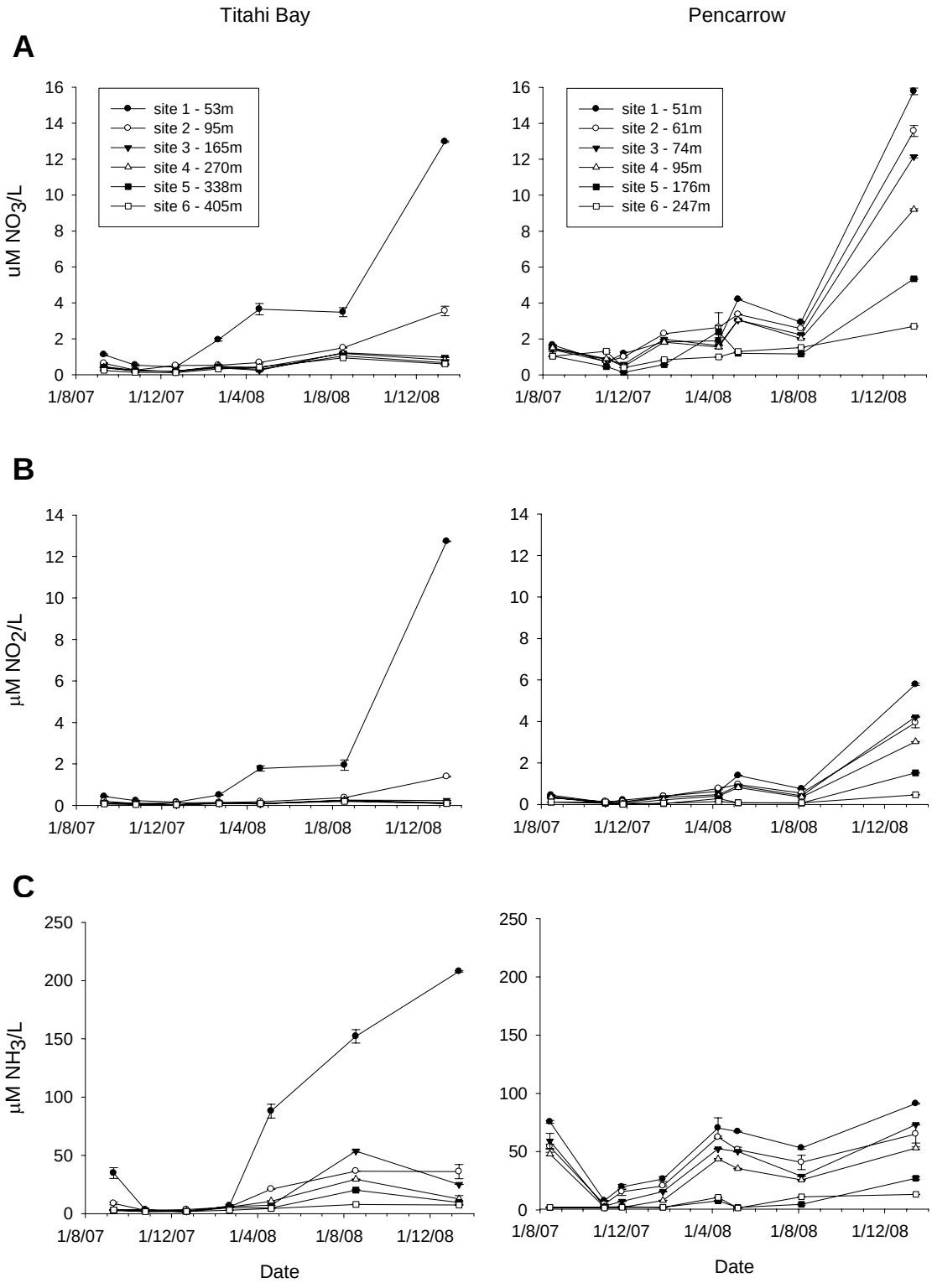
Species	**Functional group**	**Division**	**Site**					
			1	**2**	**3**	**4**	**5**	**6**
Unid. red filamentous algae	Filamentous	Rhodophyta					x	
Ulva spp.	Foliose	Chlorophyta	x	x	x	x	x	x
Dictyota kunthii	Corticated foliose	Phaeophyta		x	x	x	x	x
Petalonia fascia	Corticated foliose	Phaeophyta					x	
Zonaria turneriana	Corticated foliose	Phaeophyta		x	x	x	x	x
Champia novae-zelandiae	Corticated macrophytes	Rhodophyta				x	x	x
Codium convolutum	Corticated macrophytes	Chlorophyta		x				x
Colpomenia sinuosa	Corticated macrophytes	Phaeophyta		x	x	x	x	x
Gelidium caulacantheum	Corticated macrophytes	Rhodophyta						x
Gigartina chapmanii	Corticated macrophytes	Rhodophyta					x	
Gigartina decipiens	Corticated macrophytes	Rhodophyta	x					
Halopteris spp.	Corticated macrophytes	Phaeophyta		x	x		x	x
Leathesia spp.	Corticated macrophytes	Phaeophyta		x	x	x	x	x
Lophurella caespitosea	Corticated macrophytes	Rhodophyta			x		x	x
Streblocladia glomerulata	Corticated macrophytes	Rhodophyta	x				x	
Unid. brown turfing alga	Corticated macrophytes	Phaeophyta		x	x		x	x
Unid. red turfing alga	Corticated macrophytes	Rhodophyta			x	x	x	x
Carpophyllum maschalocarpum	Leathery macrophytes	Phaeophyta		x	x	x	x	x
Cystophora torulosa	Leathery macrophytes	Phaeophyta						x
Coralline algae	Erect coralline algae	Rhodophyta		x	x	x	x	x
Crustose Coralline Algae	Crustose algae	Rhodophyta		x	x	x	x	x
Unid. brown crustose alga	Crustose algae	Phaeophyta		x		x	x	x

B Pencarrow

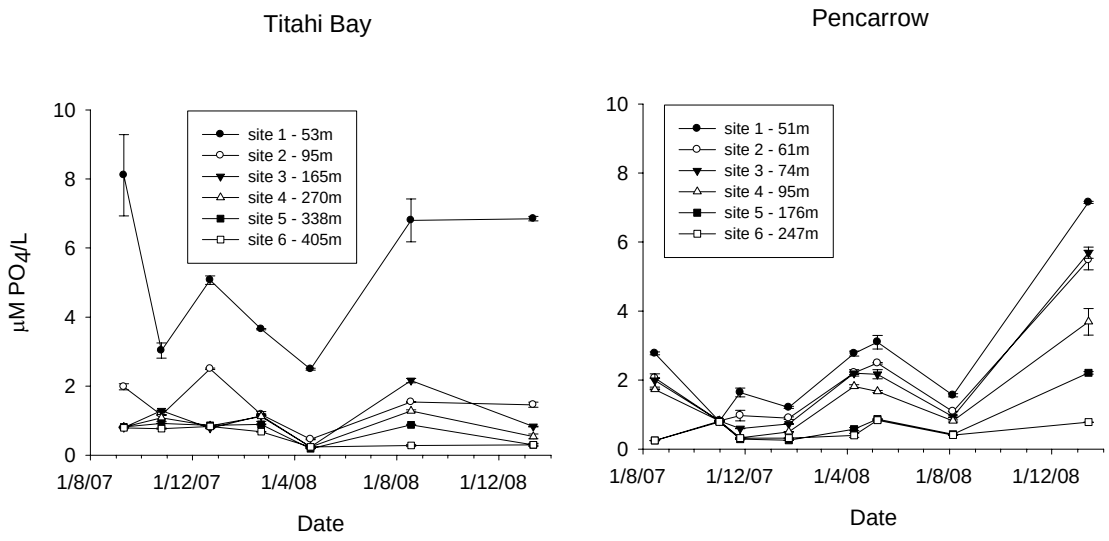
Species	Functional group	Division	Site					
			1	2	3	4	5	6
Unid. red filamentous algae	Filamentous	Rhodophyta	x	x	x			
Ulva spp.	Foliose	Chlorophyta	x	x	x	x	x	x
Porphyra spp.	Foliose	Rhodophyta					x	
Dictyota kunthii	Corticated foliose	Phaeophyta		x	x		x	
Champia novae-zelandiae	Corticated macrophytes	Rhodophyta				x	x	x
Codium convolutum	Corticated macrophytes	Chlorophyta	x		x		x	
Gigartina decipiens	Corticated macrophytes	Rhodophyta	x	x	x	x	x	x
Streblocladia glomerulata	Corticated macrophytes	Rhodophyta	x		x	x	x	
Unidentified brown turfing alga	Corticated macrophytes	Phaeophyta	x					
Carpophyllum maschalocarpum	Leathery macrophytes	Phaeophyta	x	x	x	x	x	x
Lessonia variegata	Leathery macrophytes	Phaeophyta			x	x		
Coralline algae	Erect coralline algae	Rhodophyta	x	x	x	x	x	x
Crustose Coralline Algae	Crustose algae	Rhodophyta	x	x		x	x	x
Unid. brown crustose alga	Crustose algae	Phaeophyta			x	x	x	



Appendix 3.2: *Mean nitrate (NO_3), nitrite (NO_2), and ammonia (NH_3) concentration (± S.E.) with distance from the sewage outfall (per site) over the study period. N = 7 for Titahi Bay; n = 6 for Pencarrow*



Appendix 3.3: *Mean NO_3 (A), NO_2 (B), and NH_3 (C) concentration at each site per sampling event at Titahi Bay and at Pencarrow. Error bars show S.E.; n = 2.*



Appendix 3.4: *Mean PO_4 concentration at each site per sampling event at Titahi Bay and at Pencarrow. Error bars show S.E.; n = 2.*

Appendix 3.5 A: *SIMPER results displaying the contribution of each algal species to measures of dissimilarity in species composition between sites at Titahi Bay. Procedure was based on Bray-Curtis similarity matrix of square-root transformed data. A cut-off at 90% (cumulative contribution) has been applied.*

Sites 1 and 2
Average dissimilarity = 97.77

Species	Site 1 Av.Abund	Site 2 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	9.24	0	29.44	5.51	30.11	30.11
Erect coralline algae	0	6.93	22.1	2.84	22.61	52.72
D. kunthii	0	3.17	10.08	1.01	10.31	63.03
Z. turneriana	0	2.36	7.31	0.9	7.48	70.51
bare rock	1.96	0.51	5.94	0.99	6.08	76.59
C. convolutum	0	1.06	3.29	0.55	3.36	79.95
Ulva spp.	0.81	0.31	2.85	0.72	2.91	82.86
S. glomerulata	0.82	0	2.48	0.56	2.54	85.4
Unid. brown crustose algae	0	0.81	2.46	0.55	2.52	87.92
Leathesia spp.	0	0.71	2.2	0.67	2.25	90.17

Sites 1 and 3
Average dissimilarity = 97.10

Species	Site 1 Av.Abund	Site 3 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	9.24	0	27.65	5.82	28.48	28.48
Erect coralline algae	0	5.85	17.59	1.74	18.12	46.59
Z. turneriana	0	2.67	8.18	1.13	8.42	55.02
Leathesia spp.	0	2.18	6.51	0.9	6.71	61.72
bare rock	1.96	0.35	5.71	0.99	5.88	67.61
Ulva spp.	0.81	1.45	4.55	1.15	4.68	72.29
Unid. brown turfing algae	0	1.35	4.06	0.52	4.19	76.48
Halopteris spp.	0	1.32	3.96	0.75	4.07	80.55
C. maschalocarpum	0	1.26	3.71	0.63	3.82	84.37
D. kunthii	0	1.22	3.56	0.6	3.67	88.04
C. sinuosa	0	0.87	2.66	0.79	2.74	90.78

Sites 2 and 3
Average dissimilarity = 60.13

Species	Site 2 Av.Abund	Site 3 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Erect coralline algae	6.93	5.85	8.04	1.25	13.37	13.37
D. kunthii	3.17	1.22	7.97	1.14	13.25	26.62
Z. turneriana	2.36	2.67	6.93	1.23	11.52	38.14
Leathesia spp.	0.71	2.18	5.44	1.01	9.05	47.19
Unid. brown turfing algae	0.73	1.35	4.36	0.68	7.25	54.44
C. maschalocarpum	0.55	1.26	3.72	0.77	6.19	60.63
Halopteris spp.	0.3	1.32	3.54	0.81	5.89	66.52
Ulva spp.	0.31	1.45	3.29	1.06	5.47	71.99
Crustose Coralline Algae	0.61	0.64	2.88	0.5	4.79	76.78
C. convolutum	1.06	0	2.62	0.55	4.36	81.14
C. sinuosa	0.55	0.87	2.6	0.96	4.32	85.46
Unid. red turfing algae	0.42	0.53	2.01	0.51	3.34	88.8
Unid. brown crustose algae	0.81	0	1.97	0.55	3.28	92.08

Sites 1 and 4
Average dissimilarity = 97.81

Species	Site 1 Av.Abund	Site 4 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	9.24	0	29.72	5.36	30.39	30.39
Z. turneriana	0	6.37	21.04	1.91	21.52	51.9
Erect coralline algae	0	3.27	10.07	1.41	10.3	62.2
C. maschalocarpum	0	2.8	9.17	1.53	9.38	71.57
D. kunthii	0	2.61	7.97	0.78	8.15	79.72
bare rock	1.96	0.64	6.26	1.01	6.4	86.12
Ulva spp.	0.81	0.33	2.92	0.71	2.99	89.11
Leathesia spp.	0	0.97	2.8	0.73	2.87	91.98

Sites 2 and 4
Average dissimilarity = 63.20

Species	Site 2 Av.Abund	Site 4 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Z. turneriana	2.36	6.37	13.24	1.49	20.94	20.94
Erect coralline algae	6.93	3.27	11.43	1.5	18.09	39.03
D. kunthii	3.17	2.61	9.45	1.19	14.95	53.98
C. maschalocarpum	0.55	2.8	7.01	1.41	11.09	65.07
Leathesia spp.	0.71	0.97	3.09	0.97	4.88	69.95
C. convolutum	1.06	0	2.78	0.55	4.4	74.36
bare rock	0.51	0.64	2.5	0.65	3.96	78.32
Unid. brown crustose algae	0.81	0.28	2.45	0.66	3.88	82.2
Custose Coralline Algae	0.61	0.32	2.36	0.42	3.74	85.94
Unid. brown turfing algae	0.73	0	1.86	0.48	2.95	88.88
C. sinuosa	0.55	0.3	1.8	0.74	2.84	91.73

Sites 3 and 4
Average dissimilarity = 64.54

Species	Site 3 Av.Abund	Site 4 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Z. turneriana	2.67	6.37	11.58	1.54	17.95	17.95
Erect coralline algae	5.85	3.27	10.22	1.38	15.83	33.77
D. kunthii	1.22	2.61	7.06	0.95	10.94	44.71
C. maschalocarpum	1.26	2.8	6.61	1.45	10.23	54.94
Leathesia spp.	2.18	0.97	5.54	1.02	8.59	63.53
Unid. brown turfing algae	1.35	0	3.46	0.52	5.36	68.9
Ulva spp.	1.45	0.33	3.4	1.09	5.28	74.17
Halopteris spp.	1.32	0	3.37	0.75	5.22	79.39
C. sinuosa	0.87	0.3	2.4	0.89	3.72	83.11
Crustose Coralline Algae	0.64	0.32	2.26	0.51	3.5	86.62
bare rock	0.35	0.64	2.13	0.58	3.3	89.92
Unid. red turfing algae	0.66	0.36	2.09	0.51	3.23	93.15

Sites 1 and 5
Average dissimilarity = 96.62

Species	Site 1 Av.Abund	Site 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	9.24	0	28.6	5.53	29.6	29.6
Z. turneriana	0	6.11	18.95	2.36	19.61	49.21
Erect coralline algae	0	3.95	12.06	1.67	12.49	61.69
C. maschalocarpum	0	2.85	8.91	1.07	9.22	70.92
bare rock	1.96	0.76	5.73	1	5.93	76.84
Leathesia spp.	0	1.14	3.47	0.57	3.6	80.44
D. kunthii	0	1.09	3.41	0.5	3.53	83.97
Ulva spp.	0.81	0.45	2.95	0.77	3.06	87.03
S. glomerulata	0.82	0.18	2.76	0.6	2.86	89.89
Unid. red turfing algae	0	0.82	2.26	0.44	2.34	92.23

Sites 2 and 5
Average dissimilarity = 63.07

Species	Site 2 Av.Abund	Site 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Z. turneriana	2.36	6.11	11.61	1.58	18.4	18.4
Erect coralline algae	6.93	3.95	9.59	1.44	15.2	33.6
D. kunthii	3.17	1.09	8.29	1.09	13.15	46.75
C. maschalocarpum	0.55	2.85	7.22	1.1	11.44	58.2
Leathesia spp.	0.71	1.14	3.53	0.76	5.6	63.8
C. convolutum	1.06	0	2.7	0.55	4.28	68.07
bare rock	0.51	0.76	2.63	0.76	4.17	72.25
Unid. brown turfing algae	0.73	0.43	2.56	0.57	4.05	76.3
Unid. brown crustose algae	0.81	0.23	2.32	0.62	3.69	79.99
Crustose Coralline Algae	0.61	0.26	2.12	0.4	3.37	83.35
Unid. red turfing algae	0	0.82	1.94	0.44	3.07	86.42
C. sinuosa	0.55	0.38	1.88	0.78	2.98	89.4
Ulva spp.	0.31	0.45	1.39	0.88	2.2	91.6

Sites 3 and 5
Average dissimilarity = 61.99

Species	Site 3 Av.Abund	Site 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Z. turneriana	2.67	6.11	9.98	1.59	16.1	16.1
Erect coralline algae	5.85	3.95	8.96	1.35	14.46	30.56
C. maschalocarpum	1.26	2.85	6.96	1.17	11.23	41.78
Leathesia spp.	2.18	1.14	5.76	1.02	9.3	51.08
D. kunthii	1.22	1.09	4.47	0.78	7.21	58.29
Unid. brown turfing algae	1.35	0.43	3.92	0.6	6.33	64.62
Halopteris spp.	1.32	0.2	3.35	0.8	5.41	70.03
Ulva spp.	1.45	0.45	3.23	1.09	5.21	75.24
Unid. red turfing algae	0.66	0.82	2.89	0.6	4.66	79.91
C. sinuosa	0.87	0.38	2.38	0.92	3.84	83.74
bare rock	0.35	0.76	2.33	0.69	3.75	87.5
Crustose Coralline Algae	0.64	0.26	2.06	0.51	3.32	90.82

Sites 4 and 5
Average dissimilarity = 49.86

Species	Site 4 Av.Abund	Site 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Z. turneriana	6.37	6.11	8.04	1.32	16.13	16.13
D. kunthii	2.61	1.09	7.38	0.92	14.81	30.93
Erect coralline algae	3.27	3.95	7.15	1.3	14.35	45.29
C. maschalocarpum	2.8	2.85	6.76	1.41	13.55	58.84
Leathesia spp.	0.97	1.14	3.86	0.81	7.75	66.59
bare rock	0.64	0.76	2.88	0.75	5.77	72.36
Unid. red turfing algae	0.36	0.82	2.54	0.54	5.09	77.44
C. novae-zelandiae	0.41	0.23	1.52	0.56	3.04	80.48
Ulva spp.	0.33	0.45	1.49	0.85	2.98	83.47
C. sinuosa	0.3	0.38	1.46	0.69	2.92	86.39
Crustose Coralline Algae	0.32	0.26	1.42	0.44	2.85	89.24
L. caespitosea	0	0.48	1.14	0.53	2.3	91.53

Sites 1 and 6
Average dissimilarity = 95.76

Species	Site 1 Av.Abund	Site 6 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	9.24	0	27.45	5.47	28.66	28.66
Erect coralline algae	0	3.33	10.1	0.83	10.55	39.21
Crustose Coralline Algae	0	2.75	8.36	0.76	8.73	47.95
Z. turneriana	0	2.27	6.46	0.88	6.74	54.69
bare rock	1.96	1.13	6.27	1.08	6.55	61.24
C. maschalocarpum	0	1.86	5.39	0.99	5.63	66.86
Ulva spp.	0.81	1.24	4.12	1.06	4.31	71.17
Leathesia spp.	0	1.13	3.15	0.79	3.29	74.46
C. novae-zelandiae	0	1.08	3.11	0.65	3.25	77.71
Unid. red turfing algae	0	1.04	2.97	0.49	3.1	80.81
Unid. brown crustose algae	0	0.99	2.81	0.72	2.94	83.75
Unid. brown turfing algae	0	0.91	2.5	0.46	2.61	86.36
L. caespitosea	0	0.84	2.33	0.55	2.43	88.79
S. glomerulata	0.82	0	2.32	0.56	2.43	91.22

Sites 2 and 6
Average dissimilarity = 71.64

Species	Site 2 Av.Abund	Site 6 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Erect coralline algae	6.93	3.33	12.29	1.62	17.16	17.16
D. kunthii	3.17	0.65	7.79	1.08	10.87	28.03
Crustose Coralline Algae	0.61	2.75	7.5	0.81	10.47	38.5
Z. turneriana	2.36	2.27	6.9	1.15	9.63	48.13
C. maschalocarpum	0.55	1.86	4.63	1.06	6.47	54.6
bare rock	0.51	1.13	3.32	0.73	4.63	59.23
Unid. brown crustose algae	0.81	0.99	3.31	0.89	4.62	63.85
Unid. brown turfing algae	0.73	0.91	3.29	0.66	4.59	68.45
Leathesia spp.	0.71	1.13	3.15	1	4.4	72.85
C. convolutum	1.06	0.38	3.12	0.7	4.35	77.2
Ulva spp.	0.31	1.24	2.81	0.97	3.93	81.13
C. novae-zelandiae	0	1.08	2.64	0.65	3.69	84.82

Unid. red turfing algae	0	1.04	2.52	0.49	3.52	88.34
C. sinuosa	0.55	0.63	2.17	0.93	3.03	91.37

Sites 3 and 6
Average dissimilarity = 69.77

Species	Site 3 Av.Abund	Site 6 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Erect coralline algae	5.85	3.33	11.1	1.42	15.91	15.91
Crustose Coralline Algae	0.64	2.75	6.98	0.84	10.01	25.92
Z. turneriana	2.67	2.27	6.59	1.25	9.44	35.36
Leathesia spp.	2.18	1.13	5.25	1.06	7.53	42.89
C. maschalocarpum	1.26	1.86	4.98	1.13	7.14	50.04
Unid. brown turfing algae	1.35	0.91	4.43	0.69	6.35	56.39
Halopteris spp.	1.32	0.4	3.56	0.81	5.1	61.5
D. kunthii	1.22	0.65	3.56	0.76	5.1	66.6
Ulva spp.	1.45	1.24	3.36	1.16	4.81	71.41
Unid. red turfing algae	0.66	1.04	3.32	0.64	4.76	76.17
bare rock	0.35	1.13	3	0.67	4.29	80.46
C. novae-zelandiae	0	1.08	2.52	0.65	3.61	84.07
L. caespitosea	0.44	0.84	2.45	0.67	3.51	87.58
C. sinuosa	0.87	0.63	2.44	1.04	3.5	91.08

Sites 4 and 6
Average dissimilarity = 70.22

Species	Site 4 Av.Abund	Site 6 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Z. turneriana	6.37	2.27	12.65	1.49	18.01	18.01
Erect coralline algae	3.27	3.33	9.38	1.32	13.36	31.37
Crustose Coralline Algae	0.32	2.75	7.24	0.81	10.31	41.68
D. kunthii	2.61	0.65	6.7	0.89	9.54	51.22
C. maschalocarpum	2.8	1.86	5.64	1.32	8.04	59.26
bare rock	0.64	1.13	3.5	0.73	4.98	64.24
Leathesia spp.	0.97	1.13	3.44	1.03	4.89	69.13
C. novae-zelandiae	0.41	1.08	3.07	0.79	4.37	73.5
Unid. red turfing algae	0.36	1.04	3.05	0.58	4.34	77.84
Ulva spp.	0.33	1.24	2.96	1.01	4.21	82.06
Unid. brown crustose algae	0.28	0.99	2.62	0.8	3.74	85.79
Unid. brown turfing algae	0	0.91	2.15	0.46	3.07	88.86
L. caespitosea	0	0.84	2.01	0.55	2.86	91.72

Sites 5 and 6
Average dissimilarity = 69.36

Species	Site 5 Av.Abund	Site 6 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Z. turneriana	6.11	2.27	11.09	1.56	15.99	15.99
Erect coralline algae	3.95	3.33	9.49	1.51	13.69	29.68
Crustose Coralline Algae	0.26	2.75	6.98	0.8	10.06	39.74
C. maschalocarpum	2.85	1.86	6.44	1.21	9.28	49.02
Leathesia spp.	1.14	1.13	3.81	0.86	5.49	54.52
Unid. red turfing algae	0.82	1.04	3.67	0.66	5.29	59.81
D. kunthii	1.09	0.65	3.59	0.67	5.18	64.99
bare rock	0.76	1.13	3.54	0.82	5.1	70.1
C. novae-zelandiae	0.23	1.08	2.82	0.72	4.06	74.16
Unid. brown turfing algae	0.43	0.91	2.78	0.55	4.01	78.17
Ulva spp.	0.45	1.24	2.78	0.99	4.01	82.18
L. caespitosea	0.48	0.84	2.54	0.74	3.67	85.84
Unid. brown crustose algae	0.23	0.99	2.54	0.78	3.66	89.51
C. sinuosa	0.38	0.63	1.92	0.89	2.77	92.28

Appendix 3.5 B: *SIMPER displaying the contribution of each algal species to measures of dissimilarity in species composition between sites at Pencarrow. Procedure was based on Bray-Curtis similarity matrix of square-root transformed data. A cut-off at 90% (cumulative contribution) has been applied.*

Sites 1 and 2
Average dissimilarity = 73.38

Species	Site 1 Av.Abund	Site 2 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	1.84	7.25	20.85	1.87	28.42	28.42
Ulva spp.	4.12	1.36	12.98	1.13	17.69	46.1
S. glomerulata	3.07	0	10.45	0.89	14.24	60.34
Erect coralline algae	1.52	1.27	8.13	0.6	11.08	71.42
bare rock	2.28	2.98	7.98	1.31	10.88	82.3
Unid. red filamentous algae	1.88	0.12	6.39	0.56	8.7	91

Sites 1 and 3
Average dissimilarity = 64.43

Species	Site 1 Av.Abund	Site 3 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	1.84	5.09	13.23	1.44	20.53	20.53
Ulva spp.	4.12	2.5	11.52	1.28	17.88	38.4
S. glomerulata	3.07	2.42	11.13	1.08	17.27	55.67
bare rock	2.28	4.09	8.8	1.34	13.66	69.33
Erect coralline algae	1.52	1.29	7.37	0.63	11.45	80.78
Unid. red filamentous algae	1.88	0.22	6.04	0.57	9.37	90.15

Sites 2 and 3
Average dissimilarity = 52.98

Species	Site 2 Av.Abund	Site 3 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	7.25	5.09	13.79	1.29	26.02	26.02
bare rock	2.98	4.09	8.96	1.32	16.92	42.94
S. glomerulata	0	2.42	7.9	0.71	14.91	57.85
Erect coralline algae	1.27	1.29	7.25	0.61	13.68	71.54
Ulva spp.	1.36	2.5	7.23	1.23	13.64	85.17
D. kunthii	0.53	0.12	1.94	0.29	3.66	88.83
C. maschalocarpum	0.37	0.22	1.78	0.48	3.35	92.19

Sites 1 and 4
Average dissimilarity = 73.82

Species	Site 1 Av.Abund	Site 4 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	1.84	7.62	20.57	2.06	27.87	27.87
Ulva spp.	4.12	0.32	13.12	1.06	17.77	45.64
S. glomerulata	3.07	0.12	10.06	0.89	13.63	59.27
bare rock	2.28	4.55	9.54	1.43	12.92	72.19
Erect coralline algae	1.52	0.86	6.57	0.6	8.9	81.09
Unid. red filamentous algae	1.88	0	6.01	0.53	8.14	89.23
C. maschalocarpum	0.39	0.68	2.81	0.57	3.81	93.05

