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Factors influencing the establishment and phenology of the invasive kelp *Undaria pinnatifida* in northern New Zealand

Kate James

A thesis submitted in fulfilment of the requirements for the degree of
Doctor of Philosophy in Marine Science
The University of Auckland, 2016
Abstract

Macroalgal invasions can change the structure and function of benthic habitat, dominating space, altering primary productivity, nutrient cycles, and community composition. This is a serious concern for receiving environments. A major determinant of the geographic distribution of macroalgal species is water temperature. Investigating the population ecology, genetic variation and factors controlling the density and spread of invasive macroalgae towards the extent of their thermal distribution limits can therefore provide important insights into the potential range and ecological impacts both now and with future climate change.

The kelp *Undaria pinnatifida* is a prolific and cosmopolitan invasive species. *Undaria* has invaded countries around the world across a variety of temperature regimes. *Undaria* displays a variable phenology at introduced locations; it is a winter annual in its native range, but sporophyte presence can vary from annual to year-round across its invasive range. Information is lacking on how *Undaria* phenology and impacts manifest under warm-temperate conditions. This work studies *Undaria* in northern New Zealand, one of the warmest-water populations in the world. I investigated how water temperature influenced the phenology and distribution of *Undaria*. In addition I examined some attributes of the invasion process for warm-water populations; I looked at the role mussel aquaculture plays in influencing the spread of *Undaria* to native habitats, how disturbance might facilitate the spread of *Undaria* to subtidal reefs, and the genetic composition of populations in northern New Zealand.

Monitoring over three growth seasons revealed how *Undaria* in northern New Zealand displayed an annual growth cycle. Recruitment occurred when temperatures dropped below ~15 °C and density was minimal at temperatures above 20 °C. Sporophyte size and growth rates were comparable to those of cooler water populations but the seasonal cycle was compressed into a shorter timeframe. *Undaria* was found to proliferate on mussel farms and low numbers were found on reefs adjacent to farms, in shallow habitats lacking native macroalgal canopies. *Undaria* was rare in deeper habitats dominated by native macroalgal canopies, experimental canopy removal did not facilitate the spread of *Undaria* into these habitats at the site examined. This suggests that native canopy-forming species are not the sole factor prohibiting the invasion of *Undaria* to subtidal reef sites in this region.

Genetic analysis of *Undaria* from all known populations in the North Island revealed very low genetic diversity in northern New Zealand. The presence of a single haplotype in northeastern New Zealand may indicate a particularly warm-tolerant strain and suggests thermal pre-adaptation may influence invasion success.

An investigation into the global distribution and associated phenology of *Undaria*, and how this related to water temperature regimes, demonstrated how *Undaria* only occurred where winter temperatures dropped below ~15 °C and that persistent year-round populations were only present at sites where summer temperatures did not exceed 20 °C. This analysis also revealed that there are extensive areas of the world where *Undaria* does not occur that have temperature regimes
suitable for *Undaria* colonisation. Such areas are potentially at risk from future invasion based on current temperature regimes. These thermal limits for *Undaria* indicate that populations in northern New Zealand are towards the limit of its distribution, with winter temperatures close to 15 °C, *Undaria* is unable to withstand warmer winter temperatures.

Ocean warming is likely to restrict the potential geographic distribution of *Undaria*, particularly where winter temperatures exceed 15 °C. Increases in summer temperatures, which prolong the period during the year when temperatures exceed 20 °C, will reduce the annual persistence of *Undaria*. A limited annual presence of sporophytes at warmer locations may reduce the ecological impacts of *Undaria* invasion as compared to cooler water locations where sporophytes persist for a longer portion of the year.
For Granny
Acknowledgements

I acknowledge and thank my supervisor Nick Shears, whose direction, advice, and interest in this research has been invaluable throughout the course of this project. I am grateful for the insights and knowledge you provided on marine systems as well as how to translate knowledge and research outcomes into research articles; thank-you for the many helpful comments across endless word documents and the ongoing feedback around my research and writing which has helped to shape this thesis. I also acknowledge and thank my co-supervisor Judy Sutherland for leading me through the laboratory component of this research, for being patient as I learnt about molecular biology procedures from laboratory work to software to interpreting results. Thank you for trusting me in your laboratory and for teaching me everything I needed to know for this part of my project. Thank you also to my co-supervisor Alwyn Rees for advice, guidance, and for reviewing my written work. Thank you to all three of my supervisors for believing my capabilities for research and for producing results would not be compromised by the arrival of my son during the early stages of this project.

This research would not have been possible without the skills and help from students and volunteers in the field, thank you so much to all the people who got the hands, feet and whole bodies wet and often freezing cold to find, measure, count and collect Undaria: Oriana Brine, Bhakti Patel, Igor Ruza, Blake Seers, Jenna James, Kathy Kenyon, Nathan White, Christine Kibele, Phil Ross, Caitlin Blain, Arie Spyksma, Nathania Brooke, Dave Culliford, Kirsten Rodgers, Jenni Stanley, Richard Hughes, Emily Duder, Lauren Jones, Paul Caiger, Edwin Ainley, Anna Berthelsen, Jarrod Walker, Irene Middleton, Crispin Middleton, Caroline Williams, Oliver Wade, and Jamie Quirk. Thank-you to Navdeep Bhatti, Vibhavari Thakur and Vanessa Arranz for help and advice in the laboratory. Thank-you to Brian Dobson for performing the water nutrient analysis and to Arthur Cozens and Brady Doak for facilitating this research.

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<td>Irene Middleton</td>
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Chapter 1

General Introduction

1.1 BIOLOGICAL INVASIONS

1.1.1 General background

An invasive species is one which has been introduced to an environment where it is non-native, or not naturally found, and whose establishment causes a threat to native species and ecosystems (International Union for the Conservation of Nature [IUCN] 2015). Invasive species can often establish and grow rapidly and as such may be able to outcompete or even exclude native species, causing changes in local biodiversity as well as altering ecosystem processes such as succession and nutrient cycling (Mack et al. 2000; Lockwood et al. 2007, 2013; Simberloff 2013). Invasion by introduced species is currently ranked as the second greatest threat to biodiversity on earth after habitat destruction (IUCN 2015). The spread and impacts from invasive species are often intertwined with the influence of anthropogenic stressors (Dukes and Mooney 1999); global environmental changes such as climate change will lead to different responses and interactions from invasive species which will have novel ecological implications (Hellmann et al. 2008).

In the marine environment, the threat to biodiversity by invasive species is increasing rapidly (Molnar et al. 2008; Olenin et al. 2011; Cecere et al. 2015). The number of incursions to new sites continues to increase with increased global trade and changes in trade patterns (Ruiz et al. 2000, Costello and Solow 2003, Hulme 2009). However, it is widely recognised that the impacts of marine invasive species remain poorly understood (Ruiz et al. 1999, Grosholz 2002, Molnar et al. 2008). This is in part due to the complexity of the invasion process for many marine invasive species. Successful invasive species commonly have large fundamental niches, are capable of surviving a wide range of biotic and abiotic conditions, and may even adapt to new habitats by altering their niche at invaded locations (Lockwood et al. 2007; Simberloff 2013; MacNeil and Campbell 2014). For example, an invasive species may occupy different climatic niche ranges at invaded locations as compared to the native range (Broennimann et al. 2007). Changes to a species’ niche can confound the prediction of range expansions, and exposure to different conditions in the receiving environment may also cause the growth, morphology, phenology and genetic composition of introduced populations to diverge from those displayed by native populations (Lockwood et al. 2007; Simberloff 2013). This can influence the extent of the impacts that invasive species have on the invaded community (Mack et al. 2000). For example the more favourable conditions a species is exposed to in its receiving environment the more rapidly it may
proliferate and spread, displacing native species and altering community composition and function.

Understanding the potential distribution and ecological effects of marine invasive species poses a unique and significant challenge for the management of marine ecosystems and resources. This challenge is further complicated by concurrent changes to marine ecosystems associated with additional anthropogenic stressors, such as pollution, and climate change. Once established the eradication of marine invasive species is generally impossible; current techniques available for use in the marine environment are extremely limited (Olenin et al. 2011; Forrest and Hopkins 2013) and vector management is also complicated and difficult to regulate (Williams et al. 2013). Ecosystems can only be protected from invasive species by preventing invasions in the first place and this requires well informed pre-emptive management strategies. Such strategies, which may allow early detection and management, require knowledge about the species physiology, its tolerances, growth and phenology, as well as interactions with the receiving environment (Canning-Clode et al. 2011; MacNeil and Campbell 2014).

1.1.2 Invasive macroalgae

Seaweeds, or macroalgae, make up a significant component of marine invasive species (Schaffelke et al. 2007), with over 300 species recorded as invasive (Davidson et al. 2015). The effects from introduced macroalgae are context-dependant and can vary across different environments and on different scales (Inderjit et al. 2006; Schaffelke et al. 2006, Williams and Smith 2007, Thomsen et al. 2009). Understanding impacts is complicated by interactions with receiving environments. For example, invasion by Caulerpa racemosa in the Mediterranean Sea has been facilitated through grazing by native fish (Tamburello et al. 2014), and the competitive ability of invasive Caulerpa cylindracea populations was increased at sites affected by nutrient enrichment (Bulleri and Piazzi 2015).

On a broader scale, water temperature is a key factor in determining the distribution, growth and phenology of all macroalgae (Lobban and Wynne 1981; Breeman 1988, 1990). Consequently, understanding how life history characteristics relate to water temperature is a crucial starting point in determining the potential distribution and impacts of invasive macroalgal species. In addition, interactions between invasive species and ocean warming are likely to change patterns of marine invasion (Sorte et al. 2010). In some cases the ability of invasive species to tolerate a broader thermal range than native species may give them an advantage over native species (Sutherst 2000; Stachowicz et al. 2002; Wernberg et al. 2010). Elevated temperatures have already resulted in range shifts or loss of native kelp canopy in some areas (Wernberg et al. 2011; Raybaud et al. 2013).
1.2 THE INVASIVE KELP UNDARIA PINNATIFIDA

1.2.1 Native range

The Asian kelp Undaria pinnatifida (Harvey) Suringar 1873 (hereafter ‘Undaria’) is native along the shores of the northwestern Pacific (Fig. 1.1): including the Japanese coast (Okamura 1926; Saito 1975; Akiyama and Kurogi 1982; Uwai et al. 2006), the northeastern coasts of Korea (Kang 1966), the neighbouring coasts of China (Tseng 1981; Zhang et al. 1984), and southeast Russia in Peter the Great Bay near Vladivostok and in the Okhotsk Sea (Funahashi 1973; Uwai et al. 2006; Verlaque 2007; Shibneva et al. 2013). In its native range Undaria is most commonly found to depths of ~4 m in the subtidal zone (Saito 1975; Yamada 1980). In clear water it can be found growing on reefs down to depths of 15 m (Akiyama and Kurogi 1982). In its native range water temperatures can range between ~0 - 27 °C (Akiyama and Kurogi 1982; Watanabe et al. 2014).

1.2.2 Morphology

Undaria is a golden to dark-brown, mucilaginous laminarian kelp (Fig. 1.2; Fig. 1.3). Wide morphological variation exists both between and within populations (Uwai et al. 2006; Dean and Hurd 2007). It typically grows to 1 - 2 m or less (Adams 1994). Very young juveniles (≤ 10 cm) lack a mid-rib, but maturing and mature individuals have a strap-like midrib (1 - 3 cm wide) along the full length of the thallus, (Hay 1990; Castric-Fey et al. 1999; Fig. 1.2). Edges of the midrib expand as thin membranous laminae. Laminae are undivided and lanceolated at first, later they become pinnately divided with pinnae about 2.5 - 4 cm wide (Adams 1994; Fig. 1.2). The blades are thin, mucilaginous and dotted with white cryptostomata and dark gland cells (National Introduced Marine Pest Information System [NIMPIS] 2011; Verlaque 2007). The sporophyte is fixed by a ramified holdfast with many thin root-like haptera (Adams 1994). As it grows, the naked basal section of the midrib forms the stipe. Once the sporophyte is mature, reproductive tissue called sporophylls develop laterally along the stipe. The two thickened ‘fluted’ or ‘frilled’ sporophylls, bend laterally around the stipe with the folds becoming interleaved (NIMPIS 2011; Fig.1.2).

1.2.3 Reproduction and phenology

Undaria is a winter annual; in its native range recruitment of the sporophyte occurs in autumn, the sporophyte grows rapidly through winter and spring, and senescence occurs in summer (Saito 1975; Lee and Sohn 1993; Oh and Koh 1996; Choi et al. 2007). The annual life cycle of Undaria is biphasic, consisting of a microscopic, haploid gametophyte phase and macroscopic, diploid sporophyte phase (Akiyama and Kurogi 1982; Verlaque 2007; Fig. 1.3).

As the Undaria sporophyte matures, reproductive sporophylls form at the base of the stipe (Castric-Fey et al. 1999; Choi et al. 2007) and sexual spores are produced in the sporophylls. Spore release then occurs progressively from the base of the sporophyll upwards (Schaffelke et al. 2005). Once the mature sporophyte has released all its spores, the sporophyte gradually degrades and dies (Sinner et al. 2000; NIMPIS 2011).
Mature sporophylls from a single sporophyte can release up to 700 million zoospores (Akiyama and Kurogi 1982; Schiel and Thompson 2012). These motile zoospores usually settle 1-6 hours after release, but can remain in the water column for two days and possibly remain viable in a state of quiescence for up to 14 days (Saito 1975; Forrest et al. 2000; Petrone et al. 2011). Once they have settled the zoospores secrete an adhesive and they can begin to germinate within three hours under suitable conditions (Petrone et al. 2011). The attached zoospores grow into microscopic dioecious gametophytes (Thornber et al. 2004) and a male or female gametophyte will develop within seven days of attachment in optimum conditions; the same level of growth takes closer to three weeks in less than optimum conditions; such as under heat stress (Hay and Luckens 1987; Zhang and Pang 2007; Morelisson et al. 2013). At this stage, if conditions are not suitable for gametophyte maturation and fertilisation, such as high temperatures or low light conditions, the gametophytes enter a dormancy phase (Thornber et al. 2004; Hewitt et al. 2005; Morelisson et al. 2013).

In its native range the gametophyte remains dormant over summer and, when seawater temperatures decrease, gametogenesis is initiated (Pang et al. 2008). Gametophytes then produce antherozoids (sperm) or eggs, and the egg is held in the female gametophyte until fertilised; approximately seven days after gametophyte maturation (Farrell 2003; Pang et al. 2008). After fertilisation, the zygotes develop into diploid sporophytes (Sinner et al. 2000; Fig. 1.3). The sporophyte develops at the same point of attachment as the female gametophyte (Bardach et al. 1972). Sporophytes can form 14 to 30 days after zoospores germinate (Akiyama 1965; Stuart 1997; Bite 2001), and can reach total lengths of about 1 cm in a month to 45 days (Hue et al. 1995; Wu et al. 2004). Sporophytes typically live for up to eight or nine months in their native range (Hay and Luckens 1987).

1.2.4 The influence of temperature on phenology

Overall, Undaria has a broad temperature tolerance. However, different life cycle stages have different temperature requirements (Floc’h et al. 1991). The duration of the life cycle and its components depends largely upon the local temperature regime (Hay and Luckens 1987; Floc’h et al. 1991). Within the native range the life cycle occurs over the course of a full year in coincidence with environmental cues; the sporophyte growth cycle aligns with cooler winter temperatures and senescence of the visible sporophyte occurs en masse as temperatures reach 24 – 27 °C (Akiyama and Kurogi 1982; NIMPIS 2011).

Undaria sporophytes have a broad temperature tolerance and the gametophyte has an exceptionally high temperature tolerance (Dieck 1993; Morita et al. 2003). This allows Undaria to colonise sites with a range of temperature regimes. Some introduced populations of Undaria do not adhere to a strictly winter annual life cycle, with multiple cohorts of sporophytes recruiting annually (Hay and Luckens 1987; Floc’h et al. 1991; Hay and Villouta 1993; Brown 1999; Fletcher and Farrell 1999; Casas et al. 2008; Martin and Bastida 2008; Zabin et al. 2009). It has been hypothesised that annual temperatures which remain between ~15 and 19 °C allow
gametogenesis to occur throughout the year, resulting in an extended presence of sporophytes (Hay and Villouta 1993; Stuart 2004; Thornber et al. 2004; Schaffelke et al. 2005).

Literature values for Undaria temperature tolerances are highly variable. For example, the optimum temperature range for sporophyte growth is reported from 5 - 10 °C to 15 - 20 °C, and optimum ranges for gametophyte growth could be 15 - 20 °C or 23 - 28 °C (Floc’h et al. 1991 and references therein). Understanding temperature tolerances helps predict the potential invasive range, because differences in the annual recruitment patterns and the year-round presence of Undaria occur between introduced sites with different temperature regimes (Hay and Luckens 1987; Floc’h et al. 1991; Hay and Villouta 1993; Brown 1999; Fletcher and Farrell 1999; Casas et al. 2008; Martin and Bastida 2008; Zabin et al. 2009).

1.2.5 Invasive attributes
Undaria is a high-profile marine invader; it is currently regarded as one of the worst invasive species in the world (Lowe et al. 2004). Undaria possesses traits common to highly successful invasive species (Lockwood et al. 2007). Undaria grows rapidly (Hewitt et al. 2005; Schiel and Thompson 2012) and is highly fecund (Forrest et al. 2000), it can colonise a wide variety of natural and artificial substrates (Fletcher and Manfredi 1995; Torres et al. 2004; Russell et al. 2008), and has a broad temperature tolerance (Nyberg and Wallentinus 2005). Undaria is genetically diverse with more than 30 different strains identified from its native range (Uwai et al. 2006). It is easily spread and transported (Hay and Luckens, 1987; Hunt et al. 2009) and has a cryptic (microscopic) phase which is difficult to control or kill (Thornber et al. 2004).

1.2.6 Factors that influence invasion
Undaria invasion has been linked with a range of factors including disturbance, eutrophication and other anthropogenic activities such as fishing, aquaculture and coastal development. For example, Undaria thrives on artificial structures and in areas enriched with nitrogen and phosphorous, and therefore grows prolifically in modified harbours and at sites affected by eutrophication (Campbell et al. 1999; Castic-Fey et al. 1999; Curiel et al. 2001; Torres et al. 2004; Sfrisco and Facca 2013). Native macroalgal canopy clearance or disturbance in the form of experimental canopy removal or natural canopy die-back has been shown to facilitate Undaria invasion and recruitment at some sites (Valentine and Johnson 2003, 2004; Edgar et al. 2004; Schiel and Thompson 2012; Thompson and Schiel 2012; Carnell and Keough 2014). At some benthic sites which are chronically (physically) disturbed, such as urchin barrens, the persistence of Undaria can potentially be facilitated by increased levels of sediment deposition (Valentine and Johnson 2005; Valentine et al. 2007).

The introduction of Undaria to new locations is largely dependent on human-mediated vectors of introduction. Transoceanic invasion pathways are primarily via hull fouling on large-scale, commercial fishing vessels (Hay and Luckens 1987; Voisin et al. 2005; Uwai et al. 2006). Domestic spread also occurs via hull fouling, on both recreational and commercial vessels (Hay
1990; Floerl et al. 2005; Forrest and Hopkins 2013), as well as via the movement of aquaculture equipment, stock and vessels (Hay 1990; Perez et al. 1988; Fletcher and Farrell 1999; Voisin 2005; Russell et al. 2008; Hunt et al. 2009; Forrest and Hopkins 2013; Table 1.1).

1.2.7 Current invasive range

*Undaria* has invaded warm and cool temperate marine environments in at least fourteen countries around the world (Fig. 1.1). Table 1.1 summarises introductions to countries outside its native range since 1971.

1.3 ECOLOGICAL EFFECTS OF *UNDARIA* INVASION

In general, the ecological effects and impacts from *Undaria* invasion remain poorly understood and in some cases contradictory. *Undaria* is capable of altering natural habitats and changing community composition under some circumstances (Valentine and Johnson 2003; Edgar et al. 2004; Irigoyen 2011a; Carnell and Keough 2014) and there is a perception that *Undaria* poses a high to extreme risk to environmental values, including biodiversity, and habitat and trophic interaction, through the displacement of native species and detrimental effects on community and ecosystem function (Campbell and Hewitt 2013; McLaughlan et al. 2014). However, there remains limited quantitative information from empirical or manipulative experiments to verify ecological impacts.

*Undaria* has a limited ability to outcompete established native canopy-forming species where light and space are limiting factors (Hay and Luckens 1987; Hay and Villouta 1993; Castric-Fey et al. 1993; Brown and Lamare 1994; Casas and Piriz 1996; Floc'h et al. 1996; Hay and Sanderson 1997; Forrest and Taylor 2002; Valentine and Johnson 2005; Raffo et al. 2009; Grulois et al. 2011; Thompson and Schiel 2012; South et al. 2015), but it may be able to shade out smaller understory algal species (Curiel et al. 2001; Sanderson and Barret 1989; Silva et al. 2002; Casas et al. 2004; Russell et al. 2008; Hunt et al. 2009), albeit sometimes on a transient basis where *Undaria* has an annual life cycle (South et al. 2015).

The invasion of sites previously devoid of macroalgae changes habitat architecture, and can therefore affect water movement, sediment accumulation, light penetration, nutrient dynamics and community composition (Wallentinus and Nyberg 2007; Russell et al. 2008; South et al. 2015). Quantitative data on how *Undaria* infestation affects these environmental conditions are absent from the literature, it is likely however that *Undaria* modifies the environment in the same way as other canopy-forming macroalgal species; by reducing current velocities, causing an increase in sedimentation and reducing turbidity (Kennelly 1989; Madsen et al. 2001). In addition, the presence of a kelp canopy acts to exclude or facilitate particular species, for example *Ecklonia radiata* (C. Agardh) J. Agardh can exclude sessile invertebrate species and promote the growth of encrusting coralline algae (Connell 2003). Understory assemblages are site-specific and differ among canopies of different types (Irving et al. 2004), so knowing what species *Undaria* may
exclude or facilitate requires further research. Information is also lacking on how Undaria may directly affect benthic species on which it colonises such as oyster beds (Sfriso and Facca 2013).

Epibiotic assemblages found in association with Undaria are different and less diverse in comparison to those found on native macroalgae (Raffo et al. 2009; Arnold et al. 2015; Jiménez et al. 2016) and Undaria invasion can also change native macrofaunal presence and composition (Floc'h et al. 1991; Castric-Fey et al. 1993; Baker 2011; Thornber et al. 2004; Irigoyen et al. 2011a; Hooton-Kaufman 2012; Atalah et al. 2013; Jiménez 2016).

Undaria invasion contributes nitrogen-rich material to the ecosystem, potentially in much larger amounts compared to native perennial species (Yoshikawa et al. 2001; Tait et al. 2015). Large Undaria populations can therefore impact on local nutrient cycling as increased nutrient levels are incorporated into the food chain (Yoshikawa et al. 2001; Sfriso and Facca 2013; South et al. 2015). How such changes in primary productivity modify community composition and alter the direction and magnitude of trophic interactions and species distributions remains unknown (Taylor and Schiel 2010; Irigoyen et al. 2011a; Thomsen et al. 2014; South et al. 2015; Jiménez et al. 2016).

1.4 COMMERCIAL VALUE OF UNDARIA

Undaria is one of the world’s most valuable seaweeds. In eastern Asia it is a popular and commercially valuable sea vegetable known as Wakame (Bardach et al. 1972; Akiyama and Kurogi 1982). It has been grown commercially in Japan since about 1940 and in China and Korea since the 1950s (Yamanaka and Akiyama 1993). Undaria is harvested from natural habitats and cultivated commercially, i.e. grown on ropes (Akiyama and Kurogi 1982). Undaria has also been grown commercially in France since 1983 (Hay 1990). Harvest production in recent years has been between 450,000 and 500,000 tons in Japan and Korea, with a few hundred tonnes being produced annually in China. Commercial hybrids with higher growth and nutritional characteristics have been developed in Japan (Food and Agriculture Organization of the United Nations [FAO] 2011). Recently Undaria has also gained popularity in Europe as a nutritional supplement and weight loss aid (Peteiro and Freire 2012). Research is now expanding rapidly into the potential medicinal and anti-cancer properties of Undaria (Hosokawa et al. 2004; Yang et al. 2008). In its native range Undaria suffers from a range of diseases caused by fungi and parasitic copepods which affect the quality of the end product whereas introduced populations can be free of these infections and hence may be more economically viable as crops (Neill et al. 2008).

In 2011 the Ministry of Agriculture and Forestry – Biosecurity New Zealand [MAF], predecessor to the Ministry for Primary Industries, released policy allowing for the farming and harvesting of Undaria in selected “heavily infested” areas around Wellington Harbour, Marlborough Sounds and Lyttelton Harbour (MAF 2011). To date Undaria is not commercially farmed in New Zealand, but it is harvested from mussel farm structures in southern New Zealand and sold commercially for human consumption and for use in fertiliser products (A. Pressman pers comm). Although Undaria remains an Unwanted Organism under the New Zealand Biosecurity Act 1993, there
exists the potential for Undaria to form the basis of a highly valuable aquaculture industry in New Zealand (MAF 2011). However, for Undaria aquaculture to be a sustainable and ecologically-sound enterprise in New Zealand, more information is needed on the growth and phenology of Undaria and how this relates to site-specific environmental conditions such as water temperature. In addition a better understanding of the invasion process including the potential spread of Undaria from aquaculture sites to native reefs and the impacts of Undaria on native communities is required.

