Localised population collapse of the invasive brown alga, *Undaria pinnatifida*: Twenty years of monitoring on Wellington's south coast

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Abstract

Invasive species pose a significant threat to marine environments around the world. Monitoring and research of invasive species is needed to provide direction for management programmes. This thesis is a continuation of research conducted on the invasive alga *Undaria pinnatifida* following its discovery on Wellington's south coast in 1997. By compiling the results from previous monitoring surveys (1997-2000 and 2008) and carrying out additional seasonal surveys in 2018, I investigate the distribution and spread of *U. pinnatifida* on Wellington's south coast, how this may have changed over time and what impacts it may have had on native macroalgal and invertebrate grazer communities. Intertidal macroalgal composition and *U. pinnatifida* abundance was recorded on fifteen occasions between 1997 and 2018 at two sites at Island Bay and two sites at Owhiro Bay. In addition, the subtidal abundance of six invertebrate grazers was recorded eight times within the same sampling period. Microtopography was also measured at each site to determine if topography had an influence on macroalgal composition. From 1997 to 2000 *U. pinnatifida* abundance gradually increased per year, but its spread remained localised to Island Bay. In 2008 *U. pinnatifida* had spread westward to Owhiro Bay where it was highly abundant. However, in 2018 no *U. pinnatifida* was recorded at any of the sites indicating a collapse of the invasion front. Further investigation revealed that *U. pinnatifida* was still present along the south coast with the nearest population only 500 m away from the nearest study site. The cause of the *U. pinnatifida* collapse is not known for certain, but it is unlikely that biotic resistance in the form of competitive exclusion or grazing or a change in environmental parameters such as temperature or nutrient concentration were contributing factors. It is speculated that the collapse arose from a multitude of confounding effects of which further research is needed to identify the exact cause. *U. pinnatifida* had no impact on macroalgal or grazer community composition. Additionally, microtopography also had no significant impact on macroalgal composition. This study reports the first ever invasion front collapse of *U. pinnatifida* in the world, and as a result, provides a new insight on *U. pinnatifida* distribution and invasion ecology. These findings can assist in predicting the future spread of *U. pinnatifida* populations as well as aid in formulation of new management strategies.

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Introduction

1.1. Invasive species

Invasive species pose a significant threat to marine and terrestrial ecosystems around the world (Prior et al. 2018). Alongside habitat destruction, climate change and overexploitation, invasive species have been recognised as significant contributors to global change (Vitousek et al. 1996; Chan & Brisk, 2017). Rapid population and economic growth resulting in increasing trends of trade and transport have accelerated the spread of invasive species (Hulme, 2009; Katsanevakis et al. 2014).

The ability of invasive species to tolerate a wide variety of environmental conditions coupled with a fast reproductive output enables them to survive long translocation periods and spread quickly throughout the environment (Morelissen et al. 2013). To be successful in a newly invaded area, the invading species must be well adapted to the environmental conditions of the area. Once introduced into a new environment these species can modify community structure, displace native species and alter ecological processes (Molnar et al. 2008). The control and mitigation of invasive species has been regarded as one of the most challenging aspects of conservation biology (Forrest & Hopkins, 2013). For this reason, it is paramount that invasive species are regularly monitored, and their impacts extensively documented and researched, to contribute to management actions to mitigate their impact.

Research on invasive species varies across systems, with terrestrial species often receiving the most attention, leaving a gap in our knowledge of aquatic invasive species (Jeschke et al. 2012; Lowry et al. 2012; Chan & Brisk, 2017). Anthropogenic activities such as shipping, aquaculture and habitat modification have resulted in marine and coastal environments being invaded at extraordinary rates (Molnar et al. 2008; Chan & Brisk, 2017). Globally, 7000 species are estimated to be transported daily in ballast water alone (Carlton, 1999; Lyons & Scheibling, 2009). In San Francisco Bay invasion rates have increased from one new invader per year between 1851-1960, to more than three new invaders per year between 1961-1995 (Cohen & Carlton, 1998). As of 1998 approximately 164 non-indigenous marine species were recorded in San Francisco Bay (Cohen & Carlton, 1998). Five hundred and seventy-three non-indigenous marine species have been recorded in the Mediterranean Sea (Galil, 2009), 30 off the coasts of Argentina (Orensanz et al. 2002) and 129 in Australia (Hayes et al. 2005; Lyons & Scheibling, 2009). Introduced macroalgae make up a substantial proportion of these species, with 277 species comprising 408 separate introduction events been recorded globally, one of which is the brown alga *Undaria pinnatifida* (Williams & Smith, 2007; Lyons & Scheibling, 2009). *U. pinnatifida*

has a global reputation as being one of the most invasive macroalgal species and has been listed among the world's top 100 most invasive species (Lowe et al. 2000). The increased presence of *U. pinnatifida* foreign marine environments has resulted in a demand for research regarding the species' physiology, distribution and potential ecological impacts.

1.2. Invasion ecology

Understanding the process' responsible for invasion has been a major aim of ecological research in recent years (Heger & Trepl, 2003). There are numerous factors that can contribute to the success and establishment of an invasive species in a new environment. Propagule pressure (also termed 'introduction effort') is a measure of the number of individuals released into an area to which they are not indigenous (Carlton, 1996; Lockwood et al. 2005). Propagule pressure consists of two components: (1) propagule size, the number of individuals released in a single introduction event, and (2) propagule number, the frequency of introduction events (Lockwood et al. 2005; Jeschke, 2014). Lockwood et al. (2005) stated that as the number of introductions and/or the number of individuals released increases, propagule pressure also increases. Increased propagule pressure can increase invasion success by providing colonist populations with sufficient genetic variation to adapt to local conditions (Ahlroth et al. 2003; Ricciardi et al. 2010) as well as increasing the likelihood that an invasive species will be released when abiotic variables are optimal for establishment and growth (Drake et al. 2006; Ricciardi et al. 2010).

Another contributor to invasibility is the biotic and abiotic characteristics of the receiving environment as well as the ability of the invader to overcome environmental barriers (Shea & Chesson, 2002). Invasive species are typically limited to habitats that are ecologically similar to their native habitats (Peterson & Vieglas, 2001). Subsequently, invasion success and growth is highly dependent on niche opportunities and whether the invader possess the traits required to exploit them (Peterson & Vieglas, 2001; Heger & Trepl, 2003). Shea and Chesson (2002) concluded that the main factors that contributed to an invader's growth following introduction was resource availability, natural enemies and the physical environment. Environments that have low numbers of predators/competitors, few environmental stressors, and experience high levels of disturbance are typically favoured by invasive species (Carlton, 1996).

In contrast, the ability of an invasive species to tolerate or adapt to a different or new environment can also influence invasion success. For example, the invasive Asian shore crab *Hemigraspus sanguineus* has almost identical abiotic niches in its invaded and native habitat (Lohrer et al. 2000),

whereas the European green crab *Carcinus meanus* due to its ability to survive in a wide range of water temperatures and salinities has established in regions outside of its native abiotic niche (Olyarnik et al. 2008). Additionally, species with traits associated with fast growth and large reproductive output have often been associated with increased invasion success (Carlton, 1996; South & Thomsen, 2016).

However, invasion success is not dependant on one factor alone. Propagule pressure, the characteristics of the invaded ecosystem, and the characteristics of the invader are not mutually exclusive (Carlton, 1996; Shea & Chesson, 2002; Heger & Trepl, 2003). Therefore, recognising the mechanisms responsible for invasion and how they integrate with one another is critical to understanding biological invasions (Heger & Trepl, 2003).

1.3. Importance of ecological monitoring

Monitoring is of fundamental importance to ecological management and the conservation of natural resources (Carpenter 1998; Lovett et al. 2007; Gitzen et al. 2012). Natural resource managers have increasingly recognised the importance and need for reliable scientific research in the making of management decisions (Gitzen et al. 2012). Robust scientific research is used by managers to determine the condition and status of the resources they manage, which is then used as a basis for conservation planning, deciding if current management programmes are working effectively, and informing stakeholders on the state of natural resources (Lovett et al. 2007; Gitzen et al. 2012).

Long-term monitoring is particularly useful as it provides valuable ecological information needed to comprehend and detect change in systems influenced by variability and stochasticity (Carpenter, 1998; Gitzen et al. 2012). Gitzen et al. 2012 identified five key benefits of long-term monitoring: (1) monitoring the state of system enables the best management actions to be chosen; (2) learning how an ecosystem functions and reacts to management; as part of an adaptive management system (3) communicating to the public and policy makers about long-term ecological changes; (4) involving the public in ecological issues thereby gathering support and effort; and (5) detecting idiosyncratic events that would otherwise be overlooked.

As stated previously, the accelerated spread of invasive species is a cause for concern and warrants investigation (Hulme, 2009; Katsanevakis et al. 2014). Monitoring is needed to determine the potential for non-indigenous species to become invaders and the vulnerability of environments to invasion (Shea & Chesson, 2002; Heger & Trepl, 2003). Managers can use this information to predict future invasions and thus develop mitigation strategies accordingly (Anderson, 2007). Post-invasion, invaders

need to be carefully monitored to determine their distribution and influence on ecosystem processes (Blossey, 1999**)**. This monitoring provides direction for further management action such as the allocation of resources (e.g. time and money) and the viability of eradication programmes (Blossey, 1999; Anderson, 2007).

1.4. *Undaria pinnatifida* – biology, impacts and distribution

U. pinnatifida is a species of large lamanarian kelp characterised by having a heteromorphic lifestyle with macroscopic sporophytic and microscopic gametophytic stages (Hunt et al. 2009). In its native range of Japan, Korea and north-eastern China (Silva et al. 2002; Neill et al. 2008), *U. pinnatifida* is an annual plant, however, mature plants have been observed year-round in certain regions around the world (Russell et al. 2008). The morphology of an *U. pinnatifida* sporophyte consists of a holdfast, stipe and a blade with large pinnate divided fronds (Shibneva et al. 2013). Sporophytes may have a rapid growth rate of up to 1 cm day^{-1}, typically growing to a final blade length of between 1.5 - 2 m (Silva et al. 2002; Hunt et al. 2009). Maturation occurs within 40 - 50 days of establishment, with sporophytes having a maximum life span of approximately 6 - 9 months in most regions, but not all (Saito, 1975; Stuart, 1997; Hunt et al. 2009). *U. pinnatifida* sporophytes may exhibit plastic morphology with different forms being determined by their genetic structure and environmental parameters (Shibneva et al. 2013).

U. pinnatifida growth boundaries range from 3 - 20^{o}C for sporophytes and 10 - 24^{o}C for gametophytes, with optimum growth for sporophytes being recorded between 15 - 17^{o}C (Silva et al. 2002; James & Shears, 2013). Reproduction occurs within a temperature range of 7 - 23^{o}C (Sanderson, 1990; Wallentinus, 1999). *U. pinnatifida* mainly occurs in salinities above 27 psu but has been recorded in waters down to 20 psu (Wallentinus, 1999). Reproduction occurs via sporophylls at the base of the stipe (Hunt et al. 2009; Epstein & Smale, 2017). Microscopic sacs are located at the ends of the sporophyll and release bi-flagellated zoospores approximately 5 - 6 µm in diameter (Hunt et al. 2009). A single *U. pinnatifida* sporophyte can produce one hundred million zoospores in its lifetime, meaning that the establishment of one mature sporophyte is often enough to found a new population (Akiyama & Kurogi, 1982; Hay & Luckens, 1987). In its native range, sporophyte recruitment takes place over winter, plants become reproductive in spring and the die back during the summer (Saito, 1975; Koh & Shin, 1990).

U. pinnatifida acts as a pioneer species and is part of a natural successive colonisation process (Kim et al. 2016; Epstein & Smale, 2017). However, in its non-native range it can have a severe impact on

marine ecosystems and their associated economies. *U. pinnatifida* is considered an archetype of a 'weedy' species, its life-history characteristics are more similar to fast growing ephemeral algae than that of a typical laminarian (Schiel & Thompson, 2012; South & Thomsen, 2016). Due to its ability to tolerate a wide range of conditions, in conjunction with its high fecundity and rapid growth rates, it has the potential to invade native intertidal and subtidal temperate communities (Russell et al. 2008).

U. pinnatifida has been recorded to change the structure of benthic ecosystems by excluding and competing with native macroalgal species for light and space (Stuart, 2004; Russell et al. 2008). This competition can lead to reductions in biodiversity and changes or breakdowns in food web structure (Cecere et al. 2000; Neill et al. 2008; James & Shears, 2013). *U. pinnatifida* also has the potential to displace native fishes and invertebrates by excluding the algae they rely on for food and protection (Aquenal, 2008). It poses a threat to aquaculture industries through the direct loss of commercial species and by increasing labour costs due to fouling on mussel lines, oyster racks and fin fish cages etc. (Aquenal, 2008). A survey of mussel farms in the Coromandel region, New Zealand, found that 28 of 31 farms were infested with *U. pinnatifida*, of which 11 farms were deemed to have a high level of infestation (>100 plants per 50 m of mussel line) (James & Shears, 2013).

In its native range, *U. pinnatifida* is found in abundance on protected rock coasts where it grows in the lowest intertidal zone to a depth of approximately 15 m (Saito, 1975; Silva et al. 2002). However, it also capable of invading exposed coastlines in wave exposed areas such as native kelp forests, rock pools and in low light areas beyond the vertical extent of most native algae (Russell et al. 2008). *U. pinnatifida* predominantly grows on artificial and natural hard substrates such as rocky reefs, hulls of vessels, rope and wharf pilings (NZ Ministry of Fisheries, 2001; Hunt et al. 2009). It also has the ability to grow in areas of soft sediment when attached to small cobbles and shells (NZ Ministry of Fisheries, 2001; Sliwa et al. 2006). Additionally, *U. pinnatifida* has been reported to grow on other species of seaweed and seagrass while in the small sporophyte life history stage (NZ Ministry of Fisheries, 2001). In Wellington, New Zealand, the distribution of *U. pinnatifida* primarily ranges from the low intertidal to depths of 7 m, however it has been recorded at depths up to 15 m (Hay, 1990; Adams, 1994).

Due to a combination of accidental and intentional introductions for aquaculture, *U. pinnatifida* has established in many regions around the world including New Zealand, Australia, the United States of America, Argentina, England and France (Silva et al. 2002: Morelissen et al. 2013; James & Shears, 2016). Translocation through ballast water discharge, aquaculture activities and fouling on vessels hulls are deemed to be the main vectors for the accidental release of *U. pinnatifida* (Silva et al. 2002; James & Shears, 2016). The first appearance of *U. pinnatifida* outside of the north-western Pacific was in the Etang de Thau, southern France, in 1971, having been accidently imported with Pacific Oysters

designated for cultivation (Floc'h et al. 1991). *U. pinnatifida* then proceeded to spread along the south coast of France, to two sites in Italy, and to several sites on the Atlantic Coast (Spain, Netherlands and Southern England) (Hay, 1990; Floc'h et al. 1991; Wallentinus, 1999; Silva et al. 2002). This invasion was shortly followed by establishment in New Zealand in 1987 (Hay & Luckens, 1987), Tasmania, Australia in 1998 (Sanderson, 1990) and Argentina in 1992 (Piriz & Casas, 1994). Following its introduction in the San Jose Gulf, Argentina, *U. pinnatifida* rapidly spread across 100 km of coastline in less than four years (Dellatorre et al. 2014) and in certain parts of Tasmania, local spread has been estimated to reach up to 10 km per year (Hewitt et al. 2005).

U. pinnatifida was first detected in New Zealand in Wellington Harbour in 1987 where it is believed to have been transported via a foreign international vessel, most likely of Asian origin (Hay & Luckens, 1987; James & Shears, 2013). Spread via infected aquaculture gear as well additional introductions from its native range has led to *U. pinnatifida* establishing in several regions throughout New Zealand (Hunt et al. 2009). Since its introduction it has spread to most ports and harbours along the East Coast, as well as to Taranaki, Stewart Island, Snares Island and the top of the South Island (Neill et al. 2008). The rate of spread has been variable among different locations across the country. *U. pinnatifida* has been spreading at a rate of approximately 2 km per year along the Otago Coast, hundreds of meters per year in the Marlborough Sounds, whereas in Timaru Harbour it has extended less than 1 km in over 20 years (Forrest et al. 2000; Russell et al. 2008; Epstein & Smale, 2017). Establishment on aquaculture gear has aided its spread in New Zealand waters, as well as dispersal onto adjacent natural reefs (Hunt et al. 2009). Research has determined that there are now eight different strains of *U. pinnatifida* residing in New Zealand waters (Neill et al. 2009).

1.5. Management and eradication

The invasion of *Undaria pinnatifida* in New Zealand waters has provided a unique challenge for conservationists to overcome. The dynamic nature of the ocean, accompanied by the uncertainty of founding events, makes it difficult to fully eradicate a marine pest over a long period (Hewitt et al. 2005; Hunt et al. 2009). *U. pinnatifida* is highly tolerant of environmental variability and its adaptability makes it a resilient invasive species and difficult to eradicate (Dean & Hurd, 2007; James & Shears, 2016). However, the development of management strategies and the application of appropriate removal techniques can greatly increase the chances of eradication success. Because of its strong emphasis on environmental protection, New Zealand is a world leader in biosecurity measures, having employed various techniques and strategies to eradicate and control the spread of *U. pinnatifida* (Hewitt et al. 2004). Manual removal was an effective method in temporarily reducing *U. pinnatifida*

abundance in Big Glory Bay, Stewart Island (Hewitt et al. 2005; Hunt et al. 2009). Following its discovery in Big Glory Bay in 1997, a seven-year eradication project was implemented in which *U. pinnatifida* sporophytes were continually removed by hand from the surrounding area (Hunt et al. 2009). The initial results of the project were positive with *U. pinnatifida* numbers consistently declining over time (Hunt et al. 2009). However, due to the inability to target *U. pinnatifida* in its gametophyte stage in conjunction with two new founding events, eradication could not be achieved (Hewitt et al. 2005; Hunt et al. 2009).