Sites 2 and 4
Average dissimilarity = 39.68

Species	Site 2 Av.Abund	Site 4 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	7.25	7.62	10.1	0.95	25.46	25.46
bare rock	2.98	4.55	9.51	1.39	23.97	49.43
Erect coralline algae	1.27	0.86	6.29	0.57	15.84	65.27
Ulva spp.	1.36	0.32	4.49	0.93	11.32	76.59
C. maschalocarpum	0.37	0.68	2.92	0.56	7.36	83.95
C. novae-zelandiae	0	0.58	1.79	0.44	4.5	88.45
D. kunthii	0.53	0	1.69	0.24	4.26	92.72

Sites 3 and 4
Average dissimilarity = 49.20

Species	Site 3 Av.Abund	Site 4 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	5.09	7.62	12.05	1.22	24.49	24.49
bare rock	4.09	4.55	7.75	1.21	15.76	40.25
S. glomerulata	2.42	0.12	7.7	0.72	15.64	55.89
Ulva spp.	2.5	0.32	7.34	1.22	14.91	70.8
Erect coralline algae	1.29	0.86	5.57	0.61	11.32	82.12
C. maschalocarpum	0.22	0.68	2.37	0.56	4.82	86.94
L. variegata	0.41	0.16	1.78	0.3	3.61	90.55

Sites 1 and 5
Average dissimilarity = 75.81

Species	Site 1 Av.Abund	Site 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
C. novae-zelandiae	0	5.54	16.57	1.78	21.85	21.85
Ulva spp.	4.12	4.17	10.97	1.59	14.47	36.33
S. glomerulata	3.07	0.53	9.03	0.94	11.91	48.23
Erect coralline algae	1.52	1.89	7.99	0.82	10.53	58.77
bare rock	2.28	2.14	6.66	1.31	8.79	67.56
Unid. red filamentous algae	1.88	0	5.36	0.53	7.07	74.63
G. decipiens	1.84	0.38	5.21	0.83	6.87	81.49
C. maschalocarpum	0.39	1.32	4.31	0.7	5.69	87.19
Crustose Coralline Algae	0.1	1.31	3.72	0.65	4.91	92.1

Sites 2 and 5
Average dissimilarity = 81.70

Species	Site 2 Av.Abund	Site 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	7.25	0.38	21.56	1.98	26.39	26.39
C. novae-zelandiae	0	5.54	17.45	1.77	21.36	47.75
Ulva spp.	1.36	4.17	10.16	1.54	12.44	60.19
Erect coralline algae	1.27	1.89	7.89	0.79	9.66	69.85
bare rock	2.98	2.14	7.82	1.31	9.57	79.42
C. maschalocarpum	0.37	1.32	4.5	0.7	5.51	84.93
Crustose Coralline Algae	0.18	1.31	4.05	0.67	4.96	89.89
C. convolutum	0	0.64	1.84	0.44	2.26	92.15

Sites 3 and 5
Average dissimilarity = 75.71

Species	Site 3 Av.Abund	Site 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
C. novae-zelandiae	0	5.54	16.1	1.79	21.26	21.26
G. decipiens	5.09	0.38	13.75	1.5	18.16	39.42
bare rock	4.09	2.14	8.65	1.35	11.42	50.85
Ulva spp.	2.5	4.17	8.13	1.47	10.74	61.59
S. glomerulata	2.42	0.53	7.19	0.78	9.5	71.09
Erect coralline algae	1.29	1.89	7.04	0.83	9.3	80.39
C. maschalocarpum	0.22	1.32	3.89	0.67	5.14	85.53
Crustose Coralline Algae	0	1.31	3.53	0.62	4.66	90.19

Sites 4 and 5
Average dissimilarity = 81.14

Species	Site 4 Av.Abund	Site 5 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	7.62	0.38	22.09	2.55	27.22	27.22
C. novae-zelandiae	0.58	5.54	15.71	1.59	19.36	46.58
Ulva spp.	0.32	4.17	11.5	1.79	14.17	60.75
bare rock	4.55	2.14	9.53	1.52	11.75	72.5
Erect coralline algae	0.86	1.89	6.3	0.81	7.77	80.27
C. maschalocarpum	0.68	1.32	4.75	0.75	5.85	86.12
Crustose Coralline Algae	0.1	1.31	3.8	0.65	4.68	90.8

Sites 1 and 6
Average dissimilarity = 77.72

Species	Site 1 Av.Abund	Site 6 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	1.84	6.91	18.16	1.86	23.37	23.37
Ulva spp.	4.12	0.1	13.62	1.06	17.53	40.89
C. novae-zelandiae	0	3.89	12.44	0.97	16.01	56.9
S. glomerulata	3.07	0	10.24	0.89	13.17	70.07
bare rock	2.28	3.41	8.07	1.36	10.38	80.46
Unid. red filamentous algae	1.88	0	6.09	0.53	7.84	88.29
Erect coralline algae	1.52	0.25	5.53	0.5	7.12	95.41

Sites 2 and 6
Average dissimilarity = 46.89

Species	Site 2 Av.Abund	Site 6 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
C. novae-zelandiae	0	3.89	13.14	0.97	28.03	28.03
G. decipiens	7.25	6.91	11.18	1.17	23.84	51.87
bare rock	2.98	3.41	8.61	1.36	18.35	70.22
Erect coralline algae	1.27	0.25	5.13	0.47	10.95	81.17
Ulva spp.	1.36	0.1	4.52	0.86	9.65	90.82

Sites 3 and 6
Average dissimilarity = 55.69

Species	Site 3 Av.Abund	Site 6 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
C. novae-zelandiae	0	3.89	12.06	0.97	21.66	21.66
G. decipiens	5.09	6.91	11.15	1.24	20.02	41.68
bare rock	4.09	3.41	7.97	1.23	14.31	55.99
Ulva spp.	2.5	0.1	7.75	1.22	13.92	69.9
S. glomerulata	2.42	0	7.75	0.71	13.91	83.81
Erect coralline algae	1.29	0.25	4.54	0.51	8.16	91.97

Sites 4 and 6
Average dissimilarity = 37.80

Species	Site 4 Av.Abund	Site 6 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
C. novae-zelandiae	0.58	3.89	12.77	1.04	33.78	33.78
G. decipiens	7.62	6.91	8.56	1.21	22.66	56.43
bare rock	4.55	3.41	8.07	1.21	21.36	77.8
Erect coralline algae	0.86	0.25	3.05	0.55	8.08	85.88
C. maschalocarpum	0.68	0.1	2.21	0.5	5.85	91.73

Sites 5 and 6
Average dissimilarity = 73.00

Species	Site 5 Av.Abund	Site 6 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
G. decipiens	0.38	6.91	19.91	2.41	27.27	27.27
C. novae-zelandiae	5.54	3.89	13.07	1.38	17.91	45.18
Ulva spp.	4.17	0.1	12.18	1.85	16.69	61.86
bare rock	2.14	3.41	8.04	1.4	11.01	72.88
Erect coralline algae	1.89	0.25	5.71	0.76	7.82	80.7
C. maschalocarpum	1.32	0.1	4.02	0.64	5.51	86.21
Crustose Coralline Algae	1.31	0	3.74	0.62	5.12	91.33

CHAPTER 4

RECRUITMENT OF THE INVASIVE ALGA *UNDARIA PINNATIFIDA* (HARVEY) SURINGAR IN RESPONSE TO DISTURBANCE IN A LOW-INTERTIDAL HABITAT

ABSTRACT

Disturbance has been shown to play an important role in the invasion ecology of many species. Establishment of invasive species can be facilitated and spread accelerated when resources, like space and light, become available. Disturbance that reduces the cover of native algal canopy species may facilitate the establishment of invasive macroalgae, as has been demonstrated in subtidal habitats. In this study, the invasion process of *Undaria pinnatifida* in disturbed patches in a rocky low-intertidal habitat was investigated. At an un-invaded location, but adjacent to (~150 m) sites with established *U. pinnatifida* populations, invasibility of the intertidal habitat was investigated by partially or totally clearing the native algal cover at two different times of year (summer and winter). No significant effect of clearing treatments on *U. pinnatifida* invasion was found. The fact that *U. pinnatifida* also recruited in the control treatments indicated that disturbance of the native algal cover was not a key requirement for this kelp to invade and establish in low-intertidal habitats in this study site, and suggested that neither space nor light were limiting resources in the intertidal zone of this study site. *U. pinnatifida* abundance was highest at the end of the experiment in late spring, which could indicate that the majority of the plants maintain a winter annual strategy or that by that time the invasion of the study site was progressing. Yet, the presence of young recruits in late spring indicates that *U. pinnatifida*, a winter annual in its native range, is capable of reproducing year round in this area.

INTRODUCTION

Disturbance has long been recognized as an important process structuring benthic marine assemblages and can be caused by both natural and anthropogenic agents (Dayton 1971; Sousa 1984a; Keough and Quinn 1998; Schiel and Taylor 1999; Thompson *et al.* 2002; Valentine *et al.* 2007; Araújo *et al.* 2009). Intertidal macroalgal communities are subject to a wide variety of disturbances, and the consequences of these impacts on the remaining assemblages vary. For example, macroalgal assemblages are often partially removed or thinned, e.g. through trampling by humans (Schiel and Taylor 1999; Milazzo *et al.* 2002; 2004; Schiel and Lilley 2007), while larger impacts, e.g. major storms, can completely remove canopy forming species (Underwood 1998, 1999). The impacts can cause changes in resource availability (e.g., space, light, and nutrients), which may affect species composition and abundance of local communities (Airoldi 1998; Araújo *et al.* 2009). Removal of a dominant species due to disturbance can influence direct and indirect interactions with associated species (Underwood 1998, 1999), or result in the loss of these species (Dayton 1975; Bertness *et al*. 1999; Jenkins *et al.* 2004; Lilley and Schiel 2006; Schiel and Lilley 2007).

Disturbance also appears to play a crucial role in the invasion ecology of many species (Hobbs and Huenneke 1992; Alpert *et al.* 2000; Scheibling and Gagnon 2006) by facilitating the establishment and accelerating the spread of invasive species as resources are freed (Valentine *et al.* 2007). This has been extensively hypothesised (e.g. Elton 1958; Hobbs and Huenneke 1992; Williamson 1996; Alpert *et al.* 2000; Davis *et al.* 2000) and demonstrated (e.g. Burke and Grime 1996) for plants in terrestrial ecosystems, e.g. disturbance created by cutting gaps facilitated seedling establishment of invaders in a limestone grassland in the UK (Burke and Grime 1996), and total cover of alien grasses increased after fire events in a seasonal submontane habitat in Hawai'i (Hughes *et al.* 1991).

Although the role of disturbance in mediating invasion success in marine macrophytes has been less well studied than for terrestrial plants (Valentine *et al.* 2007), there is

evidence that it can be important in the establishment of some species. For example, *Sargassum muticum* requires free space to establish successfully (e.g. Andrew and Viejo 1998; Britton-Simmons 2006), and recruitment of *Codium fragile* spp. *tomentosoides* into gaps in kelp beds is facilitated by the infestation of an invasive bryozoan which causes severe damage to kelp in the Gulf of Maine (USA) (Levin *et al.* 2002).

Disturbance that reduces the cover of native canopy forming algae also appears to be crucial for the establishment of the invasive kelp *Undaria pinnatifida* in subtidal habitats on the east coast of Tasmania (Valentine and Johnson 2003). Stable native algal canopies inhibit development of *U. pinnatifida* sporophytes primarily through competition for light (Valentine and Johnson 2003; Valentine *et al.* 2007) and disturbance seems required for the sporophytes to establish at high densities in subtidal habitats (Valentine and Johnson 2003; Edgar *et al.* 2004; Valentine and Johnson 2004). In the subtidal environment, the formation of urchin barrens, where native algae are overgrazed by sea urchins, is the major disturbance that contributes to *U. pinnatifida*'s invasion success (Valentine and Johnson 2003; Valentine and Johnson 2005). While the formation of urchin barrens does not take place in intertidal habitats, other types of disturbance promoting *U. pinnatifida* invasion could occur in this environment. Nevertheless, to my knowledge, the role of physical disturbance in *U. pinnatifida*'s invasion success has not been examined on rocky intertidal shores.

The role of disturbance in macroalgal communities and invasion success may be size-dependent. Small cleared patches may recover quickly from disturbance by rapid recruitment from neighbouring algae, mainly through vegetative propagation, which may inhibit or outcompete recruitment of invasive macroalgae (Sousa 1979, 1984a). In larger cleared areas, recolonisation usually occurs through a combination of vegetative propagation along the edges of the cleared patch bordering the intact neighbouring algal population, and recruitment through sexual propagules, in which spores dispersed from plants in adjacent areas are transported through the water column and settle in the cleared patch (Sousa 1979, 1984b; Keough 1984; Farrell 1989; Kim and DeWreede 1996). Timing of disturbance can affect community dynamics of algal assemblages due to

species-specific seasonal patterns of growth and recruitment (Kennelly 1987; Benedetti-Cecchi and Cinelli 1994; Kim and DeWreede 1996). Therefore, timing of disturbance may be important in colonisation success of invasive species into cleared areas. For example, in Valentine and Johnson's (2003) study in Tasmania, *U. pinnatifida* recruited in higher densities when the native canopy was removed immediately prior to the sporophytes growth season (winter), compared to native canopy removal prior to *U. pinnatifida* spore release (spring). However, in some populations in New Zealand, *U. pinnatifida* is not a strict winter annual (Hay and Villouta 1993; Thornber *et al.* 2004) and may release spores and reproduce year-round. Therefore, it is not clear how *U. pinnatifida* recruitment would respond to clearings in different seasons. *U. pinnatifida* recruitment success may be influenced by the seasonality of native species and competition may take place if they are recruiting at the same time.

In this study I examined the role of disturbance in the invasion success of *U. pinnatifida* on low intertidal rocky shores. Mature *U. pinnatifida* individuals can release millions of spores which disperse over a short distance (tens of metres), in the proximity of the adult plant. However, thalli dispersal can take place over long distance via drift (up to hundreds of meters to kilometres) (Forrest *et al.* 2000). Therefore, I used a field experiment where I cleared native algal assemblages from plots in a site where no *U. pinnatifida* was established at the start of the study, but was in close proximity (~ 150 m away) to a site with *U. pinnatifida* populations. I conducted experiments at two different times of year (summer and winter) to test if *U. pinnatifida* recruitment depends on the timing of the disturbance, and used clearings of different sizes (total and partial clearings) to test if recruitment in newly created space is dependent on the amount of free space. I hypothesised that *U. pinnatifida* recruitment would be higher in the total clearings, as levels of free space and light availability would be higher and these levels would be maintained for longer in this treatment compared to the partial clearings, which would recover from the disturbance more quickly by rapid propagation from neighbouring algae. In addition, I predicted that *U. pinnatifida* would recruit faster into cleared plots after clearing in winter because even if *U. pinnatifida* is able to reproduce year-round in this region, the majority of plants may still follow a winter annual strategy. Also, native

algae generally have a considerably slower growth and lower recruitment during winter and recovery from disturbance is likely to take longer in this season, and hence they are more likely to be outcompeted by *U. pinnatifida* during winter months.

MATERIALS AND METHODS

Study site

This study was conducted in the low-intertidal of the rocky shore at Breaker Bay, Wellington, New Zealand (41º20`S, 174º49`E). The rocky intertidal substratum at this site consists of sedimentary greywacke. The selection of this site was based on the presence of *U. pinnatifida* in adjacent areas but not in the study site itself. The entire study site was surveyed extensively in November and December 2008 (before experimental set-up) and no *U. pinnatifida* recruits or mature individuals were detected. Established *U. pinnatifida* populations (~15 plants m^{-2}) were present on either side of the study area at ca. 150 m distance.

This experiment was conducted twice: December 2008 (early summer) and June 2009 (early winter). Both times twenty-one 0.25 m^2 quadrats were selected at random along ~700 m of coastline at 0.4 – 0.7 m above mean low water springs (MLWS) and the corners of each quadrat were marked with buttons of marine epoxy (Z-spar brand, Splash Zone 788, Kop-Coat Inc., United States). Two clearing treatments and a control treatment were randomly allocated to the quadrats (n = 7 replicates per treatment). The first treatment was a total clearing treatment in which all algae were cleared from the substratum with a scraper, leaving bare substratum (100% clearing). Disturbance created by scraping is similar to natural (or anthropogenic) disturbance and I did not intend to remove all living matter (e.g. by burning) as this is not representative of disturbance that could happen 'naturally' (Farrell 1989; Dye 1993; Airoldi 2000). The second treatment was a partial clearing in which 50% of the algal cover was scraped off in a checkered pattern. To establish this, the quadrat was equally divided into 16 squares (12.5 x 12.5 cm) of which every other square was cleared (8 in total). Additionally, canopy forming

algae outside the quadrats that were overhanging cleared quadrats were cut back to eliminate possible edge effects. The control plots were left untouched. Due to the heterogeneous nature of the substratum with a high abundance of crevices, complete removal of algae by scraping was sometimes difficult, and small algal fragments remained in some crevices, although total percent cover of these fragments in the quadrat never exceeded 2%. Also, crustose algae were not completely removed by using the scraper and still covered ~ 15-18% in the majority of the quadrats after scraping.

The first run (clearings conducted in summer [December 2008]) was monitored 3, 6, 9, and 12 months after establishment. The second run (clearings conducted in winter [June 2009]) was monitored 3 and 6 months after establishment. Monitoring the plots consisted of extensive investigation of understory, overstory, and bare space of each quadrat to identify and count *U. pinnatifida* recruits, and record algal species. Algae larger than ca. 3 mm were included. *U. pinnatifida* individuals were measured at the last sampling event in December 2009. Digital photographs were taken of each quadrat at every sampling event. Due to time pressure in the field (incoming tide), total percentage cover of the algal species was visually estimated later, using the digital photographs. Algal species that were recorded in the quadrats and the functional groups they were classified to are shown in Appendix 4.1.

Data analysis

To test whether *U. pinnatifida* recruitment was different across treatments, I employed a permutational ANOVA design (Anderson 2001; Anderson and Ter Braak 2003) (using 9999 permutations) on raw data. I examined the effects of treatment and time after manipulation (fixed factors) and quadrats (random factor) nested within treatment to account for repeated measures, using the number of *U. pinnatifida* individuals per quadrat as the response variable. Analysis was based on a Bray-Curtis similarity matrix using a dummy variable to account for zeros in the dataset.

The effect of treatment (3 levels) on total macroalgal cover was tested for each sampling time separately using one-way ANOVA. Bartlett's test showed homogeneity of variances

of the data. I excluded crustose algae from the analysis since algal crust was hard to remove during the clearing process and because this algal group is readily overgrown by other (upright) species making underestimation of crustose cover likely in quadrats with high algal cover. When significant treatment effects were found, Tukey's post-hoc tests were performed to indicate the difference between treatments.

PERMANOVA was conducted with PRIMER v6 + PERMANOVA (PRIMER-E Ltd, Plymouth Marine Laboratory, UK). ANOVA analyses were carried out using R version 2.9.2 (R Development Core Team, R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Undaria pinnatifida *recruitment*

Undaria pinnatifida recruitment was not affected by treatment in both runs, but was by time (Table 4.1A and 4.1B). There was also a significant effect of quadrat nested within treatment (Table 4.1A and 4.1B). The number of *U. pinnatifida* sporophytes increased over the course of the experiment (Figure 4.1). In the summer run (clearing in Dec 2008) *U. pinnatifida* did not appear until 6 months after clearing (Jun 2009), whereas in the winter run (clearing in Jun 2009) it appeared 3 months after clearing (Sep 2009) (Figure 4.1). However, in the summer run *U. pinnatifida* first appeared in the total and partial clearings, but in the winter run it first appeared in the control plots. By December 2009 *U. pinnatifida* had recruited to all treatments in both the winter and summer experiments (Figure 4.1). In December 2009, plants ranged in size from ~ 10 to 37.5 cm for the summer run, and from ~ 5 to 40 cm for the winter run.

Table 4.1A: PERMANOVA for difference in U. pinnatifida *recruitment across treatments for first run (clearing in summer [Dec 2008])*

	df	***SS***	***MS***	***Pseudo-F***	***P(perm)***	***Unique perms***
Treatment	2	74.318	37.159	<<0.01	0.9765	27
Time	4	2535.4	633.85	4.3503	**0.0032**	9883
Quadrat (Treatment)	18	7499.9	416.66	2.8597	**0.0016**	7624
Treatment x Time	8	566	70.75	0.48558	0.8875	9856
Residuals	72	10491	145.7			
Total	104	21166				

Table 4.1B: PERMANOVA for difference in U. pinnatifida *recruitment across treatments for second run (clearing in winter [June 2009])*

	df	***SS***	***MS***	***Pseudo-F***	***P(perm)***	***Unique perms***
Treatment	2	98.236	49.118	0.11957	1	46
Time	2	2055.6	1027.8	4.8226	**0.0072**	8784
Quadrat (Treatment)	18	7394.2	410.79	1.9275	**0.0394**	4621
Treatment x Time	4	596.18	149.05	0.69934	0.6296	8804
Residuals	36	7672.5	213.12			
Total	62	17817				

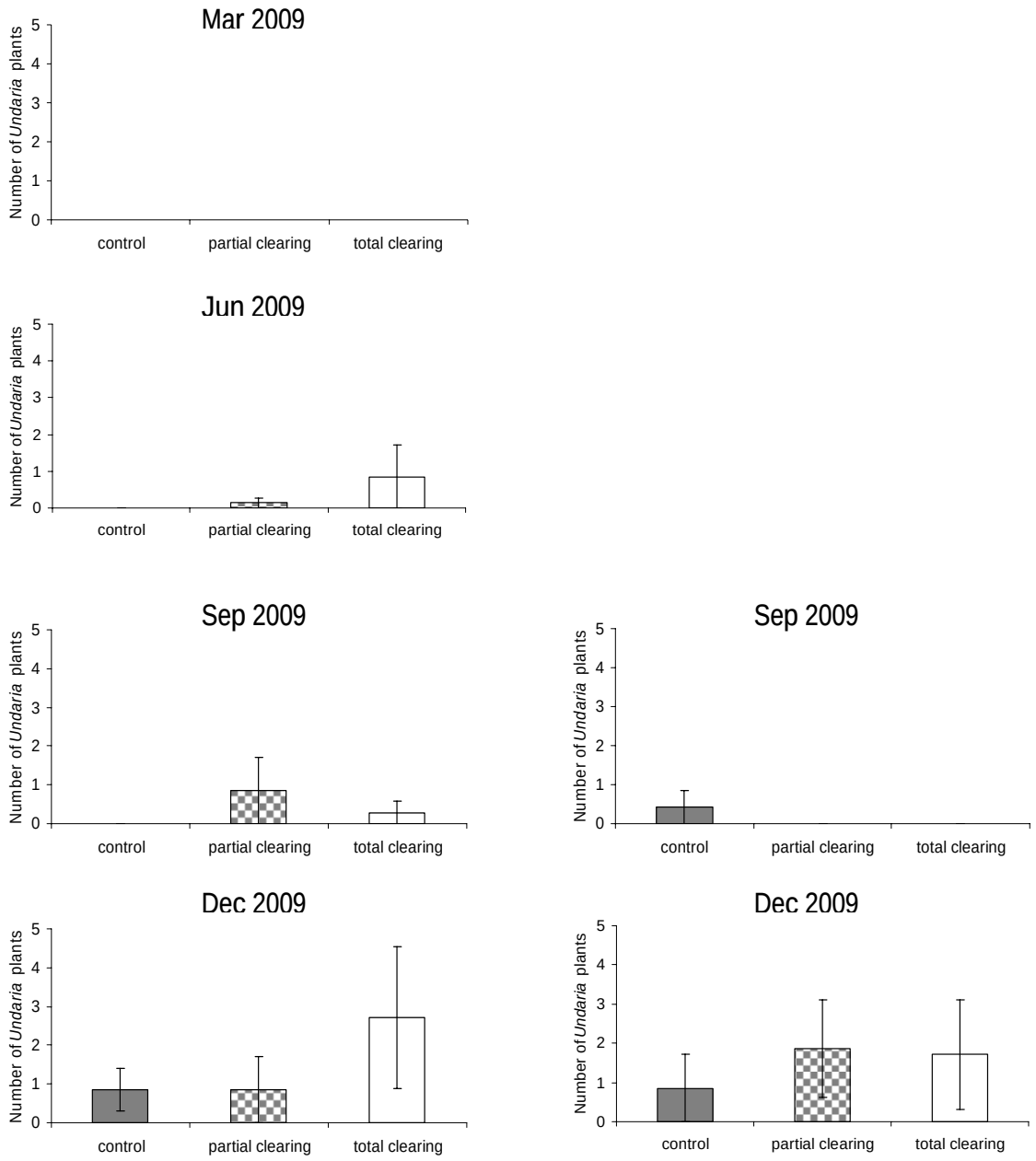


Figure 4.1: Average number of Undaria pinnatifida *individuals per 0.25 m^2 (50 x 50 cm) quadrat in control (grey), partial cleared (checkered), and total cleared (blank) treatments at 3 (Mar 09), 6 (Jun 09), 9 (Sep 09), and 12 months (Dec 09) after manipulation (for clearing in summer) (left), and 3 (Sep 09) and 6 months (Dec 09) after manipulation (for clearing in winter) (right). N = 7 for each treatment. Error bars represent standard errors.*

Macroalgal cover

In the first run, total macroalgal cover was significantly different among treatments for all sampling times except 9 months after clearing (Figure 4.2). Post-hoc tests (^{A,B}; Figure 4.2) showed that after clearing in summer, total macroalgal cover at 3 and 6 months was similar in partial and control plots, and both had around two times higher cover than totally cleared plots. By 12 months after clearing partially cleared plots had a significantly higher algal cover than totally cleared plots (Figure 4.2). The effects of clearing in winter (Figure 4.2) showed a different pattern. Three and 6 months after clearing the totally and partially cleared quadrats were not significantly different in terms of total macroalgal cover, but both had approximately 2-3 times lower algal cover than the control quadrats (Figure 4.2).

Figure 4.3 shows that the algal community composition (percent cover of algal functional groups) recovered rapidly in the partial clearings after summer clearing. Especially erect coralline algae cover increased quickly in the first six months, while corticated leathery macrophytes cover increased after 9 and 12 months. In the six months after winter clearing, only percentage cover of foliose algae increased in the partial clearings, while the other functional groups remained fairly constant. In the total clearings crustose algae and bare substratum together covered the majority of the quadrat area at all sampling events in both runs. The first colonizers after total clearing were corticated macrophytes, foliose algae, erect coralline algae, and some leathery macrophyte recruits. Mean percentage cover of large canopy species (mainly leathery macrophytes) never exceeded 24% in all treatments at all sampling times.