1.5 UNDARIA IN NEW ZEALAND

1.5.1 Distribution and spread

Undaria has been thriving in southern New Zealand since the 1980s (Hay and Luckens 1987) with a widespread and relatively well documented distribution around the lower North Island, east coast of South Island and Stewart Island (Russell et al. 2008). Spread around the upper North Island has been more recent and is not well reported. Undaria is now present at almost all major ports around the North Island and at sites as far north as Rangaunu Harbour in Northland (Appendix I). Timeframes for discovery in New Zealand are summarised in Table 1.2. Undaria has been spread around New Zealand via hull fouling (Hay 1990; Floerl et al. 2005; Forrest and Hopkins 2013) and with the transfer of mussel aquaculture stock and equipment (Forrest 2007; Table 1.2). Once present at coastal sites, annual along-shore distances of spread from source populations are highly variable. Studies by Forrest et al. (2000) and Brown (1999) in the Marlborough sounds indicate that the along-shore dispersal of Undaria in regions of low current is in the order of hundreds of metres per year. These results are within the range of between 50 m and 2 km per year estimated from other countries (Hay 1990, Casas and Piriz 1996, Floc’h et al. 1996, Curiel et al. 1998). The rate of natural spread depends on many factors, including local hydrology, the availability of suitable substrate and the ability of Undaria to settle and establish in the receiving environment; hence the highly variable and often unpredictable rate of natural dispersal (Hunt et al. 2009).

1.5.2 Phenology

Undaria has been reported to persist year-round, through overlapping generations of sporophytes, at some locations in the South Island and in Wellington Harbour in the lower North Island. These sites have summer temperatures < 20 °C (Hay 1990; Hay and Villouta 1993; Brown 1999; Stuart 2004; Thompson and Schiel 2012). The phenology of populations present further north than Wellington Harbour was unknown prior to this research.

1.5.3 Genetic variation

Undaria populations in southern New Zealand were found to represent an unusually high genetic diversity as compared to other introduced populations around the world (Uwai et al. 2006).
1.6 STUDY LOCATION: HAURAKI GULF, NORTHEASTERN NEW ZEALAND

Field research presented in this study took place in the Hauraki Gulf (36.63 N, 175.18 E), northeastern New Zealand. The Hauraki Gulf comprises 4000 km² of water space including some large sheltered embayments. It is home to a diverse and highly productive marine ecosystem, large infrastructure including the Ports of Auckland, a multitude of aquaculture sites, as well as six marine reserves. The Hauraki Gulf has a warm-temperate climate with annual water temperatures ranging from ~12 - 24 °C, with the lowest temperatures typically occurring in July and warmest temperatures in February-March (Chapter 2).

*Undaria* is known to occur at multiple sites within the Hauraki Gulf (Table 1.2), in particular at sites around the highly developed Waitemata Harbour and on mussel farm infrastructure in the Firth of Thames and around Great Barrier Island. *Undaria* was first discovered in the Hauraki Gulf in 2002, but prior to this research no quantitative information was available on the density, size, growth, phenology, or the invasion process and resultant ecological effects from *Undaria* populations in this region. Population monitoring took place at two sites approximately 64 km apart; the Westhaven Marina on the western side of the Gulf and at mussel farms and a coastal reef within Coromandel Harbour on the eastern side of the Gulf (Fig. 1.4). Westhaven Marina is the largest marina in the Southern Hemisphere with over 2000 swing moorings and berths and is situated in Waitemata Harbour, this is a highly developed urban site.

Survey work covered mussel farming sites on the eastern side of the Hauraki Gulf, around the Coromandel Peninsula and Great Barrier Island. Coastal monitoring and survey sites were located inshore from mussel farms and comprised typical reef communities present at shallow sheltered reefs in northeastern New Zealand as described by Shears and Babcock (2004).

Genetic work outlined in Chapter 4 involved analyses of *Undaria* tissue samples from monitoring and survey sites around the Hauraki Gulf and also included *Undaria* tissue samples from all known *Undaria* populations around the North Island.

1.7 RESEARCH AIMS

This thesis investigated the population ecology and factors influencing the distribution and establishment of warm water populations of *Undaria* in northern New Zealand and worldwide. Northern New Zealand was previously classified as being sub-optimal for growth of *Undaria* due to a warmer temperature regime than that of its native range (Sinner *et al.* 2000). At the beginning of this research the northern-most population of *Undaria* in the Southern Hemisphere was found in the Hauraki Gulf. However, during the course of this research *Undaria* was also recorded at Rangaunu Harbour in the far north of New Zealand, a site where water temperatures typically range between 14 and at least 24 °C (Appendix I), demonstrating that it can establish in warmer conditions than present in the Hauraki Gulf. This raised questions around the potential range of *Undaria* and how this invasive species may impact upon warm-temperate and subtropical locations around the world. *Undaria* has been recorded at sites overseas with similar temperature regimes to the Hauraki Gulf; Taranto, Italy (Cecere *et al.* 2000), Port la Nouvelle France (Floc’h *et
al. 1991) and Baja California, Mexico (Aguilar-Rosas et al. 2004), However, information on the population ecology and seasonal cycle, impacts, and genetic variability of populations under this temperature regime was lacking. Understanding the ecology of Undaria under such warm temperature regimes is vital to predicting its potential distribution and impacts on local and global scales, both now and with future changes in ocean temperature.

This research aimed to gain an understanding of how invasive Undaria populations perform in warm-temperate conditions and how its distribution and phenology related to water temperature regimes both in New Zealand and globally. I investigated aspects of population ecology such as phenology, growth and density, and analysed the genetic composition of warm-tolerant populations found in the North Island of New Zealand. I also examined how the distribution of Undaria on coastal reefs in northern New Zealand was influenced by mussel farming activities and disturbance to native macroalgal canopies.

1.8 THESIS OUTLINE

Chapter 2 aimed to determine how Undaria population ecology manifested under a warm-temperate water temperature regime, including how many recruitment events occurred annually, whether sporophytes persisted year-round, or whether it maintained a more typical winter annual cycle as seen in its native range. For this study a combination of monitoring and tagging studies were carried out over three growth seasons.

Chapter 3 investigated the role that mussel aquaculture can play in influencing the spread of Undaria. I compared population dynamics between Undaria growing on mussel farm structures and at a coastal reef site. I also investigated how the density of Undaria on mussel farms, and its presence on adjacent reefs, related to different environmental variables and physical attributes of mussel farms. I aimed to identify what influenced the spread of Undaria from mussel farms to nearby reefs and to isolate factors which may allow the prediction and mitigation of spread within the coastal marine environment. I hypothesised that larger aquaculture sites and those where structures were positioned closer to the coast may increase the likelihood of introducing Undaria to coastal reefs. This was tested by examining relationships between infestation levels on mussel farms and at coastal sites and a range of environmental factors and features of the sites. Reef surveys were used to identify coastal habitats most at risk from invasion.

Chapter 4 used a manipulative experiment to test the theory that loss of native macroalgal canopies through disturbance is important in facilitating invasion by Undaria. A macroalgal canopy removal experiment was carried out across a subtidal reef adjacent to an intertidal population of Undaria. Canopy species were removed and the responses of both native algal communities and Undaria were monitored over two growth seasons.

Chapter 5 investigated the genetic diversity of Undaria from all known populations around the North Island and related these to known strains, or haplotypes, from native and introduced populations around the world. As well as revealing the origins of invasive populations, determining
the genetic diversity of warm-tolerant *Undaria* populations may reveal links between haplotypes and temperature tolerances.

Chapter 6 provided a global synthesis of the current distribution and phenology of *Undaria*, based on available literature. I investigated how distribution and phenology related to water temperature regimes. Following validation against reported temperatures from the literature, temperature regimes were quantified for all reported locations where *Undaria* has been found around the world using satellite-derived measurements of sea surface temperature. This allowed comparison of temperature ranges between all native and introduced populations, as well as between locations with differing phenologies (winter annual vs. year-round presence). These temperature relationships were used to predict the potential global range for *Undaria* and the likely phenology for any given site.

The final chapter to this study, Chapter 7, comprises a general discussion of the preceding research and implications of the research findings. In particular, based on the findings of this research and published literature, I speculate what the likely ecological effects of *Undaria* are in warmer water regions and with regards to climate change. Chapter 7 also discusses the limitations of this work.
Table 1.1
Summary of *Undaria* discovery around the world, substrate it colonised and mode of introduction.
NB: Spaces are blank where substrate or mode of introduction were unknown or not reported.

<table>
<thead>
<tr>
<th>Year</th>
<th>Country</th>
<th>Location</th>
<th>Substrate</th>
<th>Mode of Introduction</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1983</td>
<td>France</td>
<td>Atlantic Ocean, Brittany, the islands of Groix and Ushant, La Rance estuary, Bay of St Malo, Ouessant, Abers, Trieux, Pleubian, Guilvinec, Oleron and the Chausey Islands</td>
<td>Undaria cultivation farms</td>
<td>Deliberately introduced for cultivation by the French Institute for the Exploitation of the Sea (IFREMER)</td>
<td>Perez et al. 1984; Fletcher and Farrell 1999</td>
</tr>
<tr>
<td>1986</td>
<td>France</td>
<td>Coastal sites adjacent to farms in Ouessant and other areas</td>
<td>Rocky reef</td>
<td>Natural dispersal</td>
<td>Floc’h et al. 1996; Grulois et al. 2011</td>
</tr>
<tr>
<td>1987</td>
<td>New Zealand</td>
<td>Wellington Harbour</td>
<td>Breakwaters and seawall structures</td>
<td>Fishing vessels</td>
<td>Hay 1990; Uwai et al. 2006</td>
</tr>
<tr>
<td>1988</td>
<td>Spain</td>
<td>Galicia, Ria de Arousa</td>
<td>Mussel farm infrastructure</td>
<td>Oyster transfers</td>
<td>Fletcher and Farrell 1999; Silva et al. 2001</td>
</tr>
<tr>
<td>1988</td>
<td>Australia</td>
<td>Tasmania</td>
<td>Rocky reef and urchin barrens</td>
<td>International shipping</td>
<td>Sanderson 1990</td>
</tr>
<tr>
<td>1992</td>
<td>Italy</td>
<td>Venice lagoon, Chioggia and Giudecca islands</td>
<td>Canals, artificial breakwaters</td>
<td>Oyster transfers</td>
<td>Curiel et al. 1994; Cecere et al. 2000</td>
</tr>
<tr>
<td>1992</td>
<td>Argentina</td>
<td>Puerto Madryn, Nuevo Gulf</td>
<td>Wharf piles, rocky reef and boulders</td>
<td>International shipping or fishing vessels</td>
<td>Piriz and Casas 1994; Casas and Piriz 1996</td>
</tr>
<tr>
<td>1994</td>
<td>England</td>
<td>Solent region, Hamble estuary</td>
<td>Marina structures</td>
<td>Recreational vessels</td>
<td>Fletcher and Manfredi 1995</td>
</tr>
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Table 1.2
Summary of reported *Undaria* distribution, substrate it colonised and modes of introduction around New Zealand (A) and specific sites within the Hauraki Gulf (B).

NB: Spaces are blank where substrate or mode of introduction were unknown or not reported.

<table>
<thead>
<tr>
<th>Year</th>
<th>Location</th>
<th>Substrate</th>
<th>Mode of Introduction</th>
<th>Reference</th>
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Figure 1.1

Locations of native (star) and known introduced (circle) *Undaria* populations around the world. This map is based on a review of literature presented in Chapter 6.
**Figure 1.2**

*Undaria* growth stages and morphological features: juvenile sporophyte with lanceolated lamina and lacking a midrib (<10cm) (A), juvenile sporophyte with lanceolated lamina and developing a midrib (B), young sporophyte with lamina widening and midrib thickening (C), immature sporophyte with pinnately divided lamina (D), mature sporophyte (≤ 2m in length) with sporophylls present at base of the stipe and apex eroded (E). Photographs of *Undaria* growing in the Hauraki Gulf: sporophylls on a mature sporophyte at the Westhaven Marina (F) and an immature sporophyte with pinnately divided lamina on coralline turf flats at Katherine Bay, Great Barrier Island (G). Diagram adapted from NIMPIS (2011). Photograph F taken by the author in 2012, photograph G taken by N.T. Shears in 2012.
Figure 1.3

_Undaria_ life cycle: sporophylls at the base of the mature macroscopic diploid (2n) sporophyte release haploid (1n) zoospores. Zoospores grow into male and female gametophytes (1n). Antherozoids (sperm) from mature male gametophytes fertilise mature female gametophytes to form sporophytes (2n).

Diagram adapted from Sinner _et al._ (2000).
Figure 1.4
Map of North Island, New Zealand. Inset shows locations for study sites in the Hauraki Gulf:
1 = Waitemata Harbour, 2 = Coromandel Harbour.
Chapter 2

Population ecology of the invasive kelp *Undaria pinnatifida* in warm-temperate conditions

A research paper has been published based on this chapter:


2.1 ABSTRACT

Understanding what drives the growth and phenology of an invasive species is fundamental to predicting its potential distribution and impacts. *Undaria pinnatifida* is a winter annual in its native range, but populations are known to persist year-round at some introduced locations. This variation in phenology is thought to be induced by different water temperature regimes and likely influences the extent of ecological impacts on native communities. For this chapter I investigated the phenology of *Undaria* in the Hauraki Gulf, northern New Zealand, one of the warmest water *Undaria* populations in the world. Monitoring took place over three growth seasons from June 2011 to February 2014 revealed an annual growth cycle, with one main recruitment event in winter, 1 - 2 months after water temperatures dropped below ~15 °C. Density, sporophyte length and growth rate peaked in spring, and declined rapidly at temperatures above 20 °C. Lowest densities were sustained over summer and autumn months when temperatures exceeded 20 °C and density remained low for varying periods depending on how long temperatures were above 20 °C. Overall, sporophyte size and growth rates were comparable to those of cooler water populations, but the seasonal cycle was compressed into a shorter time period. This demonstrates that *Undaria* can adjust its life cycle to maximise production when temperatures are cool enough for recruitment and growth. The requirement for water temperatures to fall below 15 °C may be an important determinant in limiting the geographical distribution of *Undaria*, the seasonal absence of *Undaria* when temperatures regularly exceed 20 °C, will likely restrict the ecological impacts of *Undaria* at warmer water sites.

2.2 INTRODUCTION

Invasive species are considered one of the foremost threats to marine ecosystems (Molnar *et al.* 2008). Amongst invasive marine species habitat-forming macroalgae are of particular concern; they can cause substantial ecological and economic impacts at introduced sites (Johnson 2008). When invasive species reach locations with different environmental conditions growth and life cycle patterns can diverge from those displayed by native populations. This flexibility in growth
and life cycle patterns can give invasive species a competitive advantage over native species (Lockwood et al. 2007; Simberloff 2013).

In the marine environment, water temperature is a major driver of species’ growth and life cycle patterns, and variation in temperature regimes between locations can lead to differing life cycle patterns between native and introduced populations. For example, the invasive alga *Sargassum muticum* (Yendo) Fensholt has a life cycle and maximum size that vary between locations with different water temperature regimes (Aguilar-Rosas and Galindo 1990; Britton-Simmons 2004). Similarly, *Undaria* exhibits varying life cycle patterns between locations, and this is hypothesised to relate to differing temperature regimes (Hay and Villouta 1993; Thornber et al. 2004; Casas et al. 2008; Martin and Bastida 2008; Zabin et al. 2009); such variability in population ecology among locations can significantly influence resultant ecological impacts (Mack et al. 2000).

*Undaria* has a broad set of environmental tolerances and adaptive capabilities, with invasive populations now present in more than fourteen countries outside its native range (Minchin and Nunn 2014). The success of *Undaria* as an invader is due in part to its resilient biphasic life cycle. *Undaria* is a winter annual in its native range (Koh and Shin 1990); macroscopic sporophytes disappear over summer and the population sustains itself in the form of vegetative gametophytes; when water temperatures drop again, gametophyte development resumes during autumn (Pang et al. 2008). Following gametophyte growth and fertilisation, the production of visible sporophytes occurs; this takes at least a month to 45 days from the onset of gametophyte growth (Hue et al. 1995). Once sporophytes have formed, *Undaria* is fast growing (Yoshikawa et al. 2001). However, reported optimal temperatures for sporophyte growth vary (see Floc’h et al. 1991). Optimum growth has been recorded at temperatures as low as 5 – 10 °C for some native populations (Zhang et al. 1984; Yoshikawa 2001) and it is generally accepted to occur at less than 20 °C (Morita et al. 2003a). Sporophytes typically live for up to eight or nine months in their native range; once the mature sporophyte has released all its spores, it dies and is detached from the substratum (Hay and Luckens 1987).

The life cycle of invasive populations of *Undaria* can vary in a number of ways. For example, in California two distinct recruitment pulses occur over the course of a year (Thornber et al. 2004) whereas, at some locations, successive generations of sporophytes have been observed forming year-round populations, e.g. in parts of New Zealand, England, Argentina, Australia, America (California), and France (Hay and Luckens 1987; Floc’h et al. 1991; Hay and Villouta 1993; Fletcher and Farrell 1999; Casas et al. 2008; Martin and Bastida 2008; Zabin et al. 2009). Interpreting growth and life cycle patterns in relation to water temperature is fundamental to predicting potential impacts from *Undaria* at introduced sites. Differences in growth and life cycle patterns have implications for the receiving environment, with a year-round presence of sporophytes potentially having greater impacts as compared to a transient annual population (Valentine and Johnson 2003; Thornber et al. 2004; South et al. 2015). Understanding how growth and phenology relate to water temperature regimes will also aid in the prediction of the potential distribution for *Undaria* under current and future climatic conditions.
Undaria was discovered in New Zealand in the 1980s, and overlapping generations of sporophytes have been documented at sites in central and southern New Zealand where temperatures remain below 20 °C year-round (e.g. Hay and Villouta 1993). In some cases this has resulted in a year-round presence of sporophytes (Hay and Luckens 1987; Hay and Villouta 1993). Prior to this study, no information existed on the phenology and life cycle of Undaria in northern New Zealand. This region was previously classified as being sub-optimal for Undaria colonisation due to warmer water temperatures compared to its native range (Sinner et al. 2000). However, Undaria was subsequently discovered in the eastern Hauraki Gulf, on mussel farm structures, in 2002 and in the Waitemata Harbour in the western Hauraki Gulf in 2004 (Stuart and McClary 2004; Russell et al. 2008). This region has a warm–temperate climate and water temperatures range from ~12 - 24 °C. Undaria has been discovered at sites with similar temperature regimes to northern New Zealand: Taranto, Italy (Cecere et al. 2000), Port la Nouvelle, France (Floc’h et al.1991) and Baja California, Mexico (Aguilar-Rosas et al. 2004), however, information on the growth and life cycles of populations under these warmer temperature regimes are lacking.

This study investigates the phenology of Undaria in the Hauraki Gulf, northern New Zealand, one of the warmest water populations in the world. I aim to determine how many recruitment events occur annually, how population cycling relates to specific water temperature cues and whether sporophytes are present year-round, or whether Undaria populations maintain a more typical winter annual cycle as seen in its native range. A combination of field monitoring and tagging studies were carried out over three growth seasons to examine the density, growth rate, recruitment and reproductive capacity of Undaria in the Hauraki Gulf.

2.3 METHODS

2.3.1 Study Sites

Undaria populations were monitored from June 2011 to February 2014 in the Westhaven Marina and at a Greenshell™ mussel, Perna canaliculus Gmelin (hereafter ‘mussel’) aquaculture site in Coromandel Harbour. Both sites are located in the Hauraki Gulf, northern New Zealand (Fig. 2.1). The Hauraki Gulf comprises ~4000 km² of water space, and is home to a diverse and highly productive marine ecosystem, large infrastructure including the Ports of Auckland, a multitude of aquaculture sites, as well as six marine reserves.

The Westhaven Marina is the largest marina in the southern hemisphere with over 2000 moorings and berths. Situated in Auckland, New Zealand’s largest city, the marina has an extensive network of swing moorings, pile moorings and a pontoon system consisting of floating concrete pontoons. Monitoring at Westhaven Marina was carried out on two different piers located ~400 m apart, Pier Z in the inner part of the marina and Pier W, on the outer pontoon structures near the marina breakwater bordering the open Waitemata Harbour (Fig 2.1). Both sites comprise lengths of concrete pontoon where Undaria was growing on the sides of the pontoons with a depth
distribution of zero to ~30 cm. Undaria sporophytes were growing directly on the concrete pontoons or attached to other organisms present such as Crassostrea gigas Thunberg, Sabella spallanzanii Gmelin, Styela clava Herdman and other encrusting algal and ascidian species. Marina management confirmed that the sub-marine portions of the pontoons are never cleaned.

The mussel farm that was monitored was positioned in 10-12 m of water within the sheltered confines of the Coromandel Harbour on the less-developed eastern side of the Hauraki Gulf (Fig. 2.1). At the mussel farm, Undaria grows on the mussel growing lines (“droppers”), the structural ropes (“backbone”) and on the floats used to suspend the mussel dropper lines. Undaria grows on the underside of the mussel farm floats, on or amongst encrusting organisms such as algal, cnidarian and ascidian species, on bare backbone ropes and amongst or on top of the mussels growing on the droppers.

2.3.2 Seasonality and population structure

Monitoring of Undaria density and population size structure employed different methods at the marina and mussel farming site to account for the different substrata on which Undaria is found. At the marina, Undaria was growing along the concrete pontoons which extend 30 cm below the water. This meant that Undaria could be counted and measured from above the pontoon by reaching into the shallow water to a depth of 30 cm. Size distribution was monitored by taking in situ measurements of haphazardly selected individuals, n = 40 at Pier Z and n = 40 at Pier W, unless total numbers present were lower, in which case all sporophytes present in the study area were measured. Recordings were made fortnightly from June 2011 – January 2013 and monthly from February 2013 to February 2014. Measurements were made for total sporophyte length, from the top of the holdfast to the end of the primary lamina; sporophyll width and length were also measured if present. Sporophyll volume for each sporophyte sampled was calculated based on width and length, and assuming a cylindrical sporophyll shape.

Density was quantified by counting Undaria from one metre sections of the designated marina pontoons, n = 24 at Pier Z and n = 12 at the smaller site of Pier W. The random number function in Microsoft Excel was used to assign sections of the pontoons for sampling, for each 1 m section all sporophytes >5 cm in length were counted to a depth of 30 cm. This was done monthly throughout the study.

At the mussel farm, in order to survey a consistent substrate area, comparable to the marina substrate, and to allow for surveys to be carried out by snorkel, the underside of the mussel floats were surveyed. Monitoring was carried out on four mussel growing lines each month. All Undaria sporophytes found on the underside of the first ten floats per mussel line were counted and measurements made as for the sporophytes at the marina. The submerged portion of the underside of one standard mussel float comprised an area of approximately 1 m² and this is the area where Undaria occurs. If lines were harvested during the course of the study new lines were haphazardly selected for monitoring to ensure 40 floats were inspected each month.
2.3.3 Growth rate
Sporophyte growth rates were only monitored at the marina site as individuals could be readily tagged and re-measured from the pontoon. At each pier 20, sporophytes ≥ 20 cm total length were haphazardly chosen and tagged in July of 2011 and 2012. These sporophytes grew as part of the main recruitment pulse observed each year. Growth of these sporophytes was measured fortnightly until they died or disappeared. Individuals were tagged around the holdfast or as close to the basal section of the stipe as possible using thin coloured cable ties. Larger individuals (>20 cm) were chosen for tagging because of damage to smaller individuals by tagging and potentially distorting growth by attaching the tag to the base of the sporophyte. Care was taken not to restrict growth by keeping the tags loose around the base of sporophytes. Tags were cut from the sporophytes and new ones attached at or before the first signs of constriction. Once sporophyll growth began, the sporophytes were generally larger and were able to be tagged between the top of the sporophyll and the base of the lamina. This allowed the rapid sporophyll growth to occur unrestricted. Despite these efforts to ensure individuals were not damaged by tagging, tagged individuals were frequently lost. The large initial number of tagged sporophytes, n = 40, resulted in successful measurements through the seasons for between 3 and 19 individuals each fortnight.

Incremental growth in blade elongation and blade erosion rates for the tagged sporophytes were tracked using the hole-punch method (Parke 1948). For each individual, a 0.5 cm diameter hole was punched 10 cm above the stipe-blade junction on one side of the midrib each fortnight. Stipe length and sporophyte length (blade plus stipe) were measured to the nearest 0.5 cm. These measurements plus the lateral displacement of the hole relative to the blade/stipe junction were recorded every two weeks (±3 days). Lamina growth rate was calculated using the lateral displacement of the hole divided by the duration of the growth period (days). This method has been commonly used to determine growth rates for Undaria as it overcomes effects from distal thallus erosion (Dean and Hurd 2007; Schiel and Thompson 2012). However, the hole-punch method cannot be applied to small individuals. Monthly measurements were confirmed to be inadequate in 2013 as sporophytes were severely damaged by the cable ties and often the hole had grown right out of the blade before successive measurements could be taken.

2.3.4 Environmental variables
HOBO® temperature loggers were deployed at Pier Z and Pier W at the marina and a raft in Coromandel Harbour near the monitored mussel farming site. At each site a sensor pendant was suspended in the water approximately 30 cm below the water’s surface and set to log temperature every thirty minutes for the duration of the study.

Seawater samples (n = 3) were collected for nutrient analysis from the sea surface fortnightly between July 2011 and December 2012 and monthly for the year of 2013 from each pier at the marina site. At the mussel farm site seawater samples (n = 3) were collected monthly from the sea surface for the duration of the study. Water samples were 60 mL and were not filtered prior to analysis. Samples were frozen before being sent to the Leigh Marine Laboratory for processing.
Ammonium and phosphate (inorganic) content were determined following methods by Grasshoff et al. (1983), nitrate and nitrite concentrations were determined using methods by Parsons et al. (1984). Analysis was performed manually on a Shimadzu UV-2450 spectrophotometer.

2.4 RESULTS

2.4.1 Environmental conditions at monitoring sites

Average daily temperatures were very similar for Pier Z and Pier W. Data were lost for the mussel farm site for much of 2011, however, the available data indicates slightly cooler daily average temperatures in summer at the mussel farm compared to the marina and slightly warmer winter temperatures (Fig. 2.2).