Aquaculture activities are often associated with the movement of invasive species from site to site, and also with the proliferation of invasive species at a given site. One of the key problem's aquaculture farmers have is removing *U. pinnatifida* from their equipment without killing or damaging their product; removing *U. pinnatifida* from mussel seed stock is one such problem (Forrest et al. 2007). Immersion of mussel ropes in freshwater for 48 hours and 4% acetic acid for <1 minute have both proven to result in complete *U. pinnatifida* mortality with minimal effect on mussel health (Forrest et al. 2007; Hunt et al. 2009). Hot water treatments have also been tested, and it was found that exposure to water at 55^{o}C for approximately 5 seconds would result in complete *U. pinnatifida* mortality while still ensuring high levels of mussel survival (Forrest et al. 2007). The development of innovative heat treatment techniques has also resulted in one of the first complete eradications of *U. pinnatifida* in New Zealand waters (Wotton et al. 2004). On the 23rd March 2000 *U. pinnatifida* sporophytes were detected on a sunken trawler in Hansen Bay, Chatham Islands. This finding was the first known detection of *U. pinnatifida* in the Chatham Islands and because of the islands' unique and pristine environment an immediate response was undertaken. A combination of manual removal and heat treatment methods were employed to eradicate the *U. pinnatifida in situ*. From March 2000 to June 2001 a total of 427 *U. pinnatifida* sporophytes were removed from the hull of the trawler and safely disposed (Wotton et al. 2004). To kill any microscopic gametophytes that resided on the ship's hull plywood boxes were attached to the vessels hull with magnets. Elements within the boxes heated the water enclosed to 70^{o}C and were left for a period of 10 minutes. Overall, the whole treatment took four weeks (June 2001) with boxes being applied 311 times to the hull (Wotton et al. 2004). Following the heat treatment, monthly monitoring which ended in March 2003 found no sporophytes on the vessel's hull (Wotton et al., 2004). Eradication or preventing the spread of an invasive species is a difficult task which requires large amounts of time, funding and knowledge (Myers et al. 2000). In contrast, the best way to prevent the invasion of the marine environment is through robust pre-border controls followed by post-border or internal border vigilance (Hewitt et al. 2004; Forrest et al. 2009) and constant monitoring and management (Anderson, 2007).

1.6. Previous research along Wellington's south coast

Wellington's south coast is a highly dynamic environment and experiences considerable wave action. Strong surges and swell are characteristic of the region, and the water conditions can change very rapidly from flat calm with a low particle load (4000 - 5000 particles in the size range 2 - 63 µm per ml) to storm conditions with a high particle load (100,000 - 120,000 particles in the size range 2 - 63 µm per ml) (Wear & Gardner, 1998). Primary productivity along the south coast is relatively low due to lack of nutrient input from watershed run-off (Helson & Gardner 2004; Morelissen, 2012). The current that runs along the south coast flows west to east, and as a result nutrient concentration follows an east to west gradient in which concentrations are highest at the entrance of Wellington Harbour and lowest at the entrance of the Cook Strait in the west (Helson & Gardner 2004; Morelissen, 2012). Wellington's south coast is home to a diverse range of marine flora and fauna. Over 180 species of fish and approximately half of New Zealand's native algae species have been recorded in the region (Gardner & Bell, 2008). Typically, the macroalgal community along the south coast is very well developed and is well represented by a large number of different species (Wear & Gardner, 1998). In 2008 the Taputeranga Marine Reserve was established on the south coast. This 'no take' marine reserve covers 854 hectares and extends approximately 2.3 km offshore (Gardner & Bell, 2008).

In less than 10 years since its first introduction into New Zealand in Wellington Harbour in 1987 *U. pinnatifida* had become well established in the harbour's nutrient rich, low energy environment (Hay & Luckens, 1987). During the winter of 1997 *U. pinnatifida* was found to have spread beyond Wellington Harbour to Wellington's south coast along the northern shores of the Cook Strait (refer to Figure 1 for map of south coast). A general shoreline survey carried out in late 1997 (Wear & Gardner, 1998) showed the open coastal occurrence of *U. pinnatifida* to be patchy, with extensive growth occurring at the eastern end of Island Bay, and around Taputeranga Island. Scattered individuals were recorded along the western side of Lyall Bay, around Houghton Bay, and in two sheltered channels behind the Sirens Rock at the western end of Island Bay but were absent elsewhere despite apparent availability of sites and suitability of habitat (Wear & Gardner, 1998). These observations prompted further investigation, with an ensuing monitoring programme initiated. The aim of the programme was to monitor the distribution, growth, spread and ecological impact of *U. pinnatifida* along Wellington's south coast, with the resulting data potentially aiding in predicting the future occurrence and spread of this species at other locations within New Zealand, and in other areas. Sampling took place over a three-year period from 1997 to 2000, incorporating 11 separate surveys across multiple locations. The results of this work were published as three monitoring reports (Wear & Gardner, 1998; Gardner & Wear, 1999; Wear & Gardner, 2000). This work has not been published in the international

peer-reviewed literature. A follow-up survey was also conducted in 2008: these data were not published in any form. A summary of the three monitoring reports revealed a gradual increase in *U. pinnatifida* abundance over time, however, its spread along the south coast remained relatively confined to eastern Island Bay. Additionally, an unpublished survey report conducted by divers from the United Kingdom (UK RAF divers, 2004) recorded the distribution and abundance of subtidal *U. pinnatifida* sporophytes at Island Bay and Owhiro Bay. Findings revealed that *U. pinnatifida* was present at 7 of 11 dive sites, however, no *U. pinnatifida* was found west of the Sirens Rock, Island Bay. Initial analyses of the 2008 survey data indicated that *U. pinnatifida* had spread over 1 km to the west of Island Bay and had established in new locations in Owhiro Bay.

Figure 1. Map of Wellington's south coast from Island Bay to Owhiro Bay.

1.7. Ongoing monitoring of *U. pinnatifida* populations along Wellington's south coast

Because of the highly invasive nature of *U. pinnatifida* and the threat it poses to New Zealand's economy and marine environment, it is imperative that the monitoring of this species continues. This thesis is an extension of research conducted at the time of the first spread of *Undaria pinnatifida* along Wellington's south coast. In it I compile the results of the 1998, 1999, 2000 and 2008 *U. pinnatifida* monitoring surveys (Wear & Gardner 1998; Gardner & Wear 1999; Wear & Gardner 2000; Gardner & Wear, unpublished data 2008) while also carrying out my own survey in 2018. In these early surveys macroalgal composition including *U. pinnatifida* abundance was recorded in the intertidal zone at two

sites in Island Bay and two sites in Owhiro Bay. Additionally, invertebrate grazer composition was also recorded in the adjacent subtidal zone at these four sites. The aim of this study is to investigate the current distribution of *U. pinnatifida* on Wellington's south coast and how this may have changed over time. Based on the results of the previous monitoring reports I hypothesised that *U. pinnatifida* abundance has increased over time and by 2018 its distribution has advanced further westward (i.e., be found at or beyond the invasion front sites at Owhiro Bay) along the south coast. To understand the possible impacts this invasive species may have on the marine environment, it is essential to study the ecological communities present within the environment. For this reason, another aim was to examine the temporal and spatial variation of native intertidal macroalgal communities and subtidal invertebrate grazers. I hypothesised that the site-specific macroalgal and invertebrate community composition would remain unchanged over time, however, would vary between sites. I also examined if the composition of the macroalgal community was related to the physical habitat characteristics of the sites (i.e., substrate topography).

Materials and Methods

2.1. Study sites

In 1997 initial surveys were conducted at four sites along Wellington's south coast in order to monitor the possible advance of *Undaria pinnatifida*. These same sites were employed in subsequent monitoring work (Gardner & Wear 1999; Wear & Gardner 2000; Gardner & Wear, unpublished data 2008). Two sites were set up where *U. pinnatifida* had recently established (Island Bay) and two sites were set up outside the leading edge of the *U. pinnatifida* invasion front (Owhiro Bay). The two sites at Island Bay comprised two parallel channels orientated east to west, located behind the Sirens Rock, 41^0 21.0' S, 174^0 46.10' E (Figure 2). The roadside channel (Island Bay 1) is 80 m long and shelves to about 1.5 m depth at low tide; the seaward channel (Island Bay 2) is 110 m long and is generally about 1 m deep but contains deeper areas to about 2.5 m. Both channels are bounded by greywacke basement rock platform and are sheltered from the prevailing northerly and southerly winds. Both sites have a well-developed and relatively permanent macroalgal fringe that runs along the sides of both channels.

The first Owhiro Bay site (Owhiro Bay 1) is located 1.25 km west of the Island Bay sites at the west side of Owhiro Bay in a small 35 m long channel in the area of an infrequently used concrete boat ramp, 41^0 21.0' S, 174^0 45.3' E (Figure 3). The channel faces east and shelves to about 1.5 m deep at low tide. Surrounding rock platforms shelter the channel from low to moderate swells. The second Owhiro Bay site (Owhiro Bay 2) is located 500 m further west adjacent to the now disused Owhiro Bay Quarry at 41^0 21.0' S, 174^0 44.95' E, faces due south, and is more exposed to the southerly surge (Figure 4). The site comprises a broad channel about 40 m long and 1.0 m deep. Both Owhiro Bay and Island Bay sites currently fall within the boundaries of the Taputeranga Marine Reserve following its establishment in 2008.

2.2. Intertidal methodology

2.2.1. Macroalgal species composition

During the 3rd week of October 1997, 37 permanent 50 cm x 50 cm quadrats were positioned about the mean low water springs (MLWS) in the study area using a random block design in 10 m blocks along each side of each of the two channels (Island Bay 1 and Island Bay 2). One quadrat was selected

at random in each 10 m block. The location of this quadrat was determined from random number tables using random numbers between 0 and 9 and locating the quadrat at the value of the random number expressed in metres. The block design avoided the possibility that either the open or closed ends of a channel would be favoured in the distribution of quadrats. In this way, 15 quadrats were established in the roadside channel (Island Bay 1), and 22 quadrats in the longer seaward channel (Island Bay 2). Of these, two quadrat locations (Q12 and Q24) were not used, as they fell in an area of open water where the rock platform separating the two channels was discontinuous. In the same way, eight quadrats were set up at the west Owhiro Bay site (Owhiro Bay 1), and seven at the 'Quarry' site (Owhiro Bay 2). The position of each quadrat was photographed, mapped and marked with a numbered plastic tag that was adhered to neighbouring bedrock with marine epoxy (Figures 2, 3 & 4). A reference booklet containing photographs of each quadrat's location was then created to assist in locating the quadrats while in the field. To assess the abundance of *U. pinnatifida* and the specific macroalgal communities within the intertidal zone, photographs of each permanent 50 x 50 cm quadrat were taken at each of the four sites. Photographs were then labelled, ready to be analysed ex-situ later. Surveys were carried out in October 1997, February 1998, April 1998, September 1998, December 1998, February 1999, May 1999, September 1999, November 1999, March 2000, June 2000, November 2008, April 2018, July 2018 and October 2018. The latter three surveys were carried out as part of the fieldwork for this thesis.

During the April 2018 survey it became apparent that 20 years of wave exposure had caused changes to the intertidal landscape making it impossible to identify the exact original location of some quadrats. In instances where a quadrat's location could not be discerned a new permanent quadrat was established in the approximate location of the original (using the original photographs permitted establishment of a new quadrat within 0.5 m of the original quadrat). New quadrats were re-tagged and photographed for future reference. Careful consideration was made to mimic the substrate and topography found in the original quadrat in the new quadrat. New quadrats were established for the following: Q1, Q2, Q3, Q9, Q19, Q22, Q23, Q34, Q36, Q37, C13, C14, and C15.

2.2.2. Substrate heterogeneity

To determine the influence that substrate microtopography may have on *U. pinnatifida* abundance and macroalgal composition a topography survey was carried out for each of the quadrats during October 2018. Two 1.5 m pieces of light chain were attached to two adjacent corners of a 50 x 50 cm

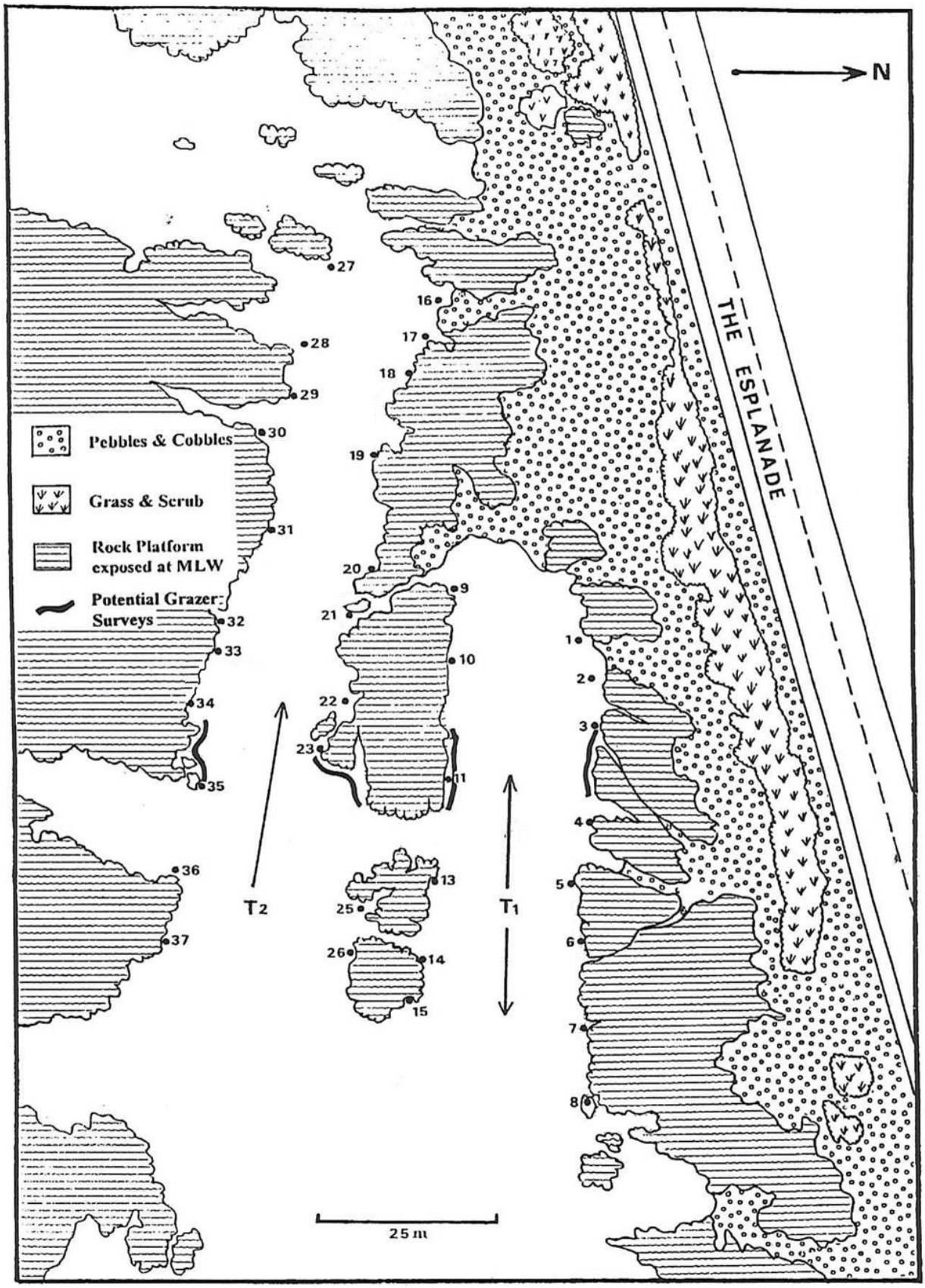


Figure 2. Sites Island Bay 1 (T1) and Island Bay 2 (T2) showing fixed quadrat locations (Q1 – Q37) and invertebrate grazer survey transects. Sourced from Wear & Gardner (1998).

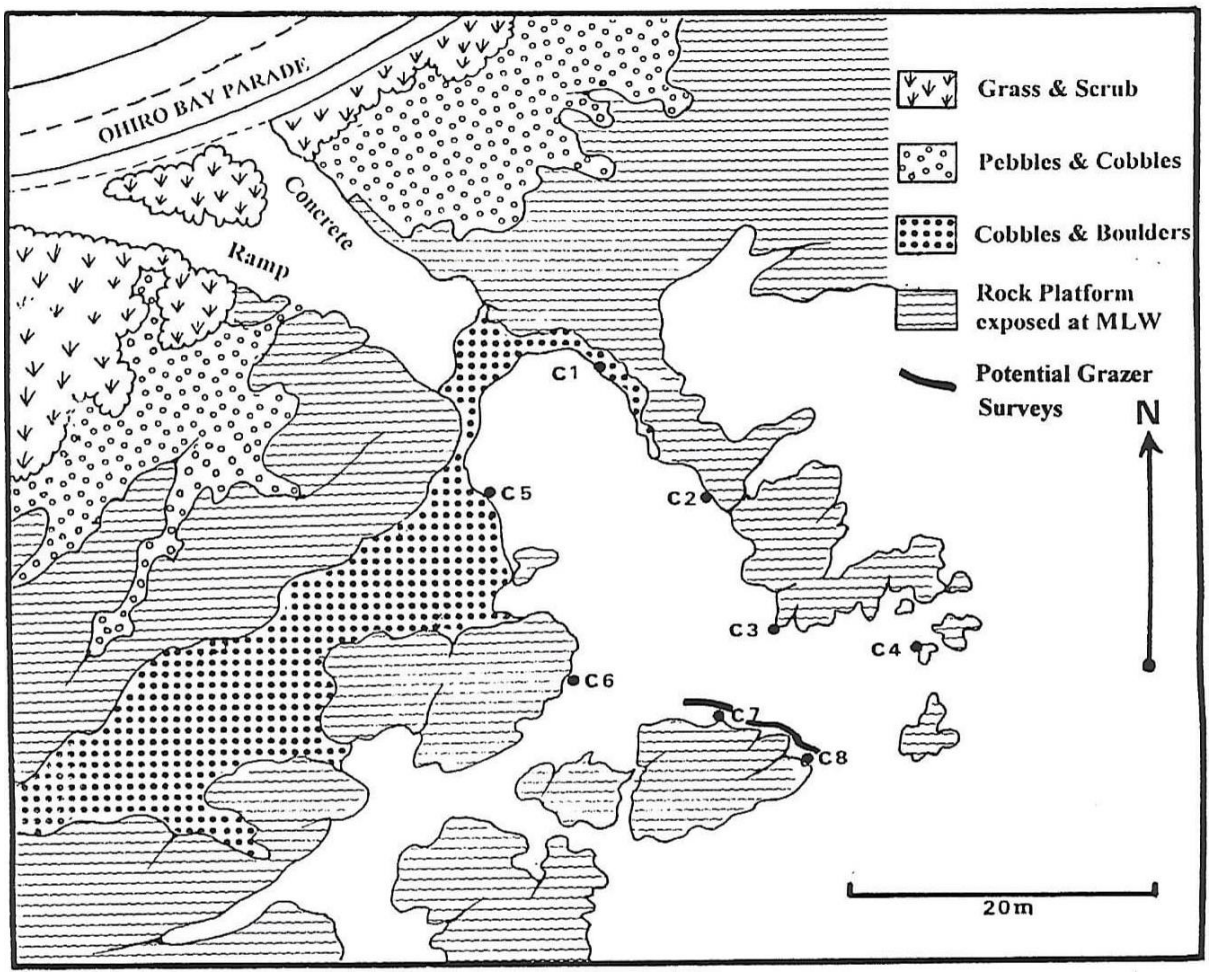


Figure 3. Site Owhiro Bay 1 showing fixed quadrat locations (C1 - C8) and invertebrate grazer survey transect. Sourced from Wear & Gardner (1998).

quadrat. At each permanent quadrat location, the greywacke reef microtopography was measured by loosely laying out each chain in a straight line to the parallel corner to which the chain was attached to, forming an 'X' shape within the quadrat that reflected the reef's structure. Each length of chain was then marked at the point at which it touched the parallel corner and pulled taut. The distance between the attached end of the chain to the point where it was marked was then measured and recorded. The microtopography measurements were then entered in an Excel spreadsheet where for each quadrat the lengths of both pieces of chain were summed (X1 + X2) to give one value of measurement.