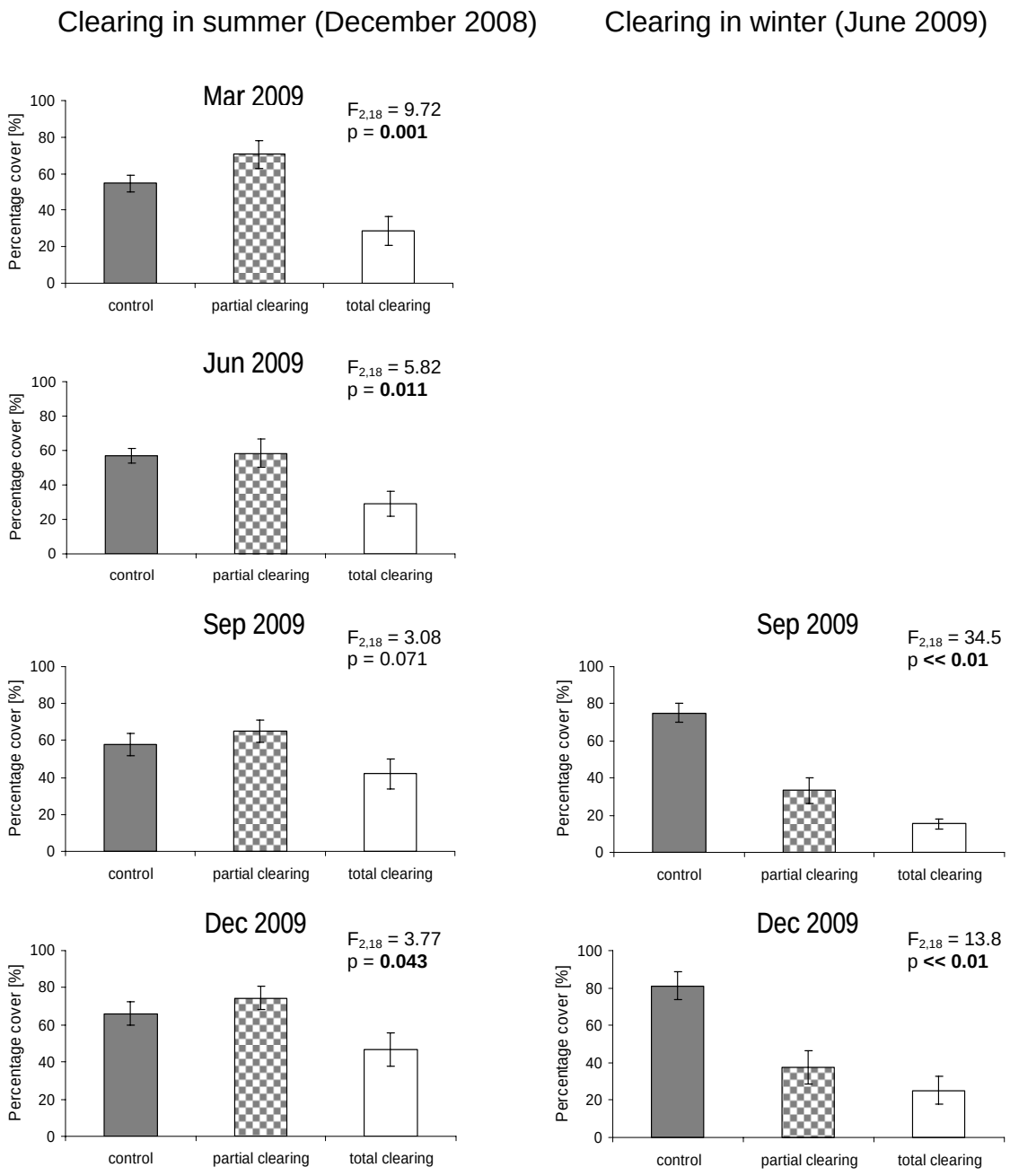


Figure 4.2: Mean total macroalgal percentage cover (excluding crustose algae) in control (grey), partial cleared (checkered), and total cleared (blank) treatments at 3 (Mar 09), 6 (Jun 09), 9 (Sep 09), and 12 months (Dec 09) after manipulation (for clearing in summer) (left), and 3 (Sep 09) and 6 months (Dec 09) after manipulation (for clearing in winter) (right). N = 7 for each treatment. Error bars represent standard errors. Results of one-way ANOVAs at each sampling time are shown in top-right corner of each panel. Significant P-values are shown in bold face. Tukey's post-hoc tests were performed to identify significant differences (P adj. < 0.05) among treatments (shown as $^{A, B}$*).*

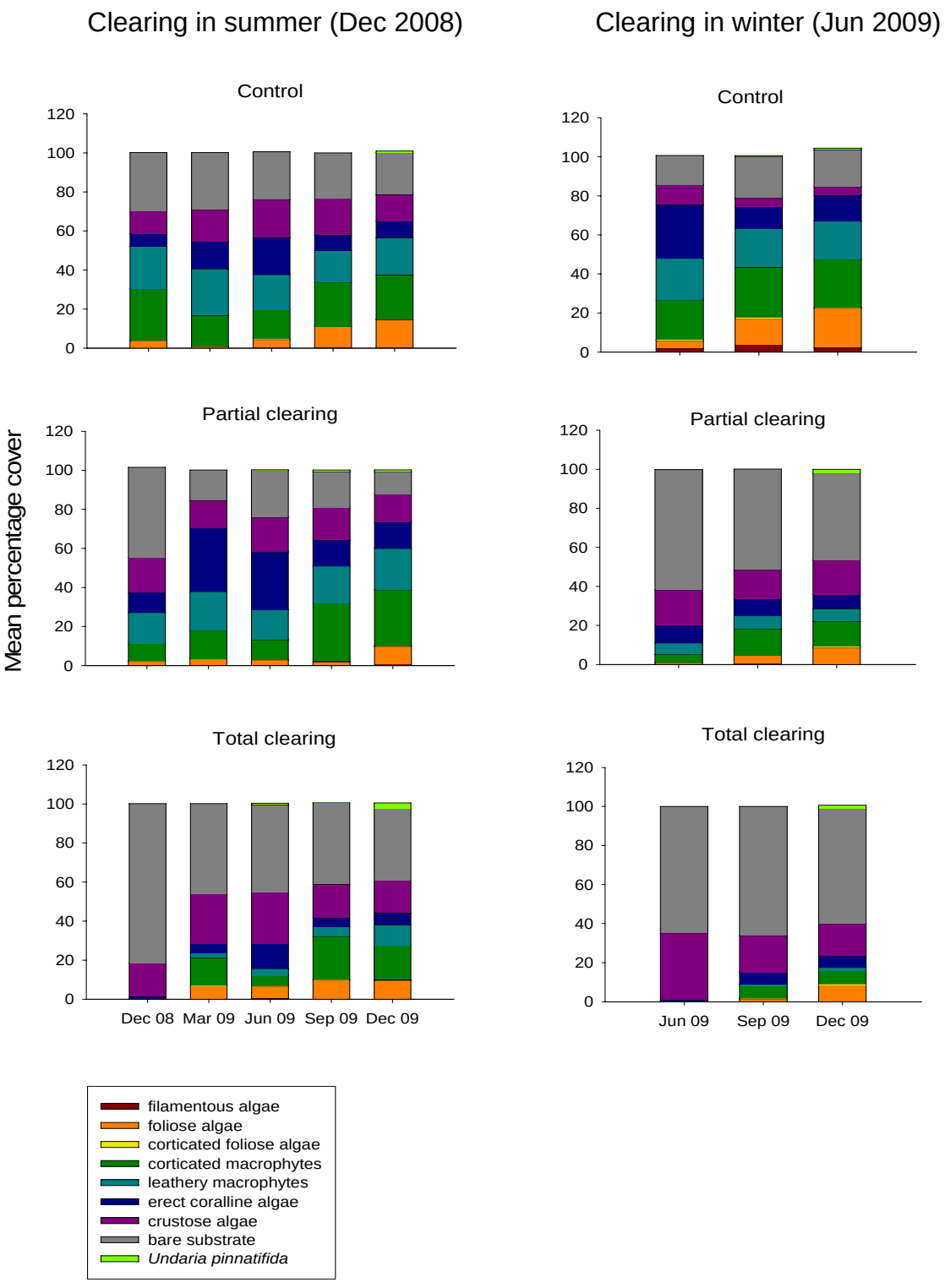


Figure 4.3: Mean percentage cover of algal functional groups over experimental period for control, partial clearing, and total clearing treatments after clearing in summer (Dec 2008) and clearing in winter (Jun 2009). N = 7 for each treatment. (Total cover can exceed 100% due to algal layering.)

DISCUSSION

Effect of disturbance on Undaria pinnatifida *recruitment*

Disturbance did not appear to affect recruitment success of *Undaria pinnatifida* in the intertidal habitat at this site. I did not find a significant effect of either partial or total clearing of the native algal cover on *U. pinnatifida* recruitment. Moreover, the fact that *U. pinnatifida* also recruited in the control treatments at both times suggests that removal of the native algal assemblage was not a key requirement for this kelp to invade and establish in the low intertidal zone in the Wellington region, or may indicate that sufficient natural disturbance was present. This result contrasts studies in subtidal habitats, where removal of native canopy species was necessary for *U. pinnatifida* establishment (Valentine and Johnson 2003; Edgar *et al.* 2004; Valentine and Johnson 2004).

Light limitation is believed to play a major role in determining algal community structure in subtidal environments, because development of gametophytes that have settled on the bottom is dependent on sufficient light for germination and growth, but they are more likely to be light limited in subtidal compared to intertidal environments. Not only does light attenuate with depth, but nearshore temperate subtidal habitats often have a high abundance of large canopy forming species (mostly laminarian and fucalean species) (Schiel 1988; Schiel and Hickford 2001) that can provide additional reduction in light availability (Reed and Foster 1984) compared to intertidal habitats. Hence, removal of canopy species can be a key requirement for recruitment and establishment of *U. pinnatifida* in subtidal habitats, which has also been shown for other kelp species (Reed and Foster 1984). Neither space nor light seem to be limiting resources in the intertidal habitat of this study site. Because algal assemblages in the rocky intertidal zone in the Wellington region are often discontinuous with bare substratum comprising a considerable proportion of total cover (>20% at this study site in control plots), my results suggest that free space may not be limiting for *U. pinnatifida* recruitment. This may, however, be different in other parts of the world, where intertidal algal assemblages

have more continuous cover and are space-limited. In these cases, disturbance that creates bare substratum may be necessary for establishment of invaders.

I observed that *U. pinnatifida* mainly colonised the outer quadrats of the study site, meaning the quadrats bordering adjacent areas. This could imply that propagules arrived into these quadrats from neighbouring populations, through spore dispersal in the water column or drift thalli (Forrest *et al.* 2000). The propagules may simply not have reached the inner quadrats as the distance from neighbouring *U. pinnatifida* populations could have been too large to bridge. However, the study site is subject to moderate wave action and spores, arguably, would have been able to be transported to the other quadrats as well.

Patterns of U. pinnatifida *recruitment*

The results of this study suggest an invasion in progress at the study site, starting in June – September 2009. By December 2009, this process appears more clearly under way with highest *U. pinnatifida* abundance across the site, regardless of clearing treatment. That invasion by *U. pinnatifida* occurred more rapidly in the second run (winter clearing) than in the first run (summer clearing) may be due to the fact that the second run started six months later than the first run. The first *U. pinnatifida* recruits had already started to establish within the site when the second run was initiated, indicating that neighbouring *U. pinnatifida* populations were expanding and invading the study site. Even though the recruits were not found in proximity of the quadrats of the second run, it could be argued that propagules from mature sporophytes may have been in closer vicinity to these quadrats compared to six months earlier when the first run was set-up, giving the second run a head start. The higher *U. pinnatifida* recruitment after six months in the second run could have been influenced by increased availability of propagules from neighbouring individuals.

U. pinnatifida has been observed to die back to lower abundance during summer months in other sites around the Wellington region (personal observation; Chapter 5). Even though I did find some young *U. pinnatifida* recruits during the last sampling in

December 2009, I noticed signs of senescence in a large number of the mature sporophytes, indicating that seasonality may be the major factor in the patterns I observed. The senescence was mainly observed in the individuals in quadrats of the first run, and the small recruits were primarily found in the quadrats of the second run. Senescence was likely caused by a combination of season and age of the individuals. However, the presence of recruits in late spring shows that *U. pinnatifida* is capable of producing multiple cohorts in this area, yet the majority of *U. pinnatifida* individuals may still follow its winter seasonality as characteristic for this alga in its native range (Hay and Luckens 1987; Thornber *et al.* 2004), resulting in a greater abundance in late spring.

Recovery of native macroalgae after disturbance

Recovery of the total macroalgal cover in partially and totally cleared plots depended on the timing of the clearing. Partially cleared quadrats that were cleared in summer recovered quickly and returned to their original cover within three months. However, when clearing was performed in winter, recovery of the partially cleared quadrats took longer. Opportunistic foliose algae (mainly *Ulva* spp.) colonised bare space, but cover of other algal functional groups remained fairly steady. Total algal cover was still lower in these quadrats than in the control plots by December 2009, six months after manipulation. Recovery of the totally cleared quadrats took longer than the partially cleared ones after summer clearing. However, after winter clearing recovery of partially and totally cleared quadrats was slower and total algal cover in these two treatments was still lower than in controls three and six months later. This could imply that when disturbance takes place in winter, cleared areas may be more susceptible to invasion as it takes longer for native macroalgae to regain cover, enabling opportunistic *U. pinnatifida* to take advantage of newly available resources like space and light. Invasion by *U. pinnatifida* was quicker following winter clearing, yet this result was likely due to a combination of an invasion already in progress across the study site, seasonality of *U. pinnatifida,* and characteristics of the native community, and not caused by clearing or speed of recovery of the native assemblage as *U. pinnatifida* also recruited into control quadrats. The native community at this site has a considerable cover of crustose algae and bare substratum, and a limited

cover of large canopy species, suggesting that space and light may not be limiting in this habitat, which may contribute to the habitat's invasibility.

Conclusion

Suitable substratum (space) is a key requirement for successful settlement and early growth of macroalgal colonists, and access to ample light and nutrients is essential for their continued development (Arenas *et al.* 2006). Previous research has shown that algal communities dominated by crustose algae showed higher or similar biomass of colonizers as bare rock (Arenas *et al.* 2006). Because communities dominated by crustose algae contain high levels of the two major resources, space and light, these habitats are more susceptible to invasions. On the contrary, canopy forming algae appear to inhibit colonization, probably due to a reduction in light reaching the substratum (Middelboe and Binzer 2004; Arenas *et al*. 2006). In this study, there was ample cover of bare rock and crustose algae in the low intertidal zone and the created disturbance may not have contributed to a significant increase of limiting resources, as these were already available before algae were cleared. In addition, the presence of large canopy forming species, which can reduce light availability, was limited in this habitat. Hence, sufficient availability of space and light at this site may have facilitated *U. pinnatifida* recruitment regardless of disturbance. Moreover, the results of this experiment show that *U. pinnatifida* is still expanding its range in the Wellington Region. In this experiment, I observed new *U. pinnatifida* recruits within 3 to 6 months after the first experiment was established. I noted that *U. pinnatifida* was becoming increasingly abundant in the study area over the experimental period, both inside and outside the quadrats, and especially in the shallow subtidal zone. Even though mean percent cover of *U. pinnatifida* did not exceed 3% (highest recorded percent cover was 12%) in the experimental plots, this study demonstrates that the alga is capable of rapid invasion and indicates that disturbance of the native macroalgal cover is not necessary for this kelp to invade low-intertidal habitats.

Appendix 4.1: *Algal species or taxonomic units recorded in the quadrats of the 'clearing' experiment and the functional group to which they were classified (modified from Steneck and Dethier 1994 and Guerry* et al. *2009; pers. comm. M. Dethier)*

Species	***Functional group***	***Division***
Ceramium spp.	Filamentous	Rhodophyta
Lophothamnion hirtum	Filamentous	Rhodophyta
Brown turf	Filamentous	Phaeophyta
Green turf	Filamentous	Chlorophyta
Red turf	Filamentous	Rhodophyta
Unidentified red filamentous	Filamentous	Rhodophyta
Unidentified red filamentous epiphyte	Filamentous	Rhodophyta
Unidentified brown filamentous	Filamentous	Phaeophyta
Porphyra spp.	Foliose	Rhodophyta
Ulva intestinalis	Foliose	Chlorophyta
Ulva lactuca	Foliose	Chlorophyta
Endarachne binghamiae	Corticated foliose	Phaeophyta
Gigartina atropurpurea	Corticated foliose	Rhodophyta
Glossophora kunthii	Corticated foliose	Phaeophyta
Hymenena spp	Corticated foliose	Rhodophyta
Pachymenia lusoria	Corticated foliose	Rhodophyta
Zonaria turneriana	Corticated foliose	Phaeophyta
Champia nova-zelandiae	Corticated macrophytes	Rhodophyta
Chondria macrocarpa	Corticated macrophytes	Rhodophyta
Codium convolutum	Corticated macrophytes	Chlorophyta
Colpomenia bullosa	Corticated macrophytes	Phaeophyta
Colpomenia sinuosa	Corticated macrophytes	Phaeophyta
Gelidium caulacantheum	Corticated macrophytes	Rhodophyta
Gigartina livida	Corticated macrophytes	Rhodophyta
Halopteris spp.	Corticated macrophytes	Phaeophyta
Laurencia thyrsifera	Corticated macrophytes	Rhodophyta
Leathesia spp.	Corticated macrophytes	Phaeophyta
Lophurella caespitosea	Corticated macrophytes	Rhodophyta
Scytothamnus australis	Corticated macrophytes	Phaeophyta
Splachnidium rugosum	Corticated macrophytes	Phaeophyta
Carpophyllum flexuosum	Leathery macrophytes	Phaeophyta
C. maschalocarpum	Leathery macrophytes	Phaeophyta
Cystophora retroflexa	Leathery macrophytes	Phaeophyta
C. scalaris	Leathery macrophytes	Phaeophyta
C. torulosa	Leathery macrophytes	Phaeophyta
Hormosira banksii	Leathery macrophytes	Phaeophyta
Undaria pinnatifida	*Undaria pinnatifida*	Phaeophyta
Coralline spp. (erect)	Erect coralline algae	Rhodophyta
Encrusting coralline algae	Crustose algae	Rhodophyta
Unidentified brown crust	Crustose algae	Phaeophyta

CHAPTER 5

INTERTIDAL COMMUNITY RESPONSE TO REMOVAL OF THE INVASIVE ALGA *UNDARIA PINNATIFIDA* (HARVEY) SURINGAR

ABSTRACT

Removal of dominant canopy species from a community can increase the availability of limiting resources, which may result in increased species diversity and richness, and changes in recruitment and abundance of understory species. In the Wellington region, *Undaria pinnatifida* is abundant on intertidal shores and could potentially have considerable impact on native communities. In this study, the response of native algal assemblages to removal of *U. pinnatifida* was investigated at low-intertidal sites in the Wellington Harbour and on the south coast. The hypothesis that the removal of this invasive kelp would result in a higher abundance of native algae and a different macroalgal species composition due to increased space and light availability was not supported. Native algal assemblage composition, species diversity and species richness were not affected by the *U. pinnatifida* removal treatment, but strong differences were found in community structure and diversity between the harbour and the south coast.

INTRODUCTION

The impact and success of an invasive species depend not only on the characteristics of the invasive species itself, but also on the characteristics of the target community and the interaction between the introduced species and the community (Lodge 1993). For example, the Chinese tallow tree (*Sapium sebiferum*) is an important invader of habitats

in southern USA. In Texas, it has a great impact on native species as it is able to develop greater competitive ability because of low herbivory, which allows it to become more abundant and hence become invasive. In contrast, in Hawai'i this does not seem to occur because herbivores (from the native range) are abundant (Siemann and Rogers 2003). Characteristics of the target habitat can also determine the invasibility and the success of an invader (Lodge 1993). For instance, the introduced European shore crab *Carcinus meanas* is a great threat to native species in sheltered lagoon habitats in South Africa. However, it appears to be unable to colonise open coast habitats and is, therefore, unlikely to have a great impact on prey species or displace native crabs on wave-exposed shores (Griffiths *et al.* 1992).

Undaria pinnatifida is a fast-growing invasive macroalgal species that could potentially displace native algal species (Battershill *et al.* 1998) and outcompete smaller or slower-growing algal species for light, which could ultimately lead to a reduction in biodiversity. Several studies in subtidal habitats have shown that *U. pinnatifida* may cause shifts in community structure and a decrease biodiversity and species richness of native algae, e.g. in Venice, Italy (Curiel *et al.* 1998), in Patagonia, Argentina (Casas *et al.* 2004), and in the Wellington Harbour, New Zealand (Battershill *et al.* 1998). The effects of *U. pinnatifida* on low-intertidal assemblages have not been investigated as often. Forrest and Taylor (2002), however, found no evidence of displacement of native canopy species by *U. pinnatifida* in low-intertidal habitats in Lyttelton harbour, New Zealand.

In this experiment I investigated how native algal communities responded to removal of *U. pinnatifida* by examining whether native algal species abundance and composition differed among treatments and between two locations, the shores of Wellington Harbour and of the south coast that faces Cook Strait. I hypothesised that the removal of this invasive kelp from low-intertidal quadrats would increase space and light resources, resulting in a higher abundance of native algae, and a different macroalgal species composition as (opportunistic) algae take advantage of the newly freed resources. I also tested whether native herbivore abundance and composition changed when *U. pinnatifida* was removed.

There are many well-known differences between the shores of the Wellington Harbour and those of the south coast. For instance, the intertidal zone in the harbour has a greater cover of barnacles and mussel beds, while these are mostly absent on intertidal shores of the south coast (Morton and Miller 1968). Although evidence for dissimilarity in algal communities between harbour and south coast is weaker, and variability in community composition was greater among sites than between these two locations (Chapter 2), there still might be a location-level response to removal of *U. pinnatifida* due to other factors, e.g. wave exposure, desiccation, temperature, and grazer abundance. Even though results in Chapter 2 did not demonstrate a significant difference in algal community composition between these two locations, some trends in abundance of algal functional groups were shown. For example, foliose and erect coralline algae were more abundant on the south coast, while harbour sites showed a greater cover of corticated macrophytes and bare substratum, which may affect how the communities respond to the removal of *U. pinnatifida.*

The approach of this study is novel as the majority of studies on *U. pinnatifida* are conducted in subtidal habitats, but little research has been conducted on this invader in intertidal habitats using experimental manipulations in the field to examine ecological impacts on native intertidal communities.

METHODS AND MATERIALS

Experimental design

Ten 0.25 m^2 quadrats (50 x 50 cm) were randomly selected in the low intertidal (0.4-0.7 m above mean low water springs [MLWS]) along ~250 m of coastline at each of four sites within the Wellington Region, New Zealand: Island Bay (41º21'S, 174º46'E) and Moa Point (41º20'S, 174º48'E) (distance between sites ~ 3.4 km) on the south coast, and two sites at Shelly Bay (41º17'S, 174º49'E) (distance between sites ~ 0.75 km) in the Wellington Harbour. The two sites within each location were considered replicates. Rocky intertidal substratum around Wellington consists of sedimentary greywacke, and is

highly heterogeneous with a high degree of vertical relief. The selection of sites was based on adequate *U. pinnatifida* presence in the low-intertidal zone within sites and suitability of the substratum for 0.25 m^2 quadrats. Sites on the south coast were selected at relatively sheltered places to minimize confounding effects of wave exposure.

The corners of the quadrats were permanently marked with buttons of marine epoxy (Z-spar brand, Splash Zone 788, Kop-Coat Inc., United States) on the substratum. Five of the quadrats at each site were randomly assigned to a removal treatment, in which all *U. pinnatifida* plants were removed by carefully chiselling the holdfast off the substratum at the start of the experiment ('pulse' removal), leaving the remaining algal assemblage intact. The other 5 quadrats were left unmanipulated (controls), and thus still contained *U. pinnatifida* cover. Mean *U. pinnatifida* density in the quadrats at the start of the experiment was 27.4 ± 4.84 m^{-2} (mean ± SE, n = 20) in the harbour and 24.6 ± 2.92 m^{-2} (mean ± SE, n = 20) on the south coast. Mean length of plants removed from the quadrats was 23.16 ± 1.56 cm (mean ± SE, n = 151); with individuals from the south coast (33.45 ± 2.83 cm; mean ± SE, n = 69) being considerable larger than the ones from the harbour (14.49 ± 1.11 cm; mean ± SE, n = 82). Mean *U. pinnatifida* dry weight per quadrat was 66.38 ± 13.76 g (mean ± SE, n = 20), with considerably greater biomass per quadrat at the south coast sites (92.16 ± 22.14 g; mean ± SE, n = 10) compared with the harbour sites (40.60 ± 12.69 g; mean ± SE, n = 10) at the start of the experiment.

To investigate whether removing *U. pinnatifida* has a different effect on (native) algal recruitment than just through increasing available bare space; five additional quadrats were established at each of the four sites. These quadrats were selected at the same tidal height as the others but only contained native algal species. An equivalent amount of cover of native algae was removed haphazardly as was taken up by the *U. pinnatifida* holdfasts in the *U. pinnatifida* removal treatments, although care was taken not to affect species richness while carrying out removal. However, statistical analysis showed that there was a difference in algal community composition between this treatment and the other two treatments in which *U. pinnatifida* was contained or removed. Therefore, this third (control) treatment was omitted from analyses. Because quadrats in each treatment

contained a considerable cover of bare substratum (17.53% ± 3.34 SE in harbour; 18.77% ± 3.09 SE on south coast before manipulation), controlling for the removal of *U. pinnatifida*, and hence creating some additional bare space, was not considered necessary.

This experiment was established in November (spring) 2008. Algal abundance and percentage cover was measured before experimental manipulation (November 2008), after four (March 2009) and six months (May 2009). All algal species larger than approximately 3 mm were included in the censuses. Censuses were conducted in the field by means of recording of algal species and visually estimating algal percentage cover using a 50 x 50cm quadrat subdivided in 25 sub-quadrats. Overstory and understory algal cover was recorded. Due to overstory canopy algae overlapping smaller understory species, the total percentage cover occasionally added up to more than 100 percent. Digital photographs of the quadrats were also taken. When conditions in the field did not allow censuses in the field, visual estimation of algal percentage cover was done from digital photographs. Invertebrate species and abundance within the quadrats were recorded at the end of the experiment (May 2009).

The Shannon diversity index was determined for every quadrat using the following equation:

$$H' = -\sum p_i (\ln p_i)$$

where p_i is the relative abundance of each macroalgal species, calculated as the cover of species *i* divided by the total macroalgal cover.

Algal species were later classified into algal functional groups (Appendix 5.1).

Data analysis

The effects of the treatments on species richness of native algal assemblages (S) and the Shannon index of diversity (H') were analysed using two-way analysis of variance (ANOVA) using the cover data of all algal species before experimental manipulation (November 2008), after four months (March 2009), and at the end of the experiment (six months, May 2009). The assumption of equal variances (using Bartlett's test) was met for

both response variables. Treatment ('*U. pinnatifida* removed' and '*U. pinnatifida* present') and location ('harbour' and 'south coast') were both considered as fixed factors with two levels. Because the focus was on the response of the native algal communities to the treatments, *U. pinnatifida* percentage cover data was omitted from the analyses. To test the effect of treatment and location on total cover of native macroalgae, two-way ANOVA was used for each sampling time. Assumptions of normality and homogeneity of variances were met. Two-way ANOVA was also used to analyse the effect of treatments on mobile invertebrate numbers and diversity from the final sample date in May 2009. The R statistical package, version 2.9.2 (R development Core Team 2009) was used for univariate analyses.

Two-way crossed analysis of similarity (ANOSIM) (Clarke 1993; Clarke and Warwick 2001; Clarke and Gorley 2006) was used on algal percentage cover data to test for differences in algal community composition between location (2 levels; harbour vs. south coast) and treatments (2 levels; *U. pinnatifida* removed vs. *U. pinnatifida* present), before experimental manipulation, 4 months, and 6 months after manipulation. Percentage cover data were square root transformed before analysis to reduce the influence of dominant species. The analyses were based on Bray-Curtis similarity matrices. When the ANOSIM test showed significant differences, two-way crossed SIMPER (similarity percentages) analysis (Clarke and Warwick 2001; Clarke and Gorley 2006) was conducted on square root transformed data to indicate which species contributed most to the dissimilarity between groups. Two-way crossed ANOSIM was also conducted for the harbour and south coast separately, using Treatment (2 levels) and Time (3 levels) as factors to test if algal community structure differed between treatments and sampling times.

Non-metric multidimensional scaling (nMDS) ordinations were used to describe the responses of the algal assemblages to the different treatments and the two locations. Percentage cover data were square root transformed before analysis. *U. pinnatifida* was omitted from the data set to check if differences between treatments were caused by changes in the native algal assemblages, and not by the presence of *U. pinnatifida.*

PRIMER v6 (Plymouth Marine Laboratory, Plymouth, UK) was used for multivariate statistical analyses.

RESULTS

Impact of U. pinnatifida *on native intertidal algal assemblages*

Two-way ANOVAs carried out before experimental manipulation (November 2008) did not detect a significant difference in species diversity and species richness among treatments or between locations prior to experimental manipulation ((P >> 0.05 for all; results not shown; Figure 5.1). Also, four months after set-up (in March 2009), no significant differences in species diversity and richness were found between treatments or locations (two-way ANOVA; P > 0.05 for all; results not shown). Six months after the experiment was established (May 2009), location had a significant effect on species diversity H' and species richness S (Table 5.1, 5.2), where the south coast had higher H' and S than the harbour (Figure 5.1). Treatment, however, did not have a significant effect on either of the two response variables (Table 5.1, 5.2; Figure 5.1).