Nutrient concentrations were highest at all sites during the spring and summer of 2011 - 2012. Nitrate peaked during winter-spring each year but in general nitrate as well as ammonium and phosphate were variable though the seasons (Fig. 2.3). Nutrient levels were generally highest at Pier Z, the most confined site within the marina and in closest proximity to the urban storm-water inputs. Average nitrate concentration (± SE) ranged from 0.068 ± 0.004 - 0.523 ± 0.012 µM. Average ammonium concentrations were 0.323 ± 0.084 - 5.263 ± 0.123 µM and average phosphate ranged from 0.532 ± 0.005 – 1.366 ± 0.035 µM. At Pier W levels of all nutrients were slightly lower; average nitrate concentration ranged from 0.067 ± 0.004 – 0.421 ± 0.003 µM, ammonium levels were 0.103 ± 0.045 – 4.497 ± 0.190 µM and phosphate levels were 0.384 ± 0.063 – 1.218 ± 0.060 µM. Average phosphate and ammonium concentrations were considerably lower at the open water mussel farm site and average nitrate concentrations were also generally lower. Average nitrate concentrations ranged from 0.057 ± 0.007 – 0.470 ± 0.007 µM, ammonium ranged from 0.021 ± 0.033 – 2.432 ± 0.030 µM and phosphate ranged from 0.280 ± 0.028 - 0.816 ± 0.063 µM at the mussel farm site.

2.4.2 Seasonality and population structure

Consistent seasonal patterns in sporophyte density were apparent across all monitoring locations (Fig. 2.4). Recruits began to appear during winter, density peaked in late spring and sporophyte numbers then dropped rapidly in mid-summer each year. Density was lowest in summer and autumn, numbers remained low during early winter. The very low numbers of sporophytes present over late summer and autumn months typically comprised the remains of adult sporophytes (with only eroded sections of midrib and sporophylls present) and occasional new recruits (Fig 2.4 and 2.5). At Pier Z, no sporophytes were found in 2013 between February and April in the haphazardly allocated pontoon sections used to calculate density (Fig. 2.4A), but a few small sporophytes were recorded on other parts of the pontoons (Fig. 2.4B; Fig. 2.5). Sporophyte densities were highest at Pier Z with maximum density (± SE) recorded at 103.5 ± 21 sporophytes m⁻² in October 2012. The mussel farm had a much lower density of sporophytes than the marina sites, maximum densities of 2.7 ± 1 sporophyte m⁻² were recorded from the mussel floats (Fig.
Density at the mussel farm was also more variable through the year than at the marina sites, displaying a more persistent density of sporophytes.

The seasonal variation in sporophyte density closely followed changes in water temperature at all sites. Densities began to increase rapidly approximately 1 – 2 months after temperatures dropped below ~15 °C (Fig. 2.4). The timing of this decrease in temperature and associated increase in sporophytes differed between 2012 and 2013. In 2012, water temperatures dropped below 15 °C in May and this resulted in an earlier rise in sporophyte presence at the marina site as compared to 2013 when temperatures remained above 20 °C for longer and did not fall below 15 °C until June. Sporophyte density was minimal at temperatures above 20 °C. The shorter period during summer when temperatures remained above 20 °C in 2012 resulted in a shorter period of minimal density as compared to 2013 when temperatures were above 20 °C for longer and density remained minimal for almost five months at the marina sites. Density was more variable through the year at the mussel farm but peaks occurred at temperatures less than 15 °C and densities were consistently lowest at temperatures above 20 °C (Fig. 2.4).

Average sporophyte lengths were similar at all locations and underwent similar seasonal variation (Fig. 2.5). Individuals at the mussel farm reached maximum lengths of 120 cm with 19% of measured sporophytes reaching lengths ≥50 cm. At the marina, sporophytes reached a maximum length of 116 cm with 16% of measured individuals reaching lengths ≥50 cm. Sporophytes which were present through autumn had an average length of ≤10 cm and, as stated above, included a mix of degrading adult sporophytes and a few new recruits. Sporophyte lengths peaked in September-October each year at all sites. Maximum average lengths were 59.1 and 75.0 cm for Pier Z and Pier W respectively and 52.1cm at the mussel farm. Peaks in sporophyte length consistently coincided with average temperatures around 13 - 17 °C (Fig. 2.5).

Sporophyll production and size were similar among sites and followed a consistent seasonal pattern, (Fig. 2.6) sporophytes typically began forming reproductive sporophylls in spring and when they reached a total length of ≥20 cm at all sites. Sporophyll volume peaked in November each year for all sites (Fig. 2.6). Sporophyll volume was variable between years with the lowest volume per plant recorded in 2013 at all sites. Individuals with sporophylls were present for almost the entire duration of monitoring at the marina and the mussel farm. The greatest percentage of individuals with sporophylls was observed from November to January/February at all sites in 2012 (Fig. 2.7). However, the high percentage over later summer months was due to the presence of very low numbers of remnant adults with degrading sporophylls and overall sporophyll volume at this time was very low (Fig. 2.6).
2.4.3 Growth rate

Growth rates were generally highest when temperatures were lowest (~14 °C, in August and September), and then declined as water temperature increased and nutrients declined (Fig. 2.3, 2.7). However, growth rate was more variable in 2012 as compared to 2011. Average growth rate for tagged individuals peaked in late August in 2011, 0.58 ± 0.08 cm day⁻¹, and then declined steadily until tagged sporophytes were highly degraded (and unable to be tagged) or gone in late November. Average growth rates in 2012 also peaked in late August, 0.91 ± 0.14 cm day⁻¹, and then began to decline. However in 2012, there was a marked reduction in growth rate in September when the average growth rate was 0.35 ± 0.09 cm day⁻¹; this was in part due to the presence of some very large individuals which had zero or very low growth rates at this time. These sporophytes were gone by the next monitoring date. Sporophytes typically survived for five months or less once they were tagged.

2.5 DISCUSSION

In general, both perennial and annual macroalgae show seasonal growth and reproduction cycles and these are most often correlated with seasonal temperature and light changes (Darley 1982). Growth rates usually begin to increase in winter or spring and decline in the summer or autumn (Darley 1982; Kain 1989). This pattern was confirmed for Undaria at the study sites. However, Undaria in the Hauraki Gulf was found to have an annual life cycle that differed slightly in timing to native populations. In its native range Undaria recruitment occurs in autumn, the sporophyte grows rapidly through winter and spring, and senescence occurs in summer (Saito 1975; Lee and Sohn 1993; Oh and Koh 1996; Choi et al. 2007). In the present study Undaria displays a somewhat delayed and compressed annual cycle, seen most clearly at the marina sites. Undaria abundance rose sharply 1 - 2 months after water temperatures fell below ~15 °C, this occurred in autumn each year at all sites and resulted in the recruitment of macroscopic sporophytes during winter. Rapid growth occurred from late winter to spring, peak abundance in late spring/early summer, followed by the rapid onset of reproductive maturity and senescence in summer. Abundance was consistently minimal when temperatures were above 20 °C; a cooler summer in 2012 as compared to 2013 saw water temperature remain above 20 °C for a shorter period of time and this corresponded with a shorter period of low abundance of sporophytes in 2012 as compared to 2013. Tagging of individuals revealed a typical lifespan for sporophytes to be less than six months, with individuals tagged at ~20 cm total length generally surviving for a maximum further 5 months.

Despite a reduced annual presence as compared to cooler water populations, Undaria in the Hauraki Gulf can form dense monospecific stands on artificial structures. Sporophyte density at the marina peaked during late spring-early summer each year with the highest densities, >100 sporophytes m⁻², recorded at Pier Z. Lower densities were found at Pier W and this appeared to be related to restricted light availability on one side of the pontoon; the orientation of Pier W restricted sun exposure as compared to pier Z and one side of Pier W was also shaded by a large visiting yacht for most of 2012 (Fig. 2.4B). In general the pontoons at the marina provide ideal
growing conditions for Undaria with high light levels and substrate which is easy to colonise. Densities were considerably lower on the mussel farm. Highest densities at the mussel farm site were ~3 sporophytes m$^{-2}$. Lower mean densities recorded at the mussel farm reflect the non-continuous substratum provided by mussel floats and may also be related to mussel farm maintenance and harvesting regimes, which could not be avoided when studying an operational mussel farm over an extended period of time. For example mussel farming operations can require adding floats to mussel lines as the mussels grow and become heavier, resulting in differing period of time in the water for floats on the same mussel line.

The higher density of sporophytes found at the marina may also be related to the length of time the population has been established on the marina pontoons. Undaria gametophytes can build up in proximity to adult sporophytes and form a ‘seedbank’ of propogules which result in a dense recruitment of sporophytes when conditions are suitable (Forrest et al. 2000; Hewitt et al. 2005). Nutrient loading at the marina was also higher than at the mussel farm. Interestingly, the presence of mussels, which can excrete large amounts of ammonium, did not appear to result in elevated ammonium concentrations at the mussel farming site (Fig. 2.3C). Undaria thrives in areas enriched with nitrogen and phosphorous (Campbell et al. 1999; Castic-Fey et al. 1999; Curiel et al. 2001; Torres et al. 2004; Sfrisco and Facca 2013) and therefore grows more prolifically at human-impacted sites where nutrient levels are higher (Torres et al. 2004; Morelisson et al. 2013). In general, peaks in growth rate coincided with elevated nutrient concentrations and nutrient levels may have also influenced sporophyte lengths and sporophyll volume, (Oh and Koh 1996; Stuart 1997; Yoshikawa et al. 2001; Kumura et al. 2006; Sfrisco and Facca 2013), both of which were greater in 2011 and 2012 as compared to 2013 when overall nutrient levels were the lowest of the study.

Highest growth rates were recorded during August-September each year at temperatures of ~14 °C, with the maximum individual growth rate recorded at 2.86 cm day$^{-1}$ in spring 2011. Growth rates were generally highly variable between sporophytes. Less annual variability among average growth rate occurred in 2011 as compared to 2012 and this was likely due to the influence of several very large sporophytes in September 2012 which had very low or zero growth rates at that time; these sporophytes were gone by October 2012. Growth rates declined as water temperature increased and nutrient levels decreased until all tagged sporophytes had disappeared in December. Once sporophytes begin to mature and form sporophylls, sporophyte length depends to a certain extent on the thallus erosion rate, which increases from the distal end as the sporophytes age. Increased distal erosion coincided with the formation of sporophylls, which is consistent with the re-direction of nutrients to reproduction but is likely also related to increasing temperature and age of the sporophytes (Yoshikawa et al. 2001; Dean and Hurd 2007; Kohtio 2008). However, There was not a clear reduction in growth rate associated with the beginning of sporophyll formation as may have been expected (Campbell and Burridge 1998; Choi et al. 2007).
The temperature ranges for sporophyte growth in this study are consistent with those from studies in native populations where temperatures of <12 – 13 °C are considered optimal for young thalli growth and 10 - 15 °C optimal for older thalli growth (Saito 1975). However, temperatures ranging between 4 and 25 °C have been recorded as allowing possible sporophyte growth (see Floc'h et al. 1991 and references therein; Morita et al. 2003b). Average growth rates were comparable to those recorded in introduced populations (Thornber 2004; Dean and Hurd 2007), but less than those recorded at Undaria cultivation sites (e.g. Yoshikawa et al. 2001).

On average, sporophytes at all sites grew to around 50 – 75 cm total length. This is consistent with lengths recorded for individuals from some introduced populations at cooler sites and from Baja California, Mexico which has a similar temperature regime to the Hauraki Gulf (Hay and Villouta 1993; Campbell and Burridge 1998; Aguilar-Rosas 2004; Merreta et al. 2012). Sporophytes are often larger at more exposed locations (Sanderson 1990; Casa and Piriz 1996; Castric-Fey et al. 1999; Schiel and Thompson 2012) and from native locations where it is cultivated to produce large thalli (Koh and Shin 1990; Choi et al. 2007). The relatively small size of Undaria at the sites examined in this study may therefore reflect the sheltered nature of the study sites and potentially the origin of the population, wild or cultivated, rather than the warm-temperate conditions.

The timing and duration of Undaria recruitment appeared to be linked to water temperature cues. Recruitment and growth were optimal at temperatures below ~15 °C at the marina sites, analogous to water temperature cues from native populations. Undaria begins to recruit in the wild as seawater temperatures decrease from ~17 to 14 °C (Hwang et al. 2004; Wantanabe et al. 2014) and individuals grow rapidly when seawater temperatures are between 10 and 16 °C (Lee and Sohn 1993; Oh and Koh 1996). An introduced population in California also exhibited recruitment pulses that correlated with a decrease in water temperature approximately 1 - 2 months prior to recruitment, with the strongest correlation when the temperature dropped to ~15 °C and recruits appeared 40 - 60 days later (Thornber et al. 2004; Kohtio 2008). Recruitment peaks have been recorded at 13 - 17 °C in France and Italy (Castic-Fey et al. 1999; Voisin 2007; Sfrisco and Facca 2013). Recruitment of sporophytes begins with gametophyte growth and fertilisation and laboratory experiments have shown Undaria gametophytes to have significantly higher growth rates when cultured at 13 – 16 °C than individuals grown at higher or lower temperatures (Stuart 1997; Thornber 2004; Stuart 2007; Kohtio 2008; Morita et al. 2003a), fertilisation is optimal at temperatures of 10 - 15 °C (Morita et al. 2003b). Recruitment of sporophytes decreases outside the ideal temperature range (~10 - 17 °C), but does not necessarily become zero (Casas and Piriz, 1996; Castric-Fey et al. 1999; Thornber et al. 2004; Zhang and Pang 2007; Pang et al. 2008; Morellisson et al. 2013). Successful recruitment was not evident in the Hauraki Gulf during months when water temperatures were above 20 °C. In general, sporophytes degraded and disappeared at temperatures above 20 °C and were gone by late summer, ~24 °C. Low numbers of juveniles recruited occasionally during summer months but these did not successfully grow. This agrees with the suggestion that introduced sites with summer maxima of 15 - 19 °C may allow sporophytes to persist year-round, as has been
observed in some introduced populations (Hay and Villouta 1993; Stuart 2004; Thornber et al. 2004; Schaffelke et al. 2005).

Whilst results from this study suggest temperature to be a significant factor in determining the timing for growth and recruitment of Undaria sporophytes, seasonal changes in day length may also influence population ecology (Pang and Lüning 2004). Changes in day length have been shown to act as a cue for Undaria sporophyll formation when temperature was held constant (Pang and Lüning 2004) and gametophyte fertilisation can be influenced by day length when temperature is held constant (Choi et al. 2005; Zang and Pang 2007). As well as affecting sporophyll and gametophyte development, changes in day length and light availability can influence growth rate, or at least the start of the faster growth period, for Undaria (NIMPIS 2011).

Whilst it appears that temperature and light interact to influence the seasonal patterns in Undaria recruitment and growth, it is evident that whilst changes in day length remain consistent inter-annually, water temperature regimes may vary considerably inter-annually. It therefore seems likely that the inter-annual variations in Undaria phenology and density observed in this and other studies are related to divergent water temperature regimes. Further studies could be done to determine how these variables, temperature and day length, interact to affect patterns of Undaria growth and density.

Light availability is also related to depth and Undaria at the study sites appeared to be more successful at shallower depths, where light availability was greater. This is also true for native species such as the laminarian Ecklonia radiata common in this region (Rodgers and Shears 2014). E. radiata growing at shallow depths (above the summer thermocline) in northern New Zealand has a similar growth pattern to Undaria; it recruits in winter, with maximum growth occurring at relatively low water temperatures (~13 – 16 °C) and when nutrient availability is highest (Taylor 1981). Other native species, such as the annual fucoid Sargassum sinclairii, also have similar growth patterns to Undaria in this region (Schiel 1985). S. sinclairii may also grow to a similar size as Undaria in these conditions within one growth season, ~ 1 m (Schiel 1985), whereas perennial native species such Carphophyllum maschalocarpum and E. radiata grow much more slowly (Novaczec 1984; Schiel 1985).

Undaria has a similar growth pattern to some native species and it grows more quickly than many native canopy-forming macroalgae, however, the requirement for winter temperatures to fall below 15 °C, and the absence of sporophytes at temperatures above 20 °C, may restrict annual presence, distribution, and the impacts Undaria could exert at warmer water sites. Populations which can only grow and persist for a short time during the year when temperatures are suitable, such as in the present study where Undaria populations are conspicuous for ~6 months of the year, may be less able to compete with more persistent native macroalgal populations in this region. Hence, these annual Undaria populations may assert a lower level of impact as compared to year-round populations found at cooler sites (Valentine and Johnson 2003; Thornber et al. 2004; South et al. 2015).
*Undaria* can successfully compress its seasonal cycle and form dense populations under warm-temperate conditions which were previously thought to be sub-optimal for colonisation. This ability to succeed under warmer temperature regimes is an invasive trait likely to be favoured as climatic conditions change (Dukes and Mooney 1999; Hellman *et al.* 2008). Kelp species can be particularly sensitive to elevated temperatures (Hatcher *et al.* 1987; Ladah and Zertuche-Gonzalez 1999; Wernberg *et al.* 2010), and therefore often have distribution limits which are fixed by cooler temperature tolerances (Lüning and Neushul 1978; Kain 1979; Lüning 1980; Dieck 1993). An adaptable life cycle may give *Undaria* an advantage over native kelp species as ocean temperatures increase. It is possible that other fast-growing kelp species may be able to maintain populations under warmer conditions by shifting to winter annual growth cycles similar to that displayed by *Undaria*. For example, *Laminaria saccharina* can adjust its perennial growth cycle and grow as an annual, remaining dormant over summer in the microscopic gametophyte stage, near the limit of its temperature range (Lee and Brinkhuis 1986; Gerard and Du Bois 1988). However, it is likely that for slower growing kelp species and those which are less temperature tolerant, increasing temperatures will eventually exclude them and they may be replaced by those, like *Undaria*, with higher temperature tolerances or more adaptable life cycles (Schiel *et al.* 2005; Ling 2008; Wernberg *et al.* 2010).
Figure 2.1
Map of the North Island, New Zealand, and details for study sites in the Hauraki Gulf: A = Westhaven Marina in Waitemata Harbour, B = mussel farming site in Coromandel Harbour. Images are from Google Earth™.
Figure 2.2
Daily average water temperatures for each monitoring site. Temperature was monitored using Hobo © temperature loggers/pendants suspended 30cm beneath the water’s surface and set to record temperature every 30 minutes 24 hours a day. Temperature loggers went missing from the mussel farm monitoring site several times, resulting in gaps in the data for up to 12 weeks. Horizontal lines show 15 and 20 °C for reference.
Concentrations of nitrate (A), phosphate (B) and ammonium (C) (± SE) found in the seawater at each monitoring site (n=3).
Figure 2.4
Density of *Undaria* sporophytes per m² (± SE) at Westhaven Marina pier Z, n=24 (A), Westhaven Marina pier W, n=12 (B) and the mussel farm, n=40 (C). Daily average water temperature is also shown (grey line) and horizontal lines show 15 and 20 °C for reference.
Figure 2.5
Average of total *Undaria* sporophyte length (± SE) at Westhaven Marina Pier Z (A), Westhaven Marina Pier W (B) and the mussel farm (C). Daily average water temperature is also shown (grey line) and horizontal lines show 15 and 20 °C for reference.
Figure 2.6
Average of total *Undaria* sporophyll volume per sporophyte (± SE) at Westhaven Marina Pier Z, (A), Westhaven Marina Pier W (B) and the mussel farm (C). Daily average water temperature is also shown (grey line) and horizontal lines show 15 and 20 °C.
Figure 2.7
Percentage of *Undaria* sporophytes with sporophylls at Westhaven Marina Pier Z (A), Westhaven Marina Pier W (B) and the mussel farm (C). Daily average water temperature is also shown (grey line) and horizontal lines show 15 and 20 °C for reference.
Figure 2.8
Average monthly growth rate for tagged *Undaria* sporophytes (± SE) in 2011 (A) and 2012 (B), n is shown above each point. Daily average water temperature at each location is also shown (grey line). Note: growth was recorded from July to November as tagged sporophytes were all gone by the end of November each year.
Chapter 3

Proliferation of the invasive kelp Undaria pinnatifida at aquaculture sites promotes spread to coastal reefs

A research paper has been published based on this chapter:


3.1 ABSTRACT
Aquaculture is a significant vector for the introduction of invasive species worldwide. Understanding factors influencing the proliferation and spread of invasive species from aquaculture sites to native habitats is necessary to develop management strategies aimed at mitigating their spread and subsequent impacts. This chapter compares population dynamics of the invasive kelp Undaria pinnatifida between mussel farms and a natural reef site in northern New Zealand (36°35'S 175°05'E), and investigates how the density of Undaria on mussel farms, and its presence on adjacent reefs, relates to different environmental variables and physical attributes of mussel farms. Monitoring from 2011 - 2014 found Undaria sporophytes on mussel farms were larger and more seasonally and reproductively persistent compared to populations on adjacent reefs. Region-wide surveys found Undaria at all mussel farming sites examined (n = 25) and at eight adjacent reefs. Coastal populations were most abundant in reef habitats lacking native macroalgal canopies. Density of Undaria on mussel farms was related to the size of mussels present, but not strongly related to wave exposure, turbidity, or spatial attributes of farms. Undaria was found on a number of native reefs adjacent to mussel farms, but its presence on these reefs was not related to the size of farms or distance from shore. These results demonstrate how marine farms provide an optimal environment for the proliferation of invasive species and management strategies must consider that farms of any size or position relative to shore pose a risk of introducing invasive species to native habitats.

3.2 INTRODUCTION
Aquaculture is one of the fastest growing sectors of the world food economy (e.g. Subasinghe et al. 2009). Rapid expansion of the industry has resulted in aquaculture becoming one of the leading vectors of introduction for aquatic invasive species worldwide (Katsanevakis et al. 2013) with introductions of seaweeds, fish, invertebrates, parasites and pathogens all linked to aquaculture activities (Naylor et al. 2001). Introductions of invasive species occur via the movement of aquaculture equipment and the transfer of farmed species among aquaculture sites. Once colonised, aquaculture sites can subsequently spread invasive species to native habitats.
(Katsanevakis et al. 2013) where it can be nearly impossible to eliminate them (Thresher and Kuris 2004; Olenin et al. 2011). Interception or removal of pathways to introduction is potentially the only effective strategy for reducing future impacts from invasive species (Carlton and Ruiz 2005; Minchin 2007; Olenin et al. 2011; Katsanevakis et al. 2013). Because aquaculture has fixed and licensed locations and operating procedures it can be more effectively controlled than other pathways such as recreational and commercial vessel movements (Savini et al. 2010). It has been shown that compulsory regulatory controls for aquaculture practices can decrease the spread of invasive species (Katsanevakis et al. 2013). Consequently, a better understanding of invasion patterns and processes will allow the development of strategies to reduce the spread of invasive species via aquaculture vectors and mitigate their ecological impacts (Molnar et al. 2008; Williams et al. 2013; Ojaveer et al. 2015).

Macroalgae form a significant component of marine invasive species and pose considerable economic and environmental risks for which there are currently limited control and management options (e.g. Davidson et al. 2015). The invasive kelp *Undaria pinnatifida* is one of the most prolific invasive macroalgal species (Nyberg and Wallentinus 2005), and is now found throughout most temperate regions of the world (Minchin and Nunn 2014). *Undaria* was first spread outside of its native Asian waters, to France, in association with Pacific oyster aquaculture (Perez et al. 1981). Following its introduction, aquaculture transfers continued to act as vectors for spread around Europe (Perez et al. 1988; Fletcher and Farrell 1999; Voisin 2005), including spread to coastal reef habitats (Floc’h et al. 1991, 1996). Similarly, since the discovery of *Undaria* in southern New Zealand in the 1980s (Hay and Luckens 1987), its spread throughout the country has been closely associated with aquaculture activities (Hay 1990; Neill et al. 2008; Russell et al. 2008; Hunt et al. 2009; Forrest and Hopkins 2013).

*Undaria* has a limited capacity for natural dispersal (Forrest et al. 2000) but is easily spread by anthropogenic vectors. Shipping and recreational vessels commonly spread *Undaria* between marinas, ports and other artificial structures (e.g. Minchin and Nunn 2014). Aquaculture activities typically rely on high water quality meaning that aquaculture transfers and practices often expose coastal areas in isolated and undeveloped areas to *Undaria* invasion (Inglis et al. 2000; Dodgshun et al. 2007; Hunt et al. 2009). These areas often have intact wilderness values and offer resources of economic, social and cultural importance and therefore can be regarded as high-value areas (Campbell and Hewitt 2013).

*Undaria* is an opportunistic and efficacious invasive species. It is highly fecund, has a fast growth rate and a plastic morphology (Dean and Hurd 2007; Schiel and Thompson 2012). It also has a hardy microscopic growth phase which makes monitoring and control efforts challenging (Hewitt et al. 2005). *Undaria* can change the structure of benthic ecosystems through domination of space and the alteration of species richness and composition (Hay and Luckens 1987; Hay 1990; Eno et al. 1997; Curiel et al. 2001; Neill et al. 2008; Raffo et al. 2009; Irigoyen et al. 2011a, b). *Undaria* is an adaptable species, displaying different life spans and seasonal growth patterns in different environments and inhabiting a broad range of both natural and artificial substrata (Floc’h
et al. 1991; Hay and Villouta 1993; Dean and Hurd 2007; Russell et al. 2008; Meretta et al. 2012). However, *Undaria* has an affinity for artificial substrata (Hay 1990; Hay and Luckens 1997; Russell et al. 2008) and often colonises man-made structures more readily than natural reef systems (Hay 1990; Russell et al. 2008; Minchin and Nunn 2014).

The New Zealand green-lipped mussel *Perna canaliculus* (hereafter called ‘mussel’) provides the largest aquaculture industry in the country with more than 600 mussel farms located throughout central and northern New Zealand covering thousands of hectares of marine space (Aquaculture New Zealand 2011). The spread of *Undaria* around New Zealand via mussel aquaculture transfers is well recognised (e.g. Forrest and Blakemore 2006). Spread can occur via transfers of aquaculture equipment or mussel seed stock, including the overland transport of spat mussels (Minchin 2007). The subsequent spread from aquaculture structures to surrounding reef areas has been observed in southern New Zealand (e.g. Hunt et al. 2009). In northern New Zealand, *Undaria* is known to occur on mussel farms in the Hauraki Gulf, being first reported in 2002 (Stuart 2004). However, limited information exists on its prevalence on native reefs in northern New Zealand (e.g. Appendix I) and more generally on the factors influencing the ability of *Undaria* to successfully spread from mussel farms to native reef habitats.