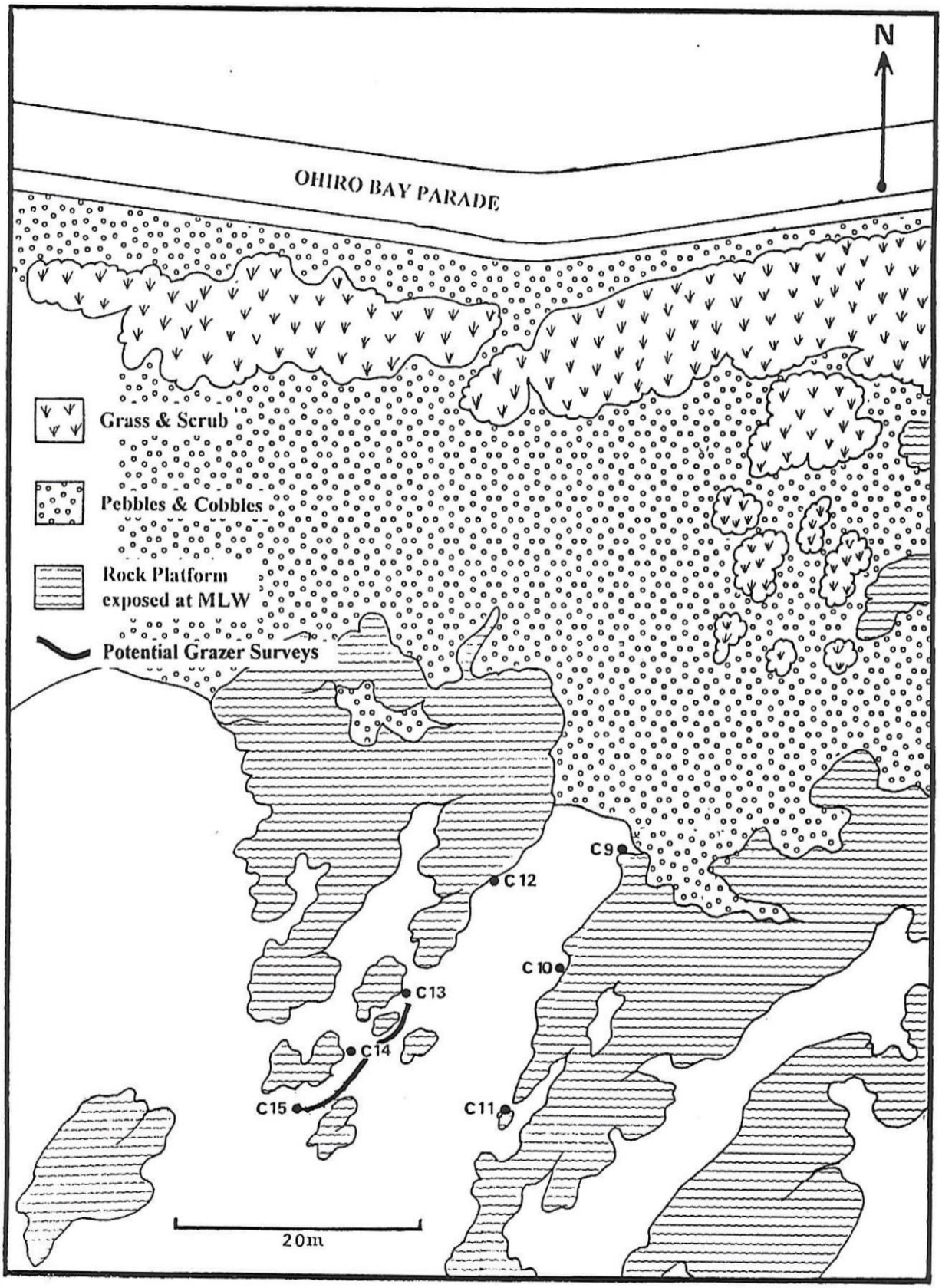


Figure 4. Site Owhiro Bay 2 showing fixed quadrat locations (C9 – C15) and invertebrate grazer survey transect. Sourced from Wear & Gardner (1998).

2.3. Subtidal methodology

2.3.1. Census of grazing invertebrates

In addition to subtidal strip transects a census of macroalgal grazers was also conducted. For the study sites in Island Bay, a 10 m transect line was run along the seafloor at the base of the rock wall at four locations from Q3 east and from Q11 west in the roadside channel (Island Bay 1), and from Q23 east and Q35 west in the seaward channel (Island Bay 2). For Owhiro Bay 1 the line was run from C8 for 10 m northwest towards C7, and in Owhiro Bay 2 from C15 north towards C13. An area of sea wall one metre above the line was carefully searched over its entire 10 m length. The abundances of 6 invertebrate grazer species (*Aplysia dactylomela, Evechinus chloroticus, Haliotis australis, Haliotis iris, Scutus breviculus* and *Lunella (Turbo) smaragdus)* were counted by a pair of SCUBA divers in 1998 - 2000 and then by a pair of snorkelers in 2018. Surveys took place in June 1998, July 1999, December 1999, February 2000, May 2000, April 2018, July 2018 and November 2018. Before analysis, to standardise the counts, the abundance data for both surveys at Island Bay 1 and Island Bay 2 were averaged to give one count per site.

2.3.2. U. pinnatifida and macroalgal species composition

Subtidally, a weighted transect line was laid along the centre of each channel at the Island Bay sites and the two Owhiro Bay sites for their full length (Island Bay 1 = 80 m, Island Bay 2 = 110 m, Owhiro Bay 1 = 35 m, Owhiro Bay 2 = 40 m). The exact location of this line along the centre of each channel was not fixed and therefore varied slightly from one sampling period to the next. One strip transect survey (2m wide - 1 m either side of a weighted transect line) was then performed at each site in order to qualitatively assess the composition of the macroalgal community and particularly the abundance of *U. pinnatifida* in the subtidal zone (if it occurred). A pair of divers swam the entire length of the transect counting the number of *U. pinnatifida* sporophytes while recording the transect swim with an underwater video camera. From 1998 – 2000 the surveys were conducted using SCUBA, but in 2018 surveys were conducted via snorkel. SCUBA or snorkel transect recordings at each site took place in November 1997, December 1997, February 1998, May 1998, December 1998, June 1999, April 2000, May 2000, April 2018, July 2018 and November 2018.

2.4. *U. pinnatifida* population status elsewhere on Wellington's south coast

To assess the current distribution of *Undaria pinnatifida* beyond the four study sites a search for *U. pinnatifida* was carried out on Wellington's south coast. Searches took place at thirteen separate locations along the south coast, ranging from Owhiro Bay to Seatoun (Figure 5). Locations were chosen for the most part haphazardly, however, consideration was made so that sites were spread out throughout the south coast. At each site approximately 50 m of coastline was examined for the presence of *U. pinnatifida* in the intertidal zone. The status of *U. pinnatifida* at each location was then classified as either present or absent. Searches were carried out on the 31st May 2018 at low tide. All sites were on suitable rocky reef habitat except for sites 5, 12 and 13 which were on artificial structure.

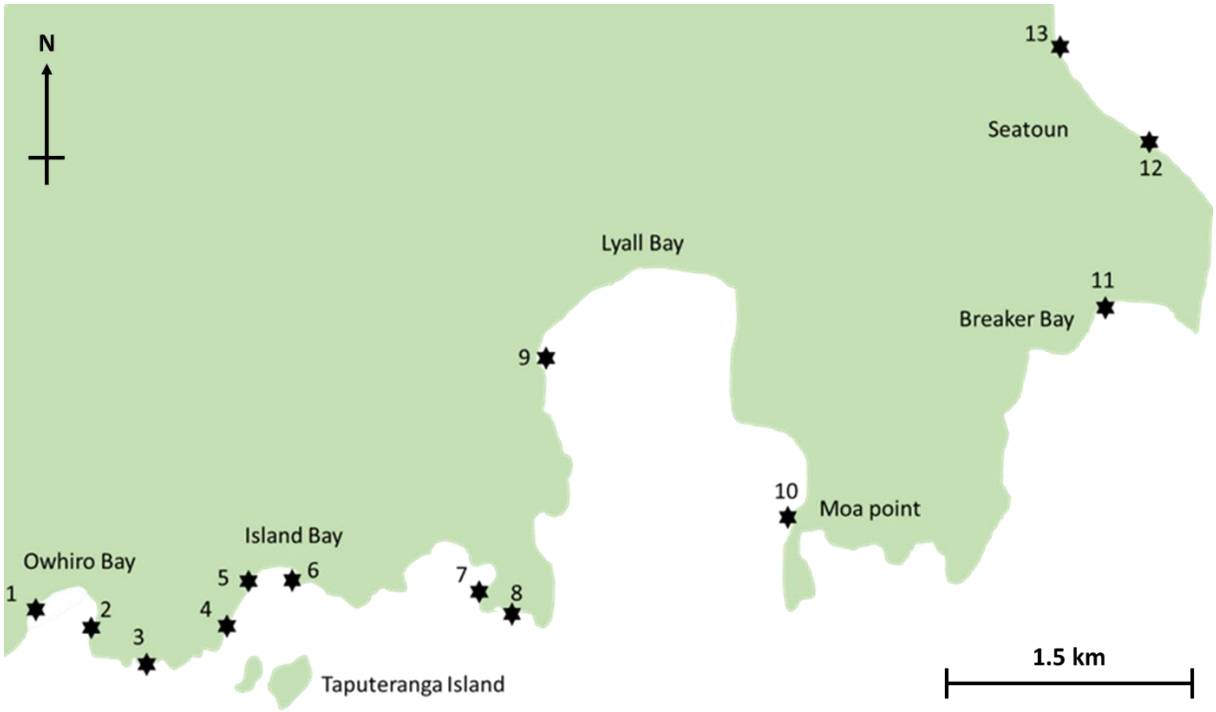


Figure 5. Map of Wellington's south coast showing locations of U. pinnatifida searches during 2018 (excludes long term survey sites Island Bay 1, Island Bay 2, Owhiro Bay 1 and Owhiro Bay 2, which are not shown on this map).

2.5. Data Analysis

2.5.1. Intertidal macroalgal species composition

From the 1997 to 2000 surveys, the 35 mm colour slides of each permanent intertidal quadrat were individually labelled with date, location and quadrat number. In a darkroom, each slide was projected onto a 50 x 50 cm grid with 100 points positioned according to x-axis and y-axis coordinates derived from random number tables. A record was made of whatever was observed at the location of each

random dot within the quadrat (Wear & Gardner, 1998). It was possible to identify most macroalgae down to species level using this approach, but certain genera (e.g. *Cystophora*, *Zonaria*, *Carpophyllum* and *Gigartina*) could not be identified to species level so were identified to genus level. In some instances where identification to genus level was not possible samples were categorised in accordance to their description (e.g. short tufting reds). Any point that fell upon reef that was devoid of macroalgae was classified as 'bare substrate'. To simplify the terminology, all macroalgae regardless of taxonomic level (including 'bare substrate') have been classed as a 'species' (refer to Appendix 1 for list of recorded macroalgal species). This data set represents an estimate of percentage cover within each quadrat, from which it is possible to determine the relative proportions of cover of individual species. Data were entered into an Excel spreadsheet to permit analysis of percentage cover data as a function of time (survey date). Means ± standard deviations (SD) were calculated for each macroalgal species and for bare substrate at each location for each sampling period. To assist with the identification of macroalgae, samples representing all species occurring within all 50 fixed quadrats were photographed in colour and then preserved in formalin. Examples of the preserved species and a colour photograph were sent to the Cawthron Institute and identified as far as possible by Dr Cameron Hay; a duplicate reference collection was retained at Victoria University's Island Bay Marine Laboratory. For the 2008 and 2018 surveys the digital photos of each intertidal quadrat were analysed using Coral Point Count with Excel extensions software (CPCe). Photos of each quadrat were uploaded onto CPCe and one hundred points were then randomly generated onto each quadrat with whatever was underneath each point being identified and recorded to its lowest possible taxonomic level, as for the slides. Identification of macroalgae was aided by the photographed reference collection made previously in 1997.

Examination of previous results found that data at Q1 for Island Bay 1 had not been recorded from September 1998 - November 2008. Q1 fell upon substrate that was heavily influenced by mobile cobble and tidal flow and for this reason was omitted from all remaining data sets and further analysis. Missing data were recorded for the following quadrats: Q7 (February 1998), Q17 (June 2000), Q28 (September 1998), Q34 (June 2000) (Island Bay sites) and C11, C13 and C15 (June 2000) (Owhiro Bay 2). As a result, two separate data sets were used for statistical analysis, an 'unbalanced' data set where Q1 was excluded from each survey, but all other quadrats included despite missing data and a 'balanced' set which excluded Q1, Q7, Q17, Q28, Q34, C11, C13 and C15 from each survey. Following all statistical analysis, it was revealed there was no substantial difference in results between the 'balanced' and 'unbalanced' data sets. However, analysis of multidimensional scaling (MDS) plots showed that the 'balanced' data set portrayed slightly more distinct patterns then the 'unbalanced'

data set, that is, that missing data in the unbalanced data set did seem to have a minor effect. For this reason, the 'balanced' data set was chosen for the presentation of results.

The following indices were calculated for each quadrat for each survey:

- **Total species**: S, the number of different species or species groups (including 'bare substrate').
- **Species richness**: d, the Margalef index which is calculated as d=(S-1)/ln N, where S is the number of species, and N is the total number of individuals in the sample.
- **Species diversity**: H', the Shannon Weiner diversity index which is calculated as H' = - ∑ pi (ln pi), where pi is the proportion of the ith species and ln is natural logs.
- **Species evenness**: J', Pielou's evenness index which is calculated as J'=H'/log(S), where H' is the Shannon diversity index, and S is the number of species (total species).

To test for differences in the indices: total species (S), species richness (d), species evenness (J') and species diversity (H') a 3-factor permutational multivariate analysis of variance (PERMANOVA) was carried out, in which the factor 'site' contained four levels (Island Bay 1, Island Bay 2, Owhiro Bay 1 and Owhiro Bay 2), the factor 'time' three levels (1997 - 2000, 2008 and 2018) and the factor 'season' four levels (spring, summer, autumn and winter). PERMANOVA is a routine for testing the simultaneous response of one or more variables to one or more factors in an analysis of variance (ANOVA) experimental design based on any resemblance matrices, using permutation methods (Anderson et al. 2008). Indices were square root transformed and tested using Bray Curtis similarity matrices and 999 permutations. Pairwise comparisons using PERMANOVA were also conducted to determine patterns between diversity indices and the levels of site, time and season.

To test the null hypothesis that macroalgal community composition does not differ over time and across multiple factors a PERMANOVA was conducted. Tests were carried out using Bray–Curtis-similarity matrices (using 999 permutations) with macroalgal percent cover data being square root transformed in order to reduce the potential effect of dominant species. A three-way design was employed, in which the factor 'site' contained four levels (Island Bay 1, Island Bay 2, Owhiro Bay 1 and Owhiro Bay 2), the factor 'time' three levels (1997-2000, 2008 and 2018) and the factor 'season' four levels (spring, summer, autumn and winter). Pairwise comparisons using PERMANOVA were conducted to determine patterns between macroalgal composition and the levels of the site, time and season.

Multidimensional scaling (MDS) ordination was performed in order to illustrate patterns of similarity in macroalgal community composition among the factors 'site' (four levels: Island Bay 1, Island Bay 2, Owhiro Bay 1 and Owhiro Bay 2), 'time' (three levels: 1997 – 2000, 2008 and 2018) and 'season' (four

levels: spring, summer, autumn and winter). Analysis was based on square root transformed macroalgal percent cover data and Bray-Curtis similarity matrices.

One-way and two-way crossed SIMPER routines tested with the factors 'site' (four levels: Island Bay 1, Island Bay 2, Owhiro Bay 1 and Owhiro Bay 2), 'time' (three levels: 1997 - 2000, 2008 and 2018) and 'season' (four levels: spring, summer, autumn and winter) were conducted to identify the primary species responsible for differences in species composition across the three factors. Similarity percentages (SIMPER) decomposes average Bray Curtis dissimilarities between all pairs of samples, one from each group, into percentage contributions from each species, listing the species in decreasing order of such contribution (Clarke & Gorley, 2006). Tests were carried out using the macroalgal percentage cover data (including 'bare substrate') which was square root transformed in order to reduce the effect of dominant species. Tests were based on Bray–Curtis similarity matrices and carried out using 999 permutations.