Table 5.1: Two-way ANOVA for effect of treatment and location on species diversity H' (Shannon index) six months after manipulation

	Df	*Sum Sq*	*Mean Sq*	*F value*	*P*
Treatment	1	0.0253	0.0253	0.2173	0.644
Location	1	0.7615	0.7615	6.5535	**0.015**
Treatment:Location	1	0.0376	0.0376	0.3235	0.573
Residuals	36	4.1832	0.1162		

Table 5.2: Two-way ANOVA for effect of treatment and location on species richness (S) six months after manipulation

	Df	*Sum Sq*	*Mean Sq*	*F value*	*P*
Treatment	1	0.225	0.225	0.0809	0.778
Location	1	70.225	70.225	25.2557	**<<0.001**
Treatment:Location	1	0.225	0.225	0.0809	0.778
Residuals	36	100.100	2.781		

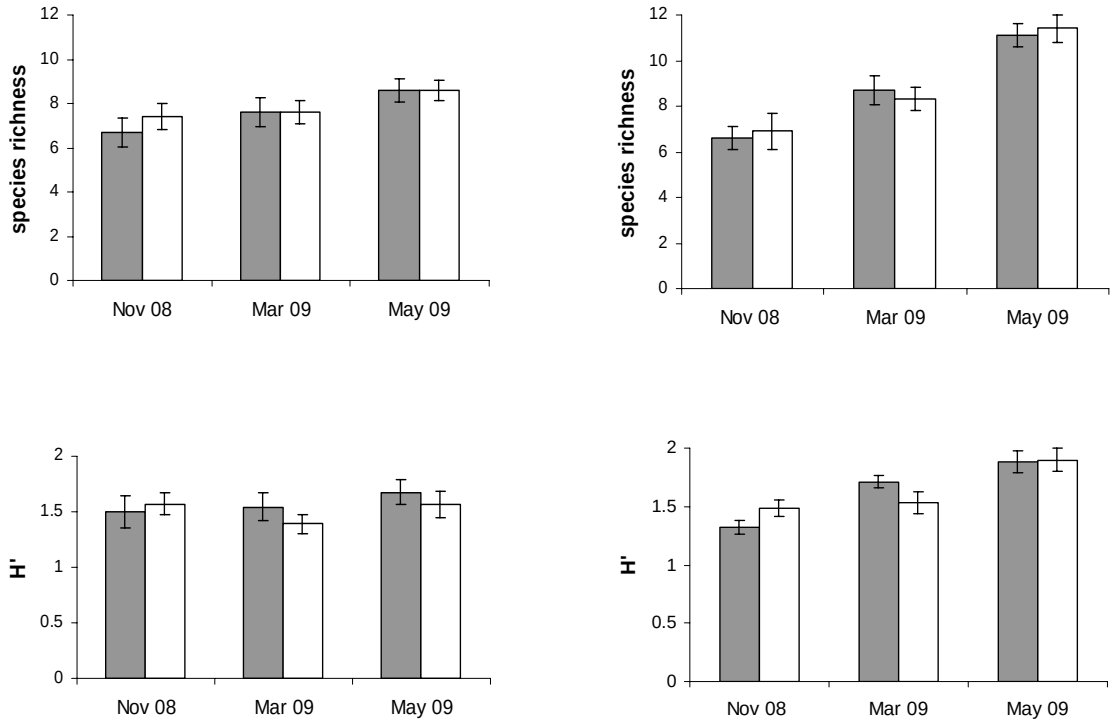


Figure 5.1: Mean species richness S (± 1 SE) (top) and mean species diversity H' (Shannon index) (± 1 SE) (bottom) at Wellington Harbour and Wellington south coast over the experimental period. Grey bars represent 'Undaria *removal' treatment; blank bare represent* 'Undaria *present' treatment. (Percent cover of* U. pinnatifida *was omitted from data set.)*

No effect of treatment on total native algal cover was found in this study, but algal cover was significantly different between the two locations before experimental manipulation and six months after manipulation (Table 5.3; Figure 5.2), with the south coast having a higher native algal cover than the harbour.

Table 5.3: Two-way ANOVA for effect of treatment and locations on total macroalgal cover

		November 2008			*March 2009*			*May 2009*		
	Df	MS	F	P	MS	F	P	MS	F	P
Treatment	1	235.2	0.628	0.433	2.0	0.004	0.948	2.0	0.005	0.945
Location	1	2356.2	6.294	**0.017**	855.6	1.854	0.182	2088.0	5.015	**0.031**
Treatment:Location	1	38.0	0.102	0.752	540.2	1.171	0.287	245.0	0.588	0.448
Residuals	36	374.4			461.5			416.4		

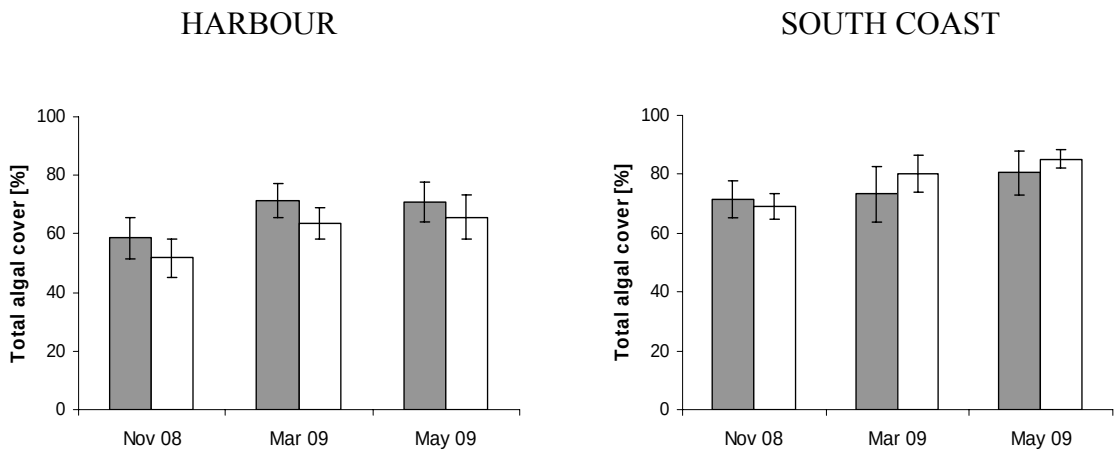


Figure 5.2: Mean algal cover (± 1 SE) at Wellington Harbour and Wellington south coast over the experimental period. Grey bars represent 'Undaria removal' treatment; blank bare represent 'Undaria present' treatment. (Percent cover of U. pinnatifida was omitted from data set.)

No significant difference in algal species composition between the different treatments was found before, 4 months after, and 6 months after manipulation using analysis of similarity, but a strong difference between the two locations was observed (Table 5.4). Two-dimensional nMDS ordinations show lack of treatment effect but strong difference between locations (Figure 5.3).

Treatment effect

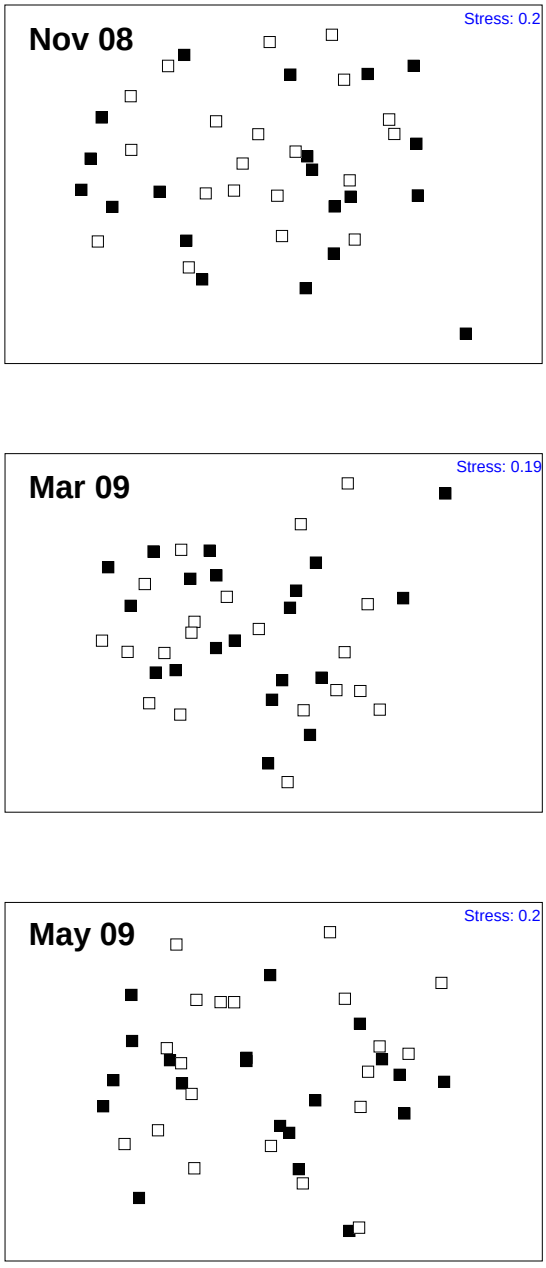


Figure 5.3A: nMDS ordinations of Treatment effect on algal community composition before experimental manipulation (Nov 08), four months after (Mar 09), and six months after (May 09) manipulation. Closed squares represent quadrats with 'Undaria removal' treatment; open squares represent quadrats with 'control' treatment.

Location effect

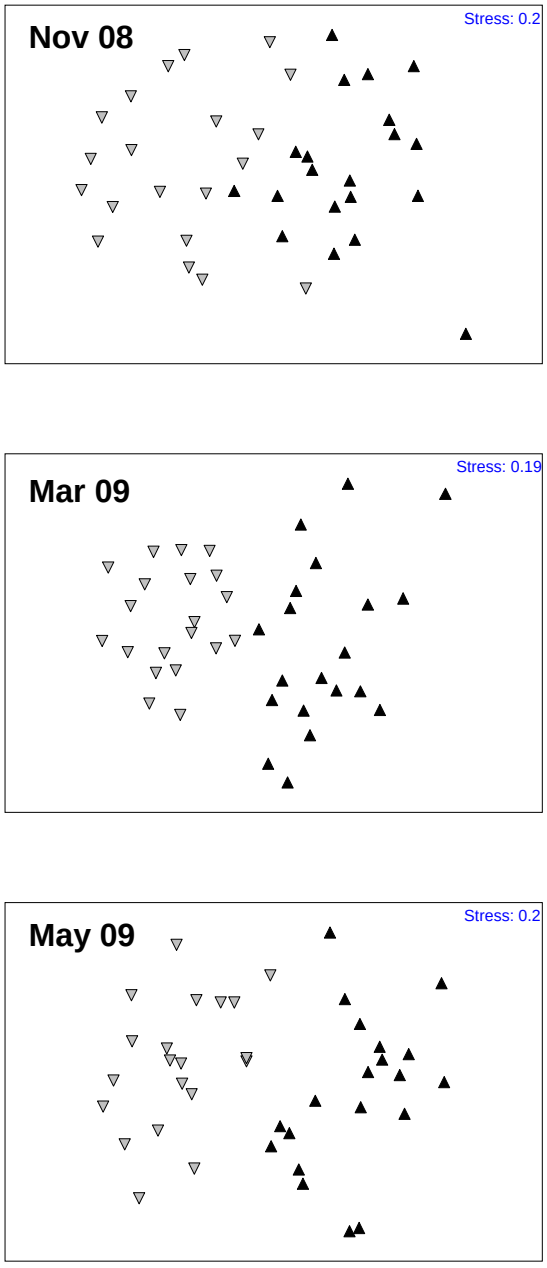


Figure 5.3B: nMDS ordinations of Location effect on algal community composition before experimental manipulation (Nov 08), four months after (Mar 09), and six months after (May 09) manipulation. Black triangles represent 'harbour' quadrats; grey triangles represent 'south coast' quadrats.

Table 5.4: Two-way crossed ANOSIM for difference in algal species composition with factors Treatment (2 levels) and Location (2 levels) before, 4 months after, and 6 months after experimental manipulation.

	Treatment		***Location***	
	R	p	R	p
Before	-0.044	0.809	0.487	<0.001
4 months	0.052	0.149	0.634	<0.001
6 months	-0.076	0.964	0.704	<0.001

Table 5.5: Two-way crossed SIMPER for each sampling time showing the relative species contribution % to the dissimilarity between locations. Only species contributing 5% or more to the dissimilarity were included.

A Before manipulation (Nov 08)

Average dissimilarity: 72.52

	Average abundance			
	Harbour	South coast	Contribution%	Cumulative %
Ulva spp.	0.3	3.25	12.12	12.12
Carpophyllum spp.	2.84	1.11	10.15	22.27
C. novae-zelandiae	1.81	3.35	9.82	32.08
Erect Coralline algae	2.78	1.65	8.79	40.87
C. macrocarpa	2.4	0.31	8.68	49.55
Cystophora spp.	0.7	1.8	6.66	56.22
Halopteris spp.	0.94	1.17	5.14	61.36

B Four months after manipulation (Mar 09)

Average dissimilarity: 65.05

	Average abundance			
	Harbour	South coast	Contribution%	Cumulative %
Ulva spp.	0.59	4.74	15.52	15.52
Carpophyllum spp.	2.93	1.01	9.94	25.46
C. sinuosa	2.88	0.73	8.62	34.08
Brown crust	1.83	1.5	7.71	41.79
Erect Coralline algae	3.23	2.85	7.3	49.09
CCA	1.52	2.94	7.06	56.15
G. caulacantheum	1.83	0.56	6.96	63.1
Cystophora spp.	1.01	1.94	6.64	69.74

C Six months after manipulation (May 09)

Average dissimilarity: 59.50

	Average abundance			
	Harbour	South coast	Contribution%	Cumulative %
Carpophyllum spp.	3.29	1.74	9.06	9.06
C. novae-zelandiae	0.65	2.9	8.3	17.35
Erect Coralline algae	3.69	3.07	8.03	25.39
Ulva spp.	0	2.09	7.5	32.89
Brown crust	2.09	1.72	7.11	39.99
Halopteris spp.	0	1.9	7	46.99
CCA	2.48	3.93	6.5	53.49
L. thyrsifera	1.95	0.55	6.31	59.8
Cystophora spp.	1.29	2.19	5.8	65.6

The species contributing most to the dissimilarity between the locations before the experiment was set up was *Ulva* spp., with the south coast having 10 times more than the harbour (Table 5.5A). After four months, *Ulva* spp. remained the species contributing most to the dissimilarity between the locations (Table 5.5B). *C. maschalocarpum* also contributes to 9-10% to the dissimilarity between the locations over all sampling periods (and has the greatest contribution after 6 months, Table 5.5C), with 2-3 times greater cover in the harbour than on the south coast at all times.

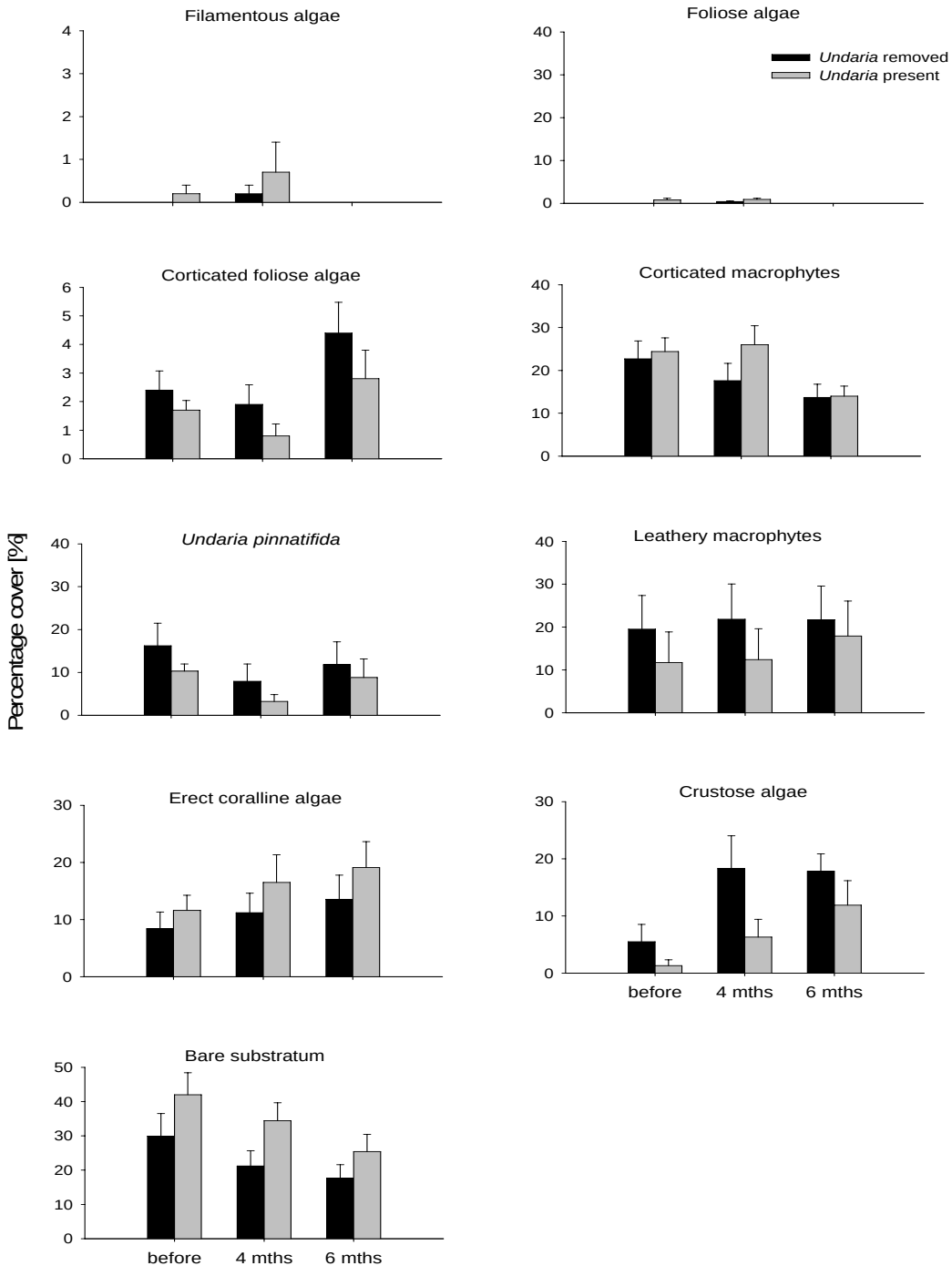
Because of the highly significant effect of Location on community composition ($p << 0.01$; Table 5.3), two 2-way crossed ANOSIMs were conducted for harbour and south coast separately with treatment (2 levels) and time (3 levels) as factors (Table 5.6). No difference in algal community composition was detected between treatments, but different sampling times did show a significant effect. Pairwise tests showed that for both locations, differences between all three sampling times were highly significant ($p < 0.001$).

Table 5.6: Two-way crossed ANOSIM for difference in algal species composition for harbour and south coast; treatment with 2 levels and time with 3 levels.

	Treatment		***Time***	
	R	p	R	p
Harbour	-0.02	0.659	0.382	<0.001
South coast	-0.025	0.713	0.274	<0.001

Figure 5.4 shows the change in the percentage cover of the algal functional groups over the experimental period. Like the SIMPER results in Table 5.5, the algal functional groups mainly responsible for the difference in algal composition between the two locations were foliose algae (e.g. *Ulva* spp.*)*, which was abundant on the south coast, but largely absent in the harbour, and the leathery macrophytes (mainly *Carpophyllum maschalocarpum)*, which were abundant in the harbour but not as abundant on the south coast. Filamentous algae made up a small percentage of the total cover but were more abundant on the south coast. After a peak at four months, there was a sharp decrease in the cover of foliose algae on the south coast at six months. At the same time, both the harbour and the south coast showed an increase in corticated foliose algae, erect coralline algae, and crustose algae, while corticated macrophytes cover decreased over the six month period. Bare substratum was higher in the harbour, and decreased over the six months, at both locations. After four months, *U. pinnatifida* had re-established in the quadrats where it had previously been removed in the harbour, and it gradually increased in cover over the remainder of the experiment. This trend, however, was not observed on the south coast, where all but one *U. pinnatifida* individuals had died off after four months, in both treatments. At six months, a small recovery in *U. pinnatifida* was observed in both treatments.

Wellington Harbour



Wellington south coast

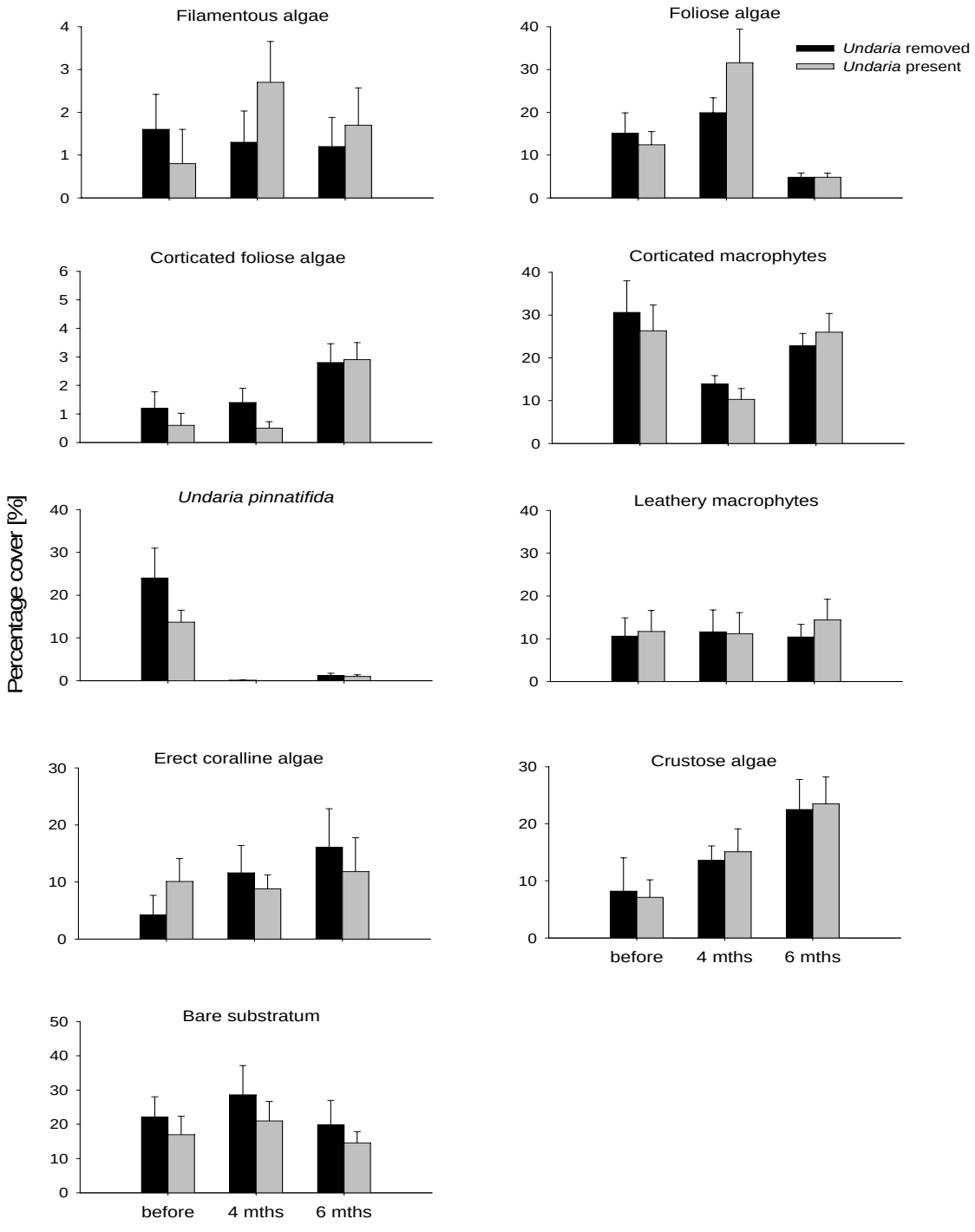


Figure 5.4: Change in algal assemblage composition (algal functional groups) over the experimental period in Wellington Harbour and on Wellington south coast, before, 4 months after, and 6 months after experimental manipulation. Black bars: 'U. pinnatifida *removed' treatment; grey bars: 'U.* pinnatifida *present' treatment (mean + 1 S.E.).*

Impact of U. pinnatifida *removal on mobile invertebrate numbers and diversity.*Two-way ANOVAs also showed a clear location effect ($p << 0.01$) on total number of invertebrate individuals (N), number of different invertebrate groups (S), and group diversity H'. Invertebrates were divided into groups as shown in Table 5.7. Wellington Harbour had much higher densities of mobile invertebrates (8.40 ± 1.11 SE individuals); species richness (S: 2.35 ± 0.18 SE); and diversity (H': 0.60 ± 0.07 SE) compared to the south coast (density: 1.95 ± 0.57 SE; S: 0.95 ± 0.21 SE; H': 0.20 ± 0.07 SE) six months after experimental manipulation. However, no treatment effect on mobile invertebrate indices was detected (Table 5.8).

Table 5.7: Mobile invertebrate group classification

Invertebrate group	***Species***
Limpets	*Cellana denticulata* *Cellana radians* *Onchidella spp*
Chitons	*Sypharochiton pelliserpentis*
Hervivorous snails	*Cookia sulcata* *Diloma spp.* *Melagraphia aethiops* *Turbo smaragdus*
Carnivorous snails (whelks)	*Cominella maculosa* *Haustrum haustorium*
Abalone (paua)	*Haliotis iris*
Sea stars	*Ophionereis fasciata* *Patiriella spp.*
Urchin	*Evechinus chloroticus*
Crab	*unidentified*

Table 5.8: Two-way ANOVA of treatment and location effects on mobile invertebrate densities and diversity in May 2009 (six months after experimental manipulation)

A Effect on total number of mobile invertebrate individuals (N)

	Df	*Sum Sq*	*Mean Sq*	*F-value*	*P*
Treatment	1	1.23	1.23	0.076	0.784
Location	1	416.02	416.02	25.853	**<<0.01**
Treatment:Location	1	7.23	7.23	0.449	0.507
Residuals	36	579.30	16.09		

B Effect on number of different invertebrate groups (S)

	Df	*Sum Sq*	*Mean Sq*	*F-value*	*P*
Treatment	1	<<0.01	<<0.01	<<0.01	0.999
Location	1	19.600	19.600	24.000	**<<0.01**
Treatment:Location	1	0.100	0.100	0.122	0.728
Residuals	36	29.400	0.817		

C Effect on invertebrate group diversity (H')

	Df	*Sum Sq*	*Mean Sq*	*F-value*	*P*
Treatment	1	0.017	0.017	0.167	0.685
Location	1	1.164	1.164	15.845	**<<0.01**
Treatment:Location	1	0.081	0.081	0.798	0.378
Residuals	36	3.667	0.102		

DISCUSSION

Removal of a dominant species from a community often results in increasing species diversity and species richness, and changes in recruitment and abundance of understory species (Dayton 1975; Lubchenco 1978; Benedetti-Cecchi and Cinelli 1992; Clark *et al.* 2004), through an increase in limiting resources (e.g., light, space, nutrients). Yet, some studies have found little effect of removal of dominant algal canopy species on community structure (Edgar *et al.* 2004; Sánchez and Fernández 2005). The results of this study showed that algal assemblage composition and diversity were not affected by the *U. pinnatifida* removal treatment.

In contradiction to the results of the algal surveys in Chapter 2, I detected a strong difference between the two research locations, harbour and south coast, indicating that algal communities significantly differed between these two locations in this study.

Interestingly, while there was no difference in species richness (S) and Shannon diversity (H') between the two coasts before the experiment was set-up in November 2008 (late spring) and after four months (March 2009; late summer), S and H' were significantly different between the two locations six months after *U. pinnatifida* was removed (May 2009; autumn) (higher S and H' on the south coast). This pattern was not observed in the surveys of Chapter 2 which were conducted a year earlier, but this does demonstrate the high spatial and temporal variability of low-intertidal communities in this region. Factors including changing temperature, wave exposure, desiccation, grazer abundance, and nutrient regimes could all play a role in the observed patterns. In this study, algal community composition was found to be different between the two locations and algal species seasonality, turnover, and response of distinct algal species to (changing) environmental conditions may vary, resulting in different algal diversity.

Four months after manipulation *U. pinnatifida* had recruited back into the '*Undaria* removed' plots at the harbour sites, and by May 2009 cover was comparable to levels before manipulation. In contrast, *U. pinnatifida* had naturally died-off in the '*Undaria* present' treatment at the south coast sites by March 2009. These events confounded the treatments and made comparison difficult. However, native algae would have had sufficient time between the manipulation in November 2008 and the sampling in March 2009 to take advantage of newly freed resources created by the removal. However, algal community composition was not different between the two treatments, which may indicate that *U. pinnatifida* was not affecting native intertidal communities, or the experiment was affected by the seasonal reproductive cycles of native algae and grazers.