This chapter aims to compare the population ecology of *Undaria* on mussel farms and native reefs, identify what influences its spread from mussel farms to nearby reefs and to isolate factors which may allow the prediction and mitigation of spread within the coastal marine environment. It was hypothesised that larger aquaculture sites and those where structures are positioned closer to the coast might increase the likelihood of introducing *Undaria* to coastal reefs. The relationship between infestation levels and a range of environmental factors and features of mussel aquaculture sites were analysed. Reef surveys also aimed to identify which coastal habitat types are most susceptible to invasion by this species in northern New Zealand.

### 3.3 METHODS

#### 3.3.1 Seasonal variation of *Undaria* on mussel farms and coastal reefs

Population monitoring was conducted at two mussel farms through monthly surveys from June 2011 until January 2014. The monitored mussel farms were positioned in 10 - 12 m of water within the sheltered confines of the Coromandel Harbour, fetch 167 Km (Fig. 3.1), annual sea surface temperatures ranged from 11.7 - 24.0 °C. Each mussel farm comprised 15 lines, each line is made up of two ‘backbone’ ropes running in parallel just beneath the surface and held up with a series of floats, suspended from the backbone ropes are the mussel growing ropes or droppers, hanging to depths of 7 – 10 m. *Undaria* growing on the underside of the floats was monitored, as opposed to that growing on the ropes, to ensure the maximum monitoring time was gained before losing the sporophytes to mussel harvesting and so a clear area (m²) of substrate could be defined. Four mussel lines were chosen for monitoring and all *Undaria* found on a series of ten floats per line were counted. Total length and sporophyll width and length were measured to the
nearest 5 mm. If lines were harvested during the course of the survey new lines were haphazardly selected for monitoring to ensure 40 floats were inspected each month.

Population monitoring was also conducted at a coastal reef site approximately 700 m from the mussel farm monitoring site within the Coromandel Harbour (Fig. 3.1). The reef site was characterised by gently sloping rocky substratum (reef, boulders and cobbles) and supported diverse stands of canopy-forming native macroalgae. The site had an Undaria population present in the shallow subtidal zone. One 50 x 2 m transect spanning the shallow subtidal zone was inspected via snorkel and all Undaria counted each month from October 2012 until January 2014. In addition to the counts, in January 2013, sporophyte measurements began. Forty randomly selected sporophytes, or all sporophytes present if numbering less than forty, were measured for total length, and sporophyll length and width, until January 2014 when no sporophytes remained at the site.

3.3.2 Distribution of Undaria on mussel farms and coastal reefs

Surveys of Undaria were carried out by snorkel and SCUBA at mussel aquaculture sites and adjacent reef sites around the Coromandel Peninsula and Great Barrier Island, northeastern New Zealand (Fig. 3.1), between July 2011 and February 2012. In this region each mussel aquaculture site typically comprised one to seven individual mussel farms with each individual farm between 0.6 and five hectares in surface area. These farms were positioned 50 to 300 m offshore. Fifty three individual mussel farms are listed by Waikato Regional Council at 24 small aquaculture sites around the region. All 24 aquaculture sites were visited and surveys were carried out on 29 individual mussel farms. In addition to the 24 afore mentioned sites was the Wilson Bay Marine Farming Zone (WBMFZ) in the Firth of Thames (Fig. 3.1); this site comprises more than 150 mussel farms which together cover more than 900 hectares of water space approximately two kilometres offshore. Seven representative farms were surveyed within the WBMFZ.

At each mussel farm surveyors swam the length of at least three mussel lines, on or near the surface, noting the presence and density of Undaria per fifty metre length of mussel line and the depth distribution of sporophytes on the dropper lines. Most backbone ropes along mussel lines were approximately 100 m so one mussel line comprised two transects. The number of Undaria sporophytes per 50 m transect was categorised as 0, 1 - 10, 10 - 50, 50 -100, 100 - 250 or 250 - 500. A total of 304 transects were run along 159 mussel lines at 36 different mussel farms. Notes were taken on the size distribution and reproductive status of the Undaria surveyed on each line. Mussels were also measured to the nearest 5 mm \((n = 5)\) on every line surveyed and the average mussel size was calculated for each of these lines.

Surveys of adjacent coastal reefs were carried out concurrently with contiguous 50 x 5 m transects run along sections of coast adjacent to all mussel farming sites surveyed. A total of thirteen kilometres of coast were surveyed via SCUBA and snorkel. In New Zealand, Undaria populations that occur on native reef habitats are typically densest from the low intertidal fringe down to approximately three metres (Brown and Lamare 1993; Russell et al. 2008). Hence,
sampling was concentrated on the shallow-subtidal margin of the reef. The depth of the surveys ranged from mean low water to four metres (MLW) with an average depth across all transects of 2.4 m. For each transect, the habitat type, substrate type and density of Undaria (using the same scale as for mussel farms) was recorded. Coastal habitat types were split into three categories by dominant species or features; urchin barrens, large brown algal canopy (primarily including the kelp Ecklonia radiata and large fucoid species of the Carpophyllum genus) coralline turf and a mixed category was allocated where none of these three habitats were obviously dominant.

3.3.3 Environmental variables

Wave exposure at each site was estimated by calculating a topographical index of fetch for each site; this was done by summing the distance to land for each 10-degree sector of the compass rose. For open sectors of water, the radial distance was arbitrarily set to be 300 km (Gorman et al. 2003). Following Shears et al. (2008), this measurement of fetch was considered the best available estimate of local exposure to ambient swell conditions for the typically shallow coastal mussel farming sites examined in this study. Water clarity was measured using a standard 25 cm diameter black and white secchi disc where the reading was taken as the depth (m) of descending disappearance and ascending reappearance. Dive notes were made on visibility and observed sediment. Information on the allocated surface area (Ha) for each mussel farm was supplied by Waikato Regional Council and confirmed using Google Earth™, distances from the shore to mussel farms were calculated using Google Earth™.

3.3.4 Statistical analysis

Distance-based linear modelling was used to investigate how both infestation levels on farms and presence on the coast related to explanatory variables using the DISTLM procedure in PRIMER v6 (Anderson et al. 2008). Explanatory variables for the analysis of infestation levels on farms included fetch, secchi depth, distance to coast (log(x+1)), size of individual farm and size of overall farming area (log(x+1)). For presence-absence on coast, explanatory variables included fetch, secchi depth, distance to coast (log(x+1)), size of overall farming area (log(x+1)), and mean density on the farm (log(x+1)). For both analyses explanatory variables were normalised and univariate analyses were based on Euclidean distance matrices. The “Best” procedure with AICc selection criterion was used to select the top models.

3.4 RESULTS

3.4.1 Seasonal variation in Undaria populations on mussel farms and coastal reefs

Monthly monitoring revealed different seasonal patterns in density and reproduction between Undaria populations on the coast and those on mussel farms (Fig. 3.2). Undaria was absent from the coastal monitoring site from late summer through to early winter whereas sporophytes were present throughout the year on mussel farm structures (Fig. 3.2A). The mussel farm population had consistently greater average sporophyte lengths as compared to the coastal population (Fig. 3.2B).
3.2B) and sporophytes on the mussel farm maintained reproductive capacity (measured by sporophyll presence) throughout the year (Fig. 3.2C).

3.4.2 Distribution and density of Undaria on mussel farms

Surveys of 36 individual mussel farms in the eastern Hauraki Gulf found Undaria was present on 33 of these farms (Fig S3.1). At the three mussel farms where Undaria was not recorded in surveys, it was observed on neighbouring mussel farms and/or mooring lines. At all mussel farms Undaria was most prevalent in the top two metres of water and declined with depth. The maximum depth for Undaria recorded on a mussel farm was 8 m at Katherine Bay, Great Barrier Island.

The highest densities of Undaria were recorded at a large offshore aquaculture area, Wilson Bay Marine Farming Zone (WBMFZ), and at three smaller mussel aquaculture sites around Coromandel Harbour and Great Barrier Island (Fig 3.3; Fig. S3.1). These sites all had farms with more than 250 sporophytes per 50 m transect on some lines, sometimes up to 500 Undaria sporophytes per 50 m of mussel line. The lowest levels of Undaria infestation were seen at Port Charles and at Kennedy Bay on the eastern side of the Coromandel Peninsula. Kennedy Bay did not have Undaria present on the mussel farms surveyed (which were newly seeded) but Undaria was identified on two mooring ropes within the bay.

Density of Undaria on mussel farms was not strongly related to any of the explanatory variables (Fig. 3.4, Table 3.1C). Mean density was significantly related to distance from shore and the overall size of the farm, but this was largely driven by the high densities at the large offshore site (WBMFZ) (Fig. 3.4C, D). There was no significant relationship between Undaria density on mussel farms and fetch or secchi depth (Table 3.1A). The “best” model based on AICc only included total farm size and this had r^2 = 0.19.

The density of Undaria on mussel lines was weakly positively related to the size of mussels on the lines (data not shown; F1,105 = 33.4, P = <0.0001). But this relationship was largely driven by the fact that farms with small and newly seeded mussels (<40 mm) had little or no Undaria and farms with very large mussels (>100 mm) had high densities of Undaria.

3.4.3 Distribution and presence of Undaria on coastal reefs

Undaria was found at eight coastal reef sites adjacent to mussel farming sites. Densities were generally low on coastal reefs (Fig. 3.3), with highest densities recorded at Katherine Bay, Great Barrier Island (~50 sporophytes per 50 m transect). Undaria was predominantly found in reef habitats lacking a native large brown macroalgal canopy, such as on coralline turf (Corallina officinalis) or urchin barrens (Table S3.1; Fig. 3.5). Coastal Undaria was typically found at highest densities between depths of 0-3 m below mean low water in the shallow subtidal or very low intertidal zone (Table S3.1).

The presence of Undaria on the coast was not clearly related to any of the explanatory variables (Table 3.1; Fig. S3.2). DISTLM indicated that presence of Undaria on coastal reefs was
significantly related to distance to shore, farm size and the mean density on the farms, but not related to secchi depth or wave exposure (Table 3.1B). The “best” model included overall farm size, secchi depth and mean density and had an $r^2 = 0.47$. This relationship was strongly influenced by Undaria being present on the coast adjacent to the Wilsons Bay Marine Farming Zone, which was the largest aquaculture area and typically had the highest Undaria density (Fig. S3.2).

3.5 DISCUSSION

3.5.1 Seasonal variation in Undaria populations on mussel farms and coastal reefs

Undaria populations on mussel farms and at the coastal monitoring site exhibited seasonal variation that is typical for this species in its native range, maximal densities occurred in late spring and lowest densities in late summer (e.g. Koh and Shin 1990). The absence of Undaria at coastal sites in summer-autumn is consistent with native populations where summer temperatures exceed 20°C (Akiyama and Kurogi 1982). However, Undaria on mussel farms was more prolific with a longer annual presence and reproductive capacity and larger average sporophyte size as compared to the monitored coastal population.

A number of factors may facilitate both the longer annual presence and larger size of Undaria on mussel farm structures. On mussel farms, sporophytes are suspended in the water column at shallow depths and subsequently subject to high light levels, with no tidal variation, and enhanced water flow, as compared to the highly turbid conditions at the more sheltered coastal site. Greater water motion can positively influence growth by replenishing in-water nutrients, such as nitrate and phosphorus, when concentrations are higher during winter and spring (Lobban and Wynne 1981; Peteiro and Freire 2011; Shibneva and Skriptsova 2012). Water motion can also prevent the build-up of fine sediments that may inhibit spore attachment and recruitment (Fletcher and Farrell 1999) as well as restrict light and nutrient penetration for sporophytes (Floc'h et al. 1996; Fletcher and Farrell 1999; Curiel et al. 2001).

In addition to differences in water motion and turbidity, competition from other macroalgal species and grazing pressure is also likely to be lower on farms as compared to coastal reefs. In its native range Undaria is a pioneer species and comprises an ordinary part of a successive colonisation process at open sites such as on urchin barrens (Agatsuma et al. 1997). Competitive interactions with native macroalgae where light and space availability are limited can reduce success at coastal sites (e.g. South et al. 2015). Undaria is also highly palatable to grazers (Peréz et al. 1981; Sanderson 1990; Sinner et al. 2000; Thornber et al. 2004; Irigoyen et al. 2011a). Large numbers of the herbivorous mollusc Lunella smaragdus, which are not present on mussel farms, were observed on Undaria sporophytes at the coastal monitoring site, especially during summer as the sporophytes were senescing. The influence of such grazing pressure can greatly reduce coastal Undaria populations at certain times of year and has been seen to affect Undaria colonisation at natural reef systems when it successfully colonises nearby floating structures (Peréz et al. 1981; Castric-Fey et al. 1993; Floc'h et al. 1991; Floc'h et al. 1996; Fletcher and
Farrell 1999; Thornber et al. 2004; Irigoyen et al. 2011a). Mussel farms provide an analogous environment to floating structures used to farm Undaria (see Peteiro and Freire 2011), reiterating the fact that such structures provide an optimal environment for Undaria colonisation and growth.

3.5.2 Distribution and density of Undaria on mussel farms

Overall, the density of Undaria on mussel farms was not strongly related to any of the explanatory variables investigated. However, many of the heavily infested farms were at more exposed sites surveyed; in particular the large offshore farm (WBMFZ). As with the monitored population, this could be related to the enhanced water motion at such sites; Undaria growth rates, sporophyte size and overall biomass are often higher in sporophytes exposed to greater wave action (Castric-Fey 1999; Nanba et al. 2011; Peteiro and Freire 2011; Shibneva and Skriptsova 2012). Although no significant relationship was found between secchi depth and overall density, Undaria was found at greater depths where water clarity was higher (Secchi depth ~8 m) compared to more turbid sites where it was restricted to shallow water (<3 m). Based on these results it is likely that Undaria will be more prevalent at aquaculture sites with high water clarity and greater water motion.

In addition to environmental factors, cultivation practices associated with different marine farming sites may also contribute to different infestation levels. Dense populations were found on mussel lines with larger mussels (80 - 120 mm); including an abandoned mussel farm (Fig. 3.7). Lines with mussels this size have been in the water for at least a year (Aquaculture New Zealand 2011) and these lines were often heavily infested with other invasive species (e.g. the tunicate Styela clava), native seaweeds (e.g., Ecklonia radiata, Sargassum ssp.) and encrusting organisms, indicating little or no cleaning maintenance had been carried out during this timeframe. Mussel harvesting also directly removes Undaria from the mussel lines. Ensuring that mussels are harvested before they become “oversized” means the accompanying Undaria also has a reduced growing time, potentially resulting in a reduction in Undaria sporophytes which reach reproductive maturity. This in turn may reduce the spore supply for subsequent generations of Undaria on the mussel farms as well as nearby reef sites.

Aquaculture transfers among farms may also drive the spread and profusion of Undaria at some sites. For example, the transfer of seed mussels (15 – 60 mm shell length) which are already heavily infested with Undaria gametophytes or other small life stages can influence the resulting density of Undaria at receiving sites (Forrest and Blakemore 2006). Mussel farms at smaller aquaculture sites, where infrastructure had little or no encrusting biofouling, generally had a lower density of Undaria present. Consequently, it may be the case that farms with floats and ropes that are cleaned or rotated out of the water to reduce encrusting biofouling may pose less of an invasion threat to the surrounding coast than those with a build-up of encrusting biofouling on the infrastructure which may allow Undaria to settle and establish more easily.
3.5.3 Distribution and presence of *Undaria* on the coast

*Undaria* was found on reefs inshore from mussel farms at a number of locations, numbers of sporophytes were relatively low compared to the numbers recorded on farms. It was slightly more likely to find *Undaria* inshore from farms positioned closer to shore. However, an exception to this was the sporophytes found on the coast adjacent to the Wilson Bay Marine Farming Zone, which is located approximately two kilometres offshore. While *Undaria* does not naturally spread long distances via spore dispersal (Forrest *et al.* 2000; Grulois *et al.* 2011; Schiel and Thompson 2012), it can spread via drifting fragments or whole sporophytes over scales of up to 10 km (Sanderson 1997). Reproductive fragments or whole sporophytes can be detached from mussel farms naturally or during routine mussel farming processes, these can then be transported both inshore and alongshore via winds, waves and currents. Furthermore, *Undaria* was found growing on mussel farm rope washed inshore from mussel farms and on mussel shells and live mussels beneath mussel farms (Fig. 3.6). These observations demonstrate how mussel farms can facilitate the spread and establishment of *Undaria* through both detached farm components and by providing additional hard substrata in areas which would otherwise consist of soft sediment unsuitable for *Undaria* colonisation (Floc’h *et al.* 1991; Hewitt *et al.* 2005; Merreta *et al.* 2012).

There did not appear to be a relationship between the density of sporophytes growing on mussel farms and the likelihood of finding *Undaria* on the adjacent coast. However, in addition to spore supply and dispersal of reproductive sporophytes or plant fragments, introduction of populations to coastal sites is dependent on appropriate receiving habitats. *Undaria* is an opportunistic species and our finding that the highest density populations were at sites devoid of native algal canopies (Table S3.1) is consistent with results of previous experiments which indicate it has a low competitive ability amongst established canopy-forming macroalgal populations which limit light and space availability (Floc’h *et al.* 1996; Johnson *et al.* 2004; Edgar *et al.* 2004; Valentine and Johnson 2003, 2004; Fletcher and Farrell 2006; Thompson and Schiel 2012). Whilst *Undaria* can inter-mingle with native canopy-forming species in some locations (Russell *et al.* 2008; Raffo *et al.* 2009), it commonly represents an addition to native macroalgal canopies in these instances as opposed to a dominating force which acts to displace or out-compete native species (South *et al.* 2015).

Most of the inshore reefs examined in this study were dominated by thick canopies of native large brown macroalgae and sea urchins were rare. This is typical of relatively sheltered reefs in northeastern New Zealand that experience high turbidity (Shears and Babcock 2004), and it seems unlikely that transient populations of *Undaria* will be able to outcompete or replace native canopy-forming macroalgal species at these sites. However, if invasive *Undaria* populations continue to increase in the Hauraki Gulf, it could represent a significant addition to macroalgal canopies at sites where conditions are suitable and potentially begin to out-compete and displace canopy-forming species at certain sites (Hay and Luckens 1987; Brown and Lamare 1994; Parsons 1995; Russell *et al.* 2008; South *et al.* 2015). Further research is needed to determine
whether Undaria may be capable of invading subtidal sites, amongst native canopy-forming species, in more sheltered and turbid waters within the Hauraki Gulf.

3.5.4 Conclusions

While quantitative research on invasive species which foul aquaculture structures is scarce, our findings are consistent with other studies in demonstrating that aquaculture structures provide optimal conditions for many invasive species. Ascidians, such as solitary tunicates (Styela clava and Ciona intestinalis) and colonial tunicate species (Botrylloides violaceus, Botryllus schlosseri and Didemnum sp), have been shown to be particularly well suited to colonising marine farming structures and can greatly hinder farming operations (McKindsey et al. 2007; Lutz-Collins et al. 2009; Zhan et al. 2015). In the present study additional invasive species, including Styela clava and Didemnum sp, were found on mussel farms and on nearby coastal reefs. Like Undaria, these species are easily spread by transfers of aquaculture equipment and stock, and pose risks to the surrounding environment as they subsequently spread from mussel farms to natural areas (e.g. Lutz-Collins et al 2009).

This work on Undaria has a number of important implications for invasive species management. Aquaculture provides vectors for invasive species introductions and physical structures with optimal growing conditions for many invasive species. Based on current practices, there is no doubt that growth in aquaculture industries and expansion of marine farms into new areas, including large offshore farms, will bring a suite of invasive species that will ultimately spread to natural coastal habitats, regardless of how far they are located from shore. As a regulated activity, the placement of aquaculture sites is one pathway for invasive species introduction which can be controlled. The development of aquaculture industry at sites currently free from invasive species must be carefully considered, integrating information about the wilderness, ecological, economic, social and cultural values of coastal marine areas. Keeping high-value areas free from aquaculture activities could play a vital role towards protecting them from invasive species. Furthermore, stricter controls and monitoring of aquaculture transfers and practices, especially regarding the maintenance and cleaning of farm infrastructure, measures to reduce the build-up of encrusting biofouling and to limit the loss and dispersal of detached farm materials (such as ropes and floats) would aid in reducing the role that aquaculture plays in the spread of invasive species to coastal ecosystems.
Table 3.1
Relationships between the density of *Undaria* on mussel farms (A) and presence of *Undaria* on the adjacent coast (B) and explanatory variables. Marginal tests from distance-based linear modelling (DISTLM).

### A

<table>
<thead>
<tr>
<th>Variable</th>
<th>SS (trace)</th>
<th>Pseudo-F</th>
<th>P</th>
<th>Prop</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fetch</td>
<td>4.6151</td>
<td>1.6059</td>
<td>0.2</td>
<td>0.0048</td>
</tr>
<tr>
<td>Distance to shore</td>
<td>13.756</td>
<td>5.3148</td>
<td>0.0</td>
<td>0.1424</td>
</tr>
<tr>
<td>Log total aquaculture area</td>
<td>18.420</td>
<td>7.5419</td>
<td>0.0</td>
<td>0.1907</td>
</tr>
<tr>
<td>Secchi depth</td>
<td>0.7767</td>
<td>0.2594</td>
<td>0.6</td>
<td>0.0080</td>
</tr>
</tbody>
</table>

### B

<table>
<thead>
<tr>
<th>Variable</th>
<th>SS (trace)</th>
<th>Pseudo-F</th>
<th>P</th>
<th>Prop</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fetch</td>
<td>0.1909</td>
<td>0.7456</td>
<td>0.3</td>
<td>0.0228</td>
</tr>
<tr>
<td>Distance to shore</td>
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<td>9.2575</td>
<td>0.0</td>
<td>0.2244</td>
</tr>
<tr>
<td>Log total aquaculture area</td>
<td>2.4904</td>
<td>13.525</td>
<td>0.0</td>
<td>0.2971</td>
</tr>
<tr>
<td>Secchi depth</td>
<td>0.4195</td>
<td>1.6860</td>
<td>0.2</td>
<td>0.0500</td>
</tr>
<tr>
<td>Log mean density on farm</td>
<td>1.8649</td>
<td>9.1564</td>
<td>0.0</td>
<td>0.2225</td>
</tr>
</tbody>
</table>
Figure 3.1
Location of mussel aquaculture areas surveyed in the Hauraki Gulf; red stars indicate smaller mussel farm sites (0.5-3 Ha), red rectangle represents the Wilson Bay Marine Farming Zone (WBMFZ; ~900 Ha), blue star represents location of the mussel farm and coastal monitoring sites in Coromandel Harbour, northern New Zealand.
Figure 3.2
Seasonal variation in density (A), sporophyte length (B) and percentage of sporophytes with sporophylls (C) for the coastal and mussel farm sites (no sampling June 2012) in Coromandel Harbour, Northern New Zealand. Error bars show standard error.
Figure 3.3

*Undaria* density (± SE) on coastal reefs and mussel farms in the Hauraki Gulf, northern New Zealand; see Fig. 1 for locations. GBI = Great Barrier Island. Densities for mussel farms are for 50 m of mussel line, densities for coastal sites are for 50 x 5 m transects on the reef. Kennedy Bay is not shown as no *Undaria* was found on the mussel farms or reefs at that site.
Figure 3.4
Relationships between Undaria density on mussel farms and explanatory variables. A linear regression line is shown for significant variables (Table 3.1). Symbols represent each mussel farm: triangles are used to indicate coastal sites adjacent to the large offshore Wilson Bay Marine Farming Zone, circles are used for all other mussel farms. Sites are in the Hauraki Gulf, northern New Zealand.
**Figure 3.5**
Density of *Undaria* in dominant reef habitat types categorised during coastal surveys (Barren = Urchin Barren, LBA= Large Brown Algae, Turf = Coralline turf (*Corallina officinalis*) at Great Barrier Island and Coromandel Peninsula sites, Hauraki Gulf, northern New Zealand. Details for individual sites where *Undaria* was recorded can be found in Table S3.1.
Figure 3.6
Photos to illustrate presence of *Undaria* on (A) mussel lines, (B) mussel beds beneath a mussel farm (in 8 m of water) and (C) inshore reefs at Katherine Bay, Great Barrier Island in the Hauraki Gulf, northern New Zealand. Photographs taken by N.T. Shears during *Undaria* surveys in 2012.
Table S3.1

Summary of coastal sites where *Undaria* was recorded during coastal surveys.