To investigate the null hypothesis that there is no difference in *U. pinnatifida* abundance over time and across multiple factors an analysis of similarity (ANOSIM) was performed. ANOSIM is a non-parametric test of significant difference between two or more multivariate groups, based on any distance measure (Clark, 1993). *Undaria pinnatifida* percentage coverage data were square root transformed to reduce the potential effect of outliers and then tested using Bray-Curtis similarity matrices (using 999 permutations). Multiple two-way crossed designs were employed (site x time, site x season and time x season), in which the factor 'site' contained four levels (Island Bay 1, Island Bay 2, Owhiro Bay 1 and Owhiro Bay 2), the factor 'time' three levels (1997 - 2000, 2008 and 2018) and the factor 'season' four levels (spring, summer, autumn and winter). Pairwise comparisons using two-way ANOSIM were also performed to test for patterns of significance between the levels of the factors: site, time and season.

2.5.2. Substrate topography

To test for differences in substrate topography between the sites Island Bay 1, Island Bay 2, Owhiro Bay 1 and Owhiro Bay 2 a PERMANOVA test was carried out. Tests were conducted using Euclidean distance matrices and normalised transformed data with 999 permutations.

2.5.3. Census of grazing invertebrates

A 3-factor PERMANOVA was conducted to test for differences in the abundance of the six invertebrate species (*Aplysia dactylomela, Evechinus chloroticus, Haliotis australis, Haliotis iris, Scutus breviculus &*

Lunella smaragdus) between 'site' (four levels: Island Bay 1, Island Bay 2, Owhiro Bay 1 and Owhiro Bay 2), 'time' (two levels: 1997 – 2000 and 2018) and 'season' (four levels: spring, summer, autumn and winter). Tests were carried out using Bray–Curtis similarity matrices with data undergoing a log(x+1) transformation before analysis. Pairwise comparisons using PERMANOVA were conducted to determine patterns of grazer abundance as a function of site, time and season

One-way and two-way crossed SIMPER routines were carried out to determine which grazer was primarily responsible for the similarities/dissimilarities among the factors site, time and season. The factor 'site' contained four levels (Island Bay 1, Island Bay 2, Owhiro Bay 1 and Owhiro Bay 2), the factor 'time' two levels (1998 - 2000 and 2018 – grazer counts were not conducted in 2008) and the factor 'season' four levels (spring, summer, autumn and winter). Tests were carried out using Bray–Curtis similarity matrices with grazer abundance data undergoing a log(x+1) transformation before analysis.

2.5.4. Relating intertidal macroalgal community composition to microtopography and grazer abundance

To investigate the relationship between quadrat-specific macroalgal composition and microtopography a RELATE procedure was undertaken. This procedure performs a multivariate regression between the topography data and algal community resemblance matrices, testing the null hypothesis that there is no relationship between the two data sets. Tests were performed independently for each of the 15 macroalgal composition surveys. Microtopography data from October 2018 were used for each analysis and thus were assumed to have remained constant throughout time. Macroalgal data for each test were square root transformed and based on Bray-Curtis resemblance matrices. Microtopography data were normalised and based on Euclidean distance matrices.

The RELATE procedure was also used to test for relationships between macroalgal composition and grazer abundances. Because grazer abundance and macroalgal composition surveys were performed at different times the macroalgal surveys that closest matched the time of the grazer surveys were chosen for testing (there was never more than a 2-month mismatch between the macroalgal and grazer data sets). The percentage cover for each macroalgal species was averaged per site for the following eight surveys: April 1998, May 1999, November 1999, March 2000, June 2000, April 2018, July 2018 and October 2018. Before analysis, macroalgal composition data were square root transformed and grazer data were log(x+1) transformed; both data types were based on Bray-Curtis similarity matrices. The following eight paired macroalgal (A) and grazer (G) data sets were tested

independently for relationships: April 1998 (A) versus June 1998 (G), May 1999 (A) versus July 1999 (G), November 1999 (A) versus December 1999 (G), March 2000 (A) versus February 2000 (G), June 2000 (A) versus May 2000 (G), April 2018 (A) versus April 2018 (G), July 2018 (A) versus July 2018 (G), October 2018 (A) versus October 2018 (G).

All statistical analyses were conducted using PRIMER v6 with PERMANOVA+ software (Clarke & Gorley 2006; Anderson et al. 2008).

Results

3.1. Intertidal macroalgal species abundance

Across all sites and time periods, *Corallina* spp. comprised the highest mean percentage cover (27.7% ± 1.1 SE) of all the species groups, followed by *Cystophora* spp. (12.7% ± 0.8 SE), bare substrate (12.2% ± 0.8 SE), *Ulva* spp. (12% ± 0.8 SE) and *Lithothamnion* spp. (6.5% ± 0.3 SE). *U. pinnatifida* had a relatively low percentage cover of 0.7% ± 0.2 SE.

Mean percent cover of bare substrate was considerably higher at the Owhiro Bay sites (Owhiro Bay 1 and Owhiro Bay 2) than at the Island Bay sites, across all sampling times (Figure 6A). For all sites except Owhiro Bay 2 bare substrate coverage appeared to have increased in 2018 (Figure 6A). *Cystophora* spp. was most abundant at Owhiro Bay 1, despite decreasing consistently over time (Figure 6B). From 1997 to 2018 *Lithothamnion* spp. had decreased in percentage cover at all sites (Figure 6C). Like bare substrate, *Lithothamnion* spp. was most abundant at the Owhiro Bay sites (Figure 6C). *Corallina* spp. had an extremely high percent cover in 1997 - 2000 at Island bay 2 (54.8% ± 2.0 SE) which decreased markedly in 2008 (Figure 6D). Across all sites *Ulva* spp. percent cover increased markedly, with *Ulva* spp. at Island Bay 2 having increased by 22.8% since 2008 (Figure 6E). In 1997-2000, *U. pinnatifida* was present in low abundances at Island Bay 1 (0.3% ± 0.2 SE) and Island Bay 2 (0.9% ± 0.4 SE) with no sporophytes being recorded at the Owhiro Bay sites (Owhiro Bay 1 and Owhiro Bay 2). In 2008, *U. pinnatifida* abundance had increased at both Island Bay sites (Island Bay 1 and Island Bay 2) and for the first time was recorded at the Owhiro Bay sites (Owhiro Bay 1 and Owhiro Bay 2), with percent cover especially high in Owhiro Bay 2 (18.3% ± 14.7 SE). However, by 2018 no *U. pinnatifida* sporophytes were recorded at any of sample sites across all three sample periods (Figure 6F).

3.2. Intertidal macroalgal diversity

Results of the three factor PERMANOVA revealed that total number of species (S) and species richness (d) were significantly different as a function of site, time, season, site x time and time x season (Table. 1A, B). Species evenness (J') differed significantly as a function of site x time (Table. 1C). As shown in Table 1D, site and season were the only factors that contribute to a significant difference in species diversity (H').

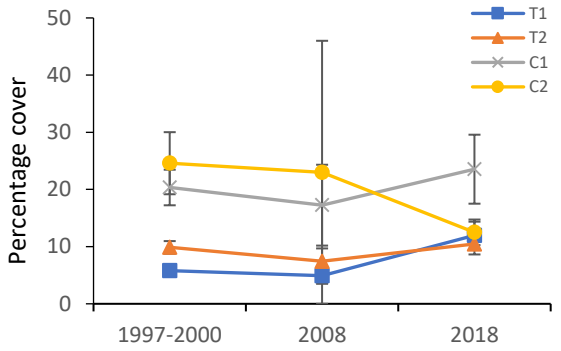


Figure 6A: Average percentage cover of bare substrate at each study site from 1997 to 2018 (mean ± se). T1 = Island Bay 1, T2 = Island Bay 2, C1 = Owhiro Bay 1 and C2 = Owhiro Bay 2

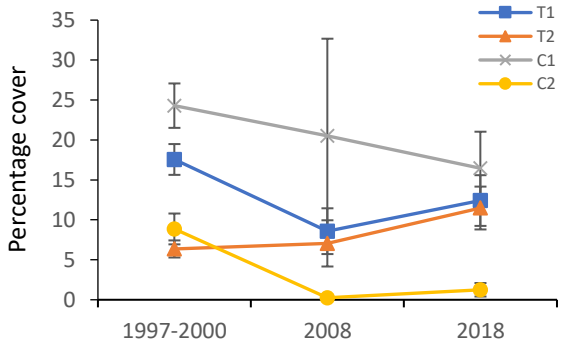


Figure 6B: Average percentage cover of Cystophora spp. at each study site from 1997 to 2018 (mean ± se).

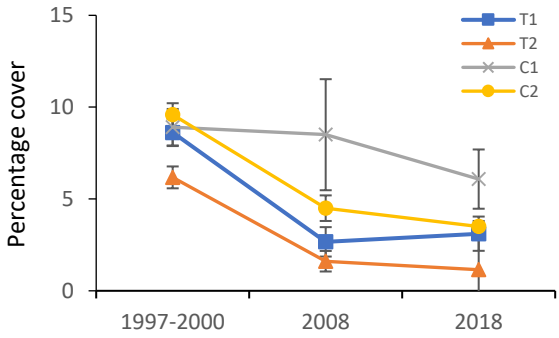


Figure 6C: Average percentage cover of Lithothamnion spp. at each study site from 1997 to 2018 (mean ± se).

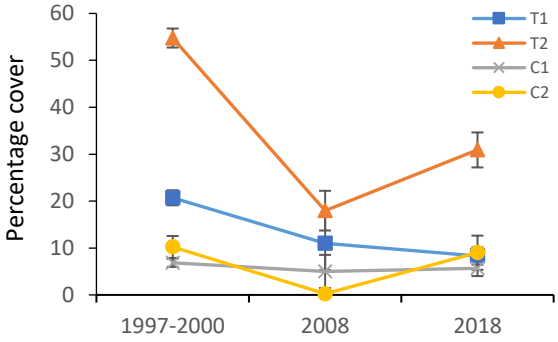


Figure 6D: Average percentage cover of Corallina spp. at each study site from 1997 to 2018 (mean ± se).

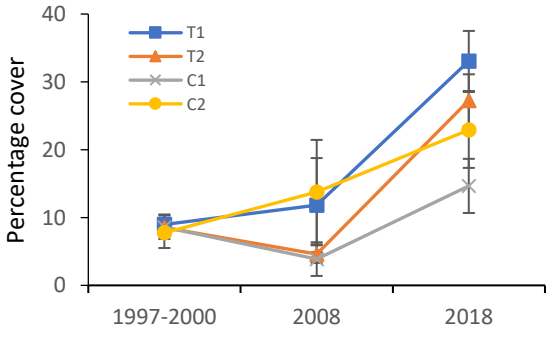


Figure 6E: Average percentage cover of Ulva spp. at each study site from 1997 to 2018 (mean ± se).

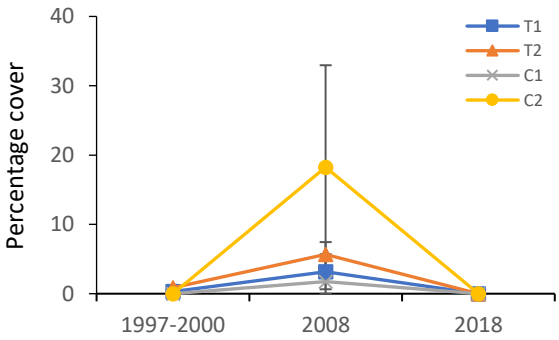


Figure 6F: Average percentage cover of U. pinnatifida at each study site from 1997 to 2018 (mean ± se).

Table 1. Three factor PERMANOVAs for diversity indices (site, time and season as factors). Data was square root transformed with analysis based on Bray-Curtis similarity matrices and 999 permutations. All non-significant terms (P > 0.05) from original analyses were excluded and PERMANOVA re-run.

A - Total Species

Source	df	SS	MS	Pseudo - F	P (perm)	Unique perms
Site	3	2410.2	803.39	9.9076	0.001	999
Time	2	2088.9	1044.5	12.88	0.001	999
Season	3	951.57	317.19	3.9117	0.008	999
Site x Time	6	2185.6	364.26	4.4921	0.001	999
Time x Season	2	1061.4	530.69	6.5446	0.003	999
Res	613	49707	81.088			
Total	629	67288				

B - Species richness

Source	df	SS	MS	Pseudo - F	P (perm)	Unique perms
Site	3	3344.3	1114.8	5.3839	0.001	999
Time	2	2827	1413.5	6.8267	0.002	999
Season	3	1771.9	590.63	2.8525	0.009	999
Site x Time	6	4115	685.83	3.3123	0.003	999
Time x Season	2	1864.2	932.09	4.5017	0.004	999
Res	613	1.269E5	207.05			
Total	629	1.5481E5				

C - Species evenness

Source	df	SS	MS	Pseudo - F	P (perm)	Unique perms
Site x Time	6	2691.6	448.59	7.3293	0.001	999
Res	617	37764	61.205			
Total	623	40455				

D - Species diversity

Source	df	SS	MS	Pseudo - F	P (perm)	Unique perms
Site	3	11889	3963.1	17.746	0.001	997
Season	2	1336.6	445.52	1.995	0.045	999
Res	623	1.3913E5	223.32			
Total	629	1.5326E5				

Two-way pairwise tests of the diversity indices revealed that the total number of species was significantly higher ($P < 0.05$) in Island Bay 1 (7.0 ± 0.2 SE) than any other site in 1997 - 2000 (site and time as factors) (Figure 7A). Total species was also significantly higher in Island Bay 1 (8.0 ± 0.5 SE) than any other site in 2008. Total species was significantly higher in Island Bay 2 (4.5 ± 0.1 SE) compared to Owhiro Bay 1 (5.0 ± 0.2 SE) and Owhiro Bay 2 (5.6 ± 0.4 SE) in 1997-2000. The only instance in which total species was significantly higher in an Owhiro Bay site was in 2018 where Owhiro Bay 1 (6.9 ± 0.5 SE) was higher than Island Bay 2 (5.7 ± 0.3 SE). In 1997 - 2000 the total number of species was significantly higher in spring (5.8 ± 0.2 SE) than autumn (5.0 ± 0.2 SE) and winter (4.4 ± 0.2 SE) (time and season as factors). The total number of species was also significantly higher in spring

(6.6 ± 0.3 SE) than in autumn (5.5 ± 0.3 SE) in 2018. Total species was significantly higher in autumn (5.0 ± 02 SE) than winter (4.4 ± 0.2 SE) in 1997- 2000. However, in 2018 total species was significantly higher in winter (6.6 ± 0.3 SE) than in autumn. In 1997 – 2000 summer (5.5 ± 0.2 SE) was significantly higher than winter (4.4 ± 0.2 SE).

Margalef's species richness was significantly higher ($P < 0.05$) in Island Bay 1 (1.3 ± 0.03 SE) than any other site in 1997 - 2000 (site and time as factors) (Figure 7B). Species richness was also significantly higher in Island Bay 1 (1.5 ± 0.1 SE) than any other site in 2008. In 1997 – 2000 species richness was significantly lower in Island Bay 2 (0.8 ± 0.02 SE) than Owhiro Bay 2 (1.0 ± 0.1 SE) However, richness was significantly higher in Island Bay 2 (1.2 ± 0.1 SE) than Owhiro Bay 2 (0.9 ± 0.3 SE) in 2008. Owhiro Bay 1 (1.3 ± 0.1 SE) had a significantly higher species richness than Island Bay 1 (1.0 ± 0.1 SE) in 2018. Species richness was significantly lower in winter (0.7 ± 0.1 SE) compared to any other season in 1997 – 2000 (time and season as factors). In 2018, species richness was significantly higher in spring (1.0 ± 0.1 SE) and winter (1.2 ± 0.1 SE) than in autumn (0.9 ± 0.1 SE).

Pielou's species evenness was significantly higher ($P < 0.05$) in Island Bay 1 (0.8 ± 0.01 SE) than any other site in 1997 – 2000 (site and time as factors) (Figure 7C). Species evenness in Owhiro Bay 1 (0.7 ± 0.02 SE) and Owhiro Bay 2 (0.7 ± 0.02 SE) was also significantly higher than Island Bay 2 (0.6 ± 0.01 SE) in 1997 - 2000. However, in 2008 species evenness was significantly higher in Island Bay 2 (0.8 ± 0.02 SE) than Owhiro Bay 2 (0.6 ± 0.02 SE). No pairwise comparisons among sites were significant in 2018.

One-way pairwise tests of Shannon Weiner's species diversity index revealed that all tests among site were significant ($P < 0.05$). Species diversity was significantly higher in Island Bay 1 (1.5 ± 0.02 SE) than any other site (site as factor) (Figure 7D). Other comparisons showed that species diversity was significantly higher in Owhiro Bay 2 (1.2 ± 0.06 SE) than in Island Bay 2 (0.4 ± 0.02 SE). However, species diversity in Owhiro Bay 1 (1.2 ± 0.04 SE) was significantly higher than Owhiro Bay 2. One-way analysis of season revealed that species diversity was significantly higher in spring (1.2 ± 0.02 SE) than summer (1.1 ± 0.04 SE) and autumn (1.1 ± 0.03 SE).

3.3. Intertidal macroalgal community composition

Three factor PERMANOVA revealed that site, time, season as well as the interaction term site x time were significant ($P < 0.05$), thus rejecting the null hypothesis that there is no difference in macroalgal community composition as a function of variation in these factors (Table 2).