In a comparable study by Sánchez and Fernández (2005), the invasive macroalga *Sargassum muticum* was removed from experimental plots on a low intertidal shore in northern Spain. They also found no significant effect of this removal on native assemblage cover, species richness and diversity. Although, similar to the results of this study, they found higher species richness and diversity in winter than in summer. Forrest and Taylor (2002) conducted surveys of sites with and without *U. pinnatifida* in Lyttelton Harbour, New Zealand. Although they did not remove the invader, they also found no

difference in number of taxa and algal assemblage composition between sites with and without *U. pinnatifida*. They reported a mean algal species richness of 4–11 taxa per site (using 0.25 m^2 quadrats), which is slightly lower, though similar to my results (Figure 5.1).

Although *U. pinnatifida* is abundant in the low intertidal zone around Wellington, it does not occur in densities found at some locations on the east coast of the New Zealand's South Island, which may explain the lack of effect in this removal study. For example, Forrest and Taylor (2002) found very high densities (up to ~130 sporophytes m^{-2}) of *U. pinnatifida* at some locations in their study on the intertidal shores of Lyttelton Harbour, New Zealand. The average density in this study was considerably lower (~26 m^{-2}), although higher than densities found in subtidal studies in the Wellington Harbour (average ~19 sporophytes m^{-2}; Battershill *et al.* 1998). Individuals in the intertidal appear substantially smaller than the ones in the subtidal zone, which are up to ~2 m (Castric-Fey *et al.* 1999; Valentine and Johnson 2003); possibly due to exposure to more extreme conditions that are characteristic of intertidal habitats. These smaller plants might not affect light availability for understory species as much as *U. pinnatifida* populations in the subtidal zone, and may explain why no effect on native assemblages was detected.

Trophic dynamics could be altered by interaction between introduced seaweeds and native herbivores. Native herbivores often have a preference for native seaweed species and when herbivores avoid eating invasive seaweeds, spread of the invader could be promoted (Keane and Crawly 2002; Williams and Smith 2007). However, it has not been shown that native herbivores avoid grazing on *U. pinnatifida*. In fact, the native abalone (paua; *Haliotis* spp.) seems to prefer it over at least some native species (Middlemass 1990; Muncaster 2002). I found a significant difference in invertebrate diversity and richness between harbour and south coast, with the harbour having a more diverse and abundant invertebrate community. Because invertebrates were only recorded at the last sampling event in May 2009, it is unclear how the *U. pinnatifida* removal treatment affected mobile invertebrates because at that time treatments had become confounded due to re-invasion by *U. pinnatifida* in both treatments.

Elton (1958) proposed, with the diversity invasibility hypothesis, that ecosystems with greater diversity have a higher resistance to invasion by other species. Diverse ecosystems generally have lower levels of limiting resources (Tilman *et al.* 1996, 1997; Knops *et al.* 1999), which may result in fewer invasive species being able to establish in diverse communities (Knops *et al.* 1999). My results showed that quadrats containing only native algae initially had a different algal community composition, but they were not more diverse than quadrats containing *U. pinnatifida* (ANOVA; $p > 0.05$; results not shown). On the contrary, they had a lower diversity than the quadrats with treatments containing *U. pinnatifida* or in which it was removed, which could suggest that higher diversity does not inhibit its recruitement in this region. It is also possible that, at least at these densities, *U. pinnatifida* canopies contribute to an increase in diversity in these locations, by increasing habitat complexity and ameliorating physical stresses by covering understory species during low tide; thereby reducing daily maximum substratum temperatures and evaporative water loss under the canopy (Dayton 1975; Bertness *et al.* 1999), which may be beneficial to understory species.

The results of this study showed that algal assemblage composition and diversity were significantly different between harbour and south coast sites, but plots in neither location responded to the *U. pinnatifida* removal treatment. This implies that even though algal communities differed between the two locations, their dynamics and turnover did not appear to be affected by the removal of *U. pinnatifida*. However, this experiment only ran for six months, which may have been too short to record significant changes in the community. Longer-term studies may show a change in native assemblage composition when press removal of *U. pinnatifida* is conducted. However, results of this study found that *U. pinnatifida* populations at the harbour sites were present year-round, forming over-lapping generations. On the south coast sites, however, populations died-off over summer and started to recruit again in May. This implies that the harbour populations may be able to reproduce year-round, as suggested by Hay and Villouta (1993). Populations at the south coast study sites, on the other hand, seemed to follow a winter annual strategy.

In this study I focused on the response of native intertidal assemblage diversity and structure to the removal of the invasive macroalga and did not investigate other parameters of the native assemblage, e.g., growth, health, fecundity, etc., which may have been affected by the presence of *U. pinnatifida.* Although I did not perceive an indication of such effects during the field observations, further research is recommended to rule out such possible interactions.

Appendix 5.1: *Algal species or taxonomic units recorded in the quadrats of the* 'Undaria pinnatifida *removal' experiment and the functional group to which they were classified (modified from Steneck and Dethier 1994 and Guerry* et al. *2009; pers. comm. M. Dethier).*

Species	***Functional group***	***Division***
Ceramium spp.	Filamentous	Rhodophyta
Brown turf	Filamentous	Phaeophyta
Red turf	Filamentous	Rhodophyta
Unidentified red filamentous	Filamentous	Rhodophyta
Unidentified red filamentous epiphyte	Filamentous	Rhodophyta
Unidentified brown filamentous	Filamentous	Phaeophyta
Ulva spp.	Foliose	Chlorophyta
Cladhymenia oblongifolia	Corticated foliose	Rhodophyta
Dictyota spp.	Corticated foliose	Phaeophyta
Endarachne binghamiae	Corticated foliose	Phaeophyta
Gigartina atropurpurea	Corticated foliose	Rhodophyta
Dictyota kunthii	Corticated foliose	Phaeophyta
Hymenena spp.	Corticated foliose	Rhodophyta
Microzonaria velutina	Corticated foliose	Phaeophyta
Zonaria turneriana	Corticated foliose	Phaeophyta
Caulerpa brownii	Corticated macrophytes	Chlorophyta
Champia nova-zelandiae	Corticated macrophytes	Rhodophyta
Chondria macrocarpa	Corticated macrophytes	Rhodophyta
Codium convolutum	Corticated macrophytes	Chlorophyta
Colpomenia bullosa	Corticated macrophytes	Phaeophyta
Colpomenia sinuosa	Corticated macrophytes	Phaeophyta
Gelidium caulacantheum	Corticated macrophytes	Rhodophyta
Gigartina chapmanii	Corticated macrophytes	Rhodophyta
Gigartina decipiens	Corticated macrophytes	Rhodophyta
Gigartina livida	Corticated macrophytes	Rhodophyta
Gigartina macrocarpa	Corticated macrophytes	Rhodophyta
Gymnogongrus torulosus	Corticated macrophytes	Rhodophyta
Halopteris spp.	Corticated macrophytes	Phaeophyta
Laurencia thyrsifera	Corticated macrophytes	Rhodophyta
Leathesia spp.	Corticated macrophytes	Phaeophyta
Plocamium microcladiodes	Corticated macrophytes	Rhodophyta
Scytothamnus australis	Corticated macrophytes	Phaeophyta
Splachnidium rugosum	Corticated macrophytes	Phaeophyta
Carpophyllum flexuosum	Leathery macrophytes	Phaeophyta
C. maschalocarpum	Leathery macrophytes	Phaeophyta
Cystophora retroflexa	Leathery macrophytes	Phaeophyta

Appendix 5.1 *continued*

Species	***Functional group***	***Division***
C. scalaris	Leathery macrophytes	Phaeophyta
C. torulosa	Leathery macrophytes	Phaeophyta
Gigartina circumcinta	Leathery macrophytes	Rhodophyta
Hormosira banksii	Leathery macrophytes	Phaeophyta
Marginariella spp.	Leathery macrophytes	Phaeophyta
Undaria pinnatifida	Leathery macrophytes	Phaeophyta
Upright coralline algae	Erect coralline algae	Rhodophyta
Encrusting coralline algae	Crustose algae	Rhodophyta
Ralfsia spp.	Crustose algae	Phaeophyta
Unidentified brown crust	Crustose algae	Phaeophyta
Unidentified red crust	Crustose algae	Rhodophyta

CHAPTER 6

DEVELOPMENT AND REPRODUCTION RATES OF CULTURED GAMETOPHYTES OF *UNDARIA PINNATIFIDA* (HARVEY) SURINGAR UNDER VARYING NUTRIENT AND LIGHT CONDITIONS

ABSTRACT

Undaria pinnatifida has the potential to thrive in a wide range of habitats. To help make predictions about *U. pinnatifida*'s population dynamics and success in different environments, it is essential to comprehend the physical and chemical dynamics that may influence its reproduction. In this laboratory study, I examined how early development and reproduction of microscopic *U. pinnatifida* gametophytes were affected by nutrient availability and light intensity. Mature sporophytes with fertile sporophylls were collected in the field and spore released was induced in the laboratory. Subsequently, released spores were exposed to different nutrient (3 levels) and light (3 levels) regimes for 22 days in a crossed factor design. Spore settlement density, gametophyte length and surface area, egg formation, zygote formation, and sporophyte formation and surface area were monitored. Under low light conditions gametophyte growth stalled within 2 days of spore settlement and development did not increase with greater nutrient concentrations. Under medium and high light levels, gametophyte growth and reproduction rate was generally reduced at low nutrient levels. Higher nutrient availability had a strong positive effect on development and growth of young sporophytes, especially in high light conditions. Outcomes of this experiment indicate that development and reproduction can occur at a high rate in environments with ample nutrient availability and where light is not limiting, and may result in greater *U. pinnatifida* abundance.

INTRODUCTION

Undaria pinnatifida is an invasive seaweed with a high dispersal potential in a wide range of environments (Nyberg and Wallentinus 2005). When *U. pinnatifida* populations establish in new habitats, they have been suggested to compete with native species directly for light (Hay and Luckens 1987; Battershill *et al.* 1998) and nutrients (Dean and Hurd 2007), and alter interactions within native algal assemblages and grazer communities (Valentine and Johnson 2003; Thornber *et al.* 2004).

Undaria pinnatifida has a biphasic life cycle in which the generation of microscopic (haploid) gametophytes alternates with macroscopic (diploid) sporophytes (Thornber *et al.* 2004). The spores settle and germinate into gametophytes, and mature gametophytes undergo sexual reproduction to produce new sporophytes (Figure 6.1), around 15-20 days after spore settlement (Pang and Wu 1996; Choi *et al.* 2005). *U. pinnatifida* is a winter annual in its native range (northwestern Pacific shores), with spore release taking place in late spring, followed by die-off of mature sporophytes in summer and autumn. However, *U. pinnatifida* is able to reproduce year-round in some populations in New Zealand (Hay and Villouta 1993). In addition, it has been suggested that settled gametophytes of this species may remain viable for up to 2 years during conditions that are not conducive to development (Stuart 2003).

Understanding the physical and chemical factors that control reproduction and recruitment in this invasive kelp is a crucial in predicting the likelihood of its spread into different habitats. Previous research in subtidal habitats has shown that removal of the native algal canopy is a requirement for the high density settlement of *U. pinnatifida*, and light is suggested to limit macroscopic sporophyte development and growth (Valentine and Johnson 2003). Hence, resident algal assemblages may be able to limit colonization and growth of *U. pinnatifida* through competition for resources (e.g. light and seawater nutrients).

Growth rates of most algae in spring and summer on temperate coastlines worldwide are limited by the availability of nutrients, predominantly nitrogen and/or phosphorus (Hanisak 1983; Galloway *et al.* 2003; Pedersen *et al.* 2010). Although, it has been suggested that overlapping generations of *U. pinnatifida* sporophytes may exist in some locations in New Zealand (Hay and Luckens 1987; Chapter 5), main vegetative growth of *U. pinnatifida* sporophytes typically takes place during winter months (Hay and Luckens 1987), when light and seawater temperatures are lower, and nutrient concentrations in New Zealand (Sherlock *et al.* 2007; Chapter 2) and temperate coastal waters worldwide are typically highest (Sharp 1983; Wafar *et al.* 1983; Oviatt 2004; Thompson *et al.* 2009). However, the gametophyte stage of *U. pinnatifida* is most common during late spring and summer, when the concentrations of limiting nutrients (particularly nitrate) tend to be lower (Sharp 1983; Sherlock *et al.* 2007). Macroalgal spores may be chemotactic to nutrients, as has been shown in different kelp species by Amsler and Neushul (1989), and may be an adaptation to facilitate settlement in benthic conditions that are suitable for growth and reproduction of gametophytes. Several laminarian species have also been shown to delay gametophyte development in conditions of low nutrient availability, and continue developing once nutrients increase (Carney and Edwards 2010; Carney 2011).

Here, I examine how the development and reproduction of *U. pinnatifida* is affected by nutrient availability and light intensity, by testing the response of spores, gametophytes, and young sporophytes to a range of nutrient conditions and different light conditions.

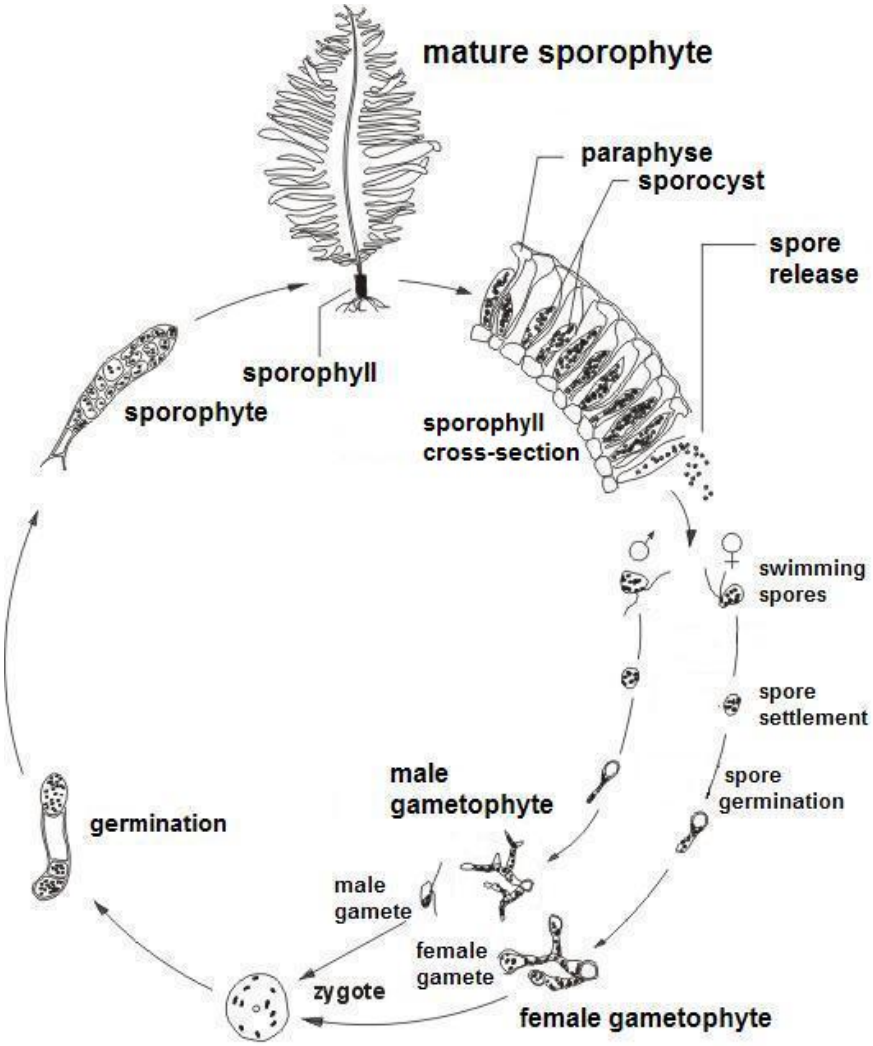


Figure 6.1: Undaria pinnatifida *life cycle (modified from Ifremer 2006)*

MATERIALS AND METHODS

Obtaining spores

Mature *U. pinnatifida* individuals were collected at low tide from low-intertidal rocks at The Sirens, Island Bay, Wellington, New Zealand (41º21'S, 174º46'E) in November 2009. The plants were cut from the substratum at the holdfast, placed in seawater, and immediately transported to the laboratory where they were placed in tanks with filtered seawater (FSW; 0.5 μm mesh size) and air bubblers and kept overnight to allow for recovery. The next day, sporophylls were cut from 5 mature plants. To obtain spores methods based on Lüning and Neushul (1978) and Choi *et al.* (2005) were followed. The sporophylls were first rinsed in FSW and then placed in a 2% bleach solution. After 5 minutes, the sporophylls were removed from the solution, rinsed with autoclaved FSW, wrapped in aluminium foil and refrigerated overnight at 4 ºC. The next day, spore release was induced by immersing each sporophyll in a beaker with autoclaved seawater at room temperature. After 1 hour, the sporophylls were removed and the solutions were stirred thoroughly. From each spore solution 200 mL was taken from the middle of each beaker using a syringe, and combined into one beaker. Spores in the combined solution were counted using a compound microscope with a haemocytometer. The average spore count was 131 spores per 0.1 ml (1 mm^2). From this combined spore solution 20 mL was added to 180 mL of medium (described below) in dishes used in the experiments, resulting in a final concentration of spores of approximately 26000 per dish. Round glass 250 mL dishes (8.5 cm Ø) were used and autoclaved before use. Glass microscope slides were cut into six equally sized pieces (ca. 25 x 12.5 mm) and 9 pieces were placed on the bottom of each dish for the spores to settle on.

Experiment

The experimental design was a two-factor fully crossed design, with nutrients and light (3 levels each) as factors, using a total of 9 treatments with 4 replicate dishes for each treatment. The experiment was conducted in a climate controlled room at a constant temperature of 15 ºC, which is within the optimal temperature range for growth and maturation of *U. pinnatifida* gametophytes (Choi *et al.* 2005).

The nutrient treatments consisted of (I) a "low" nutrient level seawater depleted of nutrients, (II) a "medium" nutrient level and (III) a "high" nutrient treatment (see Table 1 for nutrient concentrations across treatments). The low nutrient treatment was prepared by adding ~200 g (WW) *Ulva* spp. to a tank with 30 L FSW and air bubblers. This was left overnight to allow the *Ulva* spp. to take up nutrients from the seawater, effectively depleting it (after methods by Dudley *et al.* 2010). The next day the water in the tank was filtered using glass fiber filters (MN GF-3; Macherey-Nagel GmbH & Co. KG, Germany) and autoclaved. Enhanced nutrient treatments were prepared by adding the appropriate volume of liquid Guillard's fertilizer formula (Micro algae grow™, Guillard F/2 formulation Florida Aqua Farms, modified, complete, one-part, liquid Guillard's fertilizer formula) to autoclaved FSW. The medium treatment was achieved by diluting the standard F/2 concentration of formula by 5, and the high nutrient treatment was achieved by doubling the standard F/2 concentration of formula.

Three light regimes were established: low, medium, and high light. Low light treatment was accomplished by covering the dishes with 2 layers of (1mm mesh size) shade cloth and placing the dishes on the top level of a rack without a light source (light level: 8.52 μmol photons m^{-2} s^{-1} ± 0.01 SE). Medium light treatment was accomplished by covering the dishes with 2 layers of shade cloth and exposing them to a medium light source (two light tubes (Osram L 36W/865, Lumilux Cool Daylight); light level: 27.57 μmol photons m^{-2} s^{-1} ± 0.36 SE). Full light consisted of exposure to 4 light tubes and dishes were left uncovered (light level: 144.85 μmol photons m^{-2} s^{-1} ± 1.26 SE). Previous research has shown that growth and maturation of *U. pinnatifida* sporophytes is positively correlated with irradiance within 10 – 80 μmol photons m^{-2} s^{-1} (Akiyama 1965, cited in Choi *et al.* 2005). A 12:12 (light:dark) cycle light regime was used. Dishes were arranged in a randomized block design to remove any effects of unevenness of light on each rack. Light levels were checked for consistency between nutrient treatments in each light treatment on day 0 of the experiment. Light levels were measured using a LI-COR Biosciences light meter (model LI-189, Lincoln, NE, USA).

Microscope slides with settled spores were sampled at 2, 4, 6, 8, 11, 14, 18 and 22 days after inoculation. On each sampling date a new slide was sampled to prevent a handling effect, slides were never resampled. I took photos of the slides using a Leica DM LB compound microscope with a digital camera attached and QCapture PRO 6.0 image analysis software (QImaging, Surrey, BC, Canada). The location on the slide to be photographed was selected randomly on the slide and was ~ 0.11 – 0.43 mm^2 (depending on the magnification used). Photos were later analysed using ImageJ software (Rasband, U. S. National Institutes of Health, USA). Settlement density was measured by counts of settled spores (per mm^2) in each treatment two days after inoculation. Settled spores could be distinguished from swimming spores by attachment to the surface and the beginning of development of the germination tube. Initial germling growth was assessed by averaging lengths and surface areas of 10 female gametophytes intercepting a diagonal transect along each photograph. The reproductive capacity of the gametophytes in each treatment was assessed by counts of egg formation (oogonium attached to the female gametophyte), zygote formation (fertilized egg with clear membrane and organelles), and formation and surface area of sporophytes (multicellular plantlet, paddle shaped).

Medium was refreshed every 6-8 days by removing the old medium with a (50 mL) syringe and carefully pouring in 200 mL of fresh medium. On day 18, diatoms were recorded in some of the dishes. Therefore, eight drops of germanium dioxide (GeO_2) solution (250 mg/L) were added to each dish to inhibit diatom growth.

Nitrate, nitrite and ammonia concentrations in the media were analysed with a SAN^{PLUS} segmented flow analyser (SKALAR, Breda, The Netherlands). Phosphate concentrations were analysed using the method described by Koroleff (1983). Mean nutrient concentrations in the treatments are shown in Table 6.1.

Table 6.1: Mean nutrient concentrations (μM) ± 1 SE in the media.
Note there was not a filtered seawater treatment, these values are shown for comparative purposes.

Treatment	*Nitrate*	*Nitrite*	*Ammonium*	*Phosphate*
High	412.4 ± 5.89	3.4 ± 0.05	5.9 ± 0.33	44.1 ± 0.001
Medium	38.9 ± 0.37	0.4 ± 0.01	6.0 ± 0.57	5.3 ± 0.07
Low	0.03 ± 0.004	0.02 ± 0.0001	5.1 ± 0.12	0.07 ± 0.07
Filtered seawater	0.2 ± 0.01	0.1 ± 0.004	5.3 ± 0.44	0.07 ± 0.07

Data analyses

Between-treatments differences in initial settlement density on day 2, female gametophyte size (length and surface area), egg counts, zygote counts, sporophyte count and sporophyte surface area were each assessed by two-way analysis of variance (ANOVA) where treatments 'light level' and 'nutrient supply' were factors at three levels. Where there was no interaction between light and nutrient effects, Tukey's HSD post-hoc test was used to examine differences between treatment levels.

Differences in length and surface area of female gametophytes were compared at 11 days after inoculation. After this day, gametophyte density became too high to accurately measure length and surface area due to overlap. Final size of sporophytes was examined at the termination of the experiment on day 22. Count data of eggs, zygotes and sporophytes for the 8 measurements (from separate slides) over 22 days were summed prior to ANOVA analysis in order to better account for varying rates of development between treatments.

Data were examined for assumptions of normality and homogeneity of variance using quantile-quantile plots (Wilk and Gnanadesikan 1968) and homogeneity of variances was assessed by plotting residuals against fitted values (Quinn and Keough 2002). All datasets conformed to the assumptions of normality and equal variances necessary for ANOVA

analyses. All statistical analyses were performed using the R statistical package, version 2.9.2 (R development Core Team 2009).

RESULTS

Densities of settled spores on day 2 of the experiment (two days after inoculation) were not significantly different between nutrient treatments ($F_{2,27} = 0.3025$, $P = 0.7415$), or light treatments ($F_{2,27} = 0.1102$, $P = 0.8961$) and there was no significant interaction ($F_{4,27} = 0.5546$, $P = 0.6974$).

Eleven days after inoculation, both germling length (Light: $F_{2,27} = 39.50$, $P << 0.01$; Nutrients: $F_{2,27} = 55.80$, $P << 0.01$; Interaction: $F_{4,27} = 14.13$, $P << 0.01$) and surface area (Light: $F_{2,27} = 30.73$, $P << 0.01$; Nutrients: $F_{2,27} = 56.94$, $P << 0.01$; Interaction: $F_{4,27} = 9.16$, $P << 0.01$) were influenced by light and nutrient treatments. Germlings exposed to medium and high nutrient treatments grew similarly within medium and high light treatments (Figure 6.2 and Figure 6.3) and were considerably elongated and enlarged relative to those grown in 'low' nutrient seawater. Germling length and surface area were not affected by nutrient treatment under low light levels (Figure 6.2 and Figure 6.3). Egg counts, summed for the 22-day duration of the experiment were affected by light and nutrient levels, with an interaction between the two factors (Light: $F_{2,27} = 34.035$, $P << 0.01$; Nutrients: $F_{2,27} = 71.852$, $P << 0.01$; Interaction: $F_{4,27} = 10.924$, $P << 0.01$; Figure 6.4). Egg formation in 'low light' treatments was delayed and only small numbers of eggs were observed in low light treatments on days 18 and 22 of the trial. In contrast, there appeared to be only minor differences in the time of onset or density of egg formation between 'medium' and 'high' light treatments, although egg formation in both high and medium light treatments were lowest in low nutrients, on average half the density of medium and high nutrient treatments. Formation of eggs on female gametophytes was first observed after 8 days in the medium and high nutrient treatments, under high light. Under medium light exposure, egg formation was first observed after 11 days in all three nutrient treatments.

Summed zygote counts were affected by light and nutrients regimes (Light: $F_{2,27}$ = 6.5629, P = 0.005; Nutrients: $F_{2,27}$ = 14.1597, P << 0.01, and no interaction was found between the factors ($F_{4,27}$ = 2.1472, P = 0.102); Figure 6.5). Similar to egg counts, only a small number of zygotes formed across the 'low light' treatments regardless of nutrient availability; a total of 8 were observed on day 22 of the experiment. Zygotes were observed on day 11 for the high light treatment, and on day 14 for the medium light treatment, thus 3 days after eggs were noted. For both light and nutrient treatments, there was no significant difference between medium and high levels, but zygote density was ~25 times lower in the low light treatment than the medium light treatment (Tukey's, $P_{adj.}$ << 0.01), and ~20 times lower than in the high light treatment (Tukey's, $P_{adj.}$ = 0.001). High nutrient treatment produced significantly greater zygote numbers than low nutrient treatment ($P_{adj.}$ << 0.01), while medium and low nutrient treatments were weakly separated ($P_{adj.}$ = 0.100).

Germlings did not ever develop into sporophytes in the low light or low nutrient treatments during the 22 days of the study. Sporophyte counts, summed for the 22 day duration of the experiment, were affected by light and nutrient levels, with no interaction between the two factors (Light: $F_{2,27}$ = 4.38, P = 0.023, Nutrients: $F_{2,27}$ = 5.10, P = 0.013, Interaction: $F_{4,27}$ = 1.52, P = 0.224; Figure 6.6). Sporophyte counts were greatest in the high light treatment (6.04 ± 4.0 mm^{-2} across all nutrient treatments) and high nutrient treatment (6.56 ± 2.34 mm^{-2}). Tukey's post-hoc test showed no significant difference between medium and high light levels for sporophyte counts ($P_{adj.}$ > 0.05).

Nutrient and light treatments also affected subsequent sporophyte vegetative growth, and there was a significant interaction, caused by the tendency for sporophytes exposed to high light treatments to grow more in higher nutrient concentrations (Light: $F_{1,12}$ = 6.6128, P = 0.024, Nutrients: $F_{1,12}$ = 7.27, P = 0.019, Interaction: $F_{1,12}$ = 11.58, P = 0.005; Figure 6.7). Sporophytes started to develop on day 14 in 'high light/high nutrient', 'medium light/high nutrient', and 'high light/medium nutrient' treatments, ranging in size from 2 ('medium light/high nutrient' treatment) to 14 cells ('high light/high nutrient'

treatment). At the end of the experiment (day 22), the largest sporophytes (up to ~400 cells) were observed in the 'high light/high nutrient' treatment.

