

A review of the impacts from invasion by the introduced kelp *Undaria pinnatifida*

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A review of the impacts from invasion by the introduced kelp *Undaria pinnatifida*

November 2016

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A report prepared for Waikato Regional Council

EXECUTIVE SUMMARY

Invasive species are those which have evolved in one location and are introduced, often by human activities, to another location where they successfully establish, spread and cause harm to the receiving environment. Invasive species pose one of the foremost threats to marine ecosystems. An increasing number of marine ecosystems, primarily near shorelines, are being altered or even destroyed by invasive species.

Undaria pinnatifida is a highly successful invasive kelp species. It is regarded as one of the worst invasive species in the world. *Undaria* is native to the northwest Pacific and is now invasive to more than fourteen countries around the globe. *Undaria* has a set of attributes common to highly invasive species; it is easily spread and transported, can colonise a wide range of substrata, has a broad ecological niche and a typically weedy life history. Under suitable conditions *Undaria* can spread rapidly and form dense monospecific stands, with lifecycle and growth strategies varying from winter annual to year round dependant on local temperature regimes.

Undaria can substantially alter natural habitats and change community structure and trophic interactions. *Undaria* invasion often represents an addition to canopy cover at invaded sites, or invades sites naturally devoid of native canopy-forming species, where it can create a completely novel biogenic habitat. *Undaria* invasion can significantly increase local primary productivity as the high biomass turnover associated with the short life span of *Undaria* sporophytes increases carbon export to the surrounding ecosystem.

Where *Undaria* forms dense stands it can reduce the presence and diversity of smaller understory algal species and can in certain circumstances out-compete some canopy-forming species. *Undaria* invasion increases food and habitat availability for some species, including epibiotic communities. The epibionts associated with *Undaria* can be different and less diverse than those associated with native algal species and this has the potential to significantly affect the flux of materials to higher trophic levels. Macrofaunal assemblages found in association with *Undaria* habitat can also be different from those associated with un-invaded sites. *Undaria* invasion can result in an increase in the abundance of grazers, including gastropods, urchins and crabs, as well as fish. Such changes can further affect local food chains by increasing the abundance of food for predators.

The winter annual growth cycle of *Undaria* at many sites means carbon inputs and interactions with higher trophic levels will be temporally variable. An increase in fauna associated with *Undaria* habitat during its growth season could result in a lack of food or habitat for increased numbers of associated fauna when *Undaria* dies off during summer. This may in turn lead to effects from grazing pressure on native algal species post *Undaria* season.

Whilst there is evidence to illustrate how *Undaria* causes changes to community structure and function, quantifying ecological impacts can be difficult where there is a lack of baseline ecological data. Furthermore, separating changes caused by *Undaria* invasion from natural variation, over space and time, is a challenging task. In order to more effectively quantify impacts from *Undaria* invasion more manipulative experiments, including those which assess trophic interactions, are needed.

However, the effects currently reported from surveys and small scale experiments illustrate how *Undaria* invasion can have significant ecological impacts. In addition, responses of *Undaria* to climate change, and the interactions of climate change with other stressors, will further alter ecological impacts from *Undaria*. The presence and impacts from *Undaria* invasion undermine efforts to conserve biodiversity and representative native ecosystems in particular. Efforts should remain in place to protect important high value areas, such as marine protected areas, from *Undaria* invasion.

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1 RATIONALE AND SCOPE OF THIS REVIEW

Undaria is considered one of the most dangerous invasive seaweed species in the world (Nyberg and Wallentinus 2005). There is a perceived threat that *Undaria* poses a high to extreme risk to environmental values, including biodiversity, habitat and trophic interaction, through the displacement of native species and detrimental effects on community and ecosystem function (Campbell and Hewitt 2013). However, previous reviews have resulted in contradictory conclusions; from *Undaria* having limited impacts (Parsons 1995), impacts being unknown (Sinner *et al.* 2000), to *Undaria* being a very high risk invasive species (Nyberg and Wallentinus 2005; McLaughlan *et al.* 2014).

The most common impacts documented from *Undaria* invasion are monopolisation of space and changes to community composition (Appendices I, II). The addition of *Undaria* to a native community will by definition change community composition and the invasion of sites free from other canopy-forming species will result in space monopolisation due to the size and prolific growth strategy of *Undaria*. These impacts therefore require further investigation to provide a more meaningful assessment of ecological impacts from invasion.