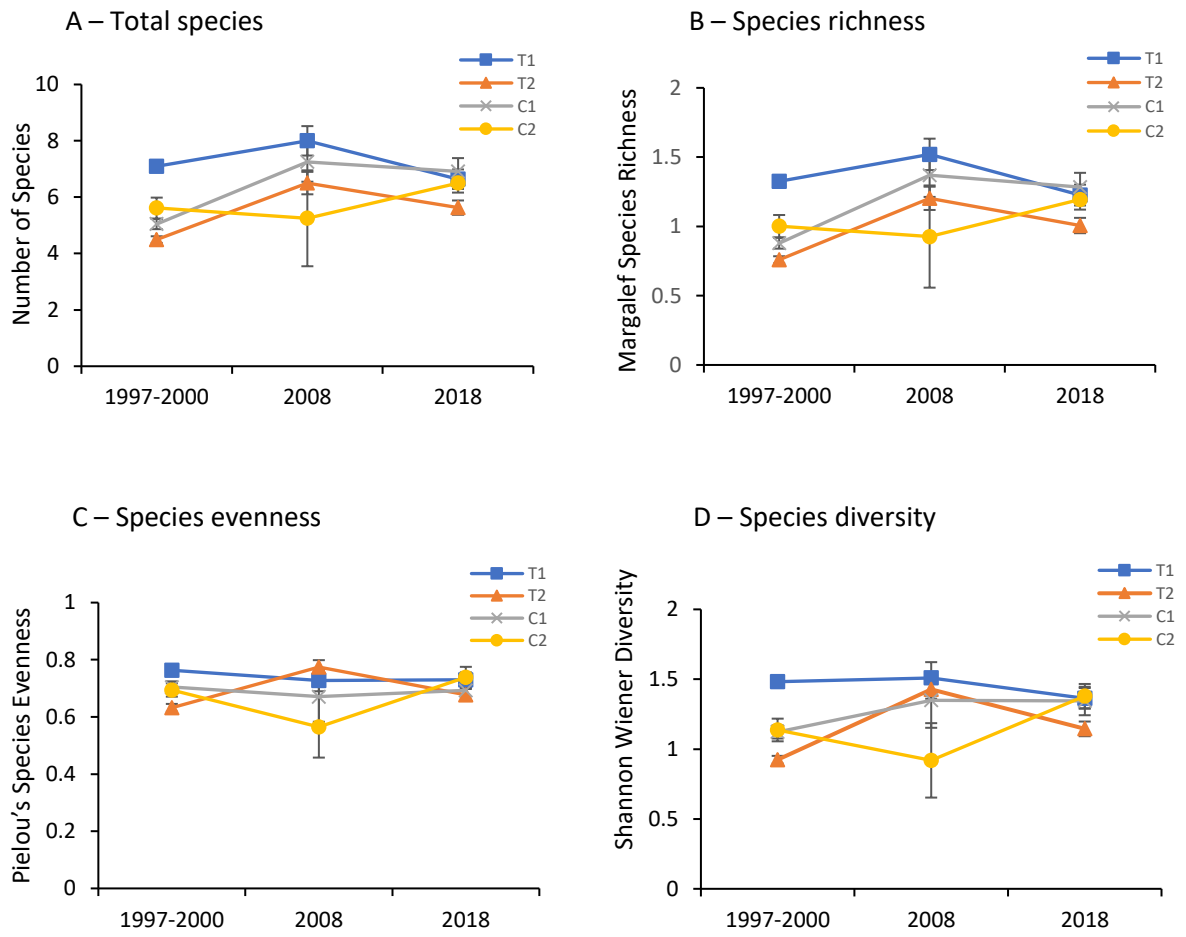


Figure 7. Total species (A), Margalef's species richness (B), Pielou's species evenness (C) and Shannon Wiener's species diversity (D) at the four study sites from 1997 to 2008 (mean ± se). T1 = Island Bay 1, T2 = Island Bay 2, C1 = Owhiro Bay 1 and C2 = Owhiro Bay 2.

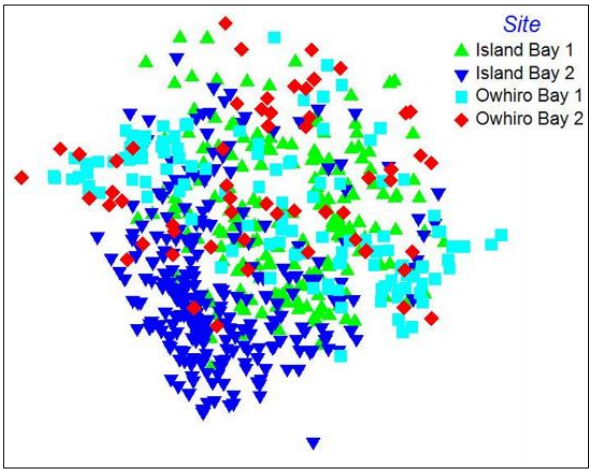
Two-way crossed pairwise tests (site and time as factors) revealed that macroalgal composition was significantly different for all pairwise site comparisons ($P < 0.05$), except for sites Owhiro Bay 1 and Owhiro Bay 2 which were not significantly different across all levels of time. All one-way pairwise tests involving season were also significant ($P < 0.05$).

Table 2. Three factor PERMANOVA testing for differences in macroalgal composition between site, time and season. Data was square root transformed with analysis based on Bray-Curtis similarity matrices and 999 permutations. All non-significant terms (P > 0.05) from original analyses were excluded and PERMANOVA re-run.

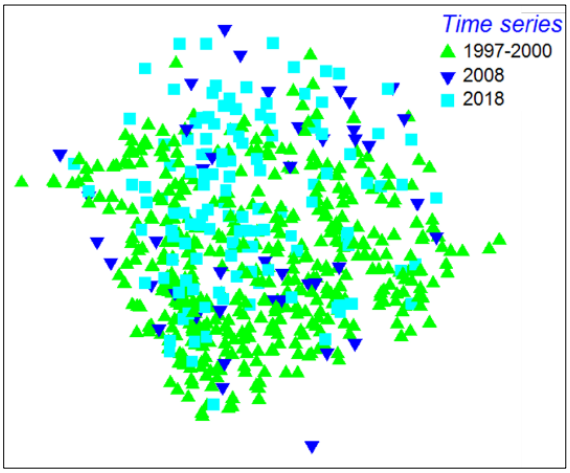
Source	df	SS	MS	Pseudo - F	P (perm)	Unique perms
Site	3	81129	27043	16.196	0.001	998
Time	2	62167	31084	18.616	0.001	999
Season	3	33941	11314	6.7757	0.001	998
Site x Time	6	27662	4610.4	2.7612	0.001	997
Res	615	1.0269E6	1669.7			
Total	629	1.3652E6				

MDS ordination plots illustrate separately the patterns of similarity in macroalgal community composition for each of the factors included in the PERMANOVA tests. Overall the plots show that there is a deal of overlap in the sample points across each of the factors, with few distinct clusters of sample points. The MDS ordination plot with sample points coded for the factor site showed that the macroalgal community of Island Bay 2 had a relatively high similarity which is indicated by clustered points at the bottom of the plot (Figure 8A). Samples of the macroalgal community of Owhiro Bay 1 also appear to be clustered in the shape of a band through the middle of the plot (Figure 8A). The MDS plot of sample points coded for time and season both appear more scattered and random with no discernible pattern of clustering by these factors (Figure 8B, C). However, the 2D stress for each MDS plot is quite high (>0.2) which suggests the data is not well represented by the plots

A - Site 2D stress: 0.24



B - Time 2D stress: 0.24



C - Season 2D stress: 0.24

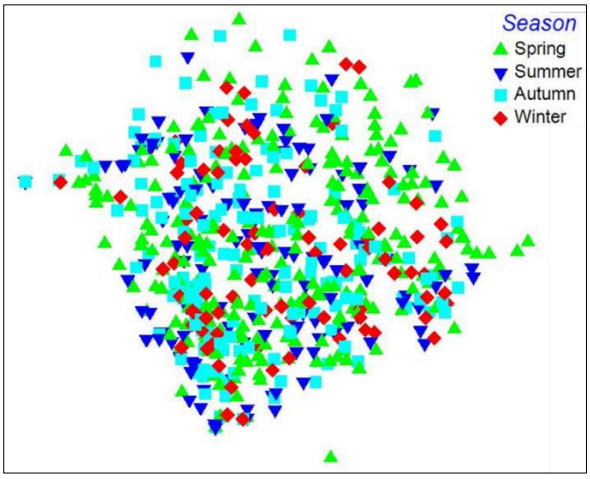


Figure 8. MDS ordination plots for Bray-Curtis similarity derived from macroalgal percent cover data. Sample points are coded for factors site (A), time (B) and season (C).

Two-way SIMPER tests (site and time as factors) revealed that 10 – 12 species contributed to dissimilarity amongst site (90% contribution cut off). Amongst these species the consistently highest contributor's to dissimilarity were bare substrate, *Corallina* spp., *Cystophora* spp*., Zonaria* spp*.* and *Ulva* spp. (Appendix 2). These five species contributions to dissimilarity ranged from 8.6 % to 20.5 % amongst all site groups (Appendix 2). *U. pinnatifida* was a not listed as a species which contributed to dissimilarity amongst the factor site. Results amongst time were similar with the exception that 12 – 13 species contributed to dissimilarity (90% contribution cut off) and *Leathesia marina* replaced *Zonaria* spp. as one of the highest contributing species (Appendix 2). Contribution of the top species ranged from 7.3% to 15.1% (Appendix 2). *U. pinnatifida* also contributed to dissimilarity between sampling times, contributing 5.3% to dissimilarity between 1997 - 2000 and 2008, and 4.8% between 2008 and 2018 (Appendix 2).

The one-way SIMPER test (season as factor) revealed that 11 or 12 species contributed to dissimilarity amongst groups. Amongst these species the highest contributors to dissimilarity ranged from 7.3 % to 15.1%. These species were bare substrate, *Corallina spp.*, *Cystophora* spp. and *Lithothamnion* spp. *U. pinnatifida* was not a contributing species amongst 'season' (Appendix 3).

The two-way crossed ANOSIM (site and time as factors) showed that *U. pinnatifida* abundance differed significantly amongst site (Global R: 0.011, P = 0.011) and time (Global R: 0.015, P = 0.03). Pairwise tests found that *U. pinnatifida* abundance was significantly higher in Owhiro Bay 2 (1.2 ± 1.1 SE) than Island Bay 2 (1.0 ± 0.3 SE). Abundance was also significantly lower in Owhiro Bay 1 (0.1 ± 0.1 SE) compared to Island Bay 1 (0.4 ± 0.2 SE) and Island Bay 2. Additionally, *U. pinnatifida* abundance was significantly higher in 2008 (5.4 ± 1.8 SE) than 2018. The interaction between site (Global R: 0.01, P = 0.024) and season (Global R: 0.013, P = 0.016) also proved to be significant ($P < 0.05$). Pairwise tests revealed that *U. pinnatifida* abundance differed significantly between Island Bay 1 and Owhiro Bay 2. *U. pinnatifida* abundance was also significantly higher in spring (1.5 ± 0.4 SE) than summer (0.03 ± 0.02 SE). These results reject the null hypothesis that there is no difference in *U. pinnatifida* abundance as a function of site, time and season.

3.4. Microtopography

One-way PERMANOVA revealed that microtopography did not differ significantly (P = 0.052) as a function of site, supporting the null hypothesis that there was no difference in quadrat microtopography between sites.

3.5. Census of invertebrate grazers

Analysis of the grazer data revealed a noticeable decrease/absence of most grazers in 2018. *Scutus breviculus* and *Aplysia dactylomela* were absent from all surveys in 2018, with *Haliotis australis* also being recorded at much lower densities compared to earlier surveys. *Lunella (Turbo) smaragdus* abundance remained constant over time, but it did decrease slightly at both Island Bay 2 and Owhiro Bay 2 in 2018. *Evechinus chloroticus* and *Haliotis iris* densities were consistent at both sites and across all sampling times. Across all surveys (mean abundance per 10 m^2 ± SE) *Lunella smaragdus* (17 ± 0.5 SE) was by far the most abundant grazer species, followed by *Scutus breviculus* (3.4 ± 0.8 SE), *Haliotis australis* (3.0 ± 0.7 SE), *Haliotis iris* (2.7 ± 0.5 SE), *Evechinus chloroticus* (0.2 ± 0.1 SE) and *Aplysia dactylomela* (0.1 ± 0.1 SE).

Results of the three factor PERMANOVA revealed that site and time as well as the interaction effect site x time explained significant ($P < 0.05$) variation in the similarity of abundance of the six species of grazer (Table 3). Although season was not significant, the interaction term site x season was significant. These results reject the null hypothesis that there was no difference in grazer abundance as a function of the factors site, time and season

Two-way crossed PERMANOVA pairwise tests (site and time as factors) using the same grazer abundance similArevealed the following pairwise comparisons were significant ($P < 0.05$): Island Bay 1 and Owhiro Bay 2, Island Bay 2 and Owhiro Bay 1 within level 1998 – 2000; Island Bay 1 and Island Bay 2, Island Bay 1 and Owhiro Bay 1, Island Bay 1 and Owhiro Bay 2, Island Bay 2 and Owhiro Bay 1, Island Bay 2 and Owhiro Bay 2 within level 2018. There were also no significant pairwise tests ($P > 0.05$) for the interaction effect site x season.

Table 3. Three factor PERMANOVA testing for differences in abundance of six species of grazers as a function of site, time and season. Data were log(x+1) transformed with analysis based on Bray-Curtis similarity matrices and 999 permutations. All non-significant terms (P > 0.05) from original analyses were excluded and PERMANOVA re-run.

Source	df	SS	MS	Pseudo - F	P (perm)	Unique perms
Site	3	15565	5188.4	9.189	0.001	996
Time	1	9493.5	9493.5	16.814	0.001	998
Site x Time	3	8174.6	2724.9	4.8259	0.001	998
Site x Season	9	8379	931	1.6489	0.038	999
Res	28	15810	564.63			
Total	47	68823				

Two-way SIMPER tests (site and time as factors) revealed that 4 - 5 species contributed to dissimilarity in grazer abundance amongst site (90% contribution cut off). Amongst these species the consistently highest contributor's to dissimilarity were *Lunella smaragdus. Scutus breviculus* and *Haliotis iris*. These three species contributions to dissimilarity ranged from 15.6 % to 67.7 % amongst all site groups (Appendix 4). Results for time were similar with the exception that only 4 species contributed to dissimilarity amongst time (90% contribution cut off) and *Haliotis australis* replaced *Haliotis iris* as one of the highest contributing species (Appendix 4). Contribution of the top species ranged from 17.8 % to 28.6 %. SIMPER analysis of site (site and season as factors) revealed that 4 species contributed to dissimilarity (90 % contribution cut off) (Appendix 5). Amongst these species the consistently highest contributor's to dissimilarity ranging from 14.7% to 47.7% were *Lunella smaragdus. Scutus breviculus* and *Haliotis iris.* The results were similar amongst season with the exception that *Haliots australis* consistently had a high contribution to dissimilarity. For both site x time and site x season *Aplysia dactylomela* was not listed among the contributing species (Appendix 5).

3.6. Relating community composition to microtopography and grazer abundance

Results of the RELATE test between macroalgal community composition data and microtopography revealed that there was a significant relationship between microtopography in March 2000 (Rho: 0.055, P = 0.023) and June 2000 (Rho: 0.031, P = 0.028) (all other tests were non-significant). However, a sample statistic (Rho) close or equal to zero suggests a very weak relationship between the biological and environmental datasets.

The RELATE test results between macroalgal composition data and grazer abundance revealed no significant relationships (P > 0.05).

3.7. Subtidal *U. pinnatifida* surveys and macroalgal community composition

Overall (across all sites and time periods), very few *U. pinnatifida* sporophytes were recorded in the subtidal transect surveys. No sporophytes were recorded at sites Owhiro Bay 1 and Owhiro Bay 2. No sporophytes were recorded at any site in all three of the surveys conducted in 2018. Island Bay 1 had the highest abundance of subtidal sporophytes with numbers fluctuating between zero and six. One sporophyte was recorded in two surveys in Island Bay 2.

The macroalgal community of Island Bay 1 was dominated mostly by *Cystophora* spp. at the shallowest end of the channel, becoming sparser with increasing depth. *Carpophyllum* spp. and large foliose red algae were present in patches, with *Ulva* spp. being present consistently along the transect. *Lessonia variegata* was abundant at the deepest end of the channel. Substrate changed from fine gravel to small cobble at the shallow end. Island Bay 2 was largely dominated by a dense cover of *Cystophora* spp. and *Carpophyllum* spp. *Ulva* spp. was present in patches with *Lithothamnion* spp. covering most rocks. Substrate was predominantly large cobble. Owhiro Bay 1 contained high densities of *Lessonia variegata* at its deepest end of the transect along with patches of *Ecklonia radiata. Cystophora* spp. was present throughout the transect, becoming extremely dense in the shallowest waters. Substrate changed from large cobble to fine gravel with increasing depth. Owhiro Bay 2 was dominated by *Lessonia variegata* which was extremely abundant in the deep end of the channel. *Carpohyllum* spp*., Zonaria* spp. and *Cystophora* spp. were present in patches throughout the shallow end. *Lithothamnion* spp. were also present in small patches on larger rocks. Substrate was predominantly large rocks mixed in with cobble. Subtidal observations remained constant throughout all 2018 surveys with the exception that *Ulva* spp. became noticeably more abundant at Island Bay 1 during spring. These results align with previous qualitative observations made by Wear & Gardner (1998, 2000) and Gardner & Wear (1999), suggesting that subtidal macroalgal composition has not differed substantially since 1997.

3.8. *U. pinnatifida* coastal survey

Undaria pinnatifida was present at 8 of 13 locations along the south coast in 2018. Sporophytes appeared healthy and reproductively active (sporophyll present) and occurred in quite high abundances in most locations. Sporophytes were present on both artificial and natural substrates. No sign of *U. pinnatifida* was recorded in Owhiro Bay and Island Bay west of the Sirens Rock (locations: 1, 2, 3, 4 & 5; Figure 5).

Discussion

This thesis describes the distribution and spread of *Undaria pinnatifida* on Wellington's south coast. This investigation was accomplished by compiling the results of previous *U. pinnatifida* monitoring surveys at four study sites (Wear & Gardner 1998; Gardner & Wear 1999; Wear & Gardner 2000; Gardner & Wear, unpublished data 2008) while concurrently carrying out additional seasonal surveys in 2018. Surveys involved the recording of macroalgal community composition in the intertidal zone, as well as invertebrate grazer counts in the adjacent subtidal zone. Results showed a gradual increase in *U. pinnatifida* abundance over time until 2008, followed by a complete disappearance from all four study sites in 2018. The most dominant intertidal macroalgal species were *Corallina* spp., *Cystophora* spp. and *Ulva* spp., with the latter having increased dramatically in abundance from 2008 to 2018. Macroalgal diversity indices differed to some extent across site, time and season, but no clear pattern emerged with the exception that species diversity did not change over time. Although macroalgal species composition differed across site, time and season *U. pinnatifida* appeared to have no influence on macroalgal composition. In addition, there was no relationship between macroalgal composition and both grazer abundance and microtopography. Abundance for almost all six grazer species decreased over time; of these species *Lunella smaragdus* was by far the most abundant.