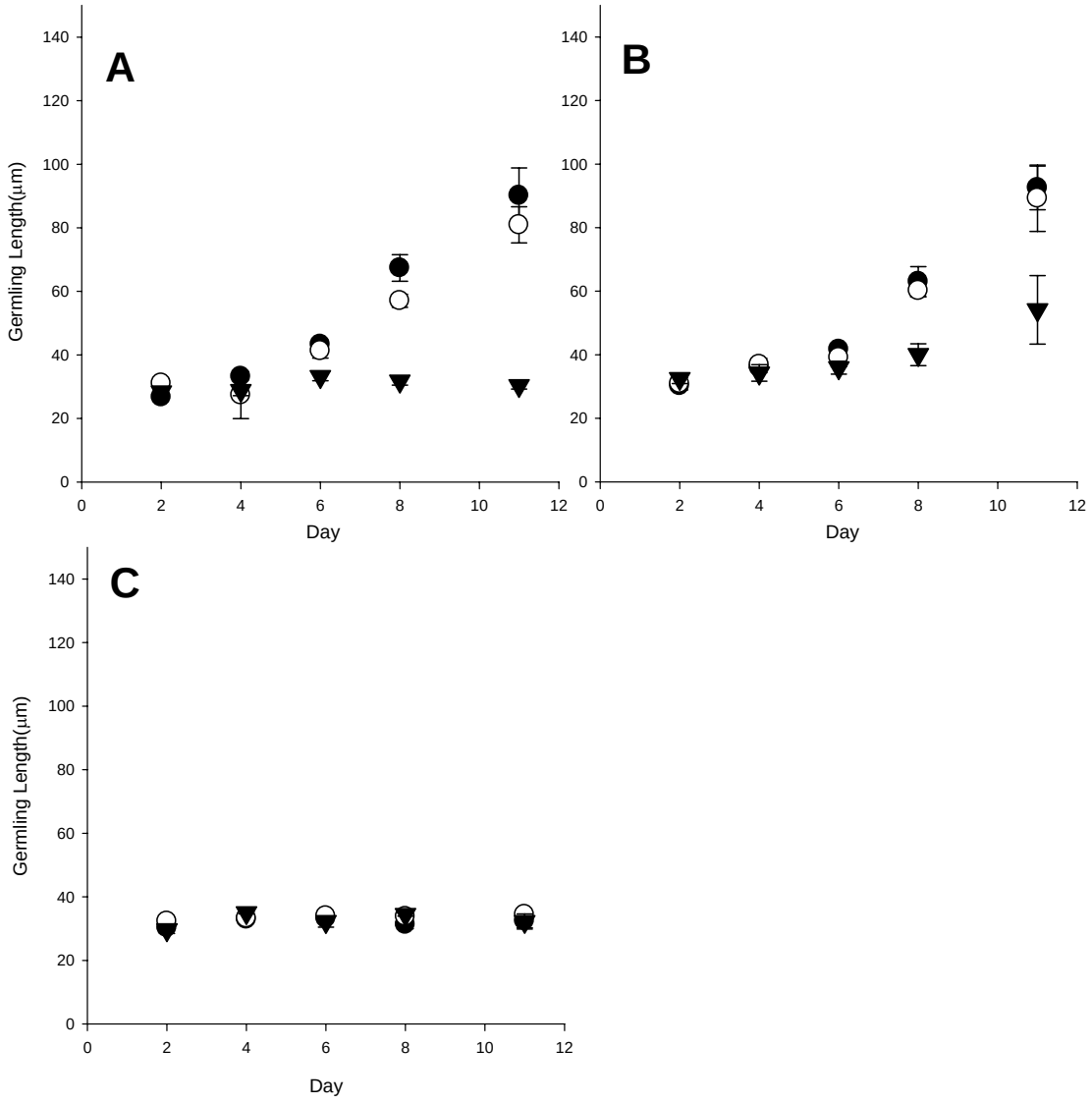


Figure 6.2: Length of female gametophytes on days 2 to 11 for high light treatments (A), medium light treatments (B), and low light treatments (C). Filled circles represent high nutrient treatments, open circles represent medium nutrient treatments, filled triangles represent low nutrient treatments.

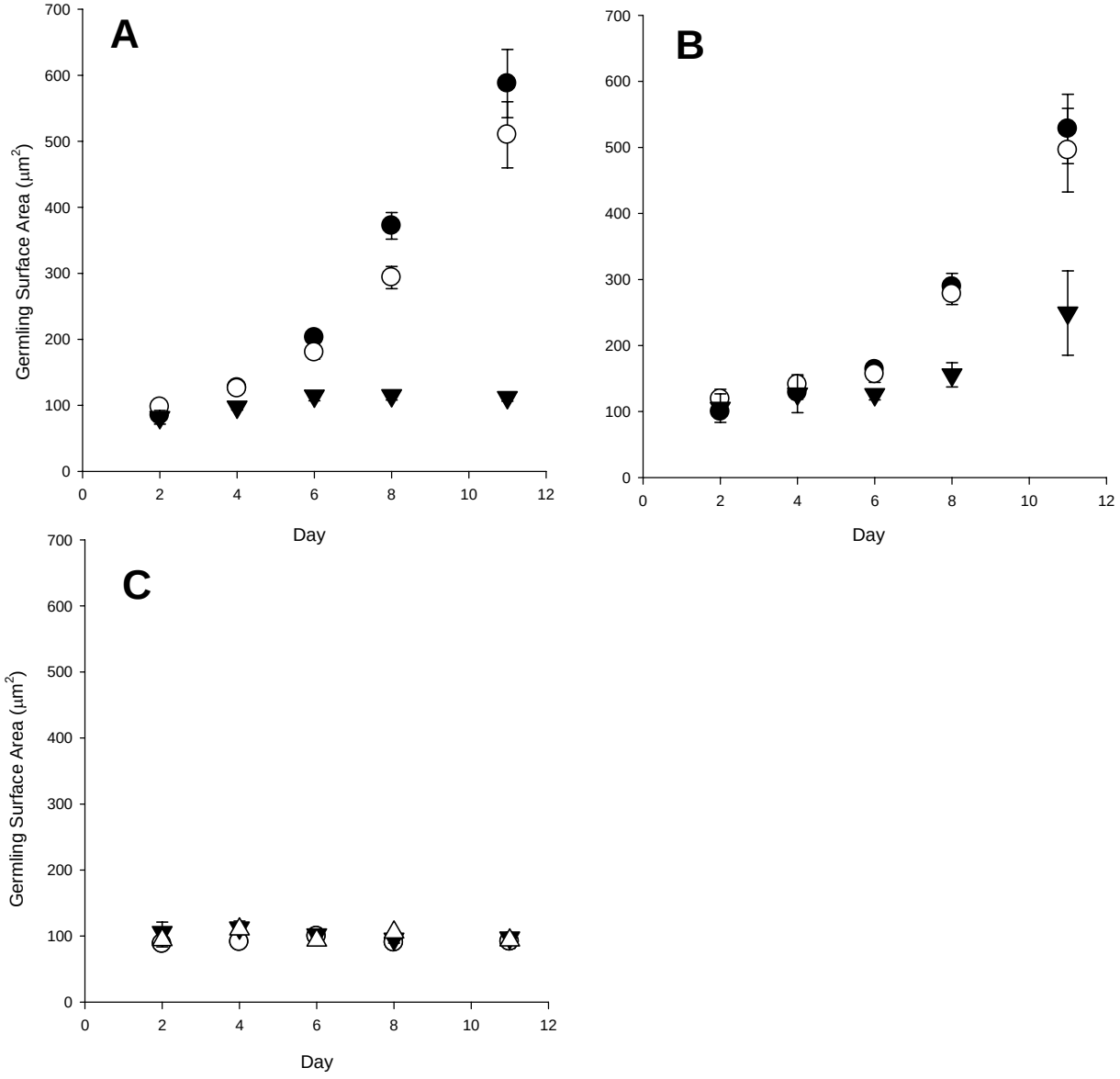


Figure 6.3: Surface area of female gametophytes on days 2 to 11 for high light treatments (A), medium light treatments (B), and low light treatments (C). Filled circles represent high nutrient treatments, open circles represent medium nutrient treatments, filled triangles represent low nutrient treatments.

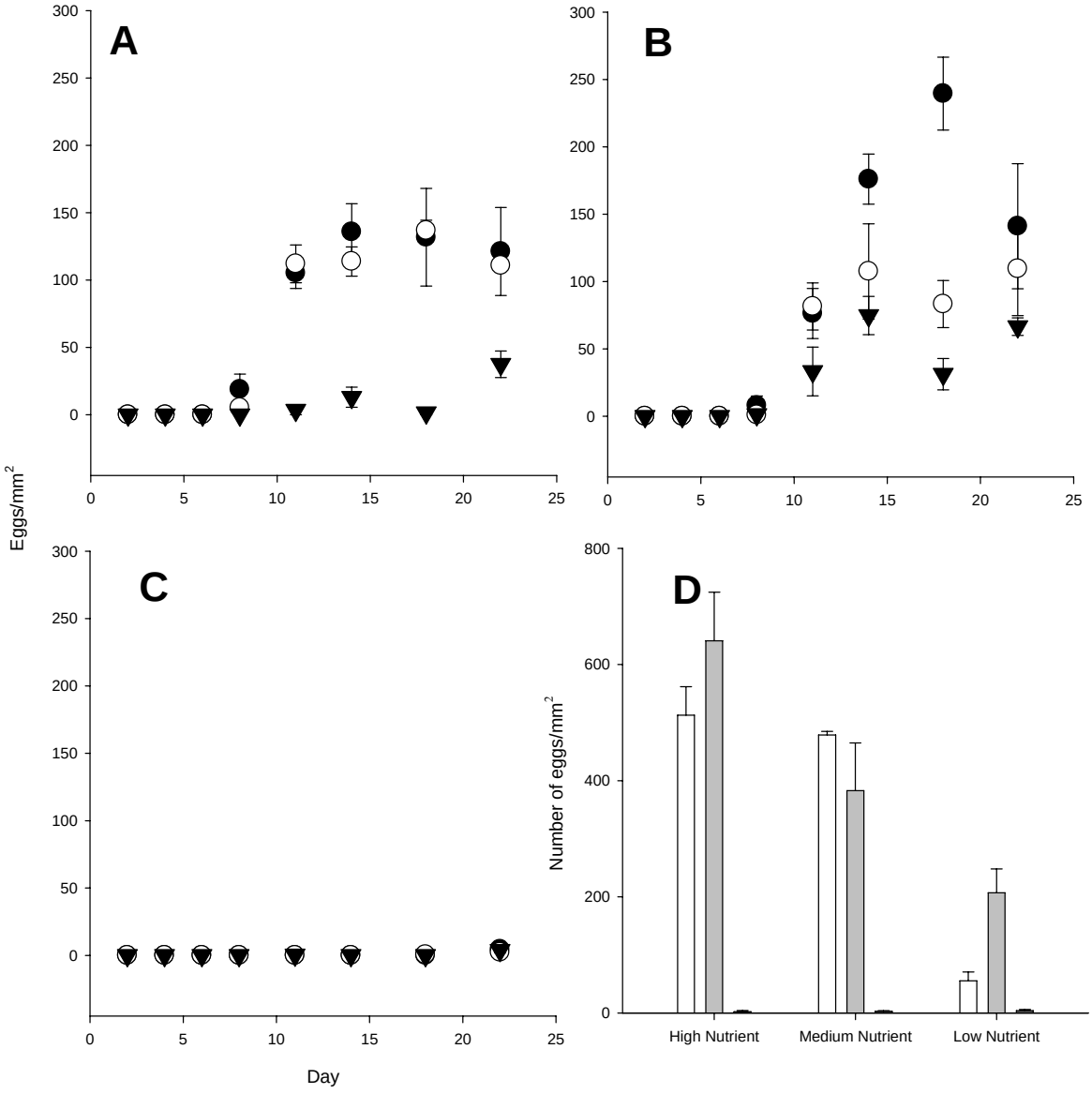


Figure 6.4: Egg density on days 2 to 22 for high light treatments (A), medium light treatments (B), and low light treatments (C). Filled circles represent high nutrient treatments, open circles represent medium nutrient treatments, filled triangles represent low nutrient treatments. Panel D shows summed egg counts for each treatment. White bars represent high light, light grey bars medium light, and dark grey bars low light egg counts. Error bars show standard error for replicates (n = 4).

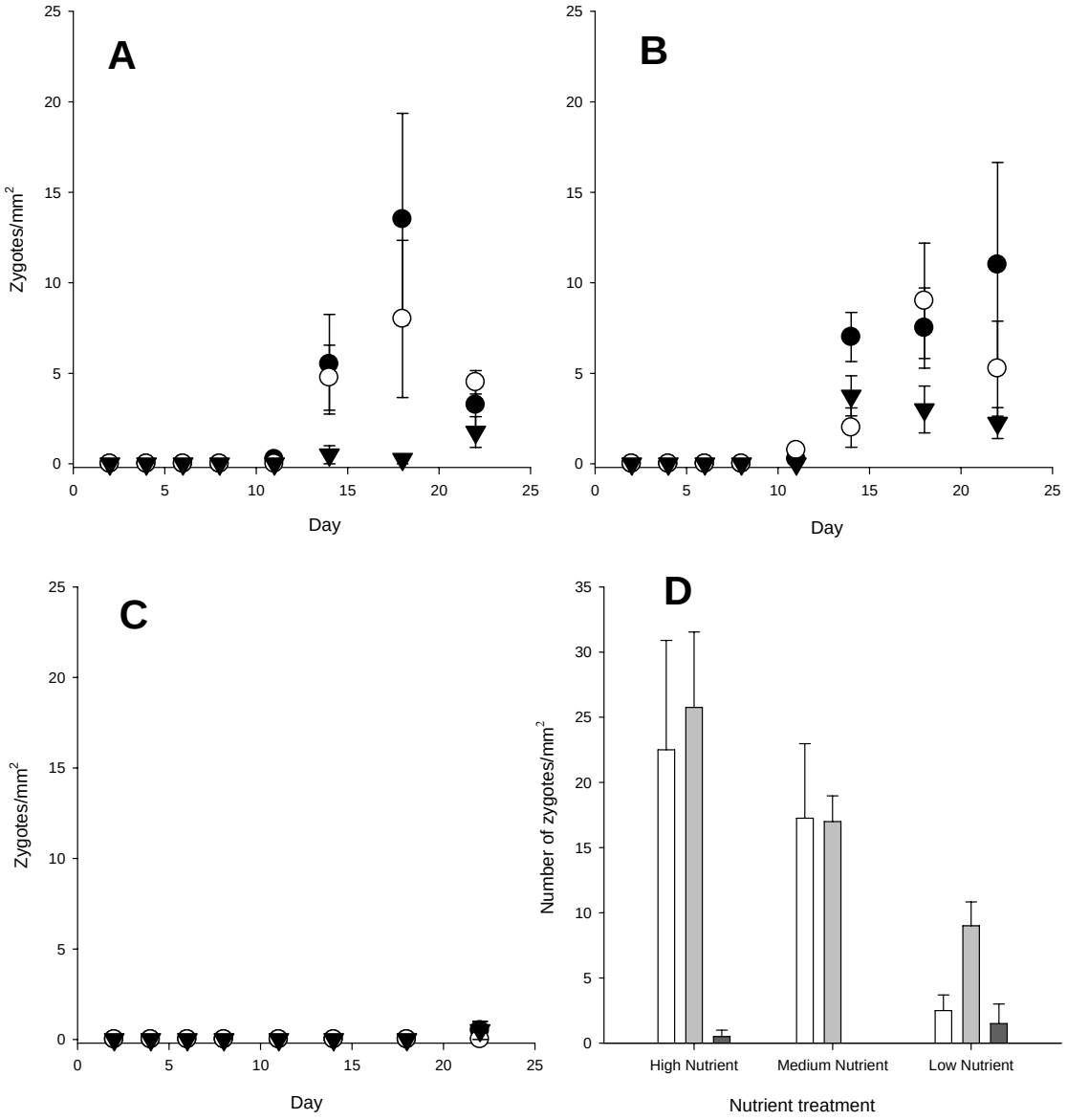


Figure 6.5: Zygote density on days 2 to 22 for high light treatments (A), medium light treatments (B), and low light treatments (C). Filled circles represent high nutrient treatments, open circles represent medium nutrient treatments, filled triangles represent low nutrient treatments. Panel D shows summed zygote counts for each treatment. White bars represent high light, light grey bars medium light, and dark grey bars low light zygote counts. Error bars show standard error for replicates (n = 4).

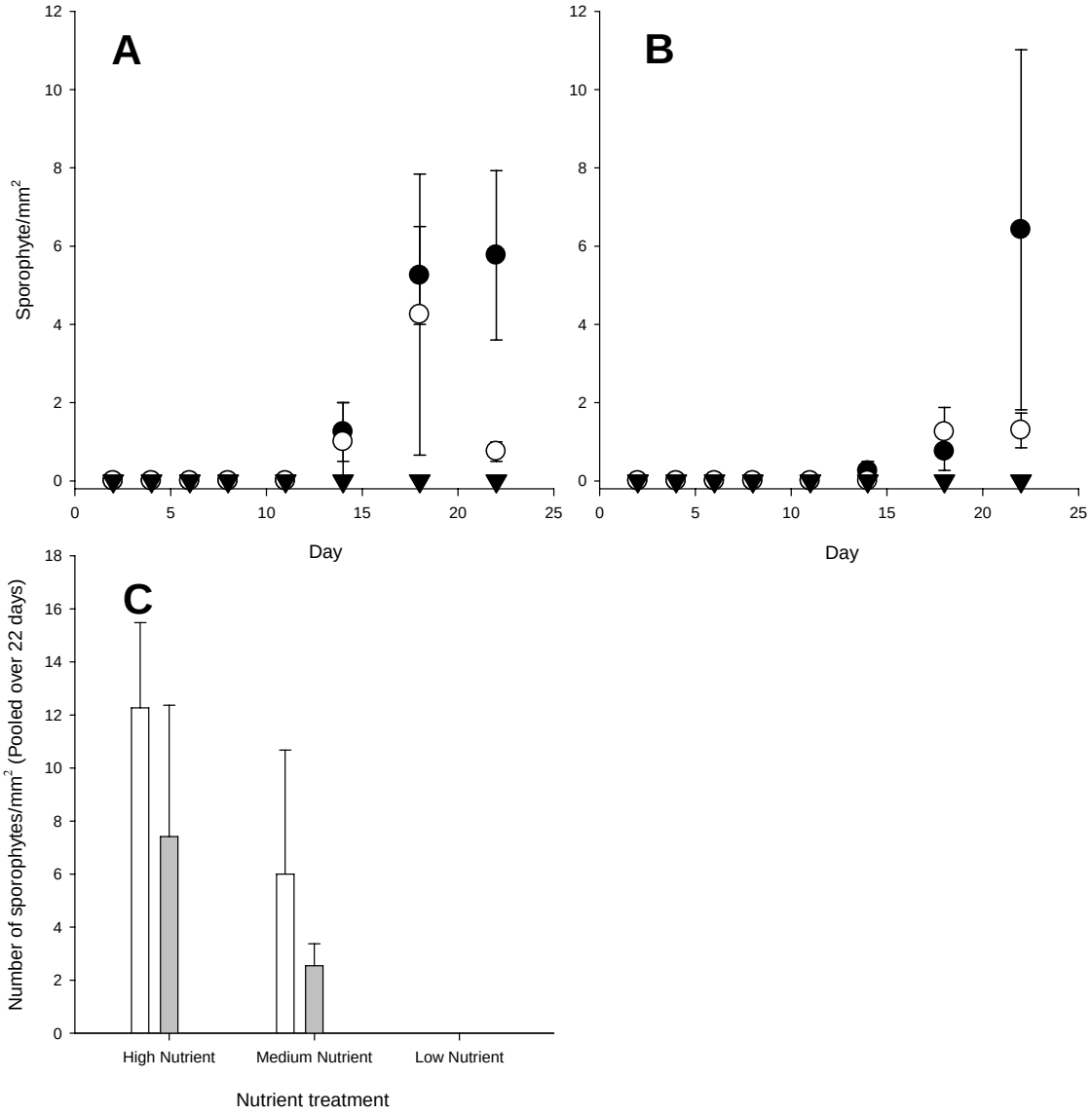


Figure 6.6: Sporophyte density for days 2 to 22 for high light treatments (A) and medium light treatments (B). Low light treatments have not been shown as no sporophytes were produced (see text). Filled circles represent high nutrient treatments, open circles represent medium nutrient treatments, filled triangles represent low nutrient treatments. Panel C shows summed sporophyte counts for each treatment. White bars represent high light, and light grey bars medium light. Error bars show standard error for replicates (n = 4).

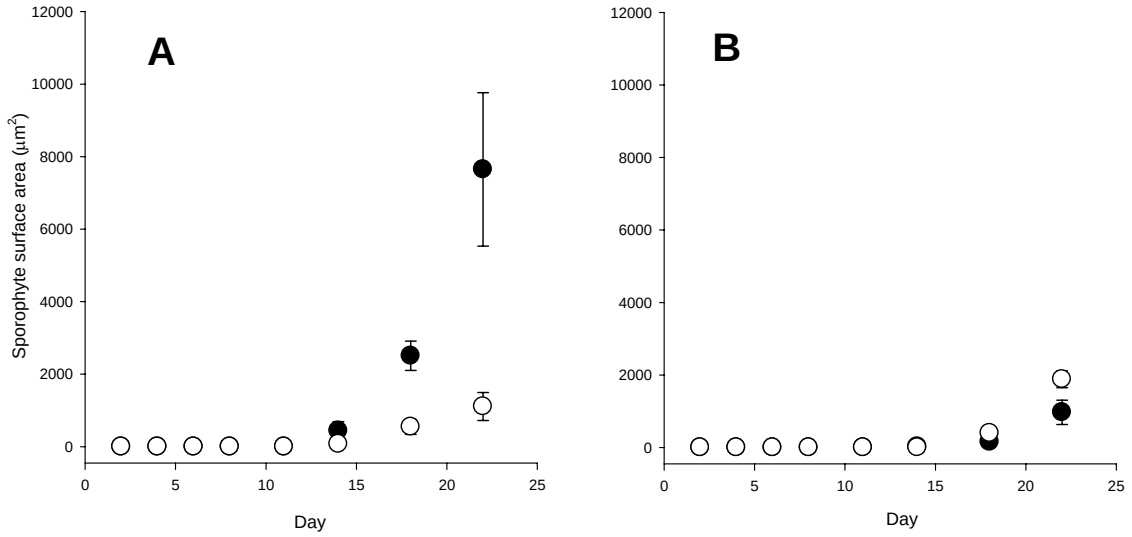


Figure 6.7: Sporophyte surface area for days 2 to 22 for high light treatments (A) and medium light treatments (B). Low light and low nutrient treatments have not been shown as no sporophytes were produced (see text). Filled circles represent high nutrient treatments, open circles represent medium nutrient treatments.

DISCUSSION

Nutrients and light both had strong effects on *U. pinnatifida* reproduction. For gametophyte length, surface area, and egg density there was an interaction of these factors whereby gametophyte growth and reproduction was retarded under low light conditions regardless of nutrient availability. Under medium and high light treatments, gametophyte length, surface area, and egg and zygote density generally increased with nutrient availability, with a notable tendency to be more tolerant to low nutrient availability under medium, rather than high light. Sporophyte development and growth appeared dependent to a greater extent on nutrient supply than gametophyte stages. Young sporophytes showed much higher vegetative growth when exposed to high nutrients, particularly in high light conditions, yet no sporophytes developed in the low nutrient treatment over the 22 days of the experiment.

Nutrient concentrations in 'low nutrient' seawater were not greatly reduced by treatment with *Ulva* spp. Limiting nutrients (inorganic biologically available N and P) in this treatment remained within the range of concentrations found in natural waters in the Wellington region (Fry *et al.* 2011; Chapter 2). N and P concentrations in the medium nutrient treatment were substantially greater, in the range of natural concentrations found in upwelling regions of New Zealand coastlines (Barr 2007), and areas affected by anthropogenic nutrient sources (Barr 2007; Dudley and Shima 2010; Chapter 3). N and P concentrations in the high nutrient treatment are uncommon in coastal New Zealand waters, but similar concentrations have been measured in eutrophic environments, e.g. in southern California, USA (Boyle *et al.* 2004).

The lack of turbulence in these experimental treatments, however, is likely to have caused small scale reductions in nutrient concentrations. Nutrients are taken up from the boundary layer of water around the alga, and hence available nutrient concentrations are depleted until the medium is refreshed. Moreover, standard nutrient analysis methods do not detect patchiness on the size scale of kelp spores (Amsler and Neushul 1990). In field conditions, marine snow (aggregates) can patchily greatly increase nutrient concentrations relative to the surrounding water (Shanks and Trent 1979) and this pattern could also be expected in the benthic boundary layer (Amsler & Neushul 1990). In addition, in field conditions, increased turbulence tends to increase the availability of nutrients to algae (Barr *et al.* 2008).

Light levels used in this experiment are representative of levels in field conditions. On sunny days, irradiance can reach up to ~1500 μmol photons m^{-2} s^{-1} in the Wellington region (K. Ryan, pers. comm.). However, overcast days are very common in this region and greatly reduce irradiance levels. Moreover, irradiance gets attenuated with water depth, and light levels reaching the substratum are further affected by water motion, turbidity, algal canopies and substratum relief.

I did not detect differences in female gametophyte density among the different treatments two days after inoculation, suggesting that rates of spore settlement were not affected by

light or nutrient availability. This result appears to contrast with results of Amsler and Neushul's (1990) study, which found that spore settlement in the kelps *Pterygophora californica* and *Macrocystis pyrifera* was stimulated by increased nutrient availability in the form of Provasoli's enriched seawater medium 14-18 hours and 5-12 hours (resp.) after release. They suggested that stimulation of spore settlement by nutrients may be an adaptation, which increases the probability of settlement in microhabitats suitable for subsequent growth and reproduction of gametophytes.

Gametophyte growth was retarded under low light conditions at all three nutrient levels, with little to no change in size over 22 days. Notably gametophytes of this species have been observed to remain viable for at least 24 months (Stuart 2003). Several other kelp species, e.g. *M. pyrifera, Laminaria farlowii, Pelagophycus porra,* and *P. califonica,* have been shown to delay development at the gametophyte stage for some months until physical and chemical conditions for growth are suitable (Carney and Edwards 2010; Carney 2011). In medium and high light the gametophyte development generally increased with nutrient availability. While gametophyte growth and reproduction was retarded when exposed to low light and in low nutrient conditions, some gametophyte development was observed in low light treatments, around two weeks later than those in medium and high light conditions. These results support those of Choi *et al.* (2005), who reported a delayed performance of *U. pinnatifida* gametophytes under low irradiance.

Gametophyte length and surface area were not significantly different between medium and high light treatments. However, for gametophytes exposed to the low nutrient treatment, surface area was higher under medium light than for high light. These medium light levels (~27 μmol photons m^{-2} s^{-1}) may be optimal for gametophyte growth under low nutrient levels. Previous research, however, has suggested that kelp gametophytes becoming multi-cellular may indicate that environmental conditions are not optimal for reproduction, and that conditions are most favourable when fertility is obtained in unicellular or few-celled gametophytes (Lüning and Neushul 1978). Hoffman and Santelices (1982) reported that the addition of nutrients to culture media affected the morphology, fertility, and development of *Lessonia nigrescens* gametophytes. They

observed that gametophytes were shorter in media with increased amount of nutrients compared to gametophytes in plain sea water.

This experiment was terminated 22 days after inoculation, by that time multi-cellular sporophytes had formed in the medium and high light treatments. Gametophytes in the low light treatment had a stunted appearance with a much lower number of cells and showed a much lower vegetative growth. Previous research by Choi *et al.* (2005) suggests that the amount of light plays a major role in the maturation of female laminarian gametophytes. Below a certain threshold, gametophytes may grow vegetatively, but maturation is inhibited (Lüning and Neushul 1978; Choi *et al*. 2005). Hoffman and Santelices (1982) also found that when light intensity is too low (10 μmol photons m^{-2} s^{-1}), gametophytes of the laminarian species *L. nigrescens* did not become fertile, regardless of nutrient addition. My results, nonetheless, showed that small numbers of eggs did develop in the low light treatment (at 8.5 μmol photons m^{-2} s^{-1}, at a 12:12 LD cycle), although their development was delayed compared to the other light treatments. This indicates that, even though the light level was very low in this treatment, it was enough to initiate gametogenesis. This suggests that *U. pinnatifida* gametophytes only require very low light levels to be able to reproduce, which may contribute to their invasive nature and ability to grow in a high variety of habitats.