<table>
<thead>
<tr>
<th>Date</th>
<th>Location</th>
<th>Co-ordinates</th>
<th>Sporophytes per 50 m (max)</th>
<th>Substrate</th>
<th>Surrounding habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>7/12/2011</td>
<td>Coromandel Harbour</td>
<td>36° 48' 27&quot; 11 E</td>
<td>5</td>
<td>Inside edge of reef on rocks bordering sand flats.</td>
<td>Rocky boulder reef, mixed algae, some <em>Ecklonia radiata</em>, <em>Carpophyllum maschalocarpum</em> and <em>Carpophyllum flexuosum</em>.</td>
</tr>
<tr>
<td>7/12/2011</td>
<td>Kiritia bay**</td>
<td>36° 51' 49&quot; 41 E</td>
<td>49</td>
<td>Coralline flats and on medium boulders between sand flats.</td>
<td>Low density mixed algal canopies. <em>Ecklonia radiata</em>, <em>Carpophyllum maschalocarpum</em> (dominant), <em>Carpophyllum plumosum</em>.</td>
</tr>
<tr>
<td>2/02/2012</td>
<td>Motukopake Island</td>
<td>36° 45' 16&quot; 11 E</td>
<td>2</td>
<td>Small boulders.</td>
<td>Small boulders with sparse <em>Sargassum sinclairii</em> and <em>Carpophyllum flexuosum</em>.</td>
</tr>
<tr>
<td>28/10/2011</td>
<td>Katherine Bay</td>
<td>36°07'50'S 175°20'56'E</td>
<td>150</td>
<td>Boulders and turfing algae.</td>
<td>Sand and reef with boulders. Low density algae - <em>Carpophyllum flexuosum</em> and <em>Ecklonia radiata</em>.</td>
</tr>
</tbody>
</table>

*Monthly survey site, **Also visited on 3/2/12 when a similar number of sporophytes were seen.*
Figure S3.1
Distribution and density of *Undaria* on (A) mussel farms and (B) the coast on the western Coromandel Peninsula, Hauraki Gulf, northern New Zealand. Distribution on the mussel farms and coast for the more northern sites at (C) Kennedy Bay, (D) Port Charles and (E) Great Barrier Island. Levels of infestation are indicated by a colour coding (green = no *Undaria*, orange = 1-100 sporophytes per 50 m transect, red = >100 sporophytes per 50 m transect). Images are from Google Earth ™.
Figure S3.2

Relationships between the presence of *Undaria* at coastal sites and explanatory variables. Symbols represent each coastal site: triangles are used to indicate coastal sites adjacent to the large offshore Wilson Bay Marine Farming Zone, circles are used for all other mussel farms. Sites are in the Hauraki Gulf, northern New Zealand.
Chapter 4

Disturbance of natural communities does not always facilitate invasion of introduced species

4.1 ABSTRACT
Disturbance has been widely demonstrated to facilitate colonisation by invasive species in terrestrial ecosystems, but relatively little is known about the influence of disturbance in promoting invasions in marine communities. A macroalgal clearance experiment was used to test the hypothesis that loss of native macroalgal canopies through disturbance plays an important role in facilitating invasion by the Asian kelp *Undaria pinnatifida* on a subtidal rocky reef. A site was chosen in northern New Zealand (36°80'S 175°45'E) where an *Undaria* population was present in the low intertidal zone, but largely absent from the subtidal reef where native macroalgal canopies dominate. Monitoring from 2012 to 2014 found *Undaria* to be common in the low intertidal zone over spring and early summer months. However, removal of macroalgal canopies across a depth gradient on the adjacent subtidal reef did not result in invasion of *Undaria*; with no *Undaria* recorded in removal or control plots over the subsequent two years. After 17 months native macroalgal canopies had recovered to ~50% of pre-removal cover, but shifts in understory communities were still evident. Whilst disturbance of native communities may promote the establishment of invasive species under certain conditions, other factors such as light availability, sediment accumulation and species interactions may be equally important in affecting establishment and ultimately the ecological impacts of invasive species.

4.2 INTRODUCTION
Once introduced to a new area, the likelihood of success and the level of impact from an introduced species are determined by interactions of the invader with the receiving environment (Simberloff 2013). This context dependency in the invasion process makes predicting impacts from invasive species inherently challenging (Ricciardi *et al.* 2013). However, understanding characteristics of the receiving environment which may contribute to invasion success could increase the ability of decision makers to weight management choices, based on the likely impacts from invasive species, more accurately. One such environmental characteristic is the disturbance regime of a site. Disturbance to a site, such that native species are removed or local environmental conditions favouring native species are changed, can promote the establishment and success of introduced species (Lockwood *et al.* 2007). While there is a wealth of evidence illustrating how disturbances facilitate colonisation by invasive species in terrestrial ecosystems (Lockwood *et al.* 2013), only a few studies have focused on the influence of disturbance in promoting successful invasion in marine communities.

Disturbance to marine environments can arise from natural events such as storms or anthropogenic impacts such as pollution and overfishing. The resulting effects from disturbance may include the
increased availability of resources (when native species are removed) and changes to abiotic conditions such that the site is less suitable for native species (for example when a site is contaminated by urban run-off) (Altman and Whitlatch 2007; Stachowicz et al. 2002). Both natural and anthropogenic disturbances can affect a community’s ability to resist invasion (Ruiz et al. 2000). Disturbance has been identified as enabling establishment of some invasive marine algal species (e.g. Mack et al. 2000; Scheibling and Gagnon 2006), yet in general there remains limited understanding around how conditions within particular receiving environments affect the likelihood of invasion following disturbance (Davidson et al. 2015).

Undaria is a marine algal invader originating from the northern Asian waters around Japan, Korea and China; it now has adventive populations established in more than fourteen countries around the globe (Minchin and Nunn 2014). Undaria possesses a set of attributes common to highly invasive species (Lockwood et al. 2007); it can occupy a broad ecological niche, has the ability to complete its life history quickly, and is tolerant to a wide range of temperatures (Nyberg and Wallentinus 2005; Chapter 2). Suitable habitats encompass a variety of natural and artificial substrates (Saito 1975; Fletcher and Manfredi 1995; Russell et al. 2008) and vary from highly urbanised enclosed harbours to semi-exposed open coastal sites, including an extensive vertical distribution, from low tide level down to 25 m in suitably clear water (Saito 1975; Russell et al. 2008; Irigoyen et al. 2011). Undaria is easily spread and transported (Hay and Luckens 1987) and the (cryptic) microscopic gametophyte phase is difficult to track, control or eradicate (Forrest and Blakemore 2006). It commonly establishes initially on artificial structures where competition is limited (Minchin and Nunn 2014). However, secondary spread and the invasion processes leading to establishment on native reefs is not well understood (Valentine and Johnson 2003, 2004; Zabin et al. 2009) and impacts on native systems are complex (Floc’h et al. 1996; Jiménez et al. 2015; South et al. 2015).

Undaria is a pioneer species in its native range and primarily colonises areas with reduced algal canopies or abundant natural open spaces (e.g. Sanderson 1990, Agatsuma et al. 1997). Consequently, disturbances that remove macroalgal canopies such as storms, urchin grazing or kelp dieback can play an integral part in facilitating the establishment of Undaria in some areas (Johnson et al. 2004; Valentine and Johnson 2004, 2005a). In south-east Asia, commercial production from wild Undaria populations is increased through the creation of open spaces for colonisation by removing other alga from rocky reefs (FAO 2011). Manipulative studies in Australia and southern New Zealand suggest that dense native macroalgal cover can inhibit invasion of Undaria and have demonstrated how disturbances to such assemblages can facilitate invasion in some environments (Valentine and Johnson 2003; Edgar et al. 2004; Thompson and Schiel 2012). Conversely, a study in France concluded that disturbance to native macroalgal canopies did not result in Undaria invasion even when reproductive Undaria sporophytes were placed in cleared benthic areas, potentially due to lack of suitable substratum (Floc’h et al.1996).

Undaria has recently been discovered at multiple sites around northeastern New Zealand (Chapter 2, Appendix I). Northern New Zealand is one of the warmest water regions of invasion for Undaria in the world (Chapter 2) and questions exist regarding how this species will affect native reef ecosystems at warmer latitudes and what factors may facilitate or inhibit the spread of Undaria. In northeastern New Zealand Undaria is most abundant on marine farms and other artificial structures and comparatively rare
on natural reefs where it is mostly found in low intertidal or subtidal reef habitats lacking large native macroalgae (Chapter 3). These patterns suggest that the perennial native macroalgal canopies common to shallow reefs in northeastern New Zealand play an important role in inhibiting the establishment of Undaria. This theory was examined using a macroalgal canopy removal experiment across a subtidal reef adjacent to an intertidal population of Undaria. Canopy species were removed to mimic a natural disturbance event and the responses of both native algal communities and Undaria were monitored over two growth seasons. I hypothesised that if native macroalgae are the main factor inhibiting Undaria from invading these shallow reef habitats, canopy removal would facilitate the establishment of Undaria.

4.3 METHODS

4.3.1 Study site

The experiment was carried out on a rocky headland within the Coromandel Harbour, northern New Zealand (36°48′26.S 175°27′41.E; Fig. 4.1). The site was located on the southern side of the harbour and was sheltered from large waves and swell. The reef extended ~15 m offshore from the intertidal to a depth of ~2 m below mean low water. Benthic habitat was characterised by gradually sloping rocky substratum; reef, boulders and cobbles, with a mix of canopy-forming native macroalgae (Fig. 4.1B) including the fucoids Cystophora retroflexa, Carpophyllum maschalocarpum and C. flexuosum, and the kelp Ecklonia radiata. The algal and invertebrate assemblage present was typical of shallow sheltered reefs in northeastern New Zealand (Shears and Babcock 2004). Undaria was present in the low intertidal and shallow subtidal zone (<0.5 m below MLW), which was dominated by coralline turf (Corallina officinalis) and a sparse native algal canopy (Fig. 4.1D). A permanent transect along the low intertidal shoreline, 50 x 2 m, was set up at this site in October 2012 and the number of Undaria sporophytes present were recorded every month until December 2014.

4.3.2 Surveys and canopy clearance

On 6th of July 2013 eight line transects, approximately 10 m apart, were established running from the intertidal zone along a depth gradient to the outer edge of the reef, 17 - 22 m (Fig. 4.1C). A 1 m² quadrat was placed at the start of each transect and quadrats were surveyed every other metre along the length of each transect (n = 7 to 11 for each transect, total n = 66). For each quadrat, depth and substrate type were recorded, algal canopy cover and substrate cover were quantified. Canopy cover was quantified by estimating the percentage area covered by different macroalgal species. The percentage area covered by understory species was also assessed by moving aside canopy-forming algae. For canopy forming algae, identification to species level was possible, whereas, for understory species it was necessary to allocate them to species complexes or guilds (e.g. foliose red algae, green turf algae). Three of the eight transects surveyed were randomly selected and manually cleared of all canopy-forming macroalgae to a width of 3 m (1.5 m either side of the transect line). Macroalgal stipes were cut just above the holdfast and understory species were left intact. The algal removal was carried out prior to the peak growth season for Undaria to allow for the growth of gametophytes already present on the substratum as well as the deposition of spores, released from nearby sporophytes during the following summer period (Valentine and Johnson 2003, 2004; Thompson and Schiel 2012). At the time of the initial clearance a HOBO®
temperature logger, set to log temperature every thirty minutes 24 hrs a day, was suspended in the water approximately 1 m below the surface from a nearby raft.

The site was visited monthly over the following 17 months to record the number of Undaria sporophytes on the shoreline transect and observations were made along the perpendicular transects. Data were downloaded from the temperature logger each month for the course of the experiment. A full survey was carried out on 11th December 2014 to investigate how the reef community had changed in control and removal transects using the same methods as the initial survey (n = 6 to 9 for each transect, total n = 61). Along the cleared transects the central 1 m was surveyed with a 1 m buffer on either side to reduce edge effects. The site was also visited in October 2015 to provide a count of Undaria along the shoreline transect and counts in the experimental transects during the third growing season post clearance.

4.4 RESULTS

The intertidal Undaria population at the site exhibited a seasonal growth pattern, with sporophytes appearing in mid-late winter, increasing in abundance through spring, and sporophytes dying off in early summer. Inter-annual variability was high, with the maximum abundances recorded in spring 2013 (Fig. 4.2) and a considerably lower number in spring 2014. Low numbers of Undaria were present in July 2013 when experimental clearances were carried out in the adjacent subtidal reef. Observations in spring (October) 2015 were also of low numbers, with eight sporophytes counted within the shoreline transect.

The removal of native canopy species did not result in Undaria recruitment into any of the cleared transects. No Undaria sporophytes were recorded in any of the removal transects during either the initial surveys, the interim observations or during the surveys 17 months after the canopy removal. Sporophytes were present inshore from the native algal canopy (Fig. 4.2) but did not extend into the removal or control transects. Undaria was also not observed in experimental transects in October 2015 (27 months after the initial clearance). Temperature measurements from the site showed conditions were consistent across years and typical for the site (Fig. 4.2).

After 17 months the native macroalgal canopy in the removal transects had recovered to about half of pre-clearance levels; average total canopy cover (± SE) was 56 ± 5 % pre-clearance and 26 ± 6% 17 months post clearance. The control plots remained constant with ~65% canopy cover. In general all native algal species were back to pre-clearance coverages after 17 months (Fig. 4.3), except the most dominant species Carpophyllum flexuosum which was not recorded in two of the cleared transects during the second survey (Fig. 4.3A). Observations in October 2015 (27 months after the initial clearance) confirmed further re-colonisation of the cleared areas by dense stands of native macroalgae and an absence of Undaria. Removal of the native macroalgal canopy also led to large changes in the understory community and these were still evident 17 months after the canopy removal (Fig. 4.4). The most obvious change in the canopy removal transects was an increase in cover of bare rock (Fig. 4.4A) and a decline in the cover of crustose coralline algae (Fig. 4.4B). The cover of crustose coralline algae and bare rock remained relatively constant in the controls (4.4).
4.5 DISCUSSION

The present study demonstrated that disturbance of native macroalgal canopies did not facilitate the invasion of Undaria at this rocky subtidal reef site. Despite complete clearance of large areas (51 - 66 m²) of canopy-forming native species across a depth gradient, no Undaria was subsequently found in the removal transects. The effect of the clearance on native macroalgal canopy cover and understory species remained evident 17 months after the canopy removal. A large decrease in the cover of crustose coralline algae occurred following canopy removal, most likely caused by increased exposure to light and bleaching once the canopy was removed (Valentine and Johnson 2003). Observations in October 2015, 27 months post clearance, confirmed the continued re-colonisation of the cleared areas by native macroalgal species and the absence of Undaria.

Although Undaria was present in the adjacent intertidal and shallow subtidal zone, in open spaces, it did not recruit into the removal transects. Canopy removal was carried out at the optimum time to allow settlement of the bare areas by Undaria spores released from mature sporophytes in the surrounding area (Valentine and Johnson 2003, 2004; Thompson and Schiel 2012) and it was hypothesised this would result in recruitment of visible sporophytes the following spring. In addition to this source of propagules, it was possible that gametophytes may be lying dormant below the intact algal canopy and these would begin to grow once exposed to light following the canopy removal (Valentine and Johnson 2003, 2004; Pang et al. 2008). Results from concurrent surveys of the adjacent intertidal and shallow subtidal zone indicated a particularly successful season for Undaria recruitment in 2013 following the clearance, but a less successful growth season in 2014.

The results of this study suggest that algal canopies are not the primary factor preventing Undaria extending into the subtidal zone at this site. This is in contrast to results from experiments in Tasmania, Australia and southern New Zealand where high densities of Undaria recruited into canopy removal plots within one growth season (Valentine and Johnson 2003; Edgar et al. 2004; Thompson and Schiel 2012). While open spaces and light availability can facilitate the invasion process, the properties of the recipient benthic community, local environmental conditions (e.g. temperature and turbidity) and propagule supply, can be equally important in determining recruitment success (Dunstan and Johnson 2007; Lockwood et al. 2007; Thompson and Schiel 2012).

Water temperature is known to influence Undaria recruitment (Chapter 2). However, relatively consistent seasonal temperature cycles during the course of the experiment (Fig. 4.2) make it unlikely that inter-annual variation in temperature was responsible for the poor recruitment success recorded in 2014 as compared to 2013. Propagule supply within the study site is unknown, but with each mature sporophyte capable of releasing up to seven hundred million zoospores (Schiel and Thompson 2012) it was assumed the population (≥289 individuals) in the nearby intertidal zone could have effectivity inoculated the study area during the 2012 and 2013 growth seasons, and potentially supplied propagules in previous years as well (Valentine and Johnson 2003; Hewitt et al. 2005). Undaria colonisation events can occur quickly, in response to light availability, following disturbance events when propagules are present beneath the canopy (Johnson et al. 2004; Valentine and Johnson 2004). However, because Undaria requires high light levels for successful growth and reproduction, the transparency and turbidity of the water affect recruitment and growth (Peteiro and Freire 2011). Observations from the current study site indicate high
turbidity; with visibility at the site commonly less than 1 m. The resultant low light levels may prevent \textit{Undaria} gametophytes from becoming fertile, restricting \textit{Undaria} to the intertidal and very shallow subtidal (<1 m depth) at this site.

Sediment loading was also relatively high at the site and on average sediment covered about 40% of the reef cover. \textit{Undaria} can tolerate sediment stress to a certain extent (Hay and Villouta 1993; Valentine and Johnson 2005b; Pang et al. 2008), and in Tasmania has been seen to colonise sites affected by sedimentation more effectively than some native species (Valentine and Johnson 2005a), but sediment loading can reduce \textit{Undaria} spore attachment and recruitment (Floc'h et al. 1991; Fletcher and Farrell 1999; Geange et al. 2014). It has been hypothesised that \textit{Undaria} can colonise sites with high sediment loading during ‘recruitment windows’ when sediment is removed by stochastic weather events (Valentine and Johnson 2005b). Variability in sediment cover over time could explain some of the inter-annual variation in the intertidal \textit{Undaria} population. However, this possibility requires further investigation.

Another factor likely to limit the recruitment of \textit{Undaria} to the canopy removal areas is the absence of suitable substrate for colonisation. In the present study there was an abundance of bare rocky substrate and crustose coralline algae which may not be suitable for spore settlement (Johnson and Mann 1986; Floc'h et al. 1996), and a low cover (<5 %) of geniculate coralline algae (or coralline turf such as \textit{Corallina officinalis}). Coralline turf can harbour \textit{Undaria} gametophytes and significantly facilitate the recruitment of sporophytes (Russell et al. 2008; Schiel and Thompson 2012; Thompson and Schiel 2012). The understorey at canopy removal experiment sites in Tasmania, where \textit{Undaria} recruited in large numbers, comprised a diverse assemblage of turfing algal species (Valentine and Johnson 2003; Edgar 2004) and in southern New Zealand recruitment into cleared sites occurred almost exclusively on coralline turf (Thompson and Schiel 2012). Recruitment of \textit{Caulerpa} sp. is facilitated by turfing algae due to the physical structure having a large surface area to catch algal fragments and spores, whilst also retaining water and providing refuge from grazers (Ceccherelli et al. 2002, Bulleri and Benedetti-Cecchi 2008, Bulleri et al. 2010). Coralline turf likely catches \textit{Undaria} spores in the same way and also provides refuge to developing \textit{Undaria} gametophytes (Schiel and Thompson 2012; Thompson and Schiel 2012). Coralline turf was present in the low intertidal and very shallow subtidal zones at the site, matching the distribution of \textit{Undaria}. Coralline turf may however be restricted from deeper water by low light and high sedimentation (Farr et al. 2009). Therefore, high turbidity may restrict \textit{Undaria} from deeper water directly (as described above) or indirectly through its effects on coralline turf which plays an important role in spore settlement and development of microscopic stages of \textit{Undaria}.

The site examined in this study has subtidal macroalgal assemblages that are typical of sheltered reefs with relatively high turbidity in this region (Shears and Babcock 2004). It appears from our study that \textit{Undaria} is not well suited to colonising such sites following disturbance, and consequently will have little impact on the native subtidal reef assemblages in such conditions. However, at more open coast sites in this region that experience higher wave action and greater water clarity \textit{Undaria} does occur in deeper reef habitats where macroalgae are lacking such as in urchin barrens and turfing algal habitat (Chapter 3). These patterns suggest that disturbance of native macroalgae could facilitate invasion of \textit{Undaria} under these conditions.
Macroalgal forests are under threat worldwide and shifts to urchin barrens and turfing algal states have been documented in many regions as a result of human-induced stressors (Connell et al. 2008, Ling et al. 2015). Further changes in disturbance regimes are likely with climate change as an increase in storms and warming events (Brynes et al. 2011, Wernberg et al. 2013) is likely. While these disturbances will provide increased opportunities for colonisation of invasive species onto temperate reefs, our findings suggest that the success and ecological impacts will be highly dependent on the characteristics of the receiving environment.

Further work is needed to experimentally investigate the complex relationships between marine algal invaders and receiving environments; effects of sediment loading, turbidity (light availability) and the importance of, and interactions with, understory species, such as turfing algal species, on macroalgal recruitment remain largely unknown. A better understanding of the factors influencing the establishment of invasive species will ultimately allow better prediction of invasion events and the impacts invasive species will have on native ecosystems in an increasing stressed marine environment. Whilst disturbance of native communities is critical in the establishment of invasive species at some sites, it is not always the determinate factor in the invasion process. When drawing on previous work to make decisions around the control and management of invasive species the complex and site specific nature of the invasion process must be taken into account.
Figure 4.1
Study site: location within the Coromandel Harbour as indicated by a star (A), typical subtidal macroalgal canopy (B), location of shoreline transect around the reef and numbers representing the location of perpendicular transects from the low intertidal to the subtidal reef edge (removal transects are 2, 4 and 7) (C), *Undaria* in the shallow subtidal zone (D). Coromandel Harbour is on the eastern side of the Hauraki Gulf, northern New Zealand.
Figure 4.2
Total number of *Undaria* sporophytes counted in the monitored intertidal shoreline transect (50 x 2 m) in Coromandel Harbour, Hauraki Gulf, northern New Zealand. Daily average water temperature (°C) is also shown (grey line).
Figure 4.3
Average changes in % cover (± SE) for the six dominant canopy-forming algal species at the monitoring site in Coromandel Harbour, Hauraki Gulf, northern New Zealand. Control transects (n = 40 for initial survey at 0 months, n = 38 for survey at 17 months) are represented by closed circles and removal transects (n = 26 for initial survey at 0 months, n = 23 for survey at 17 months) are represented by open circles. Lines are not shown for removal plots as these species were all removed following the initial survey (0 months), whereas controls were left intact.
Figure 4.4
Average changes in % cover (± SE) for the six dominant understory cover groups at the monitoring site in Coromandel Harbour, Hauraki Gulf, northern New Zealand. Control transects (n = 40 for initial survey at 0 months, n = 38 for survey at 17 months) are represented by closed circles and removal transects (n = 26 for initial survey at 0 months, n = 23 for survey at 17 months) are represented by open circles. Lines are shown between points for both treatments as none of these groups were directly manipulated.
5.1 ABSTRACT
Understanding genetic diversity in populations of the invasive Asian kelp, Undaria pinnatifida, can reveal the origins of introduced populations, indicate probable vectors of introduction and spread, as well as potentially reveal characteristics influencing invasion success at different locations. Here we investigate the genetic diversity of Undaria specimens from the North Island of New Zealand based on two mitochondrial loci, the cox3 gene and the non-coding tatC–tLeu spacer, and relate these to known strains, or haplotypes, from native and introduced populations from around the world. We found low genetic diversity, with only two closely related haplotypes (10 and 11) identified, from a possible 27 known haplotypes. In northeastern New Zealand, a region that includes some of the warmest water populations of Undaria in the world, only one haplotype (10) was found. The two haplotypes, 10 and 11, originate from Korea and China, some of the warmest populations in the Northern Hemisphere. While the lack of genetic diversity in northern New Zealand may indicate a low number of introductions from overseas and spread from southern New Zealand, we suggest that haplotype 10 is more tolerant than other strains to a wide range of temperature regimes, including subtropical conditions, and therefore the only haplotype to successfully establish in northern New Zealand. The ability of one strain of Undaria to successfully colonise locations across such a wide range of temperature regimes raises concerns that this strain may pose an increased risk to subtropical reef systems. Further investigation of the properties of each haplotype group for Undaria is needed to explore these possible relationships with temperature tolerance.

5.2 INTRODUCTION
Increasing global connectivity, volumes of international trade and exploitation of the marine environment are increasing pressure on marine ecosystems. A key environmental stressor for which awareness is rapidly growing is invasive species, sometimes referred to as biological pollution; the negative impact from invasive species is currently regarded as one of the greatest threats to coastal marine ecosystems (Olenin et al. 2011; Cecere et al. 2015).

Macroalgae are a well-recognised component of invasive marine species (Schaffelke and Hewitt 2007). Current global estimates for the number of introduced macroalgae now reach more than 300 species (Davidson et al. 2015 and references therein). It remains difficult to predict which species may become invasive and cause negative impacts at any given site of introduction, but once established some species pose significant economic and environmental risks (Anderson 2007, Hewitt and Campbell 2007; Schaffelke and Hewitt 2007; Olenin et al. 2011). Understanding the origins of introduced species and
what processes affect successful introductions allows the best chance of preventing the establishment of invasive species in the first place (e.g. Williams et al. 2013), thereby avoiding impacts resulting from invasion (Floerl et al. 2005).

Undaria is an invasive macroalgal species which is considered highly damaging to introduced environments (Nyberg and Wallentinus 2005; McLaughlan et al. 2014). Undaria impacts on native communities via space monopolisation, this in turn causes changes in community composition and can have effects on higher trophic levels (Raffo et al. 2009; Irigoyen et al. 2011a, b; South et al. 2015). The native range for Undaria is northeastern Asia; around Japan, Korea and the neighbouring coasts of some eastern parts of China and southeast Russia (Verlaque 2007 and references therein). In the past forty years Undaria has been spread beyond its native range, and it is now invasive to at least fourteen countries around the world (Minchin and Nunn 2014).

Transoceanic spread of Undaria is primarily attributed to hull fouling on large scale commercial fishing vessels (Hay and Luckens 1987; Voisin et al. 2005; Uwai et al. 2006). Once Undaria has been introduced to a new location, successful establishment relies upon suitable receiving conditions. Invasion processes often result in reduced genetic diversity in introduced populations (Voisin et al. 2005). The success of the introduced population may therefore be dependent on the arrival of individuals from a pre-adapted source population; individuals will colonise introduced sites with differing success depending on how the local environment matches native conditions (Asif and Krug 2011).

Undaria can tolerate a broad range of temperature conditions (Nyberg and Wallentinus 2005). However, it does have a requirement for winter temperatures to fall below 15 °C (Chapter 2). The northern-most Undaria population so far known in New Zealand (Rangaunu Harbour, Northland) was discovered in 2013 and experiences a temperature range of 15 - 24 °C (Appendix I). Minimum water temperatures at this site are therefore close to the thermal limit for Undaria, making it one of the warmest water populations of Undaria in the world. There is evidence for some acclimation of Undaria populations to habitat-dependent thermal stress, particularly in subtidal versus intertidal populations (Henkel and Hofmann 2008) and there is also evidence that Undaria populations from different locations of origin may have variable temperature tolerances. Gao et al. (2013) showed that different optimum growth temperatures occurred in Undaria sporophytes transplanted from populations at different latitudes to a common location in Japan. Differences persisted after three generations of cultivation in a new location, strongly suggesting that they are under genetic control rather than due to physiological adaptation. In their study, southern Japanese sporophytes had optimum growth rates at temperatures 2 - 4 °C higher than specimens from more northern locations. Lethal limits were also different for northern and southern Japanese sporophytes, with temperatures of 22 to at least 24°C proving lethal for northern sporophytes, but not to sporophytes native to warmer southern regions (Gao et al. 2013). Different strains of Undaria may therefore vary in their capacity to establish populations under different temperature regimes at introduced locations.