4.1. Patterns *of U. pinnatifida* distribution and spread

The pattern of *U. pinnatifida* distribution and spread on Wellington's south coast was comprised of three distinct phases. Firstly, an initial growth phase in 1997 - 2000 in which abundance increased gradually in Island Bay. Secondly, a rapid growth phase in the eight-year period up to 2008 in which abundance increased substantially and recruitment to Owhiro Bay occurred. Thirdly, a complete collapse and disappearance of *U. pinnatifida* from all four surveyed sites by 2018, which was not accompanied by a collapse of native macroalgal species. This lag, boom, bust pattern is not atypical for non-indigenous species invading foreign environments (Simberloff & Gibbons, 2004), but this is the first time it has been recorded for *U. pinnatifida*, even if only on a small local scale encompassing approximately 5 km of coastline.

The widespread distribution of invasive *U. pinnatifida* in most regions throughout the world has been largely facilitated by anthropogenic means (Schiel & Thompson, 2012). Hull fouling, ballast water discharge and transportation with aquaculture gear are the vectors that explain the long-distance spread of *U. pinnatifida* (Epstein & Smale, 2017; Epstein & Smale, 2018). The distribution of invasive

U. pinnatifida is typically associated with shipping routes and manmade structures such as ports and boat harbours (Stuart, 1997; Russell et al. 2008; Epstein & Smale, 2017). For example, during monitoring conducted in several southern New Zealand ports in 1998 - 2001, *U. pinnatifida* was encountered on 31 - 50% of commercial and recreational vessels (Forrest & Hopkins, 2013; South et al. 2017). Following introduction, localised spread can occur quite rapidly due to the abundance of artificial substrates and structures (Russell et al. 2008). In contrast, spread via natural dispersal without anthropogenic influence is usually much slower (Schiel & Thompson, 2012; Epstein & Smale, 2017). The rate of natural dispersal of *U. pinnatifida* varies and is dependent on numerous environment factors such as temperature, ocean currents and habitat availability (Russell et al. 2008; Epstein & Smale, 2017). Spore-mediated dispersal rates for *U. pinnatifida* have been estimated at 10 - 200 m y^{-1}, while spread through sporophyte drift has a maximum dispersal rate of 1 – 10 km y^{-1} (Forrest et al. 2000; Sliwa et al. 2006; Russell et al. 2008; Epstein & Smale, 2017). In this study, the leading edge of the *U. pinnatifida* invasion when it was first identified on Wellington's south coast was relatively confined to Island Bay from 1997 to 2000. However, in 2008 *U. pinnatifida* populations were recorded over 1.75 km to the west in Owhiro Bay. Although it is possible that unknown *U. pinnatifida* populations already existed in Owhiro Bay before 2008, dive surveys conducted in 2004 found no subtidal *U. pinnatifida* west of the Sirens Rock in Island Bay, which suggests that dispersal between these two bays took place within a four-year period (2004 – 2008). Interestingly, this westward movement is against the mean current flow in the Cook Strait, which is strongly west to east, however there is a westward component of flow which might have influenced the westward spread of *U. pinnatifida* (Helson & Gardner, 2004). If linear dispersal is assumed, the rate of spread from Island Bay to Owhiro Bay was approximately 440 m y^{-1} which is consistent with the natural dispersion rates reported above. Although it is likely this spread occurred via natural dispersion the possibility of human mediated dispersal or a combination of both cannot be ruled out.

In New Zealand spatial and temporal patterns of expansion has varied between regions (Forrest et al. 2000; Forrest et al. 2008; Epstein & Smale, 2017). Monitoring of *U. pinnatifida* at Oamaru and Timaru Harbours revealed that despite 20 years of occupancy, populations in both harbours had spread less than 1 km outside of the harbour entrance (Hay & Villouta, 1993; Russell et al. 2008; Epstein & Smale, 2017). It was hypothesised that lack of suitable substrate at the harbour's entrance restricted further spread and colonisation (Russell et al. 2008). Several populations within New Zealand harbours have also shown a lag phase before rapidly dispersing out of the harbour onto exposed coast. In Otago Harbour it took over a decade to spread to the harbour entrance, from there it spread across 15 km of exposed coast in less than 7 years (Russell et al. 2008; South et al. 2017). A similar pattern was also observed for the Moeraki Harbour population, which took almost five years to spread less than a

kilometre from a breakwater to coastal reefs, and at least another ten years for it to spread out to the exposed outer coast. However, once there it spread rapidly covering 10 km of coastline in 11 years (Schiel & Thompson, 2012). It was speculated that this pattern was most likely a reflection of wave direction, the slow build-up of large populations, and increasing propagule pressure and then greater water flow and mixing along the open coast which promoted rapid dispersal (Simberloff, 2009; Schiel & Thompson, 2012).

Slow range expansion of *U. pinnatifida* following introduction is not just specific to New Zealand populations. In France, it took 10 years for *U. pinnatifida* to disperse out of the enclosed lagoon from which it was first introduced (Floc'h et al. 1991). In California, USA, many marina populations remain localised following introductions over 10 years ago (Kaplanis et al. 2016). In the United Kingdom it took over 7 years for *U. pinnatifida* to spread to a coastline 200 m away from an established marina population (Farrell & Fletcher, 2006; Epstein & Smale, 2017). Considerably faster rates of dispersal have also been recorded overseas. In the San Jose Gulf, Argentina, *U. pinnatifida* had spread along 100 km of coastline only 4 years after its introduction (Dellatorre et al. 2014; Epstein & Smale, 2017). Along the eastern coast of Tasmania, Australia, *U. pinnatifida* has spread at a rate of 10 km y^{-1} and by 2002 had occupied more than 320 km of coastline, resulting in one of the largest recorded range expansions of *U. pinnatifida* from a founding population (Shepherd & Edgar, 2013; South et al. 2017) (refer to Figure 9 for global and regional distribution of *U. pinnatifida*). These results show that *U. pinnatifida* expansion rates are highly variable between regions, which suggest that differences in environmental factors between regions must play a key role in *U. pinnatifida* dispersal.

4.2. Response of native macroalgal communities to invasive species

In this study native macroalgal community composition was variable between the study sites and across time but did not appear to be related to changes in the abundance of *U. pinnatifida*. *Corallina* spp., *Ulva* spp. and *Cystophora* spp. consistently comprised a large percentage of the intertidal macroalgal community, with *Lithothamnion* spp*., Zonaria* spp*. and Leathesia marina* usually comprising the second most abundant group of macroalgae. Indices of total species, species richness, and species evenness varied to an extent between sites and across time, but the magnitudes of these variations were often small and no distinct pattern in their variations was discernible over time. However, one result which stood out was that species diversity (measured as H') did not change over time. This result is of note because *U. pinnatifida* has been recorded to reduce native macroalgae biodiversity (Cecere et al. 2000; Casas et al. 2004; Morelissen, 2012). For this reason, it was expected

that species diversity would have been lower in 1997 – 2000 and 2008 when *U. pinnatifida* abundance was at its highest.

Figure 9. Global distribution of *Undaria pinnatifida*. On regional map each point represents the approximate location of *U. pinnatifida*. On global map red = introduced range, green = native range. Sourced from Epstein and Smale, 2017 pp. 8626.

Morelissen (2012) investigated macroalgal composition and *U. pinnatifida* abundance on Wellington's South Coast during 2008. Erect coralline algae comprised the highest mean percent cover of all groups on the south coast (36.7% ± 2.3 SE). This species group had the highest percentage cover in the low intertidal at Island Bay (56.1% ± 2.8 SE) and at Moa Point (37.0% ± 3.7 SE), but the most abundant species at Owhiro Bay was *Zonaria turneria*. Interestingly, *U. pinnatifida* was not recorded at the Owhiro Bay and Island Bay sites in 2008 but was noted at Moa Point. Estimates of species richness S, species diversity H', and species evenness J' made by Morelissen (2012) in 2008 were almost identical to those recorded in the Gardner and Wear (2008) survey. These indices in 2008 were variable amongst site and time, but no site showed consistently higher or lower values of S, H' or J' than other sites throughout the year (Morelissen, 2012). In contrast to these results a study in the Nuevo Gulf, Argentina, revealed that species richness (S) was 2.75 times higher in plots cleared of *U. pinnatifida* (11.0 ± 1.5 SE) than those where *U. pinnatifida* was present (4.0 ± 1.0 SE) (Casas et al., 2004). Species diversity (H') was also significantly higher in *U. pinnatifida* cleared plots (0.2 ± 0.04 SE) than in plots where *U. pinnatifida* was present (0.07 ± 0.04 SE). The same pattern was recorded for species evenness (J') which was significantly higher in *U. pinnatifida* removed plots (0.06 ± 0.01 SE) than in *U. pinnatifida* present plots (0.03 ± 0.02 SE) (Casas et al. 2004). The invasive brown alga *Sargassum*

muticum has also been recorded to influence subtidal communities of native macroalgae (Britton-Simmons, 2004). A manipulation removal experiment conducted in The San Juan Islands, USA, revealed that native brown and red algae were 50 – 75% more abundant in plots from which *S. muticum* had been removed. Additionally, the native kelp *Laminaria bongardiana* grew more than twice as fast in plots where *S. muticum* was absent. Alternatively, in a study by Sánchez and Fernández (2005) removal of *Sargassum muticum* from intertidal plots in northern Spain was found to have no significant effect on native assemblage cover, species richness and diversity. These findings reveal that the ecological impact of *U. pinnatifida* as well as *S. muticum* on native macroalgae varies between regions.

4.3. Response of grazers to invasive species

Invasive species have the potential to disrupt an ecosystems food web structure (Neill et al. 2008; James & Shears, 2013), thus the abundance of six invertebrate grazers were surveyed to determine if *U. pinnatifida,* and the potential changes that it could have induced on the macroalgal community had any effect on the grazer community over time and space. Additionally, the grazers *H. iris, H. Australis and E. chloroticus* are highly valued by recreational and commercial fisherman therefore it is important to monitor these species and record any influence *U. pinnatifida* may have. In this study the abundance of almost all grazer species had decreased over time, with some species such as *Scutus breviculus* and *Aplysia dactylomela* not being recorded at all in 2018. Interestingly, the decrease of invertebrate grazers in 2018 did coincide with the apparent collapse of *U. pinnatifida*. The cause of this reduction in grazer abundance is relatively unknown, but it is unlikely that grazer abundance decreased as a result of *U. pinnatifida* collapse and vice versa. The reduction in grazer abundance may be attributable to increased fishing/collecting pressure, however this would only account for half of grazer species and doesn't explain why species such as *S. breviculus* which have no recreational/commercial importance have decreased. It may also be possible that grazer abundance decreased due to changes to study site habitat between sampling times. Although there is no direct evidence to support this claim, the south coast is a highly dynamic environment and is exposed to strong southerly swells (Wear & Gardner, 1998) which could permanently alter habitat structure via erosion over time. It is also possible this pattern arose due to investigator error caused by changes in surveying methodology from SCUBA in 1997 – 2000 to snorkelling in 2018, however this is also unlikely as all six grazers are relatively large and easy to find/identify. An across the board decrease in grazer abundance is interesting and potentially points to a wider cause. Further monitoring is needed to uncover the underlying mechanisms responsible for this pattern. The inclusion of more species would

be useful to determine if this pattern is uniform across trophic levels or just specific to the six recorded grazer species.

Several studies have investigated the potential impacts and relationships between invasive macroalgae and marine grazers/invertebrates with varying results (Wright et al. 2007; Gribben et al. 2009; Irigoyen et al. 2011a; Irigoyen et al. 2011b). In the Nuevo Gulf, Argentina, *U. pinnatifida* was associated with decreased fish abundance on low-relief reefs (Irigoyen et al. 2011a). It was suggested that this decrease was a result of *U. pinnatifida* physically obstructing access to shelters and therefore reducing reef quality for the fish populations (Irigoyen et al. 2011a). Likewise, a study in New South Wales, Australia, recorded that the survivorship, growth and condition of a native bivalve *Anadara trapezia* was significantly reduced in sediments dominated by the invasive green alga *Caulerpa taxifolia* compared to unvegetated sediment (Wright et al. 2007; Gribben et al. 2009).

Multiple choice feeding assays have been used to determine feeding rates and preferences of native grazers to both native and invasive macroalgae (Gollan & Wright, 2006; Jimenez et al. 2015). In New Zealand, a laboratory feeding assay revealed that the grazer species *Aora typica, Cookia sulcata* and *Haliotis iris* ate *U. pinnatifida* at rates similar to those of native macroalgae, whilst the isopod *Batedotea elongate* barely consumed it. This indicates that *U. pinnatifida*, has the potential to contribute organic matter to the local food web but it may also be an undesirable food for some grazers (Jimenez et al. 2015).

A common notion in invasion ecology is that invasive species reduce native invertebrate biodiversity (Molnar et al. 2008), but in some instances invasive species have been shown to increase biodiversity through increasing habitat complexity and contributing organic matter to the food web (Irigoyen et al. 2011b). In the Nuevo Gulf, Argentina, the richness and diversity of native marine fauna species was higher in plots covered by *U. pinnatifida* than those where *U. pinnatifida* was removed (Irigoyen et al. 2011b). Additionally, the abundance of two species of crustaceans, one species of sea urchin, one species of nemertine and several species of polychaetes were higher in plots containing *U. pinnatifida.* These results were attributed to the provision of new habitat structure by *U. pinnatifida* which was larger and structurally more complex than the local native macroalgae (Irigoyen et al. 2011b).

4.4. The collapse of the *U. pinnatifida* invasion front on Wellington's south coast

Undaria pinnatifida populations in New Zealand and around the world have been shown to exhibit lag growth phases after initial establishment, followed by rapid coastal spread (Russell et al. 2008; Schiel & Thomson, 2012; South et al. 2017). What is unique about the results found in this study is the

unexpected disappearance of *U. pinnatifida* following an extensive expansion. In March 2000, 219 *U. pinnatifida* sporophytes were recorded throughout the intertidal and subtidal zone of Island Bay at the two channel sites (Wear and Gardner, 2000) and by 2008 *U. pinnatifida* percent coverage at each site was the highest ever recorded in this location. However, by 2018 *U. pinnatifida* was not recorded at any of the four study sites, thus rejecting the original hypothesis that *U. pinnatifida* abundance and spread would have increased by 2018. The collapse of the *U. pinnatifida* population was not accompanied by a collapse or substantial change in the populations of the native macroalgal species, with the exception of *Ulva spp*. which had increased in abundance at all four study sites in 2018. Qualitative searches along the south coast during 2018 found that the nearest known *U. pinnatifida* population was approximately 500 m east of the Island Bay sites. Therefore, in a period of 10 years the leading edge of the *U. pinnatifida* invasion on Wellington's south coast had receded by over 1.75 km. A spontaneous collapse at an invasion front of this magnitude without human involvement has not been previously recorded for *U. pinnatifida*.

The phenomenon of invasion collapse has been observed for non-native species. The North American waterweed *Elodea canadensis* was first detected in southern Scotland in 1842 (Simpson, 1984; Simberloff & Gibbons, 2004). Following its introduction, it rapidly spread to ponds, rivers and canals throughout Great Britain and by 1900 it was highly abundant in all suitable waterways. Reports at the time revealed that the Cam River, England, was so clogged that it interfered with rowing, fouled fishing nets, and at least one swimmer drowned after being caught in it. Then it suddenly declined throughout its entire British range, for no obvious reason and with no human intervention. By the 20th century it was rare in most places and had ceased to be a problem (Simpson, 1984; Simberloff & Gibbons, 2004). Records of *E. canadensis* throughout England revealed that it showed a typical cycle of colonisation, where the plant would become established, then rapidly increase for a period of 3 - 4 years reaching pest proportions (Simpson, 1984). Following this, maximum densities would be maintained for another 3 – 10 years, then decline over 7 – 15 years where it would eventually become locally extinct or remain in low abundances (Simpson, 1984; Simberloff & Gibbons, 2004). This same pattern has also been observed with introduced *E. canadensis* in Germany (Scherer-Lorenzen et al. 2000) and Sweden (Andersson & Willen, 1999). Patterns of spontaneous collapse following expansion have also been recorded in number of terrestrial invasive species such as Cane Toads (*Bufo marinus*) in Northern Australia, the Crested Mynah (*Acridotheres cristatellus*) in Vancouver, Canada, and the Giant African snail (*Achatina fulica*) in the Pacific Islands (Simberloff & Gibbons, 2004). For these species, including *E. canadensis*, the cause of the collapse was unknown (Simberloff & Gibbons, 2004).

The *U. pinnatifida* collapse at the invasion front on Wellington's south coast is perplexing because there is no obvious reason for it. Without additional research determining the exact cause of this local site collapse is not feasible. Therefore, examining factors known to inhibit or negatively impact invasive species in other systems and discussing their relevance to this study is the next appropriate step, particularly with reference to considering the question as to whether the collapse at the invasion front is likely a to signal a wider collapse of the population on Wellington's South coast. Competitive exclusion, predation, changes to the physical environment and pathogens have been documented as determinants of invader collapse in previous studies (Simberloff & Gibbons, 2004; Lester & Grube, 2016).

Biotic resistance is a well-documented cause of preventing/restricting the establishment and spread of invasive species and has also been attributed to the collapse of several terrestrial invasive species (Stachowicz et al. 2002; Simberloff & Gibbons, 2004; Mattingly et al. 2007). However, this is unlikely to be the cause of *U. pinnatifida* collapse reported here. Native macroalgae have been recorded to exclude invasive algae by outcompeting them for light and space (Stuart, 2004; Russell et al. 2008). However, this process usually occurs shortly after the introduction of an invasive species (Thompson & Schiel, 2012). At Island Bay, *U. pinnatifida* co-occurred with native macroalgae for at least 10 years (most likely longer) before the leading edge of the population collapsed. As noted previously, other established *U. pinnatifida* populations on the south coast have not collapsed, making it still more difficult to understand the collapse of the leading edge of the invasion. Additionally, *U. pinnatifida* has been proven to be a superior competitor in macroalgal communities in other parts of New Zealand and throughout the world (Stuart, 2004; Russell et al. 2008). One study also showed that the native macroalga *Corallina officinalis* facilitated the spread of *U. pinnatifida* by providing a favourable habitat for *U. pinnatifida* gametophytes to establish on (Thompson & Schiel, 2012). This pattern is not supported in this study as *Corallina* spp. percent cover was generally higher when *U. pinnatifida* had a low abundance or was absent.