Light and nutrient conditions appeared ample for development of eggs and zygotes under medium and high light treatments, and only small differences in development rates could be observed between these treatment combinations. However sporophyte density, and to a greater extent the development of sporophyte tissue, was considerably different between high and medium nutrient treatments, suggesting greater requirements for both light and nutrients during sporophyte growth.

Settlement and germination of macroalgal spores are very important processes in the life-history of most algae (Dring 1982) and can strongly impact population dynamics (Roughgarden *et al.* 1988; Underwood and Fairweather 1989). Investigation of the performance of *U. pinnatifida* gametophytes under different light and nutrient conditions

can help explain its success in different habitats exposed to distinct light and/or nutrient environments. My results show that under low light conditions *U. pinnatifida* gametophyte growth stalls within 2 days of spore settlement, and that this development is not increased by greater nutrient concentrations. At medium and high light levels, gametophyte growth and reproduction increased with greater nutrient concentrations. In particular, sporophyte development and growth appeared highly sensitive to nutrient availability especially in high light conditions. These results have implications for *U. pinnatifida* population dynamics in intertidal habitats where light is less often a limiting resource. The results of this study show that when sufficient nutrients are available in these habitats, abundance of this invasive kelp may increase as a higher number of sporophytes will develop from the propagules and turnover time will be shorter (due to quicker development from spore to sporophyte).

CHAPTER 7

GENERAL DISCUSSION

Because it has spread to 12 countries on four continents since 1981 (Stuart 2003), several studies have speculated the ecological effects of *Undaria pinnatifida* on native assemblages. Most of these studies focused on subtidal habitats and suggest that *U. pinnatifida* can outcompete native algal species, form mono-cultures (Battershill *et al.* 1998; Forrest and Taylor 2002), and decrease faunal diversity (TAFI 2000). In contrast, it has also been suggested that the presence of *U. pinnatifida* could increase biodiversity through increased habitat complexity (Battershill *et al.* 1998). A three-year survey conducted on low-shore assemblages in Lyttelton Harbour in the South Island of New Zealand, however, found little impact from *U. pinnatifida* and no indication that it could outcompete native canopy-forming species (Forrest and Taylor 2002). Spatial variability in community structure can be very high (Coleman 2002; Fraschetti *et al.* 2005; Reichert *et al.* 2008; Chapter 2) and the effect of the presence of an invader may vary depending on the structure of resident communities. Yet, very few experimental studies have been conducted to investigate the ecological effects of this invasive kelp on resident assemblages.

Nutrients and light

Results of this thesis showed that low-intertidal algal community composition on rocky shores in the Wellington region had very high spatial variability, but no strong correlation could be detected between nutrient levels and algal assemblage structure on low-intertidal shores in the harbour and on the south coast. Nitrogen concentrations were higher in winter, but nutrient regimes of coastal waters of the Wellington Harbour and the

Wellington south coast were not significantly different. It appeared that the main contributors to increased nutrient conditions in the Wellington region were point sources like sewage outfalls. Algal assemblage structure may be affected by enriched nutrient conditions close the sewage outfall sites, but impacts on marine communities can depend on location, as shown in Chapter 3. Despite similar increases in nutrient concentrations near two sewage outfalls, effects of nutrient-enrichment on algal assemblages were not analogous across the two locations, and are likely influenced by several interacting factors, including wave exposure, grazer abundance and sedimentation (Brown *et al.* 1990). This is consistent with other studies, which have shown that besides seawater nutrient concentrations, herbivore abundance (Nielsen 2001, 2003; Worm *et al.* 2002) and physical disturbance (Kraufvelin 2007) can be important in structuring macroalgal communities on temperate rocky shores.

Besides altered nutrient regimes adjacent to sewage outfalls, the low cover of canopy-forming macrophytes found closer to the outfalls studied here could potentially facilitate invasion by non-indigenous algae as light and nutrient availability are not limited at these locations. While *U. pinnatifida* is not currently present near sewage outfalls in the Wellington region, it is possible that the sewage-enriched conditions will be suitable for the settlement and development of this species. For example, *U. pinnatifida* has been found to grow in sewage-enriched waters in Patagonia, Argentina (Torres *et al.* 2004). If *U. pinnatifida* establishes at nutrient-enriched sites, it may influence resident communities, e.g. through shading and scouring (Kennelly 1989), as large canopy species are often absent in eutrophic waters (Benedetti-Cecchi *et al.* 2001; Kraufvelin *et al.* 2006; Kraufvelin 2007). It has, however, been suggested that *U. pinnatifida* could aid in the removal of nutrients from the water column (Torres *et al.* 2004) due to its rapid nutrient uptake rate (Torres *et al.* 2004; Dean and Hurd 2007), acting as a helophyte filter. Further research is needed to investigate whether this invasive kelp can assist in nutrient reduction.

The laboratory experiment in Chapter 6 indicated that nutrient concentrations in coastal waters can affect *U. pinnatifida* reproductive development, which has implications for

enriched conditions *in situ*, especially as coastal nutrient regimes are altered through eutrophication or run-off. If *U. pinnatifida* gametophyte development and reproduction occurs at a higher rate when exposed to higher nutrient regimes, *U. pinnatifida* populations may expand in nutrient enriched waters as sporophytes may be produced at higher rates. Other (opportunistic) algae may also benefit from increased nutrient concentrations in a specific environment, and competition for space may occur among macroalgal species. The faster growing species may outcompete the slower growing ones. However, *U. pinnatifida* is capable of growing on a variety of substrata (Floc'h *et al.* 1996; Wotton *et al.* 2004) that may not be suitable for other algae to grow on. This characteristic may enable it to expand its range fast when ample nutrients are available. In addition, it has been suggested that gametophytes can remain viable for at least 24 months (Stuart 2003), giving them the opportunity to take advantage of favourable nutrient conditions for development if they arise.

The laboratory experiment also showed that *U. pinnatifida* gametophytes performed best at medium and high light levels (~28 - 145 μmol photons m^{-2} s^{-1}; constant over 12 hours). Irradiance *in situ* (above water, at midday) in Wellington can be ten-fold higher than levels in the laboratory (~1500 μmol photons m^{-2} s^{-1} in summer and ~1100 μmol photons m^{-2} s^{-1} in winter at midday on sunny days). On cloudy days light levels can be much lower, ~300 μmol photons m^{-2} s^{-1} (K. Ryan, pers. comm.). Water attenuates light levels and the level of irradiance under water is dependent on several factors, including depth and turbidity. However, light levels in intertidal habitats during submergence are probably still higher than the levels in the laboratory experiment. This suggests that in intertidal habitats, *U. pinnatifida* gametophytes would be able to develop and reproduce in conditions where light levels are lower, like in crevices, or under canopy species.

Disturbance

Disturbance is considered to be an important process in the establishment of invasive macroalgae (e.g. Levin *et al.* 2002; Valentine and Johnson 2003, 2004; Valentine *et al.*

2007). *Undaria pinnatifida* exhibits many features characteristic of opportunistic species, like rapid growth, short lifespan, small propagule size, the release of a large quantity of propagules, and a single reproductive period (Grime 1977; Valentine *et al.* 2007), traits which are often linked to disturbance. While it is difficult, or impossible, to predict invasiveness of different seaweed species based on life history characteristics (as their life history traits are wide ranging), it has been suggested that increasing invasibility may generally be associated with increases in resource availability and/or variance in resource availability within the recipient community (Davis *et al.* 2000; Dunstan and Johnson 2007). For example, both space availability and nutrient-enrichment have been shown to facilitate the establishment and spread of invasive *Sargassum muticum* in a low-intertidal macroalgal assemblage in northern Spain (Sánchez and Fernández 2006).

My results indicated that invasion dynamics may be different in intertidal versus subtidal habitats and different processes may be important in facilitating establishment of invasive seaweeds. Disturbance through canopy removal has been shown to be a key requirement for *U. pinnatifida* invasion in subtidal habitats, suggesting that reduction in light limitation facilitated *U. pinnatifida* recruitment in habitats previously dominated by native canopy-forming species (Valentine and Johnson 2003, 2004). Results from this study showed that *U. pinnatifida* was able to rapidly invade into new intertidal habitats and disturbance of the existing native algal assemblages was not a prerequisite for *U. pinnatifida* to establish in this environment, suggesting that light and space were not limiting in the intertidal habitat. This indicates that as long as there is a limited cover of large macrophytes, removal of these canopy species appears unnecessary for *U. pinnatifida* to be able to establish on rocky intertidal shores, or shows that natural removal rates or disturbances are sufficient in this habitat. The disturbances already naturally present in this environment may play a role in the relative invasibility of intertidal communities compared to subtidal communities.

Cover of large canopy species is usually higher in nearshore subtidal habitats (Schiel 1988; Schiel and Hickford 2001), which may cause light limitation and may inhibit *U. pinnatifida* development. In France, for example, a dense cover of indigenous kelp

species limited *U. pinnatifida* cover in the subtidal zone (Floc'h *et al.* 1996). While it seems likely that *U. pinnatifida* populations will be able to spread more quickly in intertidal habitats, due to the disturbance regime and the resulting frequent release of resources, consequences of increasing *U. pinnatifida* populations in subtidal habitats may be more severe due to more intense light limitation in the understory when dense *U. pinnatifida* canopies are formed, especially in habitats otherwise devoid of native kelp species (Battershill *et al.* 1998).

Undaria pinnatifida *removal*

Chapter 5 showed that the experimental removal of *U. pinnatifida* from low-intertidal habitats did not affect resident communities. This result was consistent across two distinct locations with different intertidal community structures, and may be because *U. pinnatifida* did not form dense canopies or monocultures in the study locations, or because it is generally an annual species, allowing native species to grow unaffected for part of the year. This result is coherent with a study by Sánchez and Fernández (2005), who found that the removal of the invasive *Sargassum muticum* from low intertidal assemblages on rocky shores in northern Spain had a negligible effect on the native macroalgal community. Whether the results are the same for other locations around New Zealand and other countries needs to be investigated. *U. pinnatifida* populations have been reported to be denser in other locations, e.g. in certain locations on the eastern coast of New Zealand's South Island (Forrest and Taylor 2002). In these areas removal of *U. pinnatifida* may more significantly alter community structure, as the difference in availability of resources like light and space before and after removal are likely to be larger. The annual nature of *U. pinnatifida* may also reduce its effects on native algal communities, as its influence on light and nutrient availability is only present for half of the year.

In addition, this study indicated that removal of established *U. pinnatifida* individuals is ineffective as it is able to quickly re-colonise after removal. However, no significant

change in resident community structure was found when this invader was removed; hence its effect on native communities may be limited in intertidal habitats if monocultures fail to form.

Conclusion

This thesis contributed to a better knowledge of ecological effects, invasion dynamics, and distribution of the invasive kelp *U. pinnatifida* on low-intertidal assemblages in the Wellington region of New Zealand. In addition, it gave insight into seawater nutrient regimes in this region, both natural and derived from sewage outfalls, and how these affect low-intertidal algal assemblage composition. The outcomes of this research could assist in the design of environmental protection and conservation strategies for marine habitats. Coastal marine habitats are very important to New Zealand in terms of their ecological, cultural, recreational, and economic aspects. The Taputeranga Marine Reserve, which was established in 2008, protects the marine environment on Wellington's south coast from human-induced disturbance and provides an interesting study system to investigate ecosystem processes in a natural environment. *Undaria pinnatifida,* considered a threat to biodiversity of native species by many, is abundant within the marine reserve.

This research also contributed to the understanding of ecological traits that favour invasion by *U. pinnatifida*, and showed that traits of the invasive species itself, traits of the recipient community, and the physical environmental regime of the habitat all play a role in the success of this invasive species.

Environments exposed to regular disturbances, like intertidal habitats, may have a higher invasibility due to a combination of limiting resources regularly being released within the recipient communities, and the frequent disturbances putting the resident biological communities under stress. These disturbances can be in physical (e.g. wave exposure, trampling), biological (e.g. herbivory, predation), and chemical (e.g. nutrient enrichment

through run-off, pollution) form, and may result in increased availability of open patches, reduction in cover of canopy forming species, and decrease in native species diversity.

The intrinsic trait of this invader to be able to reproduce year-round and grow in intertidal and subtidal habitats may increase its invasive success. *Undaria pinnatifida* is capable of colonising space quickly and may be able to outcompete native species which may have a distinct seasonality, and more specific habitat requirements.

A strong response of the invader to available resources, such as a quicker nutrient assimilation or growth rate than native competitors can result in overshadowing or smothering of native assemblages, where resident species may be outcompeted. In addition, the ability to utilise (limiting) resources quickly and efficiently may increase the success of the invader when this promotes rapid reproduction and development/growth, which can result in quickly succeeding generations, and consequently increasing abundance, especially when reproduction is not seasonal. Moderate disturbance may fuel and maintain the invading process through frequent freeing of limiting resources.

Further, this research hints that invasion dynamics of *U. pinnatifida* differ across different habitats (intertidal versus subtidal habitats) and that different processes may be important for the successful establishment of this invader in distinct environments. This could have parallel implications for other species in other habitats, e.g. introduced species in freshwater or terrestrial habitats.

Future directions

Recommendations for future research are (long-term) addition of nutrients *in situ* in algal assemblages without *U. pinnatifida* to investigate if nutrient enrichment facilitates *U. pinnatifida* invasion, and in assemblages with *U. pinnatifida* to investigate if *U. pinnatifida* abundance increases, and growth and development of sporophytes is accelerated in enriched conditions. Another opportunity for further research would be to

investigate if exposure of *U. pinnatifida* sporophytes to high nutrient conditions affects gametophyte growth and development and reproduction in the next generation, in particular gametophyte development under low nutrient levels. Finally, investigation into delayed development in gametophytes could assist in understanding the role of nutrient regimes in *U. pinnatifida* reproduction. Gametophytes exposed to low nutrient and light levels in a resistant state may be able to resume development when nutrient and light levels increase, as shown in other kelps, e.g. *Macrocystis pyrifera* (Carney and Edwards 2010; Carney 2011), yet minimum nutrient and light levels required for this resumption in *U. pinnatifida* gametophytes are not known.

REFERENCES

Adams, N.M. 1994. Seaweeds of New Zealand: an illustrated guide. Canterbury University Press, Christchurch. 360 pp.

Airoldi, L. 1998. Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. Ecology 79: 2759-2770

Airoldi, L. 2000. Responses of algae with different life histories to temporal and spatial variability of disturbance in subtidal reefs. Marine Ecology Progress Series 195: 81-92

Alpert, P., Bone, E., Holzapfel, C. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. Perspectives in Plant Ecology Evolution and Systematics 3: 52-66

Altman, S. and Whitlatch, R.B. 2007. Effects of small-scale disturbance on invasion success in marine communities. Journal of Experimental Marine Biology and Ecology 342: 15-29

Amsler, C.D. and Neushul, M. 1989. Chemotactic effects of nurients on spores of the kelps *Macrocystis pyrifera* and *Pterygophora californica*. Marine Biology 102: 557-564

Amsler, C.D. and Neushul, M. 1990. Nutrient stimulation of spore settlement in the kelps *Pterygophora californica* and *Macrocystis pyrifera*. Marine Biology 107: 297-304

Anderson, M.J. 2001. Permutation tests for univariate or multivariate analysis of variance and regression. Canadian Journal of Fisheries and Aquatic Sciences 58: 626-639

Anderson, M.J. and Ter Braak, C.J.F. 2003. Permutation tests for multi-factorial analysis of variance. Journal of Statistical Compuation and Simulation 73: 85-113

Andrew, N.L. and Viejo, R.M. 1998. Ecological limits to the invasion of *Sargassum muticum* in northern Spain. Aquatic Botany 60: 251-263

Araújo, R., Vaselli, S., Almeida, M., Serrão, E., Sousa-Pinto, I. 2009. Effects of disturbance on marginal populations: human trampling on *Ascophyllum nodosum*

assemblages at its southern distribution limit. Marine Ecology Progress Series 378: 81-92

Archambault, P., Banwell, K., Underwood, A.J. 2001. Temporal variation in the structure of intertidal assemblages following the removal of sewage. Marine Ecology Progress Series 222: 51-62

Arenas, F., Sánchez, I., Hawkins, S.J., Jenkins, S.R. 2006. The invasibility of marine algal assemblages: role of functional diversity and identity. Ecology 87: 2851-2861

Arévalo, R., Pinedo, S., Ballesteros, E. 2007. Changes in the composition and structure of Mediterranean rocky-shore communities following a gradient of nutrient enrichment: Descriptive study and test of proposed methods to assess water quality regarding macroalgae. Marine Pollution Bulletin 55: 104-113

Barr, N.G. 2007. Aspects of nitrogen metabolism in the green alga *Ulva*; Developing an indication of seawater nitrogen loading. PhD thesis, University of Auckland, 219 pp.

Barr, N.G., Kloeppel, A., Rees, T.A.V., Scherer, C., Taylor, R.B., Wenzel, A. 2008. Wave surge increases rates of growth and nutrient uptake in the green seaweed *Ulva pertusa* maintained at low bulk flow velocities. Aquatic Biology 3: 179-186

Battershill, C., Miller, K., Cole, R. 1998. The understorey of marine invasions. Seafood New Zealand 6: 31-33

Bax, N., Carlton, J.T., Mathews-Amos, A., Haedrich, R.L., Howarth, F.G., Purcell, J.E., Rieser, A., Gray, A. 2001. The control of biological invasions in the world's oceans. Conservation Biology 15: 1234-1246

Begg, J.G. and Johnstone, M.R. (compilers) 2000. Geology of the Wellington area. Institute of Geological and Nuclear Sciences 1:250 000 geological map 10. 1 sheet + 64p. Lower Hutt, New Zealand:Institute of Geological and Nuclear Sciences Limited.

Bellgrove, A., Clayton, M.N., Quinn, G.P. 1997. Effects of secondarily treated sewage effluent on intertidal macroalgal recruitment processes. Marine and Freshwater Research 48: 137-146

Benedetti-Cecchi, L. 2001. Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. Marine Ecology Progress Series 215: 79-92

Benedetti-Cecchi, L. and Cinelli, F. 1992. Canopy removal experiments in *Cystoseira*-dominated rockpools from the Western coast of the Mediterranean (Ligurian Sea). Journal of Experimental Marine Biology and Ecology 155: 69-83

Benedetti-Cecchi, L. and Cinelli, F. 1994. Recovery of patches in an assemblage of geniculate coralline algae: variability at different successional stages. Marine Ecology Progress Series 110: 9-18

Benedetti-Cecchi, L., Pannacciulli, F., Bulleri, F., Moschella, P.S., Airoldi, L., Relini, G., Cinelli, F. 2001. Predicting the consequences of anthropogenic disturbance: large-scale effects of loss of canopy algae on rocky shores. Marine Ecology Progress Series 214: 137-150

Benedetti-Cecchi, L., Maggi, E., Bertocci, I., Vaselli, S., Micheli, F., Osio, G.C., Cinelli, F. 2003. Variation in rocky shore assemblages in the northwestern Mediterranean: contrasts between islands and the mainland. Journal of Experimental Marine Biology and Ecology 293: 193-215

Bertness, M.D., Leonard, G.H., Levine, J.M., Schmidt, P.R., Ingraham, A.O. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. Ecology 80: 2711-2726

Bishop, M.J., Underwood, A.J., Archambault, P. 2002. Sewage and environmental impacts on rocky shores: necessity of identifying relevant spatial scales. Marine Ecology Progress Series 236: 121-128

Bokn, T.L., Moy, F.E., Christie, H., Engelbert, S., Karez, R., Kersting, K., Kraufvelin, P., Lindblad, C., Marba, N., Pedersen, M.F., Sørensen, K. 2002. Are rocky shore ecosystems affected by nutrient-enriched seawater? Some preliminary results from a mesocosm experiment. Hydrobiologia 484: 167-175

Bokn, T.L., Duarte, C.M., Pedersen, M.F., Marba, N., Moy, F.E., Barrón, C., Bjerkeng, B., Borum, J., Christie, H., Engelbert, S., Fotel, F.L., Hoell, E.E., Karez, R., Kersting, K., Kraufvelin, P., Lindblad, C., Olsen, M., Sanderud, K.A., Sommer, U.,

Sørensen, K. 2003. The response of experimental rocky shore communities to nutrient additions. Ecosystems 6: 577-594

Borowitzka, M.A. 1972. Intertidal algal species diversity and the effect of pollution. Australian Journal of Marine en Freshwater Research 23: 73-84

Borum, J. and Sand-Jensen, K. 1996. Is total primary production in shallow marine water stimulated by nitrogen loading? Oikos 76: 406-410

Boudouresque, C.F., Meinesz, A., Ribera, M.A., Ballesteros, E. 1995. Spread of the green alga *Caulerpa taxifolia* (Caulerpales, Chlorophyta) in the Mediterranean: possible consequences of a major ecological event. Scientia Marina 59: 21-29

Boudouresque, C.F. and Verlaque, M. 2002. Biological pollution in the Mediterranean Sea: invasive versus introduced macrophytes. Marine Pollution Bulletin 44: 32-38

Bowman, M.J., Kibblewhite, A.C., Murtagh, R.A., Chiswell, S.M., Sanderson, B.G. 1983. Circulation and mixing in greater Cook Strait, New Zealand. Oceanologica Acta 6: 383-391

Boyle, K.A., Kamer, K., Fong, P. 2004. Spatial and temporal patterns in sediment and water column nutrients in a eutrophic southern California estuary. Estuaries 27: 378–88.

Britton-Simmons, K.H. 2006. Functional group diversity, resource pre-emption and the genesis of invasion resistance in a community of marine algae. Oikos 113: 395-401

Brown, V.B., Davies, S.A., Synnot, R.N. 1990. Long-term monitoring of the effects of treated sewage effluent on the intertidal macroalgal community near Cape Schanck, Victoria, Australia. Botanica Marina 33: 85-98

Bruno, J.F., Stachowicz, J.J., Bertness, M.D. 2003. Inclusion of facilitation into ecological theory. Trends in Ecology and Evolution 18: 119-125

Burke, M.J.W. and Grime, J.P. 1996. An experimental study of plant community invasibility. Ecology 77: 776-790

Bustamante, R.H. and Branch, G.M. 1996. The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. Journal of Experimental Marine Biology and Ecology 196: 1-28

Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M., Atkinson, I.A.E., Seastedt, T.R., Williamson, M., Chornesky, E., Hayes, D. 2002.

Directing research to reduce the impacts of nonindigenous species. Conservation Biology 16: 630-640

Campbell, S.J. and Burridge, T.R. 1998. Occurrence of *Undaria pinnatifida* (Phaeophyta: Laminariales) in Port Phillip Bay, Victoria, Australia. Marine and Freshwater Research 49: 379-381

Carlton, J.T. 1989. Man's role on changing the face of the ocean: biological invasion and implications for conservation of near-shore environments. Conservation Biology 3: 265-273

Carlton, J.T. 1996. Biological invasions and cryptogenic species. Ecology 77: 1653-1655

Carlton, J.T. 1999. Scale and ecological consequences of biological invasions in the world's oceans. In: Sandlund, O.T., Schei, P.J., Viken, A. (Eds.). Invasive Species and Biodiversity Management. Kluwer Academic Publishers, Dordecht, pp. 195–212

Carlton, J.T. and Geller, J.B. 1993. Ecological roulette - the global transport of nonindigenous marine organisms. Science 261: 78-82

Carney, L.T. 2011. A multispecies laboratory assessment of rapid sporophyte recruitment from delayed kelp gametophytes. Journal of Phycology 47: 244-251

Carney, L.T. and Edwards, M.S. 2010. Gametophyte reproduction by *Macrocystis pyrifera* (Phaeophyceae) in southern California. Journal of Phycology 46: 987-996

Carter, L., Laing, A., Bell, R. 2002. Wild southerlies of summer. Water & Atmosphere 10: 22-23

Casas, G., Scrosati, R., Luz Piriz, M. 2004. The invasive kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). Biological Invasions 6: 411-416

Castric-Fey, A., Beaupoil, C., Bouchain, J., Pradier, E., L'Hardy-Halos, M.Th. 1999. The introduced alga *Undaria pinnatifida* (Laminariales, Alariaceae) in the rocky shore ecosystem of the St Malo area: growth rate and longevity of the sporophytes. Botanica marina 42: 83-96

Chapman, M.G., Underwood, A.J., Skilleter, G.A. 1995. Variability at different spatial scales between a subtidal assemblage exposed to the discharge of sewage and two

control assemblages. Journal of Experimental Marine Biology and Ecology 189: 103-122

Choi, H.C., Kim, Y.S., Lee, S.J., Park, E.J., Nam, K.W. 2005. Effects of daylength, irradiance and settlement density on the growth and reproduction of *Undaria pinnatifida* gametophytes. Journal of Applied Phycology 17:423-430

Clark, R.P., Edwards, M.S., Foster, M.S. 2004. Effects of shade from multiple kelp canopies on an understory algal assemblage. Marine Ecology Progress Series. 267: 107-119

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143

Clarke, K.R. and Ainsworth, M. 1993. A method of linking multivariate community structure to environmental variables. Marine Ecology Progress Series 92: 205-219

Clarke, K.R. and Warwick, R.M. 2001. Changes in marine communities - An approach to statistical analysis and interpretation (2nd ed.): PRIMER_E Ltd, Plymouth, UK

Clarke, K.R. and Gorley, R.N. 2006. PRIMER-E Ltd. User manual/Tutorial: PRIMER-E Ltd. Plymouth, UK

CliFlo, NIWA's National Climate Database on the Web, URL http://cliflo.niwa.co.nz

Cohen, A.N. and Carlton, J.T. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279: 555-558

Colautti, R.I., Grigorovich, I.A., MacIsaac, H.J. 2006. Propagule pressure: a null model for biological invasions. Biological Invasions 8: 1023-1037

Coleman, M.A. 2002. Small-scale spatial variability in intertidal and subtidal turfing algal assemblages and the temporal generality of these patterns. Journal of Experimental Marine Biology and Ecology 267: 53-74

Correll, D.L. and Ford, D. 1982. Comparison of precipitation and land runoff as sources of estuarine nitrogen. Estuarine, Coastal, and Shelf Science 15: 45-56

Corzo, A. and Niell, F.X. 1992. Inorganic nitrogen metabolism in *Ulva rigida* illuminated with blue light. Marine Biology 112: 223-228

Cranfield, H.J., Gordon, D.P., Willan, R.C., Marshall, B.A., Battershill, C.N., Francis, M.P., Nelson, W.A., Glasby, C.J., Read, G.B. 1998. Adventive species in New Zealand. NIWA Technical Report #34, Wellington, New Zealand

Crooks, J.A., Chang, A.L., Ruiz, G.M. 2011. Aquatic pollution increases the relative success of invasive species. Biological Invasions 13: 165-176

Curiel, D., Bellemo, G., Marzocchi, M., Scattolin, M., Parisi, G. 1998. Distribution of introduced Japanese macroalgae *Undaria pinnatifida*, *Sargassum muticum* (Phaeophyta) and *Antithamnion pectinatum* (Rhodophyta) in the Lagoon of Venice. Hydrobiologia 385: 17-22

D'Antonio, C.M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. Ecology 74: 83-95

Davis, M.A., Grime, J.P., Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88: 528-534

Dayton, P.K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecological Monographs 41: 351-389

Dayton, P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecological. Monographs. 45: 137-159

Dean, P.R. and Hurd, C.L. 2007. Seasonal growth, erosion rates, and nitrogen and photosynthetic ecophysiology of *Undaria pinnatifida* (heterokontophyta) in southern New Zealand. Journal of Phycology 43: 1138-1148

Denny, M.W. 1985. Wave forces on intertidal organisms: a case study. Limnology and Oceanography 30: 1171-1187

Denny, M.W. and Gaines, S.D. 1990. On the prediction of maximal intertidal wave forces. Limnology and Oceanography 35: 1-15

Dring, M.J. 1982. The biology of marine plants. Edward Arnold. London, 199 pp.