The morphology of Undaria sporophytes is plastic and highly variable; it is influenced by environmental conditions (Shibneva et al. 2013). Hence, strains of Undaria of different origins cannot necessarily be identified by morphological differences. Genetic classification is the only way to reliably identify and differentiate Undaria strains. Genetic compositions of invasive Undaria populations can then be used to
identify the origins of introduced populations, probable vectors of introduction and spread, as well as potentially revealing characteristics that determine invasion success at different sites.

Genetic diversity in *Undaria* has been investigated previously by Uwai et al. (2006), who examined 260 specimens from native and introduced populations around the world, revealing 27 combined cox3 and tatC - tLeu haplotypes, or sets of DNA variations, which represent different strains. These haplotypes were consequently assigned to four genetic and biogeographical groups. The highest genetic diversity for any introduced area, 10 haplotypes, was found in southern New Zealand. The study by Uwai et al. (2006) included 25 samples from four populations in the North Island and identified one haplotype from these samples. High diversity in southern New Zealand has been attributed to multiple introductions from native locations (Voisin et al. 2005; Uwai et al. 2006). This high genetic diversity in southern New Zealand, and a consequent pool of different haplotypes, may increase the likelihood of adaptive genetic variants being present (Sakai et al. 2001; Uwai et al. 2006). Differing temperature tolerances, and indeed other variable physiological parameters, could have significant impacts on the capacity of *Undaria* for range expansion.

Since the study of Uwai et al. (2006), *Undaria* has spread to numerous other locations in northern New Zealand (Chapter 1) including the recently discovered population in Northland, the northern-most and warmest part of New Zealand (Appendix I). The present study builds on work by Uwai et al. (2006) and investigates the genetic diversity of these northern New Zealand populations. We use the mitochondrial gene sequences of the cox3 and tatC - tLeu regions, and results are directly related to haplotypes identified by Uwai et al. (2006). Analyses included samples from all known sites of invasion around the North Island, including the newly discovered Northland population. As well as revealing the origins of invasive populations, determining the genetic diversity of *Undaria* populations towards the upper extreme of its temperature range may reveal links between haplotypes and temperature tolerances.

5.3 METHODS

Analysis involved 40 samples from sites within the Hauraki Gulf (Fig. 5.1; Table 5.1). Sampling was concentrated at the two main sites of *Undaria* infestation; Waitemata Harbour (n = 15) and the Firth of Thames (n = 15), an additional ten samples were analysed from mussel farms and coastal reef sites around Great Barrier Island and Coromandel Harbour in the eastern Hauraki Gulf (Table 5.1). In addition, samples were collected from all other known populations around the North Island (Fig. 5.1; Table 5.1); five samples were processed from each North Island location except Gisborne where only one *Undaria* sporophyte was found. Samples were collected between 2011 and 2015. Sporophytes were randomly chosen for sampling and were taken from a range of substrata at different areas across each individual site where-ever practicable (Table 5.1).

Sampling involved taking small pieces of tissue from the basal blade of *Undaria* sporophytes and immediately placing tissue into bags of desiccant silica gel beads to dry. DNA extractions were carried out on the dried sample material using the CTAB-proteinase K extraction protocol (Zuccarello and Lokhorst 2005). The polymerase chain reaction was used to amplify two regions encoded in the mitochondrial genome; the partial cox3 gene and the tatC - tLeu region (from the 3` end of the tatC gene to the 5` end of the tLeu gene). Primers used were CAF4A (5`-ATGTTTACTTGGTGAGRGA-3`) and CAR4A (5`-
CCCCACCARTAWATNGTNAG-3’) for the cox3 gene (Kogame et al. 2005; Uwai et al. 2006) and tatCEF (5’-AATAATATATGAGATTATCTATTCTATT-3’) and tLeuR (5’- ACCTAAACACCGCGTGTATACC-3’) for the tatC-tLeu region (Uwai et al. 2006). PCR was carried out using an iCycler (BioRad Laboratories, Hercules, CA, USA) machine as follows for cox3: initial denaturation step of 96 °C for 2 minutes, 35 cycles of denaturation at 96 °C for 15 seconds, 50 °C annealing for 30 seconds, 72 °C extension for 60 seconds and final 72 °C extension for 10 minutes. For the tatC-tLeu marker we used an initial denaturation step of 96 °C for 2 minutes, 35 cycles of denaturation at 96 °C for 15 seconds, 55 °C annealing for 30 seconds, 72 °C extension for 2 mins and final 72 °C extension for 10 minutes. Products were inspected on agarose gels and purified using Exonuclease I/alkaline phosphatase digestion. Sequencing was carried out using the Applied Biosystems 3130XL Genetic Analyzer at the University of Auckland Sequencing facility. Sequences were assembled into contigs and aligned with haplotypes from Uwai et al. (2006) in Geneious 7.1.5 (Biomatters, Auckland). Sequences were assigned to haplotypes identified by Uwai et al. (2006) based on 100% sequence homology over the sequenced region.

5.4 RESULTS

Sixty-two concatenated cox3 and tatC-tLeu sequences resulted from 69 cox3 and 65 tatC-tLeu spacer sequences. These were obtained from 74 specimens collected from around the North Island of New Zealand between August 2011 and June 2015. Six samples from Westhaven Marina (Hauraki Gulf), two from the Firth of Thames (Hauraki Gulf), three from Northland and the one sample from Gisborne did not successfully amplify (these are not shown in table 5.1).

All specimens had a single cox3 haplotype assignment (Table 5.1) that corresponded to a common cox3 haplotype from Korea, China and northern Japan (sensu Uwai et al. 2006). This cox3 sequence corresponds to previously identified haplotypes 14, 12, 11, 10, 9, 8, 7, 6, 5, 4 and 3 from Uwai et al. (2006) which are lodged in GenBank© (Benson et al. 2006). Two distinct haplotypes were present in the concatenated cox3 and tatC-tLeu sequences, corresponding to haplotypes 10 and 11 from Uwai et al. (2006). These haplotypes differ by one substitution.

All 47 samples from the east coast of the North Island including the Hauraki Gulf, Northland, Tauranga and Napier were assigned to haplotype 10 (Table 5.1). Haplotype 10 was also present at the other three locations in southern and western parts of the North Island (Taranaki, Wellington and Porirua) as well as Haplotype 11 (Table 5.1).

5.5 DISCUSSION

The present study found very low genetic diversity in Undaria populations from northern New Zealand; with only two haplotypes identified from 62 samples. By contrast, Uwai et al. (2006) identified eight haplotypes from 75 samples from New Zealand and an additional two haplotypes from herbarium specimens. Our analysis found no genetic variation among all east coast populations examined. While samples collected from Gisborne did not successfully amplify in this study, Uwai et al. (2006) found only Haplotype 10 at this location, consistent with our findings with populations to the north (Tauranga) and south (Napier) only having Haplotype 10 identified. Haplotype 10 was common to all locations around the
North Island including the northern-most population at Rangaunu Harbour. Haplotype 11 was identified from the west coast and southern parts of the North Island.

The two haplotypes identified in this study, haplotypes 10 and 11, are closely related and have long histories in New Zealand as noted by Uwai et al. (2006). Haplotype 10 was identified from multiple sites around Wellington in the late 1980s and is common throughout New Zealand from Northland to Stewart Island, ~34 – 47 °S (Uwai et al. 2006; Table 5.1) including four North Island areas; Wellington, Napier, Gisborne and Auckland. Haplotype 11 is common around southern New Zealand and was identified from Taranaki to Stewart Island, ~39 – 47 °S (Uwai et al. 2006; Table 5.1). Both haplotypes (10 and 11) were found on the hull of a Korean trawler in Wellington Harbour in 1987, the year Undaria was discovered in New Zealand (Hay and Luckens 1987) and hence are some of the earliest established haplotypes in the country. To date haplotypes 10 and 11 are the only two haplotypes to be identified north of Christchurch, 43 °S (Uwai et al. 2006; Table 5.1).

Haplotypes 10 and 11 are native to continental Asia, found in Korea and China, and were not identified from 100 samples analysed by Uwai et al. (2006) from around Japan. Haplotype 10 is common around the eastern and western coasts of Korea from ~35 - 38 °N, and was also found at Kuko Island (30 °N), China, in what is likely one of the southern-most Undaria populations in the Northern Hemisphere (Dellatorre et al. 2014). Haplotype 11 was less common from continental Asia but was found on the eastern Korean coastline, at 35 °N (Uwai et al. 2006).

The limited diversity in northern New Zealand potentially indicates a low number of successful introductions from native locations or limited domestic spread from the South Island. Alternatively, it is possible that only a limited number of haplotypes can cope with the warmer temperature regime in northern New Zealand, indicating the presence of strains pre-adapted to warmer water temperatures. Multiple introductions of Undaria occurred at South Island ports in the 1980s and 1990s (Voisin et al. 2005); following these introductions the secondary spread of Undaria around southern New Zealand occurred rapidly via domestic routes (Stuart et al. 2004). The spread of Undaria around the North Island has occurred in later years (Chapter 1) and was previously expected to be limited by warmer water temperatures (Sinner et al. 2000).

The slower and more recent spread of Undaria around the North Island is inconsistent with the considerably larger population size in the North Island (North Island ~3.5 million vs South Island ~1 million) and consequent boat traffic, and the fact that the North Island has more and larger ports than the South Island (Ministry of Transport 2011). There are also major centres of aquaculture (mussels) in both islands. Therefore, the mechanisms and frequency of introduction and spread for Undaria in the North Island are likely to be similar to, if not greater than, those for southern New Zealand where multiple introductions of Undaria have occurred from different origins. The identification of only one strain (haplotype 10) in northern New Zealand therefore may indicate that haplotype 10 is the only strain which can tolerate the warmer temperature regime in northern New Zealand. Water temperatures in southern New Zealand (e.g. Otago) can range from 7.6 - 15.6 ºC annually as compared to sites north of Wellington which commonly fall within an annual range of ~12 - 22 ºC (Chapter 6). Analysis of herbarium samples by Uwai et al. (2006) revealed that dominant haplotypes at different locations change over time, and it may be that strains which are better able to cope with local temperature regimes are the ones which persist.
*Undaria* is generally acknowledged to have a broad temperature tolerance; water temperatures in its native range undergo large seasonal temperature fluctuations (Akiyama and Kurogi 1982). However, reports of temperatures suitable for the optimal growth of *Undaria* sporophytes vary across the literature; for example 5 - 10°C (Zhang et al. 1984), 10 -15 °C (Bardach et al. 1972), 15 - 17 °C (Saito 1975), 10 – 20 °C (Akiyama and Kurogi 1982), 20 °C (Morita et al. 2003b) and *Undaria* from different locations have different temperature tolerances and preferences (Gao et al. 2013). It is possible that some of this variability in temperature tolerances between studies and between populations is related to the different strains present within a region. Haplotype 10 was identified in China (Uwai et al 2006) near the southern distribution limits for *Undaria*, where water temperatures range from 9.3 - 27.3°C (Dellatorre et al. 2014) and the invasive range for haplotype 10, including sites from the southern South Island to Northland in New Zealand, demonstrates an ability to cope with a wide range of different temperature regimes.

Whilst Uwai et al. (2006) linked haplotypes to different biogeographical regions of origin; it is not known whether different temperature tolerances directly correlate with these haplotypes or haplotype groups. The present study suggests thermal pre-adaptation may influence invasion success for differentiated source populations. This indicates a link between temperature tolerance and the genetic classification for *Undaria*. The ability of one strain of *Undaria* to successfully colonise locations across such a wide range of temperature regimes raises concerns that this strain may pose an increased risk to subtropical reef systems.
Figure 5.1
Locations of North Island sample collection sites indicated by red stars (A). Locations of Hauraki Gulf sample collection sites indicated by stars and a rectangle delineating the Wilson Bay Marine Farming Area (B). Haplotypes identified at each site (Sensu Uwai et al. 2006) are shown with the number of samples given in brackets. Haplotypes recorded from northern New Zealand in Uwai et al. (2006) are shown in italics.
Table 5.1
Sampling location information and haplotype assignments (*sensu* Uwai et al. 2006) from the concatenated *cox3* and *tatC*-t*Leu* sequences. The number of each haplotype is shown in parentheses if multiple haplotypes were found.

<table>
<thead>
<tr>
<th>Region</th>
<th>Habitat and Location</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Date collected</th>
<th>No. of samples</th>
<th>Haplotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northland</td>
<td>Reef, Puheke Beach, Karikari Peninsula</td>
<td>34°51.314</td>
<td>173°19.484</td>
<td>18.6.15</td>
<td>2</td>
<td>10</td>
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<td>10</td>
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<td>175°20.561</td>
<td>28.10.11</td>
<td>2</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Reef, Katherine Bay, Great Barrier Island (Fig. 5.1 northern site)</td>
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<td>175°20.519</td>
<td>28.10.1</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
<td></td>
<td>Reef, Oneura Bay, Great Barrier Island (Fig. 5.1 southern site)</td>
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<td>175°18.492</td>
<td>28.1011</td>
<td>1</td>
<td>10</td>
</tr>
<tr>
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<tr>
<td></td>
<td>Reef, Coromandel Harbour</td>
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<td>175°27.683</td>
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<td>Mussel Farm C, Coromandel Harbour</td>
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<td>Longitude</td>
<td>Date</td>
<td>Time</td>
<td>Licence</td>
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<td>Waitemata Harbour</td>
<td>Service barge at Pier A, Westhaven Marina, Waitemata Harbour</td>
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<td>174°44.925</td>
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<td>175°24.120</td>
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<td>Mussel farms with no licence numbers displayed, Wilson Bay, Firth of Thames</td>
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<td>176°10.424</td>
<td>6.8.14</td>
<td>3</td>
<td>10</td>
</tr>
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<td></td>
<td>Breakwater, Butters Crane Wharf, Tauranga Harbour</td>
<td>37°40.043</td>
<td>176°10.778</td>
<td>6.8.14</td>
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<td>Napier</td>
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<td>176°90.550</td>
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<td>Taranaki</td>
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<td>10(2) 11(1)</td>
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Chapter 6

Using satellite-derived sea surface temperature to predict the potential global range and phenology of the invasive kelp *Undaria pinnatifida*

A research paper has been published based on this chapter:


6.1 ABSTRACT

Understanding the temperature tolerances and phenology of an invasive species is essential to predicting its potential range and impacts on receiving environments. *Undaria pinnatifida* is a kelp species native to Northern Asian waters where it has a winter annual growth cycle. At some introduced sites *Undaria* can persist year-round, which potentially exacerbates its impacts. In this study we synthesise information on the global distribution and phenology of *Undaria* and use satellite-derived sea surface temperature (SST) measurements to investigate how distribution and phenology relate to temperature regime. These relationships are used to predict the potential global range and phenology of *Undaria*. The overall thermal limits of *Undaria* were considered to be the areas where the range in SST minima overlaps with the range in SST maxima for existing populations. *Undaria* was found to occur in regions with maximum temperatures of 13.5 - 29.5°C and minimum temperatures of 0.1 - 15.5°C. The SST regime differed between native and introduced locations, and between locations with year-round and annual populations. All locations with year-round populations had a maximum SST less than 20°C, whereas annual populations had maximum SST greater than 20°C; a finding consistent with the reported thermal parameters for *Undaria* gametogenesis. These results demonstrate that extensive areas of the world’s coastline have SST regimes suitable for *Undaria* colonisation and are potentially at risk from invasion. When considered in combination with additional environmental factors influencing distribution success, this type of prediction mapping provides a valuable tool for invasive species management.

6.2 INTRODUCTION

Ecological niche modelling is widely used to predict the potential distribution of invasive species (e.g. Peterson and Vieglais 2001). However, it is increasingly clear that invasive species can alter their niche at invaded locations. For example, they may occupy different climatic niche ranges at invaded locations (Broennimann et al. 2007) and when exposed to new environmental conditions, the growth and life cycle patterns of introduced populations can diverge from those displayed by native populations (Lockwood et al. 2007; Simberloff 2013). Divergent species traits can, in turn, exacerbate the impacts these species have on receiving environments (Mack et al. 2000). Therefore, understanding what drives variations in
species life cycles at introduced sites is fundamental to predicting range expansions and the concurrent impacts, biotic and abiotic, of invasive species.

In the marine environment, algae comprise a significant component of invasive species (Schaffelke et al. 2007) and water temperature is a primary factor which influences both their distribution and life cycle patterns (Lobban and Wynne 1981; Breeman 1988; Breeman 1990). Broad temperature tolerances allow invasive species to spread over wide introduced ranges (Dukes and Mooney 1999; Nyberg and Wallentinus 2005; Williams and Smith 2007; Poloczanska et al. 2013). Some of the most high risk invasive algal species in the world, such as Caulerpa taxifolia (M. Vahl) C. Agardh, and the large brown seaweeds Sargassum muticum (Yendo) Fensholt, and Undaria pinnatifida, have adventive distributions which extend beyond those anticipated from looking at water temperatures in their native range (Aguilar-Rosas and Galindo 1990; Floc'h et al 1991; Nyberg and Wallentinus 2005).

Undaria is native to Northern Asian waters (Kang 1966; Funahashi 1973; Yamada 1980). It has a wide temperature tolerance and is invasive to several regions around the world (Hay and Luckens 1987; Sanderson 1990; Piriz and Casas 1994; Fletcher and Manfredi 1995; Campbell et al. 1999; Cecere et al. 2000; Silva et al. 2002; Minchin and Nunn 2014). In its native range Undaria has an annual life cycle comprised of a macroscopic sporophyte phase in winter and a microscopic gametophyte phase in summer (e.g. Koh and Shin 1990). The sporophyte growth cycle aligns with cooler winter temperatures and senescence of the visible sporophyte occurs en masse as temperatures reach 24 - 27 °C; at these temperatures the growth rate of gametophytes also slows and the small male and female germlings adopt a resting phase (Tamura 1966, Saito 1975; Dieck 1993; Morita et al. 2003b; Gao et al. 2013). We found no reports in the literature of Undaria populations persisting year-round within its native range. At some introduced locations however Undaria does not adhere to a strictly winter annual life cycle, with successive generations of sporophytes being observed year-round in parts of New Zealand, South England, Argentina, Australia, California, and on the French Atlantic coast (Hay and Luckens 1987; Floc'h et al. 1991; Hay and Villouta 1993; Fletcher and Farrell 1999; Casas et al. 2008; Martin and Bastida 2008; Zabin et al. 2009). While these year-round populations can still exhibit a high degree of seasonality in the abundance of sporophytes (Hay and Villouta 1993; Brown 1999; Casas et al. 2008; Martin and Bastida 2008), unlike native populations, there is no autumnal hiatus, and adult individuals are present year-round. The maximum summer sea surface temperatures at these introduced locations range between 15 - 19 °C and it has been hypothesised that at these temperatures macroscopic sporophytes are able to recruit and be present year-round (Hay and Villouta, 1993; Stuart 2004; Thornber et al. 2004; Schaffelke et al. 2005).

Undaria is a pervasive and proficient invasive species (e.g. Wallentinus 2007). It can form dense assemblages which dominate light, space and nutrient resources, altering the structure and character of marine environments (Sinner et al. 2000; Stuart 2004; Raffo et al. 2009; Irigoyen et al. 2011a, b). It can also disrupt aquaculture activities and foul vessel hulls and other marine structures (Fletcher and Farrell 1999; Cecere et al. 2000; Verlaque 2007). In regions where Undaria can persist year-round these impacts are likely to be greater than in areas where it is only seasonally present (Thornber et al. 2004; Raffo et al. 2009; Irigoyen et al. 2011a, b). Consequently, predicting the potential range and phenology of introduced Undaria populations is key to predicting the potential impacts of invasion.
This paper provides a global synthesis of the current distribution of Undaria and investigates how both the distribution and phenology of Undaria are related to water temperature regimes. Following validation against reported temperatures from the literature, temperature regimes were quantified for all reported locations where Undaria is found using satellite-derived measurements of sea surface temperature (SST). This allowed comparison of temperature ranges between all native and introduced populations, as well as between locations with differing phenologies (winter annual vs. year-round persistence). These temperature relationships were then used to predict the potential range and phenology of Undaria globally. This study differs from typical niche modelling approaches (e.g. Peterson and Vieglais 2001) as we use satellite-derived sea surface temperature data to predict both the range and phenology of an invasive algal species on a global scale. The approach used has value in not only assessing the potential range of an invasive species, but also the likely levels of impact associated with different phenologies at different locations.

6.3 METHODS

6.3.1 Compilation of global distribution and phenology information

Information on the current distribution and phenology of Undaria populations was synthesised based on a systematic review of population studies on Undaria. Literature was searched through the University of Auckland Library system including the use of databases such as NZ Science, Scopus and Google Scholar. Japanese, South American and French literature was searched using Google Scholar, the Hokkaido University Collection of Scholarly and Academic Papers (HUSCAP) and the Archive Institutionnelle de l’Ifremer. Some Japanese, Spanish and French research papers were available with only the abstract in English. Some of the Spanish and French papers could be translated using online translation tools and many of the more recent publications are printed entirely in English. Research articles were sought pertaining to the distribution and life cycle patterns of Undaria both within and outside its native range, effort was concentrated on adventive populations with a representative set of native sites selected. Worldwide distribution information was collated for the time period from 1981 to 2014, using the search terms “Undaria pinnatifida”. Material published on the physical composition of Undaria tissue, medicinal and nutritional properties surrounding Undaria were omitted from this review.

Information for this paper was derived from 69 published articles, four student research theses, six books, six published government agency commissioned technical reports, two extracts from conference proceedings and the Global Invasive Species Database.

From each study, the location, and when available, the phenology of Undaria populations and temperature regime at the location was recorded. Phenology was classified as being annual; one main recruitment pulse and macroscopic sporophytes not present throughout the year, or year-round; multiple recruitment pulses and some macroscopic sporophytes present throughout the year. Locations were considered to be distinct spatially if they were recorded as comprising discrete populations. In total, Undaria was reported from 51 locations worldwide (Table 6.1; Fig. 6.1) and information was available on the phenology of populations at 25 locations. Information on the annual temperature regime (i.e. SST minima and maxima) was available at 25 of the locations (Table 6.1). Native sites where temperature information was available encompassed the geographical limits of the species and its temperature
tolerances, and were therefore considered sufficient to enable accurate predictions. The endemic range of *Undaria* has its southern boundary in the centre of Mie Prefecture, southern Honshu, Japan (Morita et al. 2003a), although it has been introduced further south in Asian waters for mariculture (Uwai et al. 2006). The northern limit of distribution is southern Russia, Primorye region, Peter the Great Bay (Skriptsova et al. 2004) giving a latitudinal range of ~34° to 42° N (Table 6.1).

### 6.3.2 Global temperature data

Temperature data reported in the literature from field studies were collected using a range of methods, sampling frequencies, and over varying temporal and spatial scales, making it difficult to compare among studies and locations. Therefore, in order to predict the temperature limits for *Undaria* worldwide, satellite-derived sea surface temperature (SST) data was used to provide a consistent and standardised approach to estimating temperature regime for all identified *Undaria* locations. Because *Undaria* typically grows in shallow water or near the surface (e.g. Saito 1975), sea surface temperature was considered an appropriate proxy for temperature at a site. Satellite-derived SST data has previously been shown to be adequate at inferring broad-scale benthic climatology at depths less than 10m (Smale and Wernberg 2009). *Undaria* field studies define water temperature regimes by the yearly maxima and minima values, which typically define the survivable limits for different life history stages of *Undaria* (e.g. Morita et al. 2003a, b). Therefore, we characterise the SST regime using global maxima and minima values.

National Oceanic and Atmospheric Administration (NOAA) Optimum Interpolation (OI) SST V2 time series data were obtained from NOAA/OAR/ESRL PSD, Boulder, Colorado, USA, via their web site (http://www.esrl.noaa.gov/psd/). Weekly average SST values are available on a 1° global grid from 1990-2013. Minimum and maximum weekly averages from each year were used to provide an estimate of the long-term minimum and maximum temperatures. Mean yearly minimum and mean yearly maximum grids were then calculated based on annual minimum and maximum values from 1990 - 2013. The 90th percentile of yearly maxima and 10th percentile of yearly minima were calculated as an additional estimate of maximum and minimum temperature for each location. This resulted in two global estimations of yearly maximum SST (mean maximum and 90th percentile maximum) and two global estimations of yearly minimum SST (mean minimum and 10th percentile minimum).

To determine which of the satellite-derived estimates of SST minima and maxima best predicted the SST regime at coastal locations; these were compared to the reported SST minima and maxima values from the literature (see additional details in Fig. 6.2 legend). The 10th percentile minima better represented literature minima than the mean of yearly minima, with a higher $R^2$ and lower mean absolute error (10th percentile minima: $r^2 = 0.710$, $p<0.001$, MAE = 1.61 °C vs. Mean yearly minima: $r^2 = 0.700$, $p<0.001$, MAE = 2.09 °C). In contrast, there was little difference in how well the 90th percentile maxima or mean yearly maxima represented the literature maxima (90th percentile maxima: $r^2 = 0.789$, $p<0.001$, mean absolute error (MAE) = 1.50 °C vs. Mean yearly maxima: $r^2 = 0.799$, $p<0.001$, MAE = 1.54 °C). Therefore, for consistency the 10th percentile values were used to represent SST minima (Fig. 6.1A) and 90th percentile values were used to represent SST maxima (Fig. 6.1B) in all subsequent calculations. SST range was calculated as the difference between the 90th percentile maximum and 10th percentile minimum (Fig. 6.1C). In general, the strong concordance between satellite-derived SST and measured
temperature data (Fig. 6.2) meant that SST regime could be reliably estimated for all locations where Undaria has been reported. Minimum satellite-derived temperatures were, however, often higher than minimum temperatures reported in the literature. This is most likely due to greater terrestrial influence on inshore temperature values that are not captured in the larger-scale satellite-derived data. For example, Ise Bay and Toyama Gulf, Honshu in Japan have recorded annual minimums of 7.9 °C and 4.0 °C respectively, whereas satellite-derived minimum temperature values were 15.5 °C and 8.3 °C respectively. Both of these sites have high freshwater and snowmelt input from local mountains, which likely results in cooler recorded temperatures inshore compared to satellite-derived values.