A key concept in invasion biology is that a community's resistance to invasion increases with its species diversity (Elton, 1958; Tilman, 1999; Mattingly et al. 2007). It is hypothesised that species rich communities offer fewer vacant niches for invaders to exploit and/or will have a higher probability that an invader will be excluded by a superior native competitor (Tilman, 1999; Wardle, 2001; Fargione & Tilman, 2005). On Wellington's south coast macroalgal diversity (Shannon Wiener's index) remained unchanged over time. However, it is important to note that macroalgal composition did differ over time despite diversity remaining unchanged. Dominant species are known to exert a strong influence over ecosystem function and community dynamics (Crawley, 1987; Dangles & Malmqvist, 2004; Emrey & Gross, 2007). Thus, the presence and relative abundance of these species maybe key to regulating

invasion rather than diversity (Emery & Gross, 2007). In this study the percent cover of the dominant macroalgae e.g. *Cystophora* spp., *Ulva* spp., *Lithothamnion* spp. and *Corallina* spp. did fluctuate over time. However, with the exception of *Ulva* spp. no apparent pattern arose to suggest that a change in macroalgae composition caused the decline of *U. pinnatifida*. For these reasons it is unlikely that competitive exclusion by native macroalgae resulted in the *U. pinnatifida* collapse.

Marine herbivores are known to be able to limit native macroalgal abundance and/or distribution through grazing pressure (Gollan & Wright, 2006; Cacabelos et al. 2010). Results of laboratory feeding assays have shown that some grazers in New Zealand waters feed on *U. pinnatifida* at rates similar to those of native macroalgae which suggests that grazers may have the ability to limit *U. pinnatifida* abundance (Jimenez et al. 2015). This theory was supported by an eradication programme conducted in Sunday Cove, Fiordland, SW New Zealand, which used the endemic sea urchin (*Evechinus chloroticus*) as a biological control agent to reduce the invading population of *U. pinnatifida* (Atalah et al. 2013). Despite this, it is doubtful that grazing pressure resulted in the collapse of *U. pinnatifida* on Wellington's south coast. Similar to competitive exclusion by macroalgae, if grazing pressure was a dominant force in reducing the spread of the *U. pinnatifida* on Wellington's south coast then its effects should have been noticed shortly after introduction (Atalah et al. 2013). In addition, if grazing pressure was responsible than one would expect to see a negative relationship between grazer density and *U. pinnatifida* abundance (e.g., Atalah et al. 2013). However, in 2018 for almost all grazer species abundance was lower when *U. pinnatifida* was absent. It could be argued that grazer abundance in 2018 declined following overgrazing of their *U. pinnatifida* food source, but this is also unlikely as there was no shortage of alternative native macroalgae to graze on. Grazing by organisms not quantified in this study could have contributed to the *U. pinnatifida* collapse. However, besides a small number of invertebrate species there is little information pertaining to what other organisms graze on *U. pinnatifida* in New Zealand waters (Jimenez et al. 2015). With this in mind, the grazer species chosen for this study did compose a large majority of the macrofauna observed in the field during 2018 and thus are most likely a good representation of the south coast's grazer community.

What is most perplexing about the invasion front collapse reported in this study is that *U. pinnatifida* was abundant at neighbouring locations only 500 m east of the Island Bay sites and along the rest of the south coast. The majority of these locations had similar physical characteristics (wave exposure, depth and topography) to the Island Bay and Owhiro Bay sites. Because of relative uniformity between these sites it is highly improbable that the collapse of *U. pinnatifida* at Island Bay and Owhiro Bay was caused by some change in natural environmental parameter over time. *U. pinnatifida* in New Zealand typically dies back in summer as a result of warmer temperatures but this is part of an annual cycle in

which a new generation of *U. pinnatifida* appears in autumn/winter (James & Shears, 2013). Sea water temperature in the Island Bay and Owhiro Bay area in 2018 ranged between 10 and 19°C (Greater Wellington Regional Council, 2019). These temperatures are well within the tolerance of *U. pinnatifida* growing conditions and have remained relatively constant over time, so this is unlikely to be the cause of collapse (Silva et al. 2002; James & Shears, 2013). Pollution can also be ruled out as a potential factor. Castric-Fey et al (1999) and Cecere et al (2000) concluded that *U. pinnatifida* growth was not prevented by organic pollution after it was found to have colonized areas close to urban sewerage emissions in their studies. Additionally, in 2008, no difference in total inorganic nitrogen (TIN) and phosphate concentrations was detected between Owhiro Bay, Island Bay and Moa Point as well as multiple locations within Wellington Harbour (Morelissen, 2012). If nutrient levels did have a substantial impact on *U. pinnatifida* by 2018 than it is expected that these impacts would have been experienced throughout the rest of the south coast and may also be reflected in the native macroalgal populations. One observation worth further investigation was the large increase in abundance of *Ulva* spp. recorded in 2018. Increased *Ulva* spp. growth is often a sign of nutrient enrichment (e.g., Villares et al. 2001), but further research would be needed to confirm that this increase in *Ulva spp*. abundance is associated with a localised nutrient input, and that this nutrient input and/or increase in the *Ulva spp*. is related to the decline of *U. pinnatifida*. A deficit of nutrients is also an unlikely cause for collapse. The westward spread of *U. pinnatifida* along Wellington's south coast was into (along) a gradient of reducing nutrient and particulate concentrations (Helson & Gardner, 2004). It's possible that low nutrient concentrations may limit the spread of *U. pinnatifida* to the west, but this doesn't explain why it established by 2008 at Owhiro Bay and then died back by 2018.

Pathogens, parasitism and disease have also been accredited to the collapse of several terrestrial invaders (Simberloff & Gibbons, 2004; Lester & Grube, 2016). In its native range *U. pinnatifida* is susceptible to outbreaks of 'shot hole' and 'green spot' disease which cause decay of the thallus and fronds (Tsukidate, 1991; Vairappan et al. 2001; Neill et al. 2008). Review of literature in 2018 revealed no record of any disease, pathogen or parasite being found *on U. pinnatifida* in New Zealand waters (Neill et al. 2008). It is possible that a previously undiscovered disease/parasite led to the collapse of *U. pinnatifida* at the invasion front. However, if this was the case then it expected that evidence of this disease/parasite would be present in other locations along the south coast and Wellington Harbour. *U. pinnatifida* was not inspected for disease/parasitism in this study so further investigation is needed to confirm this claim.

Ultimately the cause of the collapse of *U. pinnatifida* at the invasion front on Wellington's south coast as with many other invasive species, is uncertain (Simberloff & Gibbons, 2004). Perhaps a localised

disturbance event such as severe storm reduced *U. pinnatifida* abundances below population viability (e.g., a density-dependent affect that negatively impacted reproductive success) at the leading edge of this invasion front, whereas the older more establish populations further east had high enough densities to quickly re-establish. It may also be possible that *U. pinnatifida* across the entire south coast and into Wellington Harbour are in the process of declining and what we are observing is the smaller more vulnerable populations at the leading edge collapsing first. Alternatively, this collapse could just be part of a natural process that is unique to *U. pinnatifida* on Wellington's south coast and has arisen due to a multitude of confounding factors (e.g., Simberloff & Gibbons, 2004). To fully understand the underlying mechanisms responsible for this collapse as well as to predict the future occurrence of *U. pinnatifida* on Wellington's south coast further investigation is needed. Recording the distribution and abundance of *U. pinnatifida* in additional locations along the south coast and in Wellington Harbour and repeatedly measuring them over time is suggested.

Conclusion

This study investigated the distribution and spread of *U. pinnatifida* on Wellington's south coast. Results of intertidal surveys revealed a gradual increase in *U. pinnatifida* abundance over time until 2008, followed by a complete disappearance from all study sites in 2018. This finding rejects the original hypothesis that *U. pinnatifida* abundance would have increased by 2018 and its distribution had advanced further westward along the south coast. The cause of the *U. pinnatifida* collapse is not known for certain. However, it was unlikely a result of biotic resistance in the form competition or herbivory, as well as pollution or changes in temperature. An additional aim of this study was to examine the temporal and spatial variation of native intertidal macroalgal communities and subtidal invertebrate grazers. Macroalgal and grazer composition was found to have varied significantly amongst the four study sites and across time. Notably, *Ulva* spp. had increased substantially by 2018 whereas overall grazer abundance had greatly decreased by 2018. These results partially support the second hypothesis that macroalgal and invertebrate community composition would remain unchanged over time, however, would vary between sites. Additionally, *U. pinnatifida* was revealed to have no influence on native macroalgal and grazer composition.

5.1. Monitoring, management and future research

Monitoring is a vital component of the management of invasive species. The acquisition of data related to a newly established invasive species' distribution, physiology and impacts provides a baseline for management programmes (Blossey, 1999; Epstein & Smale, 2017). It is important to understand how changes in species abundance influence ecosystem processes which, in turn, will help guide management decisions (Blossey, 1999). However, this can only be achieved through precise monitoring and research. Long term monitoring is particularly useful as it can provide valuable ecological information which would otherwise go unnoticed. This study reports a localised collapse of *U. pinnatifida* on Wellington's south coast. It is the first recorded collapse of the leading invasive edge of this species in the world. If not for repeated measuring in 2018 and the continuation of earlier monitoring reports than this phenomenon would have been missed (Gitzen et al. 2012).

This study provides a novel and exciting outlook on *U. pinnatifida* distribution and invasion ecology. If collapses such as the one observed in this study became common, then a potential management decision could be a 'do-nothing' option (Simberloff & Gibbons, 2004). However, this approach should not be undertaken without further investigation. In the meantime, events like these should be considered as a viable outcome when formulating management regimes for *U. pinnatifida* and thus

be tailored accordingly. *U. pinnatifida* is renowned for its global distribution however rates of regional expansion and its recorded effects on native ecosystems have been highly variable (Forrest et al. 2000; Forrest et al. 2008; Epstein & Smale, 2017; South et al. 2017). This study supports this knowledge and confirms that *U. pinnatifida* invasion dynamics is heavily influenced by ecological and anthropogenic processes.

Additionally, this thesis contributes a better understanding on the status of intertidal macroalgal communities and subtidal grazers in the Wellington region of New Zealand. The Taputeranga Marine Reserve encompasses a large area of the south coast including the study sites used in this thesis. The decrease in grazer's recorded in 2018 is concerning and points to a wider cause (e.g. habitat destruction, climate change etc.). The outcome of this knowledge could assist in future decision making and management of protected areas.

Recommendations for future research would be the addition of more survey sites along Wellington's south coast and Wellington Harbour. This would provide a more in-depth understanding of how *U. pinnatifida* populations vary spatially in the Wellington region as well as determine if the invasion front is continuing to recede. Another opportunity for further research would be to investigate the possibility that disease/parasitism was responsible for the *U. pinnatifida* collapse. Finally, further investigation of the dynamics influencing the south coast (e.g. water flow, nutrient levels) may help in explaining the lag, boom, bust pattern observed for *U. pinnatifida* in this study.

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Appendix

Appendix 1. Intertidal macroalgal species and species groups list.

Species/Groups	Division
Bare substrate	
Leathesia marina	Phaeophyta
Hormosira banksii	Phaeophyta
Cystophora spp.	Phaeophyta
Zonaria spp.	Phaeophyta
Carpophyllum spp.	Phaeophyta
Halopteris spp.	Phaeophyta
Ralfsia verrucose	Phaeophyta
Dictyota kunthii	Phaeophyta
Lessonia variegata	Phaeophyta
Xiphophora gladiata	Phaeophyta
Ecklonia radiata	Phaeophyta
Undaria pinnatifida	Phaeophyta
Desmarestia ligulate	Phaeophyta
Splachnidium rugosum	Phaeophyta
Papenfussiella lutea	Phaeophyta
Adenocystis utricularis	Phaeophyta
Microzonia velutina	Phaeophyta
Spatoglossum chapmanii	Phaeophyta
Ulva spp.	Chlorophyta
Ulva compressa	Chlorophyta
Caulerpa brownie	Chlorophyta
Caulerpa geminate	Chlorophyta
Codium convolutum	Chlorophyta
Chaetomorpha coliformis	Chlorophyta
Cladophora spp.	Chlorophyta
Gigartina spp.	Rhodophyta
Champia novae-zelandiae	Rhodophyta
Corallina spp.	Rhodophyta
Lithothamnion spp.	Rhodophyta
Short tufting reds	Rhodophyta
Pachymenia lusoria	Rhodophyta

Appendix 2. Two-way SIMPER results showing the contribution of species to dissimilarities between sites and times. Species contribution cut off – 90%.

Site Island Bay 1 versus Island Bay 2
Average dissimilarity = 61.44%

	Island Bay 1	Island Bay 2				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corallina spp.	3.50	6.40	9.36	1.49	15.24	15.24
Cystophora spp.	2.94	1.42	7.70	1.08	12.54	27.77
Ulva spp.	2.47	2.02	6.01	0.91	9.79	37.56
Carpophyllum spp.	2.29	0.82	5.59	1.05	9.10	46.66
Bare substrate	1.93	2.30	5.28	1.18	8.60	55.26
lithothamnion spp.	2.15	1.48	4.63	1.29	7.54	62.80
Champia novae-zelandiae	1.54	0.23	3.95	0.77	6.44	69.23
Hormosira banksii	1.56	0.69	3.62	1.00	5.90	75.13
Short tufting reds	1.17	0.91	3.50	0.84	5.69	80.82
Leathesia marina	0.65	1.22	3.08	0.95	5.00	85.83
Zonaria spp.	0.89	0.13	2.58	0.61	4.19	90.02

Site Island Bay 1 versus Owhiro Bay 1
Average dissimilarity = 64.02%

	Island Bay 1	Owhiro Bay 1				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Cystophora spp.	2.94	3.57	8.20	1.25	12.81	12.81
Bare substrate	1.93	3.24	7.32	1.08	11.43	24.24
Corallina spp.	3.50	1.84	6.6	1.28	10.32	34.56
Zonaria spp.	0.89	2.49	6.42	0.97	10.03	44.58
Ulva spp.	2.47	1.87	5.82	0.95	9.09	53.67
Carpophyllum spp.	2.29	0.91	5.46	1.07	8.53	62.20
lithothamnion spp.	2.15	2.30	4.53	1.37	7.08	69.29
Champia novae-zelandiae	1.54	0.38	3.82	0.78	5.97	75.25
Short tufting reds	1.17	0.97	3.41	0.81	5.33	80.58
Hormosira banksii	1.56	0.46	3.40	0.98	5.31	85.89
Gigartina spp.	0.37	0.62	2.18	0.57	3.41	89.30
Ralfsia verrucosa	0.82	0.43	2.08	0.67	3.25	92.56

Site Island Bay 2 versus Owhiro Bay 1
Average dissimilarity = 70.19%

	Island Bay 2	Owhiro Bay 1				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corallina spp.	6.40	1.84	14.39	1.69	20.50	20.50
Cystophora spp.	1.42	3.57	9.71	1.17	13.83	34.33
Bare substrate	2.30	3.24	8.70	1.10	12.39	46.73
Zonaria spp.	0.13	2.49	7.02	0.84	10.01	56.74
Ulva spp.	2.02	1.87	6.30	0.86	8.97	65.71
lithothamnion spp.	1.48	2.30	5.48	1.30	7.81	73.51
Carpophyllum spp.	0.82	0.91	3.66	0.75	5.21	78.72
Short tufting reds	0.91	0.97	3.39	0.74	4.82	83.55
Leathesia marina	1.22	0.51	3.18	0.88	4.53	88.08

Gigartina spp.	0.26	0.62	2.23	0.51	3.17	91.25

Site Island Bay 1 versus Owhiro Bay 2
Average dissimilarity = 64.44%

	Island Bay 1	Owhiro Bay 2				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Bare substrate	1.93	3.32	7.76	0.96	12.04	12.04
Cystophora spp.	2.94	1.64	6.90	1.10	10.71	22.75
Corallina spp.	3.50	2.13	6.75	1.28	10.48	33.23
Zonaria spp.	0.89	2.80	6.56	1.01	10.18	43.41
Ulva spp.	2.47	2.10	5.56	0.93	8.62	52.04
Carpophyllum spp.	2.29	0.83	5.24	1.05	8.13	60.17
Champia novae-zelandiae	1.54	1.41	5.19	0.87	8.05	68.21
lithothamnion spp.	2.15	2.27	4.15	1.26	6.44	74.66
Hormosira banksii	1.56	0.36	3.47	0.96	5.38	80.04
Short tufting reds	1.17	0.88	3.31	0.81	5.13	85.17
Ralfsia verrucosa	0.82	0.73	2.28	0.72	3.54	88.71
Leathesia marina	0.65	0.32	1.96	0.79	3.04	91.75

Site Island Bay 2 versus Owhiro Bay 2
Average dissimilarity = 69.12%

	Island Bay 2	Owhiro Bay 2				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corallina spp.	6.40	2.13	13.8	1.56	19.97	19.97
Bare substrate	2.30	3.32	9.18	0.97	13.28	33.25
Zonaria spp.	0.13	2.80	7.13	0.89	10.32	43.57
Cystophora spp.	1.42	1.64	6.08	0.99	8.80	52.37
Ulva spp.	2.02	2.10	5.92	0.83	8.57	60.94
lithothamnion spp.	1.48	2.27	5.27	1.28	7.62	68.56
Champia novae-zelandiae	0.23	1.41	3.81	0.55	5.51	74.07
Short tufting reds	0.91	0.88	3.25	0.74	4.70	78.77
Leathesia marina	1.22	0.32	3.10	0.85	4.49	83.26
Carpophyllum spp.	0.82	0.83	3.03	0.75	4.39	87.65
Hormosira banksii	0.69	0.36	1.83	0.58	2.65	90.3

Site Island Bay 1 versus Owhiro Bay 2
Average dissimilarity = 63.97%

	Island Bay 1	Owhiro Bay 2				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Bare substrate	3.24	3.32	10.05	1.08	15.71	15.71
Cystophora spp.	3.57	1.64	8.64	1.17	13.51	29.21
Zonaria spp.	2.49	2.80	8.42	1.10	13.16	42.37
Ulva spp.	1.87	2.10	5.79	0.88	9.06	51.43
Corallina spp.	1.84	2.13	5.55	1.20	8.68	60.11
lithothamnion spp.	2.30	2.27	5.08	1.32	7.94	68.05
Champia novae-zelandiae	0.38	1.41	3.66	0.56	5.72	73.77
Carpophyllum spp.	0.91	0.83	3.38	0.78	5.28	79.06

Short tufting reds	0.97	0.88	3.06	0.69	4.78	83.84
Gigartina spp.	0.62	0.41	2.68	0.56	4.19	88.03
Dictyota kunthii	0.06	0.58	1.67	0.42	2.62	90.60