Duarte, C.M. 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia 41: 87-112

Dudley, B.D., Barr, N.G., Shima, J.S. 2010. Influence of light intensity and nutrient source on $\delta^{13}C$ and $\delta^{15}N$ signatures in *Ulva pertusa*. Aquatic Biology 9: 85-93

Dudley, B.D. and Shima, J.S. 2010. Algal and invertebrate bioindicators detect sewage effluent along the coast of Titahi Bay, Wellington, New Zealand. New Zealand Journal of Marine and Freshwater Research 44: 39-51

Dunstan, P.K. and Johnson, C.R. 2007. Mechanisms of invasions: can the recipient community influence invasion rates? Botanica Marina 50: 361-372

Dye, A.H. 1993. Recolonization of intertidal macroalgae in relation to gap size and molluscan herbivory on a rocky shore on the east coast of southern Africa. Marine Ecology Progress Series 95: 263-271

Edgar, G.J., Barrett, N.S., Morton, A.J., Samson, C.R. 2004. Effects of algal canopy clearance on plant, fish and macroinvertebrate communities on eastern Tasmanian reefs. Journal of Experimental Marine Biology and Ecology. 312: 67-87

Elton, C.S. 1958. The ecology of invasions by animals and plants. Methuen, London, 181 pp.

Fairweather, P.G. 1990. Sewage and the biota on seashores: assessment of impact in relation to natural variability. Environmental Monitoring and Assessment 14: 197-210

Farrell, T.M. 1989. Succession in a rocky intertidal community: the importance of disturbance size and position within a disturbed patch. Journal of Experimental Marine Biology and Ecology 128: 57-73

Floc'h, J.-Y., Pajot, R., Mouret, V. 1996. *Undaria pinnatifida* (Laminariales, Phaeophyta) 12 years after its introduction into the Atlantic Ocean. Hydrobiologia 326-327: 217-222

Forrest, B.M. 2007. Managing risks from invasive marine species: is post-border management feasible? PhD Thesis, Victoria University of Wellington, 199 pp.

Forrest, B.M., Brown, S.N., Taylor, M.D., Hurd, C.L., Hay, C.H. 2000. The role of natural dispersal mechanisms in the spread of *Undaria pinnatifida* (Laminariales, Phaeophyceae). Phycologia 39: 547-553

Forrest, B.M. and Taylor, M.D. 2002. Assessing invasion impact: survey design considerations and implications for management of an invasive marine plant. Biological Invasions 4: 375-386

Fraschetti, S., Terlizzi, A., Benedetti-Cecchi, L. 2005. Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. Marine Ecology Progress Series 296: 13-29

Fry, B., Rogers, K., Barry, B., Barr, N., Dudley, B. 2011. Eutrophication indicators in the Hutt River Estuary, New Zealand. New Zealand Journal of Marine and Freshwater Research 45: 665-677

Fujita, R.M. 1985. The role of nitrogen status in regulating transient ammonium uptake and nitrogen storage by macroalgae. Journal of Experimental Marine Biology and Ecology 92: 283-301

Fujita, R.M., Wheeler, P.A., Edwards, R.L. 1989. Assessment of macroalgal nitrogen limitation in a seasonal upwelling region. Marine Ecology Progress Series 53: 293-303

Galloway, J.N., Aber, J.D., Erisman, J.W., Seitzinger, S.P., Howarth, R.W., Cowling, E.B., Cosby, B.J. 2003. The nitrogen cascade. Bioscience 53, 341-356.

Gardner, J.P.A. 2000. Where are the mussels on Cook Strait (New Zealand) shores? Low seston quality as a possible factor limiting multi-species distributions. Marine Ecology Progress Series 194: 123-132

GESAMP (IMO/FAO/UNESCO-IOC/WMO/IAEA/UN/UNEP joint group of Experts of the Scientific Aspects of Marine Environmental Protection) and Advisory Committee of Protection of the Sea. 2001. Protecting the oceans from land-based activities - Land-based sources and activities affecting the quality and uses of marine, coastal and associated freshwater environment. Rep. Stud. GESAMP No. 71

Graham, W.M. and Bayha, K.M. 2007. Biological invasions by marine jellyfish. In: Nentwig, W. [Ed.] Biological Invasions, Ecological Studies 193. Springer-Verlag, Berlin Heidelberg, pp. 239-255

Griffiths, C.L., Hocky, P.A.R., Van Erkom Schurink, C., Le Roux, P.J. 1992. Marine invasive aliens on South Affrican shores: implicaitons for community structure and trophic functioning. South African Journal of Marine Science 12: 713-722

Grime, J.P. 1977. Evidence for the Existence of Three Primary Strategies in Plants and Its Relevance to Ecological and Evolutionary Theory. The American Naturalist 111: 1169-1194

Grosholz, E. 2002. Ecological and evolutionary consequences of coastal invasions. Trends in Ecology & Evolution 17: 22-27

Guerry, A.D., Menge, B.A., Dunmore, R.A. 2009. Effects of consumers and enrichment on abundance and diversity of benthic algae in a rocky intertidal community. Journal of Experimental Marine Biology and Ecology 369: 155-164

Hanisak, M.D. 1983. The nitrogen relationships of marine macroalgae. In: Carpenter, E.J. and Capone, D.G. [Eds.] Nitrogen in the marine environment. New York, Academic Press, pp. 699-730.

Harris, L.G. and Tyrrell, M.C. 2001. Changing community states in the Gulf of Maine: synergism between invaders, overfishing and climate change. Biological Invasions 3: 9-21

Hay, C.H. and Luckens, P.A. 1987. The Asian kelp *Undaria-Pinnatifida* (Phaeophyta, Laminariales) found in a New-Zealand harbor. New Zealand Journal of Botany 25: 329-332

Hay, C.H. and Villouta, E. 1993. Seasonality of the adventive Asian kelp *Undaria pinnatifida* in New-Zealand. Botanica Marina 36: 461-476

Helson, J.G. and Gardner, J.P.A. 2004. Contrasting patterns of mussel abundance at neighbouring sites: does recruitment limitation explain the absence of mussels on Cook Strait (New Zealand) shores? Journal of Experimental Marine Biology and Ecology 22: 285-298

Helson, J.G., Pledger, S., Gardner, J.P.A. 2007. Does differential particulate food supply explain the presence of mussels in Wellington Harbour (New Zealand) and their absence on neighbouring Cook Strait shores? Estuarine Coastal and Shelf Science 72: 223-234

Henkel, S.K. and Hofmann, G.E. 2008. Thermal ecophysiology of gametophytes cultured from invasive *Undaria pinnatifida* (Harvey) Suringar in coastal California harbors. Journal of Experimental Marine Biology and Ecology 367: 164-173

Hobbs, R.J. and Huenneke, L.F. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology 6: 324-337

Hoffman, A.J. and Santelices, B. 1982. Effects of light intensity and nutrients on gametophytes and gametogenesis of *Lessonia nigrescens* bory (Phaeophyta). Journal of Experimental Marine Biology and Ecology 60:77-89

Hoffmann, A.J. and Ugarte, R. 1985. The arrival of propagules of marine macroalgae in the intertidal zone. Journal of Experimental Marine Biology and Ecology 92: 83-95

Hughes, F., Vitousek, P.M., Tunison, T. 1991. Alien grass invasion and fire in the seasonal submontane zone of Hawai'i. Ecology 72: 743-746

Ifremer. 2006. http://en.aquaculture.ifremer.fr/filieres/filiere_algues/la_decouverte_des_algues/macroalgues/undaria

Jaschinski, S. and Sommer, U. 2010. Positive effects of mesograzers on epiphytes in an eelgrass system. Marine Ecology Progress Series 401: 77-85

Jenkins, S.R., Norton, T.A., Hawkins, S.J. 2004. Long term effects of *Ascophyllum nodosum* canopy removal on mid shore community structure. Journal of the Marine Biological Association of the United Kingdom 84: 327-329

Kavanaugh, M.T., Nielsen, K.J., Chan, F.T., Menge, B.A., Letelier, R.M., Goodrich, L.M. 2009. Experimental assessment of the effects of shade on an intertidal kelp: do phytoplankton blooms inhibit growth of open-coast macroalgae? Limnology and Oceanography 54: 276-288

Keane, R.M. and Crawley, M.J. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 17: 164-170

Kendrick, G.A. 1991. Recruitment of coralline crusts and filamentous turf algae in the Galapagos Archipelago: effect of simulated scour, erosion and accretion. Journal of Experimental Marine Biology and Ecology 147: 47-63

Kennelly, S.J. 1987. Physical disturbances in an Australian kelp community. 1. Temporal effects. Marine Ecology Progress Series 40: 145-153

Kennelly, S.J. 1989. Effects of kelp canopies on understorey species due to shade and scour. Marine Ecology Progress Series 50: 215–224

Kennelly, S.J. and Underwood, A.J. 1992. Fluctuation in the distributions and abundances of species in sublittoral kelp forests in New South Wales. Australian Journal of Ecology 17: 367-382

Keough, M.J. 1984. Effects of patch size on the abundance of sessile marine invertebrates. Ecology 65: 423-437

Keough, M.J. and Quinn, G.P. 1998. Effects of periodic disturbance from trampling on rocky intertidal algal beds. Ecological Applications 8: 141-161

Kevekordes, K., Clayton, M.N. 2000. Development of *Hormosira banksii* (Phaeophyceae) embryos in selected components of secondarily-treated sewage effluent. Journal of Phycology 36: 25-32

Kim, J.H. and DeWreede, R.E. 1996. Effect of size and season of disturbance on algal patch recovery in a rocky intertidal community. Marine Ecology Progress Series 133: 217-228

Knops, M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E., Groth, J. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecology Letters 2: 286-293

Koroleff, F. 1983. Determination of phosphorus. In: Grasshoff, K., Ehrhardt, M., Kremling, K. [Eds.] Methods of seawater analysis, 2nd edn. Verlag Chemie, Weinheim, pp. 125-139

Kraufvelin, P. 2007. Responses to nutrient enrichment, wave action and disturbance in rocky shore communities. Aquatic Botany 87: 262-274

Kraufvelin, P., Moy, F.E., Hartvig, C., Bokn, T.L. 2006. Nutrient addition to experimental rocky shore communities revisited: delayed response, rapid recovery. Ecosystems 9: 1076-1093

Levin, P.S., Coyer, J.A., Petrik, R., Good, T.P. 2002. Community-wide effects of nonindigenous species in temperate rocky reefs. Ecology 83: 3182-3193

Levin, S.A. and Paine, R.T. 1974. Disturbance, patch formation, and community structure. Proceedings of the National Academy of Sciences of the United States of America 71: 2744-2747

Lewis, P.N., Hewitt, C.L., Riddle, M., McMinn, A. 2003. Marine introductions in the Southern Ocean: an unrecognised hazard to biodiversity. Marine Pollution Bulletin 46: 213-223

Lilley, S.A. and Schiel, D.R. 2006. Community effects following the deletion of a habitat-forming alga from rocky marine shores. Oecologia 148: 672-681

Littler, M.M. and Murray, S.N. 1975. Impact of sewage on the distribution, abundance and community structure of rocky intertidal macro-organisms. Marine Biology 30: 277-291

Littler, M.M. and Murray, S.N. 1978. Influence of domestic waste on energetic pathways in rocky intertidal communities. Journal of Applied Ecology 15: 583-595

Lobban, C.S. and Harrison, P.J. 1994. Seaweed Ecology and Physiology. Cambridge University Press, Cambridge, 365 pp.

Lodge, D.M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution 8: 133-137

Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. The American Naturalist 112: 23-39

Lubchenco, J. and Menge, B.A. 1978. Community development and persistence in a low rocky intertidal zone. Ecological Monographs 59: 67-94

Lüning, K. and Neushul, M. 1978. Light and temoerature demands for growth and reproduction of laminarian gametophytes in southern and central California. Marine Biology 45:297-309

Mann, K.H. 2000. Ecology of coastal waters: with implications for management - 2nd ed. Blackwell Science, Inc., Malden, MA, 406 pp.

Meinesz, A., de Vaugelas, J., Hesse, B., Mari, X. 1993. Spread of the introduced tropical green alga *Caulerpa taxifolia* in northern Mediterranean waters. Journal of Applied Phycology 5: 141-147

Menge, B.A. and Olsen, A.M. 1990. Role of scale and environmental factors in regulation of community structure. Trends in Ecology and Evolution 5: 52-57

Menge, B.A., Daley, B.A., Wheeler, P.A., Strub, P.T. 1997. Rocky intertidal oceanography: an association between community structure and nearshore phytoplankton concentration. Limnology and Oceanography 42: 57-66

Middelboe, A.L. and Binzer, T. 2004. Importance of canopy structure on photosynthesis in single-and multi-species assemblages of marine macroalgae. Oikos 170: 422-432

Middlemass, S. 1990. Algal feeding preferences in juvenile paua, *Haliotis iris* Martyn (Mollusca: Haliotidae). BSc Thesis, Victoria University of Wellington, 101 pp.

Milazzo, M., Chemello, R. Badalamenti, F., Riggio, S. 2002. Short-term effect of human trampling on the upper infralittoral macroalgae of Ustica Island MPA (western

Mediterranean, Italy). Journal of the Marine Biological Association of the United Kingdom 82: 745-748

Morton, J. and Miller, M. 1968. The New Zealand Sea Shore. Collins, Auckland, 638 pp.

Muncaster, S. 2002. Feeding interactions of *Haliotis iris* and *Evenchinus chloroticus* with the invasive seaweed *Undaria pinnatifida.* MSc Thesis, Otago University, Dunedin, 121 pp.

Nielsen, K.J. 2001. Bottom-up and top-down forces in tide pools: test of a food chain model in an intertidal community. Ecological Monographs 71: 187-217

Nielsen, K.J. 2003. Nutrient loading and consumers: agents of change in open-coast macrophyte assemblages. Proceedings of the National Academy of Sciences of the United States of America 100: 7660-7665

Nyberg, C.D. and Wallentinus, I. 2005. Can species traits be used to predict marine macroalgal introductions? Biological Invasions 7: 265-279

Oh, S.-H. and Koh, C.-H. 1996. Growth and photosynthesis of *Undaria pinnatifida* (Laminariales, Phaeophyta) on a cultivation ground near Korea. Botanica Marina 39: 389-393

Oviatt, C.A. 2004. The changing ecology of temperate coastal waters during a warming trend. Estuaries 27: 895-904

Paine, R.T. and Levin, S.A. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs 51: 145-178

Pang, S.-J. and Wu, C.-Y. 1996. Study on gametophyte vegetative growth of *Undaria pinnatifida* and its applications. Chinese Journal of Oceanology and Limnology 14: 205-210

Pedersen, M.F. and Borum, J. 1996. Nutrient control of algal growth in estaurine waters. Nutrient limitation and the importance of nitrogen requirements and nitrogen strorage among phytoplankton and species of macroalgae. Marine Ecology Progress Series 142: 261-272

Pedersen, M.F., Borum J., Fotel F.L. 2010. Phosphorus dynamics and limitation of fast- and slow-growing temperate seaweeds in Oslofjord, Norway. Marine Ecology Progress Series 399: 103–115.

Phillips, N.E. and Hutchison, E. 2008. Grazer effects on algal assemblages and mussel recruitment in two different mid-intertidal communities in the Cook Strait, New Zealand. New Zealand Journal of Marine and Freshwater Research 42: 297-306

Piazzi, L., Ceccherelli, G., Cinelli, F. 2001. Threat to macroalgal diversity: effects of the introduced green alga *Caulerpa racemosa* in the Mediterranean. Marine Ecology Progress Series 210: 149-159

Piazzi, L. and Cinelli, F. 2003. Evaluation of benthic macroalgal invasion in a harbour area of the western Mediterranean Sea. European Journal of Phycology 38: 223-231

Piazzi, L. and Ceccherelli, G. 2006. Persistence of biological invasion effects: recovery of macroalgal assemblages after removal of *Caulerpa racemosa* var. *cylindracea*. Estuarine, Coastal and Shelf Science 68: 455-461

Plymouth Marine Laboratory. 2009. PRIMER v6, version 6.1.13 & PERMANOVA, version 1.0.3. PRIMER-E, Plymouth, UK

Quinn, G., Keough, M. 2002. Experimental design and data analysis for biologists. Cambridge, Cambridge University Press.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org

Rasband, W.S., ImageJ, U. S. National Institutes of Health, Bethesda, Maryland, USA, http://imagej.nih.gov/ij/, 1997-2011

Reed, D.C. and Foster, M.S. 1984. The effects of canopy shading on algal recruitment and growth in a giant kelp forest. Ecology 65: 937-948

Reichert, K., Buchholz, F., Bartsch, I., Kersten, T., Giménez, L. 2008. Scale-dependent patterns of variability in species assemblages of the rocky intertidal at Helgoland (German Bight, North Sea). Journal of the Marine Biological Association of the United Kingdom 88: 1319-1329

Roberston, B. and Stevens, L. 2010. Hutt River Estuary, fine scale monitoring 2009/10. Report to Wellington Regional Council. Nelson, Wriggle Limited, 24 pp.

Roughgarden, J., Gaines, S., Possingham, H. 1988. Recruitment dynamics in complex life cycles. Science 241: 1460-1466

Ruiz, G.M., Carlton, J.T., Grosholz, E.D., Hines, A.H. 1997. Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. American Zoologist 37: 621-632

Ruiz, G.M., Fofonoff, P, Hines, A.H., Grosholz, E.D. 1999. Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. Limnology and Oceanography 44: 950-972

Russell, L.K., Hepburn, C.D., Hurd, C.L., Stuart, M.D. 2008. The expanding range of *Undaria pinnatifida* in southern New Zealand: distribution, dispersal mechanisms and the invasion of wave-exposed environments. Biological Invasions 10: 103-115

Sánchez, Í. and Fernández, C. 2005. Impact of the invasive seaweed *Sargassum muticum* (Phaeophyta) on an intertidal macroalgal assemblage. Journal of Phycology 41: 923-930

Sánchez, Í., Fernández, C., Arrontes, J. 2005. Long-term changes in the structure of intertidal assemblages after invasion by *Sargassum muticum* (Phaeophyta). Journal of Phycology 41: 942-949

Sánchez, Í. and Fernández, C. 2006. Resource availability and invasibility in an intertidal macroalgal assemblage. Marine Ecology Progress Series 313: 85-94

Sanderson, J.C. 1990. A preliminary survey of the distribution of the introduced macroalga *Undaria pinnatifida* (Harvey) Suringer on the east coast of Tasmania. Botanica Marina 33: 153-157

Schaffelke, B., Smith, J.E., Hewitt, C.L. 2006. Introduced macroalgae - a growing concern. Journal of Applied Phycology 18: 529-541

Scheibling, R.E. and Gagnon, P. 2006. Competitive interactions between the invasive green alga *Codium fragile* ssp. *Tomentosoides* and native canopy-forming seaweeds in Nova Scotia (Canada). Marine Ecology Progress Series 325: 1-14

Schiel, D.R. 1988. Algal interactions on shallow subtidal reefs in northern New Zealand: a review. New Zealand Journal of Marine and Freshwater Research 22: 481-489

Schiel, D.R. 2004. The structure and replenishment of rocky shore intertidal communities and biogeographic comparisons. Journal of Experimental Marine Biology and Ecology 300: 309-342

Schiel, D.R. and Taylor, D.I. 1999. Effects of trampling on a rocky intertidal algal assemblage in southern New Zealand. Journal of Experimental Marine Biology and Ecology 235: 213-235

Schiel, D.R. and Hickford, M.J.H. 2001. Biological structure of nearshore rocky subtidal habitats in southern New Zealand. Science for Conservation 182, 54 pp.

Schiel, D.R. and Lilley, S.A. 2007. Gradients of disturbance to an algal canopy and the modification of an intertidal community. Marine Ecology Progress Series 339: 1-11

Schmidt, A.L. and Scheibling, R.E. 2007. Effects of native and invasive macroalgal canopies on composition and abundance of mobile benthic macrofauna and turf-forming algae. Journal of Experimental Marine Biology and Ecology 341: 110-130

Shanks, A.L. and Trent, J.D. 1979. Marine snow: microscale nutrient patches. Limnology and Oceanography 24: 850-854

Sharp, J.H. 1983. The distributions of inorganic nitrogen, and dissolved and particulate organic nitrogen in the sea. In: Carpenter, E.J. and Capone, D.G. [Eds.] Nitrogen in the marine environment. New York, Academic Press, pp. 1-35.

Sherlock, V., Pickmere, S., Currie, K., Hadfield, M., Nodder, S., Boyd, P.W. 2007. Predictive accuracy of temperature nitrate relationships for the oceanic mixed layer of the New Zealand region. Journal of Geophysical. Research 112: C06010, 13 pp, doi:10.1029/2006JC003562

Siemann, E. and Rogers, W.E. 2003. Increased competitive ability of an invasive tree may be limited by an invasive beetle. Ecological Applications 13: 1503-1507

Smith, S.V. 1981. Marine macrophytes as a global carbon sink. Science 211: 838-840

Smith, S.V. 1984. Phosphorus versus nitrogen limitation in the marine environment. Limnology and Oceanography 29: 1149-1160

Sousa, W.P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecological Monographs 49: 228-254

Sousa, W.P. 1980. The responses of a community to disturbance: the importance of successional age and species' life histories. Oecologia 45: 72-81

Sousa, W.P. 1984a. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15: 353-391

Sousa, W.P. 1984b. Intertidal mosaics: patch size, propagule availability, and spatially variable patterns of succession. Ecology 65: 1918-1935

Steneck, R.S. and Dethier, M.N. 1994. A Functional-group approach to the structure of algal-dominated communities. Oikos 69: 476-498

Stuart, M.D. 2003. Review of research on *Undaria pinnatifida* in New Zealand and its potential impacts on the eastern coast of the South Island. DOC Science Internal Series 166. Department of Conservation, Wellington. 40 p.

Tasmanian Aquaculture and Fisheries Institute (TAFI) 2000: Tasmanian Aquaculture and Fisheries Institute Annual Report 1999/2000, University of Tasmania. 61 p.

Thomas, T.E. and Harrison, P.J. 1985. Effects of nitrogen supply on nitrogen uptake, accumulation and assimilation in *Porphyra perforate* (Rhodophyta). Marine Biology 85: 269-278

Thomas, T.E. and Harrison, P.J. 1987. Rapid ammonium uptake and nitrogen interactions in five intertidal seaweeds grown under field conditions. Journal of Experimental Marine Biology and Ecology 107: 1-8

Thompson, P.A., Baird, M.E., Ingleton, T., Doblin, M.A. 2009. Long-term changes in temperate Australian coastal waters: implications for phytoplankton. Marine Ecology Progress Series 394: 1-19

Thompson, R.C., Crowe, T.P., Hawkins, S.J. 2002. Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. Environmental Conservation 29: 168-191

Thornber, C.S., Kinlan, B.P., Graham, M.H., Stachowicz, J.J. 2004. Population ecology of the invasive kelp *Undaria pinnatifida* in California: environmental and biological controls on demography. Marine Ecology Progress Series 268: 69-80

Tilman, D., Wedin, D., Knops, J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. Nature 379: 718-720

Tilman, D., Knops, J., Wedin, D. Reich, P. Ritchie, M., Siemann, E. 1997. The influence of functional diversity and composition on ecosystem processes. Science 277: 1300-1302

Torres, A.I., Gil, M.N., Esteves J.L. 2004. Nutrient uptake rates by the alien alga *Undaria pinnatifida* (Phaeophyta) (Nuevo Gulf, Patagonia, Argentina) when exposed to diluted sewage effluent. Hydrobiologia 520: 1-6

Trowbridge, C.D. 1995. Establishment of the green alga *Codium fragile* ssp *tomentosoides* on New Zealand rocky shores: current distribution and invertebrate grazers. Journal of Ecology 83: 949-965

Underwood, A.J. 1998. Grazing and disturbance: an experimental analysis of patchiness in recovery from a severe storm by the intertidal alga *Hormosira banksii* on rocky shores in New South Wales. Journal of Experimental Marine Biology and Ecology 231: 291-306

Underwood, A.J. 1999. Physical disturbances and their direct effect on an indirect effect: responses of an intertidal assemblage to a severe storm. Journal of Experimental Marine Biology and Ecology 232: 125-140

Underwood, A.J., Fairweather, P.G. 1989. Supply-side ecology and benthic marine assemblages. Trends in Ecology and Evolution 6:16-19

Underwood, A.J. and Chapman, M.G. 1998a. Variation in algal assemblages on wave-exposed rocky shores in New South Wales. Marine and Freshwater Research 49: 241-254

Underwood, A.J. and Chapman, M.G. 1998b. Spatial analyses of intertidal assemblages on sheltered rocky shores. Australian Journal of Ecology 23: 138-157

Valentine, J.P. and Johnson, C.R. 2003. Establishment of the introduced kelp *Undaria pinnatifida* in Tasmania depends on disturbance to native algal assemblages. Journal of Experimental Marine Biology and Ecology 295: 63-90

Valentine, J.P. and Johnson, C.R. 2004. Establishment of the introduced kelp *Undaria pinnatifida* following dieback of the native macroalga *Phyllospora comosa* in Tasmania, Australia. Marine and Freshwater Research 55: 223-230

Valentine, J.P. and Johnson, C.R. 2005. Persistence of the exotic kelp *Undaria pinnatifida* does not depend on sea urchin grazing. Marine Ecology Progress Series 285: 43-55

Valentine, J.P., Magierowski, R.H., Johnson, C.R. 2007. Mechanisms of invasion: establishment, spread and persistence of introduced seaweed populations. Botanica Marina 50: 351-360

Valiela, I., Foreman, K., Lamontagne, M., Hersh, D., Costa, J., Peckol, P., Demeoandreson, B., Davanzo, C., Babione, M., Sham, C.H., Brawley, J., Lajtha, K. 1992. Couplings of watersheds and coastal waters: sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. Estuaries 15: 443-457

Valiela, I., Collins, G., Kremer, J., Lajtha, K., Geist, M., Seely, B., Brawley, J. Sham, C.H. 1997a. Nitrogen loading from coastal watersheds to receiving estuaries: new method and application. Ecological Applications 7: 358-380

Valiela, I., McClelland, J., Hauxwell, J., Behr, P.J., Hersh, D., Foreman, K. 1997b. Macroalgal blooms in shallow estuaries: controls and ecophysiological and ecosystem consequences. Limnology and Oceanography 42: 1105-1118

Vergara, J.J., Bird, K.T., Niell, F.X. 1995. Nitrogen assimilation following NH_4^+ pulses in the red algae *Gracilariopsis lemaneiformis:* effect on C metabolism. Marine Ecology Progress Series 122: 253-263

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Westbrooks, R. 1996. Biological invasions as global environmental change. American Scientist 84: 468-478

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M. 1997. Human domination of Earth's ecosystems. Science 277: 494-499

Wafar, M.V.M., Le Corre, P., Birrien, J.L. 1983. Nutrients and primary production in permanently well-mixed temperate coastal waters. Estuarine, Coastal and Shelf Science 17: 431-446

Walker, D.I. and Kendrick, G.A. 1998. Threats to macroalgal diversity: marine habitat destruction and fragmentation, pollution and introduced species. Botanica Marina 41: 105-112

Wilk, M. B. and Gnanadesikan, R. 1968. Probability plotting methods for the analysis of data. Biometrika 55:1-17

Williams, S.L. and Smith, J.E. 2007. A global review of the distribution, taxonomy, and impacts of introduced seaweeds. Annual Review of Ecology, Evolution, and Systematics 38: 327-359

Williamson, M. 1996. Biological Invasions. Chapman & Hall, London, 244 pp.

Worm, B. and Sommer, U. 2000. Rapid direct and indirect effects of a single nutrient pulse in a seaweed-epiphyte-grazer system. Marine Ecology Progress Series 202: 283-288

Worm, B., Lotze, H.K., Hillebrand, H., Sommer, U. 2002. Consumer versus resource control of species diversity and ecosystem functioning. Nature 417: 848-851

Wotton, D.M., O'Brien, C., Stuart, M.D., Fergus, D.J. 2004. Eradication success down under: heat treatment of a sunken trawler to kill the invasive seaweed *Undaria pinnatifida*. Marine Pollution Bulletin 49: 844-849

Zardi, G.I., Nicastro, K.R., McQuaid, C.D., Rius, M., Porri, F. 2006. Hydrodynamic stress and habitat partitioning between indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels: constraints of an evolutionary strategy. Marine Biology 150: 79-88