Sea surface temperature calculations were done in Python using the netCDF4 library to access data and the Pandas library (McKinney 2010) for aggregation. Sea surface temperature metrics (maximum, minimum and annual range) were compared between native and introduced populations, and between populations with year-round and annual presence of sporophytes using a Welch’s t-test in Python statsmodels v0.6.0. This test was used as it allows for different variances in the underlying populations by adjusting the degrees of freedom.

6.3.3 Using satellite-derived SST to map global distribution and phenology
The potential global range where SST regimes are likely to support Undaria populations was estimated based on the SST regimes for existing populations and the global grids of 90th percentile maximum SST and 10th percentile minimum SST from OISST V2 (as outlined above). The overall thermal limits of Undaria were considered to be the area where the range in SST minima for existing populations overlaps with the range in SST maxima for existing populations. Areas with SST maxima and minima outside of these ranges were considered to be too hot or too cold for Undaria to establish viable populations. Within the predicted thermal range of Undaria, phenology was predicted based on the reported differences in SST regime between populations with year-round and annual presence of sporophytes. Due to separation in the ranges of SST maxima between year-round and annual populations, a small area was classified as having no prediction for phenology. The results were interpolated to 0.125° latitude x 0.125° longitude for display as a global map of thermal limits and predicted phenology.

6.4 RESULTS
6.4.1 Global distribution and temperature regimes
Sea surface temperature regime in the native range of Undaria is characterised by a large annual range (Table 6.1; Fig. 6.1) with temperatures commonly fluctuating by 20 to 25 °C annually, ranging from 0.1 °C in the winter, to 29.5 °C in the summer (Fig. 6.3). Introduced Undaria populations occur at locations with a variety of temperature regimes (Fig. 6.1 and 6.3), but overall have a narrower annual temperature range (c. 7 – 15 °C) compared to native populations (Table 6.1; Fig. 6.1 and 6.3; Literature: t = -6.64, df = 8.10, p = <0.001; Satellite-derived: t = -7.83, df = 7.47, p = <0.001).

Maximum temperatures at locations within the native range are significantly higher than at introduced locations, based on both literature and satellite-derived temperature values (Literature: t = -4.08, df = 11.15, p = 0.002, Satellite-derived: t = -6.81, df = 9.16, p = <0.001). There are however a few introduced locations, such as the Lagoon of Venice, Italy (8.3 - 28.0°C) and Baja California, Mexico (14.6 - 22.4 °C),
that have similar maximum temperatures to native populations. Minimum temperatures among the introduced locations were quite variable (0.1 - 15.5 °C) and typically higher than those from native locations (Fig. 6.3). Based on reported data in the literature this difference in minimum temperatures was significant (t = 3.58, df = 6.27, p = 0.011), but there was no significant difference based on satellite-derived data (t = 1.75, df = 6.63, p = 0.125).

6.4.2 Variation in phenology
All Undaria populations reported within the native range had a winter annual life cycle, whereas introduced populations had a mix of annual and year-round presence of sporophytes (Table 6.1). There were clear differences in temperature regime between locations with annual and year-round presence of sporophytes, and these patterns were consistent based on both the literature and satellite-derived temperature values (Fig. 6.4). Based on satellite-derived temperature data there was no difference in minimum temperature between populations with annual and year-round presence (t = -0.43, df = 12.01, p = 0.676), but annual populations had significantly higher maximum temperatures than year-round populations (t = 8.07, df = 14.06, p < 0.001). Consequently, locations with annual populations also had a greater range in temperature (Fig. 6.4, t = 4.93, df = 10.88, p < 0.001). All Undaria populations known to have an annual life cycle for which reported temperatures were available in the literature had reported maximum temperatures ≥22.0 °C and satellite-derived maximum temperatures ≥20.6 °C. All year-round populations had reported maximum temperatures ≤20.2 °C and satellite-derived maximum temperatures ≤19.4 °C (Fig. 6.4).

6.4.3 Prediction of global distribution and phenology
Based on the above analysis of the reported distribution, the thermal limits of Undaria were estimated to be where maximum temperatures were between 13.5 and 29.5 °C and minimum temperatures were between 0.1 and 15.5 °C. To predict the potential global distribution of Undaria these were conservatively adjusted, such that areas with maxima greater than 30 °C or minima greater than 16 °C were deemed too hot to support Undaria populations, and areas where maxima was less than 13 °C or minima less than 0 °C were deemed too cold to support Undaria populations (Fig. 6.5). Within these thermal limits, populations were characterised as having a year-round phenology where maxima were ≥19.4 °C, and as having an annual phenology where maxima were ≥20.6 °C (Fig. 6.5). Phenology was not predicted for areas with maxima between 19.4 and 20.6 °C, and these sites are referred to as having unknown phenology. For the 26 locations where Undaria populations occur, but the phenology is currently not recorded in the literature, 12 were predicted as annual, 9 were predicted as being year-round, and for 5 locations no prediction was made (Table 6.1; Fig. 6.5).

Based on the global temperature data set, large stretches of the world’s coastline were found to have temperature regimes suitable for Undaria establishment (Fig. 6.5). Prediction bands for the two different phenologies covered a relatively similar extent and the current distribution of Undaria is relatively evenly split between these two bands. Notable areas with suitable temperatures where Undaria has not yet invaded include the east coast of North America and the west coasts of South America and Africa. The phenology in each of these areas would be predicted to vary along the coast in relation to SST with year-round populations at higher latitudes and annual populations at lower latitudes.
6.5 DISCUSSION

Invasive species can have significant impacts on receiving environments and often invasions and impact assessments cannot keep up with rates of introduction and spread of invasive species to new locations. Hence, risk analysis for invasive species often relies on information around the fundamental and realised niches of these species using baseline knowledge about sensitivities, tolerances and behaviour of the invasive species (MacNeil and Campbell 2014). One of the issues with this approach is that invasive species often have very large fundamental niches and are capable of surviving a wide range of environmental conditions. Understanding how wide the fundamental niche is for a specific species is sometimes only realised once an invader starts to spread within and beyond its new territory (Sinner et al. 2000; MacNeil and Campbell 2014).

Over the past 32 years Undaria has gained an extensive global distribution and now occurs across a variety of temperature regimes (Fig. 6.1). Undaria was found to be limited to sites where maximum water temperatures are between 13.5 and 29.5 °C and where minimum water temperatures are between 0.1 and 15.5 °C. In its introduced range Undaria exhibits variable seasonal growth patterns, displaying a winter annual phenology at some locations, consistent with native populations, and a persistent year-round phenology at other locations. Our findings are consistent with the hypothesis that the seasonality of the macroscopic sporophyte population is dependent on the local temperature regime, specifically the maximum annual sea surface temperature (Saito 1975; Hay and Villouta 1993; Stuart et al. 1999). Based on satellite-derived temperatures, where summer maxima exceeded 20.6 °C, populations exhibited a winter annual phenology, whereas at locations where summer maxima were below 19.4 °C, populations were classified as being year-round, meaning that some adult sporophytes were present throughout the year. Undaria has not been recorded at locations where maximum temperatures exceed 29.5 °C or where temperatures drop below 0 °C. This is consistent with the critical temperature limits known to kill all life stages of Undaria (Tamura 1966, Saito 1975; Dieck 1993). Sites with annual temperature regimes falling inside the determined limits (0 - 30 °C) must include a period of time during the year where temperatures are between 10 - 20 °C in order to support effective reproduction (Saito 1975; Lobban and Wynne 1981; Bite 2001; Morita et al. 2003a and references therein; Thornber et al. 2004; Kohtio 2008). Mature Undaria sporophytes are tolerant of a wide range of temperatures (5 - 27 °C) and following the maturation of the sporophyte, the release and germination of zoospores can occur at temperatures between 5 - 25 °C (Saito 1975; Floc’h et al. 1991; Castic-Fey et al. 1999; Petrone et al. 2011). Zoospores then grow into gametophytes. Although gametophytes may continue to grow at temperatures as high as 27 °C and may survive at temperatures of 0 - 29 °C (Saito 1975; Dieck 1993), gametophyte maturation and gametogenesis take place at temperatures between 5 - 20 °C (Saito, 1956a, b; Lobban and Wynne 1981; Pang et al. 2008) and the optimal temperature range for maturation of gametophytes is between 10 and 20 °C (Saito 1956a, b; Morita et al. 2003a and references therein; Brown 1999; Bite 2001; Thornber et al. 2004; Kohtio 2008). This upper temperature threshold is consistent with our finding that in locations where summer temperatures exceed 20 °C populations experience a summertime hiatus and are therefore largely restricted to a winter annual life cycle. Locations which experience a narrow annual water temperature range with a summer maximum below 20 °C may allow gametogenesis to occur continually during the year; for warmer locations the amount of time during the year when temperatures remain above 20 °C will affect the persistence of Undaria populations. Undaria sporophytes have a
maximum lifespan of around 6 - 8 months, (Hay and Luckens 1987; Castric-Fey et al. 1999; Morita et al. 2003b) so a recruitment period of four months or longer, or multiple recruitment pulses per year can result in a year-round presence of macroscopic sporophytes.

Peaks of sporophyte recruitment and growth in introduced populations consistently occur when temperatures are between 10 - 17 °C (Casas and Piriz, 1996; Castric-Fey et al. 1999; Kohtio 2008; Thornber et al. 2004; Jessop 2006). Consequently, even year-round populations typically experience seasonal variations in growth and reproduction in coincidence with this temperature range (Hay 1990; Hay and Villouta 1993; Thornber et al. 2004; Casas et al. 2008). Factors such as light and nutrient availability vary with seasons and years and also affect the resulting size and abundance of plants at different times of year (Dean 1998; Stuart et al. 1999; Choi et al. 2007). However, our results suggest that temperature is an underlying regulator of whether populations are able to persist year-round. It is therefore expected that inter-annual variation in Undaria phenology will occur in regions where maximum summer temperatures are around 20 °C; during cooler years (max. SST <20 °C) populations would be expected to persist year-round, whereas in years when temperatures exceed 20 °C populations would be expected to experience a hiatus in recruitment.

The relationships between both the distribution and phenology of Undaria, and sea surface temperature, allowed prediction of the thermal distributional limits of Undaria and its expected phenology globally. The satellite-derived SST data was generally effective in predicting overall SST regimes at locations where Undaria occurs, due to the confirmed relationship between the SST regimes reported in the literature and those predicted from satellite-derived data. Satellite-derived estimates of SST minima were higher than reported SST minima for a number of locations, such as those around Japan where snowmelt may influence recorded water temperatures (Coastal Oceanography Research Committee, Oceanographical Society of Japan 1985). Inshore SST can be highly variable across small scales (e.g. Yamada 1980; Morita et al. 2003a) as it is more frequently influenced by terrestrial and climatic factors than offshore SST and therefore can show greater fluctuations than oceanic waters (Thomas et al. 2002). Adventive Undaria populations commonly occupy shallow water and artificial marine structures (Fletcher and Manfredi 1995; Floc’h et al. 1991; Floc’h et al. 1996; Verlaque 2007) where these small-scale temperature fluctuations are not captured at the relatively coarse resolution of the satellite-derived data (Smale and Wernberg 2009). Nevertheless, the relationship between satellite-derived and literature SST values in the present study was considered strong enough to allow the use of satellite-derived estimates as a standardised measure of SST regime to make broad-scale predictions for distribution and phenology of Undaria.

All populations known to be year-round had satellite-derived maximum SST ≤19.4 °C, whereas all of the annual populations had satellite-derived maximum SST ≥20.6 °C. Due to this separation in maximum temperatures, no predictions of phenology were made for locations where maximum SST fell between 19.4 and 20.6 °C. This approach allows for the fact that we do not know the critical temperature within this range that would determine the realised phenology, that the duration of time spent above a critical temperature will also be important, and that maximum SST for any given location will vary inter-annually such that populations within this range could have a variable phenology from year to year. It is also important to note that within the broad prediction bands for annual and year-round populations, local-scale variation in SST (e.g. associated with shallow sheltered embayments or marinas) will ultimately
influence the distribution and phenology of Undaria. For example, within the range where Undaria is expected to occur year-round, local-scale factors could result in summer maximum SST >20 °C, which would be predicted to result in an annual population. Therefore, while this method provides a global prediction of regions where SST regimes are suitable for Undaria and defines temperature limits for the likely phenology of populations at some sites, additional information on local SST regimes is important for small-scale predictions of both distribution and phenology. Within the designated thermal limits the realised distribution of Undaria will also depend upon suitable receiving conditions for survival, for example; habitat, salinity, water motion and nutrient levels must all be appropriate (e.g. Lobban and Wynne 1981).

The ability to predict the potential phenology of new populations has implications for understanding impacts at invasion sites. Whether generations of Undaria sporophytes are overlapping or discrete and whether the life history is strictly annual or not, has important consequences for the success of Undaria populations, its impact on native flora and fauna, and its influence on marine community structure. For example, if macroscopic stages only appear in winter when fewer native kelp species are reproductively active, Undaria might compete less directly with native species (Valentine and Johnson 2004); whereas if generations are persistent and overlapping throughout the year, the potential for negative effects on native species is much greater (Thornber et al. 2004; Thompson and Schiel 2012). Such impacts have been documented in Nuevo Gulf, Argentina where persistent Undaria populations dominate reef sites year-round and impact on community structure and composition, excluding some native species (Raffo et al. 2009; Irigoyen et al. 2011a, b). This study predicts many populations, particularly around Northern Atlantic Europe, could have populations which persist year-round, potentially putting native benthic communities at greater risk from the impacts of Undaria invasion at these sites.

Understanding how temperature affects Undaria phenology and mapping temperatures and temperature ranges allows large-scale predictions of where Undaria can survive and the probable life cycle patterns of populations within these regions. This study identified a number of large regions where temperature regimes are suitable, but Undaria has not yet been documented. These sites include the east coast of North America and the west coasts of South America and Africa. Mapping these regions where temperatures are suitable Undaria survival is only the first step in defining particular coastal locations which may be at risk from Undaria invasion. Further research is needed to understand additional local factors which may determine areas within these broad regions which are at risk from invasion. As well as suitable receiving conditions, in order for Undaria to successfully colonise a new site it requires a transport mechanism or vector for introduction, so factors such as the proximity of shipping ports and marinas need to be considered to determine the actual likelihood of Undaria invasion.

Understanding differences in temperature regimes between native and introduced populations is vital when making predictions about the potential distribution of an invasive species. A species in its native range will likely have a reported distribution which is relatively complete, while a species colonising new areas may spread beyond known temperature limits (Simberloff 2013). The present example revealed how sea surface temperature regimes generally differ between sites of native and introduced Undaria populations. While this study outlines the potential global range for Undaria, these estimates may still be conservative. Undaria gametophytes can potentially survive at 0 °C for at least two weeks (Dieck 1993),
which may allow it to colonise colder sites if conditions are otherwise suitable, including reaching temperatures warm enough for reproduction. Further research is needed to determine the extent to which *Undaria* may be cold-tolerant, especially in its gametophyte form, and how this could influence a greater distribution to cold-water sites.

Incorporating different species traits into more traditional ecological niche modelling provides a further advance in predicting invasive species distributions and likely impacts (Guisan and Thuiller 2005). In this case, incorporating *Undaria* phenology, lead to the novel finding that these differences in temperature regime can result in different life cycle patterns, which can ultimately influence the magnitude of invasion impacts. This type of approach to modelling species distribution will be of increasing importance under a changing climate regime as the potential distribution of invasive species is also likely to change (Sutherst 2000; Stachowicz et al. 2002; Wernberg et al. 2010). Understanding how the functional attributes of species, such as phenology, may vary under such scenarios will greatly increase the value in such projections.
Table 6.1
Summary of locations for all known adventive Undaria populations around the world and seven representative native sites: reported (where available) and satellite-derived sea surface temperature data for each site and reported (where available) and predicted phenology for each population

<table>
<thead>
<tr>
<th>Location, Country</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Native</th>
<th>Reported SST</th>
<th>Reported phenology</th>
<th>Reference</th>
<th>Satellite-derived SST</th>
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<tr>
<td></td>
<td></td>
<td></td>
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<td>Min</td>
<td>Rang e</td>
<td></td>
<td>Max</td>
<td>Min</td>
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90
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**The Americas**

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**Australasia**

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<th>Year</th>
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Figure 6.1
Global distribution of *Undaria* in relation to global patterns in annual minimum (A), maximum (B) and range (C) in sea surface temperature (°C). Native (star) and introduced (circle) populations are shown.
Figure 6.2
Satellite-derived estimates vs. literature records of maximum (A) and minimum (B) sea surface temperature at Undaria study locations. Each point represents a study on Undaria where the maxima and minima temperature has been reported for a location (Table 6.1). The error bars on the satellite-derived measurements represent the range of maximum (A) and minimum (B) annual values observed across the time series (1990 - 2013). The points indicate the 90th percentile for maxima and 10th percentile for minima. Diagonal line depicts a 1:1 relationship.
Figure 6.3
Comparison of temperature regimes (minimum, maximum and range) between native and introduced populations of *Undaria* based on literature records (left) and satellite-derived estimates (right). The box shows the interquartile range (25 - 75 percentiles, with horizontal red line as median) and the whiskers show the 5 - 95 percentiles.
Figure 6.4
Comparison of temperature regimes (minimum, maximum and range) between annual and year-round life cycle patterns of *Undaria* based on literature records (left) and satellite-derived estimates (right). The box shows the interquartile range (25 - 75 percentiles, with horizontal red line as median) and the whiskers show the 5 - 95 percentiles.

Note: literature values are only shown for a subset of the populations where temperature information was available, whereas satellite-derived estimates are given for all locations where phenology information was available (Table 6.1).
Figure 6.5
Potential global range and phenology for *Undaria* based on satellite-derived sea surface temperature (Blue = area predicted to support year-round sporophyte presence, Red = area predicted to support annual sporophyte presence, Yellow = no prediction). The predicted phenology for locations where *Undaria* is present, but the phenology is not documented (black symbols), is given in Table 6.1.
Chapter 7

General Discussion

This thesis used a range of methods including population monitoring and surveys, experimental manipulations, genetic analysis and a synthesis of literature to investigate the population ecology and factors influencing the distribution and establishment of Undaria in northern New Zealand and worldwide. Research was conducted on the northern most populations of Undaria in the Southern Hemisphere, located in a region previously classified as sub-optimal for Undaria establishment due to a warmer temperature regime than that of its native range (Sinner et al. 2000). Prior to this research, information on invasive Undaria populations under such warm-temperate conditions was lacking.

7.1 THE INFLUENCE OF TEMPERATURE ON UNDARIA PHENOLOGY

This study clearly demonstrates how the seasonal cycle of Undaria is closely tied to variations in water temperature (Chapter 2). Monitoring of Undaria populations in the Hauraki Gulf revealed a winter annual phenology in this warm-temperate region. Populations had one main recruitment event in winter, which occurred 1 - 2 months after water temperatures decreased below ~15 °C. Effective recruitment was not observed at temperatures in excess of 20 °C. Population densities, average sporophyte length and growth rates declined rapidly at temperatures above 20 °C, and lowest densities were sustained over summer and autumn months when temperatures remained above 20 °C. Direct links between these temperature thresholds, <15 °C for recruitment and >20 °C for sporophyte absence, were evident through inter-annual variation in population cycling. The timing of recruitment and the duration of sporophyte absence varied from year to year depending on when temperatures decreased below 15 °C and how long temperatures were above 20 °C respectively. The phenology of Undaria in the Hauraki Gulf was similar to that seen in its native range, but the life cycle was compressed into a shorter annual period (Saito 1975; Lee and Sohn 1993; Oh and Koh 1996). This annual cycle differed from that of other invasive Undaria populations in parts of southern New Zealand, England, Argentina, Australia, California, and France, where sporophytes can be present year-round (Hay and Luckens 1987; Floc’h et al. 1991; Hay and Villouta 1993; Fletcher and Farrell 1999; Casas et al. 2008; Martin and Bastida 2008; Zabin et al). This variability among regions demonstrates how Undaria can adjust its life cycle and phenology to maximise its growth output when temperatures are suitable for recruitment and growth.

The observed temperature thresholds for recruitment are consistent with temperature requirements of the microscopic life cycle phase of Undaria. The optimal temperature range for gametogenesis is between 10 and 20 °C (Saito 1956a, b; Floc’h et al. 1991; Morita et al. 2003a; Brown 1999; Bite 2001; Thornber et al. 2004; Kohtio 2008). Temperatures aligning with maximal
growth rate and densities in the Hauraki Gulf were ≤17 °C, consistent with Undaria populations from around the world (10 - 17 °C, Hay 1990; Hay and Villouta 1993; Casas and Piriz, 1996; Castric-Fey et al. 1999; Thornber et al. 2004; Jessop 2006; Casas et al. 2008; Kohtio 2008). This optimal temperature range for growth and abundance results in seasonal variations in sporophyte presence even in populations which persist year-round (Casas et al. 2008). Locations with annual temperature regimes which stay within these, 10 - 17 °C, limits are most likely to have sporophytes present year-round.

A synthesis of the current distribution and phenology of Undaria populations around the world revealed how phenology varied between locations according to water temperature regime (Chapter 6). Sites with a summer maxima below 20 °C can allow sporophytes to persist year-round and at sites where summer temperatures are above 20 °C, such as the Hauraki Gulf, Undaria has a winter annual life cycle. In its native range populations maintain a winter annual cycle because they are exposed to summer temperatures above 20 °C. Temperature regimes differ between native and introduced locations and this variation determines differences in phenology between native and invasive populations (Chapter 6). The phenology of populations present at sites where maximum temperatures were estimated to be 19.4 and 20.6 °C could not be confirmed (Chapter 6). Maximum temperatures for any given location vary inter-annually such that populations at sites where maximum temperatures are ~20 °C could have a variable phenology from year to year; during cooler years (summer temperatures <20 °C) populations would be expected to persist year-round, whereas in years when temperatures exceed 20 °C populations would be expected to experience a hiatus in recruitment. Potential implications around the different seasonal growth patterns of Undaria populations are discussed in section 7.3.

7.2 ESTABLISHMENT OF UNDARIA POPULATIONS

Undaria is well established on mussel aquaculture and marina structures in the Hauraki Gulf (Chapter 2, 3). Undaria is known to colonise man-made structures more readily than natural reef habitats (Hay 1990; Russell et al. 2008; Minchin and Nunn 2014) and Chapter 3 found that Undaria was more widespread and present at higher densities on artificial structures as compared to adjacent coastal reef habitats in the Hauraki Gulf. On natural reefs Undaria was typically found in reef habitats such as coralline turf flats and urchin barrens that did not have dense stands of canopy-forming macroalgae (Chapter 3). This is consistent with patterns observed in invasive populations around the world (Castric-Fey et al. 1993; Hay and Villouta 1993; Casas and Piriz 1996; Fletcher and Manfredi 1995; Valentine and Johnson 2004; Miller and Engle 2009; Schiel and Thompson 2012) and suggests that Undaria has a limited ability to establish amongst dense stands of canopy-forming species which restrict space and light availability (Castric-Fey et al. 1993; Floc’h et al. 1996; Grulois et al. 2011; Schiel and Thompson 2012). Furthermore, Undaria is considered a pioneer species in its native range, primarily colonising areas with reduced algal canopies or abundant natural open spaces (Agatsuma et al. 1997).

The absence of Undaria on many sheltered subtidal reefs examined in this study, where native canopies of large brown algae were dominant, suggested that these dense canopies could inhibit the establishment of Undaria and that canopy disturbance may therefore lead to the
establishment of Undaria. Subsequently, an experiment was designed to test this hypothesis (Chapter 4). It was thought that an intertidal Undaria population would supply propagules for the colonisation of subtidal reef areas cleared of native canopy-forming species and this may then allow an assessment of impacts at this site. However, Undaria did not recruit into any of the three large subtidal plots cleared of canopy-forming macroalgae and monitored over two successive growth seasons. These results differ markedly from other experimental macroalgal canopy removal or native canopy die-back studies which have shown how disturbance can facilitate the establishment of Undaria populations (Valentine and Johnson 2003, 2004; Edgar et al. 2004; Schiel and Thompson 2012; Thompson and Schiel 2012; Carnell and Keough 2014). While canopy removal may facilitate the growth and establishment of Undaria at some sites, there are additional factors which determine the success of Undaria at subtidal sites in this part of the Hauraki Gulf.

Spread to and establishment on native reefs is dependent on propagule supply and the suitability of the receiving environment. It was assumed for the experiment in Chapter 4 that propagule supply within the study site, provided by the adjacent Undaria population (≥289 individuals) would be sufficient to inoculate the study area during the 2012 and 2013 growth seasons, and potentially propagules would have been spread to the study site in previous years as well (Valentine and Johnson 2003; Hewitt et al. 2005). However, it may have been the case that gametophytes did not encounter suitable substrate on which to settle or grow in the cleared areas. The results of this experiment indicate how environmental factors which vary even on small scales, i.e. between adjacent intertidal and subtidal zones, affect the presence or absence of Undaria on native reefs. It appears that Undaria in this region is most likely to establish in native habitats with clear water and in habitats such as urchin barrens or shallow areas dominated by coralline turf. High abundances of Undaria were found in urchin barrens habitat in clear water at Great Barrier Island (Chapter 3), indicating loss of algal canopies due to impacts from over fishing and associated urchin grazing (Shears and Babcock 2002), could potentially facilitate Undaria establishment in areas where conditions were otherwise suited to Undaria establishment. Suggestions for further research to better understand what factors affect Undaria establishment are covered in section 7.6.