Time 1997-2000 versus 2008
Average dissimilarity = 61.34%

	1997-2000	2008				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corallina spp.	4.73	2.76	7.69	1.42	12.55	12.55
Leathesia marina	0.84	2.51	6.36	1.11	10.37	22.92
Cystophora spp.	2.33	1.88	5.81	0.95	9.47	32.39
Ulva spp.	1.57	1.84	5.56	1.06	9.07	41.46
Bare substrate	2.38	2.35	5.47	1.09	8.92	50.38
Carpophyllum spp.	1.24	1.81	4.57	0.94	7.45	57.83
Short tufting reds	0.85	1.47	4.27	0.90	6.96	64.79
lithothamnion spp.	2.19	1.29	4.19	1.17	6.83	71.62
Hormosira banksii	0.65	1.25	3.58	0.76	5.84	77.47
Champia novae-zelandiae	0.73	1.73	3.36	0.68	5.48	82.95
Undaria pinnatifida	0.11	1.29	3.26	0.67	5.31	88.26
Zonaria spp.	1.13	0.62	2.01	0.50	3.29	91.55

Time 1997-2000 versus 2018
Average dissimilarity = 60.50%

	1997-2000	2018				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Ulva spp.	1.57	4.27	9.79	1.30	16.19	16.19
Corallina spp.	4.73	3.21	7.91	1.27	13.07	29.26
Cystophora spp.	2.33	2.25	6.81	1.01	11.26	40.52
Bare substrate	2.38	2.85	6.36	1.15	10.51	51.02
lithothamnion spp.	2.19	1.04	4.57	1.19	7.56	58.59
Hormosira banksii	0.65	1.52	4.01	1.06	6.62	65.21
Carpophyllum spp.	1.24	1.13	3.99	0.81	6.60	71.81
Short tufting reds	0.85	1.35	3.83	0.88	6.33	78.14
Leathesia marina	0.84	0.27	2.57	0.80	4.25	82.38
Zonaria spp.	1.13	0.92	2.15	0.51	3.55	85.93
Champia novae-zelandiae	0.73	0.47	1.98	0.50	3.28	89.21
Gigartina spp.	0.38	0.42	1.70	0.56	2.81	92.02

Time 2008 versus 2018
Average dissimilarity = 62.74%

	2008	2018				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Ulva spp.	1.84	4.27	8.20	1.36	13.08	13.08
Leathesia marina	2.51	0.27	6.67	1.13	10.63	23.71
Corallina spp.	2.76	3.21	5.97	1.24	9.52	33.23
Cystophora spp.	1.88	2.25	5.90	1.00	9.41	42.64
Bare substrate	2.35	2.85	5.37	1.20	8.57	51.20

Carpophyllum spp.	1.81	1.13	4.56	0.91	7.27	58.47
Short tufting reds	1.47	1.35	4.51	0.99	7.19	65.66
Hormosira banksii	1.25	1.52	4.26	1.00	6.78	72.44
Champia novae-zelandiae	1.73	0.47	3.61	0.72	5.75	78.19
Undaria pinnatifida	1.29	0.00	3.00	0.65	4.79	82.98
lithothamnion spp.	1.29	1.04	2.68	1.01	4.27	87.25
Ralfsia verrucosa	0.58	0.69	1.68	0.70	2.67	89.92
Zonaria spp.	0.62	0.92	1.49	0.46	2.38	92.3

Appendix 3. One-way SIMPER results showing the contribution of algal species to dissimilarities between seasons. Species contribution cut off – 90%.

Season Spring versus Summer
Average dissimilarity = 64.46%

	Spring	Summer				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corallina spp.	3.89	4.50	9.04	1.24	14.03	14.03
Ulva spp.	1.86	2.92	7.67	1.07	11.90	25.93
Cystophora spp.	2.43	2.11	7.16	1.05	11.11	37.04
Bare substrate	2.27	2.23	6.69	0.98	10.38	47.42
Carpophyllum spp.	1.49	1.21	4.68	0.91	7.27	54.69
lithothamnion spp.	1.91	1.66	4.51	1.25	6.99	61.68
Zonaria spp.	1.10	0.92	3.99	0.68	6.18	67.86
Champia novae-zelandiae	1.04	0.82	3.54	0.68	5.50	73.36
Short tufting reds	1.25	0.63	3.51	0.85	5.44	78.80
Leathesia marina	1.08	0.93	3.39	0.92	5.27	84.07
Hormosira banksii	0.74	0.68	2.59	0.78	4.02	88.08
Gigartina spp.	0.49	0.39	1.85	0.51	2.87	90.96

Season Spring versus Autumn
Average dissimilarity = 63.60%

	Spring	Autumn				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corallina spp.	3.89	4.73	9.20	1.26	14.46	14.46
Cystophora spp.	2.43	2.00	7.22	1.02	11.35	25.81
Bare substrate	2.27	2.96	7.08	1.08	11.13	36.94
Ulva spp.	1.86	1.97	6.55	0.95	10.30	47.24
lithothamnion spp.	1.91	2.17	4.76	1.29	7.48	54.72
Carpophyllum spp.	1.49	0.90	4.30	0.88	6.77	61.49
Zonaria spp.	1.10	1.05	4.30	0.69	6.77	68.26
Short tufting reds	1.25	0.73	3.75	0.84	5.89	74.15
Leathesia marina	1.08	0.60	3.20	0.81	5.03	79.18
Champia novae-zelandiae	1.04	0.54	3.20	0.62	5.03	84.20
Hormosira banksii	0.74	1.02	3.17	0.83	4.99	89.19
Ralfsia verrucosa	0.47	0.40	1.70	0.58	2.68	91.87

Season Summer versus Autumn
Average dissimilarity = 62.31%

	Summer	Autumn				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corallina spp.	4.50	4.73	9.41	1.24	15.1	15.10
Ulva spp.	2.92	1.97	8.09	1.06	12.99	28.10
Bare substrate	2.23	2.96	7.42	1.07	11.91	40.01
Cystophora spp.	2.11	2.00	6.97	0.99	11.18	51.19
lithothamnion spp.	1.66	2.17	4.98	1.25	8.00	59.19
Zonaria spp.	0.92	1.05	4.03	0.66	6.46	65.65
Carpophyllum spp.	1.21	0.90	3.95	0.82	6.33	71.98
Hormosira banksii	0.68	1.02	3.16	0.84	5.07	77.06
Leathesia marina	0.93	0.60	2.92	0.85	4.69	81.75
Champia novae-zelandiae	0.82	0.54	2.76	0.58	4.43	86.18
Short tufting reds	0.63	0.73	2.70	0.72	4.33	90.51

Season Spring versus Winter
Average dissimilarity = 63.98%

	Spring	Winter				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corallina spp.	3.89	4.32	8.63	1.26	13.49	13.49
Cystophora spp.	2.43	2.70	7.60	1.10	11.88	25.37
Ulva spp.	1.86	2.08	6.57	0.98	10.26	35.63
Bare substrate	2.27	2.44	6.42	1.06	10.04	45.67
Carpophyllum spp.	1.49	1.35	4.88	0.93	7.63	53.30
lithothamnion spp.	1.91	1.69	4.77	1.22	7.46	60.76
Short tufting reds	1.25	1.31	4.44	0.93	6.94	67.70
Zonaria spp.	1.10	1.12	4.41	0.69	6.90	74.59
Hormosira banksii	0.74	1.21	3.39	0.94	5.29	79.88
Leathesia marina	1.08	0.41	2.94	0.78	4.60	84.49
Champia novae-zelandiae	1.04	0.15	2.63	0.53	4.11	88.60
Ralfsia verrucosa	0.47	0.60	2.00	0.67	3.13	91.73

Season Summer versus Winter
Average dissimilarity = 63.24%

	Summer	Winter				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corallina spp.	4.50	4.32	8.95	1.24	14.15	14.15
Ulva spp.	2.92	2.08	8.07	1.08	12.76	26.91
Cystophora spp.	2.11	2.70	7.55	1.08	11.94	38.85
Bare substrate	2.23	2.44	6.72	1.04	10.63	49.47
lithothamnion spp.	1.66	1.69	4.83	1.14	7.63	57.11
Carpophyllum spp.	1.21	1.35	4.65	0.87	7.35	64.46
Zonaria spp.	0.92	1.12	4.15	0.67	6.57	71.03
Short tufting reds	0.63	1.31	3.76	0.82	5.94	76.97
Hormosira banksii	0.68	1.21	3.38	0.95	5.35	82.31
Leathesia marina	0.93	0.41	2.65	0.85	4.19	86.50

Champia novae-zelandiae	0.82	0.15	2.12	0.48	3.35	89.85
Ralfsia verrucosa	0.32	0.60	1.78	0.65	2.82	92.67

Season Autumn versus Winter
Average dissimilarity = 61.59%

	Autumn	Winter				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Corallina spp.	4.73	4.32	9.06	1.27	14.72	14.72
Cystophora spp.	2.00	2.70	7.63	1.05	12.40	27.11
Ulva spp.	1.97	2.08	7.00	0.97	11.37	38.48
Bare substrate	2.96	2.44	6.97	1.11	11.31	49.79
lithothamnion spp.	2.17	1.69	5.25	1.24	8.52	58.31
Zonaria spp.	1.05	1.12	4.47	0.68	7.27	65.57
Carpophyllum spp.	0.90	1.35	4.22	0.83	6.86	72.43
Short tufting reds	0.73	1.31	3.98	0.81	6.46	78.89
Hormosira banksii	1.02	1.21	3.81	0.98	6.19	85.09
Leathesia marina	0.60	0.41	2.12	0.65	3.44	88.52
Ralfsia verrucosa	0.40	0.60	1.97	0.64	3.20	91.73

Appendix 4. Two-way SIMPER results showing the contribution of grazers to dissimilarities between site and time. Grazer contribution cut off – 90%.

Site Island Bay 1 versus Island Bay 2
Average dissimilarity = 34.74%

	Island Bay 1	Island Bay 2				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lunella smaragdus	3.36	2.55	12.58	0.72	36.21	36.21
Haliotis iris	1.07	0.61	7.73	1.25	22.26	58.48
Scutus breviculus	1.31	0.72	6.24	0.90	17.97	76.45
Haliotis australis	0.81	0.51	4.97	0.95	14.31	90.76

Site Island Bay 1 versus Owhiro Bay 1
Average dissimilarity = 37.24%

	Island Bay 1	Owhiro Bay 1				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lunella smaragdus	3.36	1.43	20.79	0.84	55.84	55.84
Haliotis iris	1.07	0.95	6.55	1.12	17.59	73.43
Haliotis australis	0.81	1.28	4.75	0.88	12.75	86.18
Scutus breviculus	1.31	1.33	3.37	0.69	9.04	95.22

Site Island Bay 2 versus Owhiro Bay 1
Average dissimilarity = 47.73%

	Island Bay 2	Owhiro Bay 1				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lunella smaragdus	2.55	1.43	18.21	0.80	38.14	38.14

Haliotis iris	0.61	0.95	9.66	0.91	20.24	58.38
Scutus breviculus	0.72	1.33	7.77	0.95	16.28	74.67
Haliotis australis	0.51	1.28	7.48	0.94	15.68	90.35

Site Island Bay 1 versus Owhiro Bay 2
Average dissimilarity = 45.05%

	Island Bay 1	Owhiro Bay 2				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lunella smaragdus	3.36	2.02	14.53	0.82	32.25	32.25
Haliotis iris	1.07	1.39	12.64	1.35	28.05	60.31
Scutus breviculus	1.31	0.00	10.75	1.37	23.86	84.17
Haliotis australis	0.81	1.18	5.44	1.03	12.07	96.24

Site Island Bay 2 versus Owhiro Bay 2
Average dissimilarity = 44.10%

	Island Bay 2	Owhiro Bay 2				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Haliotis iris	0.61	1.39	17.11	0.90	38.80	38.80
Lunella smaragdus	2.55	2.02	9.52	0.90	21.58	60.38
Haliotis australis	0.51	1.18	8.76	1.11	19.86	80.24
Scutus breviculus	0.72	0.00	6.51	0.80	14.77	95.01

Site Owhiro Bay 1 versus Owhiro Bay 2
Average dissimilarity = 45.54%

	Owhiro Bay 1	Owhiro Bay 2				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Haliotis iris	0.95	1.39	16.04	0.77	35.21	35.21
Scutus breviculus	1.33	0.00	11.58	1.20	25.42	60.64
Lunella smaragdus	1.43	2.02	10.27	1.30	22.55	83.19
Haliotis australis	1.28	1.18	5.18	0.82	11.37	94.55

Time 1998-2000 versus 2018
Average dissimilarity = 56.15%

	1998-2000	2018				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Lunella smaragdus	2.97	1.79	16.23	1.12	28.91	28.91
Scutus breviculus	1.48	0.00	15.06	1.48	26.81	55.72
Haliotis australis	1.33	0.06	11.76	1.33	20.94	76.66
Haliotis iris	1.04	0.76	9.64	1.19	17.18	93.84

Appendix 5. Two-way SIMPER results showing the contribution of grazers to dissimilarities between site and season. Grazer contribution cut off – 90%.

Site Island Bay 1 versus Island Bay 2
Average dissimilarity = 40.15%

	Island Bay 1	Island Bay 2				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Turbo smaragdus	3.36	2.55	12.56	0.83	31.27	31.27
Scutus breviculus	1.31	0.72	9.12	1.04	22.72	53.99
Haliotis iris	1.07	0.61	8.86	1.30	22.07	76.07
Haliotis australis	0.81	0.51	6.23	0.98	15.51	91.58

Site Island Bay 1 versus Owhiro Bay 1
Average dissimilarity = 46.03%

	Island Bay 1	Owhiro Bay 1				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Turbo smaragdus	3.36	1.43	19.54	0.93	42.46	42.46
Haliotis australis	0.81	1.28	8.44	1.08	18.34	60.81
Scutus breviculus	1.31	1.33	8.15	0.91	17.72	78.52
Haliotis iris	1.07	0.95	7.23	1.45	15.71	94.24

Site Island Bay 2 versus Owhiro Bay 1
Average dissimilarity = 56.93

	Island Bay 2	Owhiro Bay 1				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Turbo smaragdus	2.55	1.43	20.99	1.05	36.86	36.86
Scutus breviculus	0.72	1.33	10.92	0.98	19.18	56.05
Haliotis australis	0.51	1.28	10.69	0.95	18.78	74.83
Haliotis iris	0.61	0.95	9.61	1.01	16.88	91.71

Site Island Bay 1 versus Owhiro Bay 2
Average dissimilarity = 44.48%

	Island Bay 1	Owhiro Bay 2				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Turbo smaragdus	3.36	2.02	14.62	0.93	32.87	32.87
Scutus breviculus	1.31	0.00	10.96	1.28	24.63	57.50
Haliotis iris	1.07	1.39	9.59	1.03	21.56	79.07
Haliotis australis	0.81	1.18	7.73	1.10	17.39	96.46

Site Island Bay 2 versus Owhiro Bay 2
Average dissimilarity = 49.32%

	Island Bay 2	Owhiro Bay 2				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Haliotis iris	0.61	1.39	15.74	1.07	31.91	31.91
Turbo smaragdus	2.55	2.02	13.77	1.01	27.93	59.84
Haliotis australis	0.51	1.18	10.78	1.17	21.86	81.70
Scutus breviculus	0.72	0.00	6.74	0.77	13.66	95.36

Site Owhiro Bay 1 versus Owhiro Bay 2
Average dissimilarity = 53.36%

	Owhiro Bay 1	Owhiro Bay 2				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Haliotis iris	0.95	1.39	15.75	1.07	29.53	29.53
Turbo smaragdus	1.43	2.02	14.81	1.58	27.75	57.27
Scutus breviculus	1.33	0.00	11.84	1.13	22.18	79.46
Haliotis australis	1.28	1.18	8.47	0.94	15.87	95.33

Season Winter versus Summer
Average dissimilarity = 37.72%

	Winter	Summer				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Scutus breviculus	0.97	1.57	9.74	1.07	25.83	25.83
Haliotis australis	0.90	1.37	8.69	1.28	23.04	48.87
Turbo smaragdus	2.64	2.87	8.57	0.78	22.73	71.60
Haliotis iris	0.98	0.89	8.06	1.22	21.37	92.97

Season Winter versus Autumn
Average dissimilarity = 38.01%

	Winter	Autumn				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Turbo smaragdus	2.64	2.46	10.56	0.90	27.78	27.78
Scutus breviculus	0.97	0.68	8.89	0.89	23.39	51.16
Haliotis iris	0.98	1.05	7.99	1.03	21.02	72.18
Haliotis australis	0.90	0.70	7.25	0.94	19.08	91.26

Season Summer versus Autumn
Average dissimilarity = 36.99%

	Summer	Autumn				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Scutus breviculus	1.57	0.68	9.48	1.08	25.64	25.64
Haliotis australis	1.37	0.70	9.40	1.30	25.41	51.05
Haliotis iris	0.89	1.05	7.97	1.04	21.53	72.59
Turbo smaragdus	2.87	2.46	7.61	0.70	20.56	93.15

Season Winter versus Spring
Average dissimilarity = 50.77%

	Winter	Spring				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Turbo smaragdus	2.64	1.69	17.53	1.10	34.54	34.54
Haliotis iris	0.98	0.70	11.19	0.95	22.05	56.58
Scutus breviculus	0.97	0.00	9.75	0.83	19.21	75.79
Haliotis australis	0.90	0.00	7.87	0.75	15.50	91.29

Season Summer versus Spring
Average dissimilarity = 62.91%

	Summer	Spring				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Turbo smaragdus	2.87	1.69	17.88	1.28	28.41	28.41
Scutus breviculus	1.57	0.00	17.07	1.71	27.13	55.54
Haliotis australis	1.37	0.00	13.88	1.68	22.06	77.60
Haliotis iris	0.89	0.70	11.64	1.14	18.49	96.09

Season Autumn versus Spring
Average dissimilarity = 49.06%

	Autumn	Spring				
Species	Av.Abund	Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
Turbo smaragdus	2.46	1.69	18.19	1.30	37.08	37.08
Haliotis iris	1.05	0.70	12.50	1.02	25.49	62.57
Scutus breviculus	0.68	0.00	7.79	0.66	15.87	78.44
Haliotis australis	0.70	0.00	6.61	0.70	13.47	91.91