7.3 ECOLOGICAL EFFECTS OF UNDARIA INVASION IN WARM-TEMPERATE CONDITIONS

Results from Chapters 3 and 4 suggest that Undaria is not currently out-competing or displacing native canopy-forming species at the reef sites surveyed in the Hauraki Gulf. However, effects on the wider community at sites with large Undaria populations, such in Katherine Bay, Great Barrier Island may be significant. Undaria can re-engineer habitats, where it grows at sites previously devoid of canopy-forming algae, changing the native community structure and function. When Undaria populations reach high numbers, such as those observed on the mussel farms and coast at Katherine Bay, it can make a significant but inconsistent contribution of food and habitat to native communities (Jimenez et al. 2014; South et al. 2015), for example large numbers of Lunella smaragdus were observed on Undaria sporophytes at the coastal monitoring site in
Coromandel Harbour (Chapter 3). Undaria invasion can increase primary productivity, and at coastal sites it can reduce the abundance and diversity of understory algal assemblages (Hay and Villouta 1993; South et al. 2015; Hooton-Kaufman 2012; Casas et al. 2004), affect the abundance and composition of associated epibionts (Raffo et al. 2009; Arnold et al. 2016) and have varying effects on the presence and abundance of associated macrofaunal species.

The provision, by Undaria, of both habitat and food can result in an increase in the abundance of grazers and fish during the Undaria growth season (Thornber et al. 2004; Irigoyen et al. 2011a; Hooton-Kaufman 2012). Such changes could have further effects on local food chains by increasing the abundance of food for predators (Irigoyen et al. 2011a). At sites such as those within the Hauraki Gulf, where populations maintain a winter annual growth pattern, Undaria provides a temporally variable supply of resources. This could result in a lack of food or habitat for increased numbers of associated species, such as L. smaragdus, when Undaria dies off during summer (McLaughlan et al. 2014). This may in turn lead to effects from grazing pressure on native algal species post Undaria season (Dean 1999). Conversely, it may be that winter annual Undaria populations in the Hauraki Gulf, exert less evident impacts on associated species as compared to those occurring at cooler water sites where populations are present throughout the year (Valentine and Johnson 2003; Thornber et al. 2004; South et al. 2015). For example annual populations may contribute smaller amounts of nitrogen-rich material to the ecosystem, potentially having a smaller effect on primary productivity (Tait et al. 2015).

Predicting which sites Undaria may invade, and understanding how Undaria invasion can impact on native communities is a challenging task (Chapter 3, 4). In general, the ecological effects and impacts from Undaria invasion remain poorly understood and in some cases contradictory. Impacts from Undaria invasion are context dependant and factors such as turbidity, sediment accumulation and species interactions are likely important in affecting the establishment, level of infestation and ultimately the ecological effects of Undaria invasion. Whilst further research is needed to understand how such factors influence Undaria invasion in the Hauraki Gulf, evidence is available to warrant concern over Undaria invasion in the Hauraki Gulf and the subsequent ecological impacts on native communities. The presence of Undaria undermines efforts to conserve native biodiversity and representative native ecosystems in particular. Whilst the low numbers of Undaria sporophytes seen on reef habitats in sheltered parts of the eastern Hauraki Gulf, more than ten years after its introduction to the region, suggest it may have limited ecological effects under these environmental conditions, as mentioned above, the site specific nature of invasion and establishment of Undaria as well as the limited research carried out in this area must be taken into account when drawing such conclusions. Large populations of Undaria were found on artificial structures in the Hauraki Gulf and further surveys and research are needed to determine the risks posed by Undaria to coastal reef sites in this region.
7.4 WILL **UNDARIA** CONTINUE TO SPREAD IN WARMER REGIONS?

Results from Chapters 2 and 6 suggest that the *Undaria* populations in northeastern New Zealand where winter temperatures range from ~12 – 14 °C, are near the extent of its temperature limit as it would not be able to tolerate much of an increase in winter temperatures (>15 °C). While temperatures below 15 °C induce successful gametogenesis, gametogenesis does occur in some populations albeit at a reduced efficacy between 15 and 20 °C (Saito 1975; Yamanaka and Akiyama 1993; Morita *et al.* 2003a; Thornber *et al.* 2004; Henkel and Hofmann 2008a; Gao *et al.* 2013b). Therefore, this threshold is potentially conservative. In addition, the presence of a small number of reproductive sporophytes in the far north of New Zealand during summer (Appendix I) suggests a low rate of recruitment occurs when temperatures are potentially above 20 °C. While it seems unlikely dense populations would succeed in such warm summer temperatures, this may indicate a certain level of local acclimatisation (Henkel and Hofmann 2008), which could lead to greater impacts if populations adapt to warmer conditions.

Genetic analysis of northern New Zealand populations (Chapter 5) suggested that there may be certain strains of *Undaria* that are more tolerant of warmer temperatures. The majority of strains found in southern New Zealand waters are likely more suited, or pre-adapted, to colder water and cannot survive in the warmer waters of the upper North Island (Chapter 5). Experiments with *Undaria* originating from different Japanese source populations revealed differences in temperature tolerance of ~2 - 4 °C for growth and survival (Gao *et al.* 20013a), it is therefore possible that strains originating from native populations pre-adapted to warmer conditions have higher temperature tolerances. This raises concerns around the introduction of new strains of *Undaria* which may be more temperature tolerant and capable of colonising warmer locations.

Another factor which may allow *Undaria* to spread into warmer regions is its ability to colonise deep water sites, beneath warmer surface waters. At sites with suitable water clarity and light penetration *Undaria* populations can grow at depths of up to 26 m (Aguilar-Rosas *et al.* 2004; Miller and Engle 2009), much deeper than the commonly reported depth distribution from both native and introduced populations (Saito 1975; Silva *et al.* 2002). This could potentially extend the distribution of *Undaria* into clear-water subtropical regions.

A number of large areas of the world’s coastlines have been identified where temperature regimes are suitable, but *Undaria* has not yet been documented (Chapter 6). These sites are mostly in cold and cold-temperate regions, including the east coast of North America and the west coasts of South America and Africa. Many of these cooler sites would be expected to sustain year-round *Undaria* populations if it reaches these regions (Chapter 6). As mentioned above there is a potential risk that warm-tolerant strains of *Undaria* could invade subtropical sites and it may colonise deeper water at warmer sites (Miller and Engle 2009). However, evidence to date suggests *Undaria* will have limited success or be excluded from sites where winter temperatures do not decrease below 15 °C and therefore *Undaria* poses a greater risk to cooler water sites.
7.5 HOW WILL *UNDARIA* POPULATIONS BE AFFECTED BY CLIMATE CHANGE?

Global climate changes are causing an accelerated rate of ocean warming (e.g. Poloczanska *et al.* 2013). Macroalgae generally have well-defined upper temperature tolerances, meaning that temperature increases are likely to cause shifts in distribution as they are restricted within zones that suit their specific temperature tolerances (Stachowicz *et al.* 2002; Ladah and Zertuche-Gonzalez 2004; Staehr and Wernberg 2009; Sorte *et al.* 2010; Tanaka *et al.* 2012; Duarte *et al.* 2013). Kelp species may be particularly vulnerable to ocean warming due to their affinity for cold water and limited natural dispersal ability (Breeman 1988; Merzouk and Johnson 2011; Komatsu *et al.* 2014).

*Undaria* has a similar upper temperature limit for growth to that of a number of other kelp species (Luning and Neushul 1978; Kain 1979; Luning 1980). But unlike other species, *Undaria* sporophytes have a broad temperature tolerance and it has an exceptionally high temperature tolerance in its gametophyte form (Dieck 1993). *Undaria* can persist at temperatures up to 29 °C in its gametophyte form and can vary its phenology to succeed under different temperature regimes (Chapter 6). Hence *Undaria* may adapt to warming conditions to maintain invasive populations, even if only on a transient basis. Therefore as water temperatures increase, invasive *Undaria* populations may have an advantage over native perennial kelp species which are less able to adapt and could completely disappear from sites (Ladah *et al.* 1999). At introduced sites with summer maxima <20 °C, year-round presence of *Undaria* will be reduced to a winter annual cycle if summer temperatures increase above 20 °C. At warmer sites (summer maxima >20 °C) elevated temperatures over summer and autumn will cause sporophyte presence to remain minimal for longer periods during the year until such a time as *Undaria* is excluded. *Undaria* growing at the edge of its range limits, such as in northern New Zealand, will likely disappear if winter temperatures increase above 15 °C (Chapter 2, 6).

Climate change is also expected to have other impacts on coastal waters such as increasing turbidity in the oceans, reducing light penetration and increasing sedimentation (Fletcher and Farrell 1999; Harley *et al.* 2006; Geange *et al.* 2014). *Undaria* requires high light levels for successful growth and reproduction (Stuart 1997) and elevated turbidity may therefore reduce its success and depth distribution (Duder 2009; Peteiro and Freire 2012; Shibneva and Skriptsova 2012). *Undaria* can persist at shallow sites with high turbidity, although with reduced sporophyte size (Floc’h *et al.* 1996; Fletcher and Farrell 1999; Curiel *et al.* 2001). *Undaria* can also outperform native species to colonise sites affected by sedimentation in some regions (Valentine and Johnson 2005; Valentine *et al.* 2007; Carnell and Keough 2014; Geange *et al.* 2014). This ability of *Undaria* to colonise intertidal sites and sites affected by sedimentation may give it additional advantages over native kelp species.

A further consideration which intertwines with the effects of climate change is the ability of invasive species to thrive in degraded or disturbed ecosystems (Byers 2002; Stachowicz *et al.* 2002; Sorte *et al.* 2010). Global climate change will interact with smaller scale stressors, such as eutrophication and overfishing, to result in new and different patterns and combinations of
environmental stress (Harley et al. 2006; Wahl et al. 2015; Tamburello et al. 2014). *Undaria* possesses an effective set of invasive attributes which make it likely to out-perform native species under such conditions (Byers 2002; Fletcher and Farrell 2006; Curiel et al. 1998; Curiel et al. 2001; Sliwa et al. 2006; Sorte et al. 2010).

Climate-driven changes to the marine environment are particularly difficult to study and predict, but even small temperature increases could significantly affect kelp populations, and particularly those growing towards the extent of their temperature tolerances (Kain 1979; Hatcher et al. 1987; Gerard and Bois 1988; Ladah and Zertuche-Gonzalez 1999; Wernberg et al. 2010). It is possible that some other fast growing kelp species and other invasive species may be able to maintain populations under warmer conditions by shifting to winter annual growth cycles similar to that displayed by *Undaria* (Lee and Brinkhuis 1986; Aguiar-Rosas and Galindo 1990). However, it is likely that for slower growing kelp species and those which are less temperature tolerant, increasing temperatures will eventually exclude them and they may be replaced by those with higher temperature tolerances or more adaptable life cycles such as *Undaria* (Schiel et al. 2005; Ling 2008; Wernberg et al. 2010).

### 7.6 LIMITATIONS OF THIS STUDY AND SUGGESTIONS FOR FUTURE RESEARCH

While this thesis revealed new information on how water temperature influences the phenology and distribution of *Undaria*, it also highlighted the need for further investigation into the potential invasive range of *Undaria* and how *Undaria* will affect invaded sites. Predictions for the potential invasive range of *Undaria* made in Chapter 6 outline broad areas where *Undaria* may be able to establish. Further research is needed to experimentally investigate the relationships between *Undaria* establishment and receiving environments such as the effects of sediment loading, turbidity (light availability), depth and the importance of, and interactions with, substrate types and understory species such as turfing algal species. In particular the microscopic life stages of *Undaria* require further study and investigation in order to determine how and where they may settle and survive at reef sites. In addition, the extent to which *Undaria* gametophytes are cold tolerant should be studied in order to understand the potential invasive range of *Undaria* on a wider scale. This information will allow an understanding of which areas within the broad regions predicted as suitable for *Undaria* colonisation in Chapter 6 are at risk from invasion.

The context dependant relationship with invasion was highlighted by results from Chapters 3 and 4. It was not possible to predict *Undaria* presence or absence at native reef sites from survey data, nor did *Undaria* recruit into subtidal clearances in what was thought to be suitable habitat near an intertidal *Undaria* population. Results from the experimental study outlined in Chapter 4 contradict the established idea that disturbance promotes invasion, particularly in the case of *Undaria*. However, the experiment involved only a manipulation of canopy-forming species, followed by no appearance of *Undaria* in treatment or control conditions. Because of the single treatment, it was not possible to gain further insights into the factors restricting *Undaria* at this depth, relative to shallower depth where *Undaria* was present. No data was collected to address the reasons behind the lack of *Undaria* in the cleared areas. Incorporating multiple sites into the
experimental design would be more likely to provide insights into specific site characteristics which might facilitate or inhibit the spread of *Undaria* in this region.

As well as suitable receiving conditions, *Undaria* requires a transport mechanism or vector for introduction to colonise new sites (e.g. Minchin and Nunn 2014), so factors such as the proximity of aquaculture areas, shipping ports and marinas should be considered to determine the actual likelihood of *Undaria* invasion to new areas. *Undaria* populations in the Hauraki Gulf were found to be prevalent on artificial structures (Chapter 2, 3) and this leads to an increased risk of introduction to the surrounding environment (Glasby *et al.* 2007; Floerl *et al.* 2009; Dafforn *et al.* 2009; Katsanevakis *et al.* 2013). Chapter 3 indicated that proliferation of *Undaria* on mussel farms could facilitate invasion to native reef habitats. Populations on artificial structures act as population reservoirs from which *Undaria* can spread naturally via spore dispersal and detached sporophytes and spread to coastal sites can also occur via the spread of sporophytes attached to floats or ropes which detach and wash inshore from mussel farms.

Analysis of the genetic diversity of *Undaria* populations in northern NZ (Chapter 5) revealed only one haplotype, or strain, in this region. Although this may suggest the strain is tolerant to higher temperatures, the exclusive link between temperature tolerance and the identified strain remains unclear. A better understanding around how temperature thresholds for *Undaria* may vary between different source populations is required to confirm this. If there are genetically defined variations in temperature thresholds amongst populations this may allow further analysis to better predict the threats posed to warmer regions by different strains of *Undaria*.

Experimental research is required to better understand the ecological impacts of *Undaria* in warm-temperate regions, and for invasive populations in general. *Undaria* is a highly successful and cosmopolitan invasive species but it remains unknown if the purported serious ecological effects from *Undaria* (e.g. Campbell and Hewitt 2013) are tangible. Understanding impacts becomes increasingly important for an opportunistic species such as *Undaria* under changing environmental conditions. Because *Undaria* can display a competitive advantage over native species in disturbed eutrophic environments (Curiel *et al.* 2001; Sliwa *et al.* 2006), and has a high temperature tolerance which also provides an advantage as ocean temperatures increase, the potential impacts of invasion may increase as marine environments continue to be compromised by anthropogenic impacts. Furthermore, as trophic levels are skewed by increasing forces on top predators by humans and high introduction rates of producers and primary consumers (Duffy 2003; Byrnes *et al.* 2007; Tamburello *et al.* 2014), the interactions among primary producers, such as *Undaria*, and intermediate trophic levels will play a greater role in regulating community dynamics and species diversity (Jones and Thornber 2010). Future research should focus on understanding ecological impacts from *Undaria* invasion, including community-level interactions and food web impacts in invaded ecosystems (McLaughlan *et al.* 2014; Ehrenfeld 2010).
7.7 CONCLUDING REMARKS

It remains a major challenge to accurately evaluate how invasive marine species will impact on recipient communities now and under future climatic conditions. This study confirmed how the spread and impacts from invasive species are intertwined with the influence of local scale anthropogenic influences (Dukes and Mooney 1999; Chapter 2, 3). The additional effects of global environmental changes such as climate change and increases in global connectivity will lead to different responses and interactions from invasive species, which will have novel ecological implications and further complicate the prediction of spread and impacts from invasive species (Hellmann et al. 2008; Hulme 2009).

Predictions around which species will persist or dominate and which species will be excluded under elevated temperature regimes rely on baseline information around individual species temperature tolerances. Differences in phenology between native and introduced populations revealed in this study (Chapter 6) illustrate how invasive species traits cannot always be predicted from native populations. This is a significant consideration for invasive species management; detailed knowledge of invasive species’ sensitivities and tolerances are required when profiling species for the modelling and prediction of invasion patterns and ultimately their potential impacts (MacNeil and Campbell 2014). For species with multiple life cycle stages, understanding the temperature requirements across different parts of the life cycle is necessary to understand the characteristics of distribution patterns for individual species and how these may change under different environmental conditions outside their native range. Understanding the extent to which species will acclimatise or adapt to climate change and multiple anthropogenic stressors is also fundamental for predicting future ecological changes associated with invasive species (Root et al. 2003; Harley et al. 2012).

The set of attributes which make Undaria one of the most invasive species in the world (Lowe et al. 2004), and a current lack of tools or methods to control or eradicate Undaria post invasion (e.g. Forrest and Hopkins 2013), make interception or removal of pathways to introduction the only effective approach for limiting impacts from Undaria invasion. Better understanding around the invasion patterns and processes associated with the spread of Undaria, human mediated pathways in particular, will allow the development of strategies to reduce the spread of Undaria and hence mitigate ecological impacts. The potential to limit the spread of Undaria via recreational and commercial vessel movements and aquaculture transfers, which often expose coastal areas in isolated and undeveloped areas to Undaria invasion, could be crucial to conserving native ecosystems in high value areas, such as Marine Protected Areas, by keeping them free from Undaria.
References


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Nanba N, Fujiwara T, Kuwano K, Ishikawa Y, Ogawa H, Kado R (2011) Effect of water flow velocity on growth and morphology of cultured Undaria pinnatifida sporophytes (Laminariales,


Appendix I

Discovery of *Undaria pinnatifida* in northern New Zealand indicates increased invasion threat in subtropical regions

A research note has been published based on this appendix:

ABSTRACT
In March 2013 the Asian kelp *Undaria pinnatifida* (Harvey) Suringar, 1873 was discovered in Rangaunu Harbour, northern New Zealand (34º 53’S 173º 17’E), a site where water temperatures typically range between 14 and at least 24 ºC. This is the first report of *Undaria* in subtropical parts of New Zealand and demonstrates that *Undaria* is capable of invading marine environments throughout the country. The presence of healthy juvenile and reproductive sporophytes during late summer (SST >21 ºC) is of particular concern as juvenile *Undaria* sporophytes have previously only been recorded during summer in cooler water regions. This discovery indicates a previously unreported deviation from a winter annual lifecycle at subtropical temperatures and an increased risk of invasion impacts for subtropical sites worldwide.

INTRODUCTION
*Undaria* is an invasive kelp that alters ecosystem composition and function through domination of benthic communities (Eno et al. 1997; Curiel et al. 2001; Sinner et al. 2000; Russell et al. 2008; Raffo et al. 2009; Irigoien et al. 2011a, b). *Undaria* is native to Northern Asia where annual water temperatures range between ~0 - 27ºC (Akiyama and Kurogi 1982). Regular seasonal temperature shifts in its native range have caused *Undaria* to develop temperature cues for growth and reproduction (Saito 1975; Akiyama and Kurogi 1982). These temperature cues align with a heteromorphic lifecycle comprising a microscopic haploid gametophyte phase and a macroscopic diploid sporophyte phase (Saito 1975). In its native range *Undaria* is a winter annual; the sporophyte recruits in winter, becomes reproductive and sporulates in spring-early summer and subsequently dies off and disappears, only the microscopic life stages persist during the late-summer and early autumn (Akiyama and Kurogi 1982; Koh and Shin 1990).

Since the late 1980s, with increases in international maritime and aquaculture activities, *Undaria* has invaded warm and cold temperate marine environments around the World (CABI [Centre for Agricultural Bioscience International] 2013). *Undaria* can alter its winter annual life cycle under
different temperature regimes and sporophytes can be present year-round in parts of its introduced range where seasonal variations in water temperatures are less extreme than those in its native range (Floc’h et al. 1991; Hay and Villouta 1993; Fletcher and Farrell 1999; Casas et al. 2008; Zabin et al. 2009; Scheil and Thompson 2012).

In northern New Zealand Undaria establishment was thought to be constrained by warm sea water temperature (Hay and Villouta 1993; Sinner et al. 2000). In this note we report on the discovery of healthy and reproductive Undaria sporophytes in the northern-most subtropical waters of New Zealand during late summer (Fig. 1). We suggest that this observation establishes an increased risk of invasion impacts for subtropical sites worldwide.

DISCOVERY

On 15 March 2013, Undaria was discovered growing on Scheigis Rocks, a subtidal rocky outcrop at the entrance to Rangaunu Harbour, Northland, New Zealand (34° 53’S 173° 17’E) (Fig. 1). Eight Undaria sporophytes were found growing at a depth of three metres on a one metre square area of reef (Fig. 2A). The sporophytes ranged from 100 to 300 mm in total length. Sporophylls were present on three of the larger sporophytes (Fig. 2B). The rocky outcrop was dominated by a mixed algal assemblage consisting of the native kelp Ecklonia radiata and large endemic fucoids Carpophyllum maschalocarpum and Sargassum sinclairii. Undaria was found in a clearing in the algal canopy that was otherwise dominated by crustose coralline algae, articulated coralline turfs including Corallina officinalis, a number of ephemeral species including Colpomenia sinuosa, Ulva sp. and some small unidentified fleshy red algal species. The common sea urchin Evechinus chloroticus was also present but largely restricted to crevices. Several smaller Undaria sporophytes (~100 mm) were also seen growing attached to shells on nearby sand flats suggesting that Undaria may already be widely distributed in the Rangaunu harbour.

Water temperature at the site was 21.3 °C at the time of discovery. Based on long-term remote sensing information, monthly average sea water temperatures peak at between 21 and 23 °C in February, and drop to 14 to 16 °C in August (www.niwa.co.nz). Sea surface temperatures inside the harbour are likely to be more variable and Undaria present at Schelgis Rocks during summer are likely to be exposed to water temperatures greater than 24 °C (Northland Regional Council Data, 1998).

DISCUSSION

The discovery of Undaria in Rangaunu Harbour, northern New Zealand, represents the northern-most known population in the Southern hemisphere. This shifts the northern range limit of Undaria within New Zealand approximately 250 km (Fig. 1) beyond the previously reported northern limit of the Waitemata Harbour (Russell et al. 2008). This discovery of Undaria in the far north of New Zealand shows that the spread of Undaria around northern New Zealand is not limited by warm sea water temperatures, as previously thought (Hay and Villouta 1993; Sinner et al. 2000).

Within its native range Undaria sporophytes can tolerate temperatures up to 27 °C (Morita et al. 2003a), but effective recruitment of the sporophytes from the microscopic gametophyte stage generally requires temperatures between 10 and 20 °C (Saito 1975; Morita et al. 2003b).
Consequently, in regions where summertime water temperatures rise above 20 °C, such as in its native range in Asia as well as in Port la Nouvelle (France), Venice Lagoon (Italy), and Port Philip Bay (Australia), *Undaria* has a winter annual lifecycle and reproduction and recruitment do not occur over the summer months (Akiyama and Kurogi 1982; Floc’h et al. 1991; Curiel et al. 2001; Primo et al. 2010). The discovery of healthy juvenile and reproductive *Undaria* sporophytes in subtropical New Zealand waters in late summer is a significant deviation from this winter annual cycle. Previously, *Undaria* sporophytes have only been seen to recruit during summer in locations where annual water temperatures do not exceed 20 °C (e.g. Southern New Zealand, Brittany (France), Nuevo Gulf (Argentina) and Monterey Harbour (USA); Hay and Villouta 1993; Floc’h et al. 1991; Casas et al. 2008; Zabin et al. 2009).

*Undaria* is a highly adaptable and plastic species (Nyberg and Wallentinus 2005). Across regional scales *Undaria* sporophytes and gametophytes can have different temperature tolerances. In its native range, *Undaria* populations at warmer latitudes exhibit higher temperature tolerances than those at cooler latitudes (Gao et al. 2013). These differences in high temperature tolerance have been attributed to genetic differentiation rather than phenotypic plasticity. Populations can also become locally acclimatised to different thermal stress among habitats; for example *Undaria* can tolerate higher thermal stress in intertidal habitats where populations experience more extreme daily and seasonal heating than populations on nearby subtidal reefs (Henkel and Hofmann 2008). Further research is needed to determine whether the population at Rangaunu Harbour is a genetically thermal-tolerant strain or whether local adaptation may be behind the ability of the population to recruit during summer. Regardless of the mechanism, this population appears to be a relatively unique variant that is capable of reproducing and recruiting at higher temperatures than previously reported.

A wide range and flexibility of temperature tolerance is a significant characteristic of successful invasive species, especially with regards to persisting under future climate change scenarios. While kelps in general may be eliminated from warmer latitudes by warming ocean temperatures (Wernberg et al. 2013), it appears that *Undaria* may be capable of adapting to and persisting at warmer temperatures than previously thought. An ability to recruit and persist through the summer months allows *Undaria* to compete more directly with native species and increases the impact of *Undaria* on native ecosystems (Thornber et al. 2004; Thompson and Schiel 2012). Such impacts have already been documented at cooler-water sites (summer temperatures <20 °C) such as Nuevo Gulf (Argentina) where persistent *Undaria* populations dominate reef sites year-round and exclude native species (Raffo et al. 2009; Irigoyen et al. 2011a,b). A greater than expected temperature tolerance for the recruitment process indicates that year-round populations could become established in subtropical regions worldwide, and that these populations will have greater ecological impacts on subtropical reef systems than previously anticipated.
Figure 1
North Island of New Zealand showing location of previously recorded northern most *Undaria* population (star) and newly discovered *Undaria* population (square) (A). Exact location of newly discovered *Undaria* population within Rangaunu Harbour, northern New Zealand (B).
Figure 2

Juvenile *Undaria* sporophytes (A) and a reproductively mature sporophyte with sporophylls (B) at Scheigis rocks, Rangaunu Harbour, northern New Zealand. Photographs taken by Irene Middleton in March 2013.