Understanding invasion impacts from *Undaria* first requires an understanding of the attributes underpinning the invasive success of the species. These aspects are covered in Section 2. It is also important to understand the invasion process: the introduction, establishment and spread of *Undaria*, including understanding what sites are at risk from invasion. Section 3 investigates sites which are at risk from invasion as well as examining mechanisms and rates of spread.

Ecological impacts from *Undaria* invasion occur following introduction and establishment at new sites. Impacts from *Undaria* invasion are summarised for different functional groups in Section 4. Information on the impacts from *Undaria* invasion was synthesised based on a systematic review of literature around *Undaria* invasion. Literature was searched through the University of Auckland Library system including the use of databases such as NZ Science, Scopus and Google Scholar. Thirty-four studies were identified which included information on impacts from *Undaria* invasion, these are summarised in Appendix I.

A brief discussion on issues surrounding the quantification of ecological impacts from *Undaria* invasion is included in Section 5. While this review concentrates on ecological impacts from *Undaria* invasion, impacts on social and cultural values are briefly discussed in section 6, along with how climate change may influence *Undaria* invasion. Conclusions, along with recommendations for further research and potential methods for mitigating impacts from *Undaria* invasion are also discussed in Section 6.

2 INTRODUCTION

2.1 General background

Invasive species are those which have evolved in one location and are introduced, often by human activities, into another location where they successfully establish, spread and cause harm to the receiving environment (Lockwood *et al.* 2013). Invasive species are considered one of the foremost threats to marine ecosystems (Molnar *et al.* 2008). As international shipping, fishing and maritime trade activities continue to expand and increase on a global scale, so to do the associated introductions of marine species to new locations. The rate at which human-mediated translocation is introducing species to regions beyond their native ranges has never been greater (Johnson 2008; Simberloff 2013). Whilst many introduced species may fail to succeed at new locations, some become invasive and problematic (Simberloff 2013). Macroalgae are a significant component of marine invasive species and continue to establish beyond native limits with increasing frequency; posing a major threat to native ecosystems (Williams and Smith 2007; Davidson *et al.* 2015).

Kelp forests comprise one of the most extensive biological habitats across temperate coasts around the world; kelps are foundation species which act as ecosystem engineers through the provision of habitat structure and food (Nelson 2013). The composition of a kelp forest affects the diversity of understory flora and fauna. Kelp species contribute significantly to primary production. The introduction and establishment of an invasive kelp species therefore can have significant impacts on the receiving environment at many trophic levels.

2.2 *Undaria pinnatifida*

The Asian kelp *Undaria pinnatifida* (Harvey) Suringar 1873 (hereafter *Undaria*) is a cosmopolitan macroalgal invader. *Undaria* is native to north-eastern Asia (Japan, Korea and China) and south-eastern Russia. It is now invasive to more than fourteen countries around the globe and it has the potential to expand its distribution further (James *et al.* 2014, 2015). *Undaria* is one of only two introduced macroalgae listed among the world's 100 worst invasive species (Lowe *et al.* 2004; <http://www.iucngisd.org/gisd/species.php?sc=68>), it is considered one of the most dangerous invasive seaweed species in the world, due to its purported ecological and economic impacts (Nyberg and Wallentinus 2005; McLaughlan *et al.* 2014).

The life history of *Undaria* is typical for laminarian kelp (Fig. 1), with a large sporophyte phase and microscopic filamentous male and female gametophytes. Growth stages and morphological features of *Undaria* are shown in Figure 2. *Undaria* is most similar in appearance to the native kelp *Ecklonia radiata* but has a thinner, membranous, and mucilaginous lamina. *Undaria* has an easily recognisable midrib which also distinguishes it from *Ecklonia* once it is larger than ~10 cm in length.

Undaria is a winter annual species in its native range; the sporophyte typically grows rapidly during winter and spring, when it can form dense monospecific stands, and degenerates in summer and autumn. In its native range, *Undaria* gametophytes remain dormant over late summer-autumn when temperatures exceed those suitable for development and fertilisation. However, at sites where temperatures are suitable, multiple generations can recruit throughout the year. This results in a year round presence of sporophytes (James *et al.* 2015).

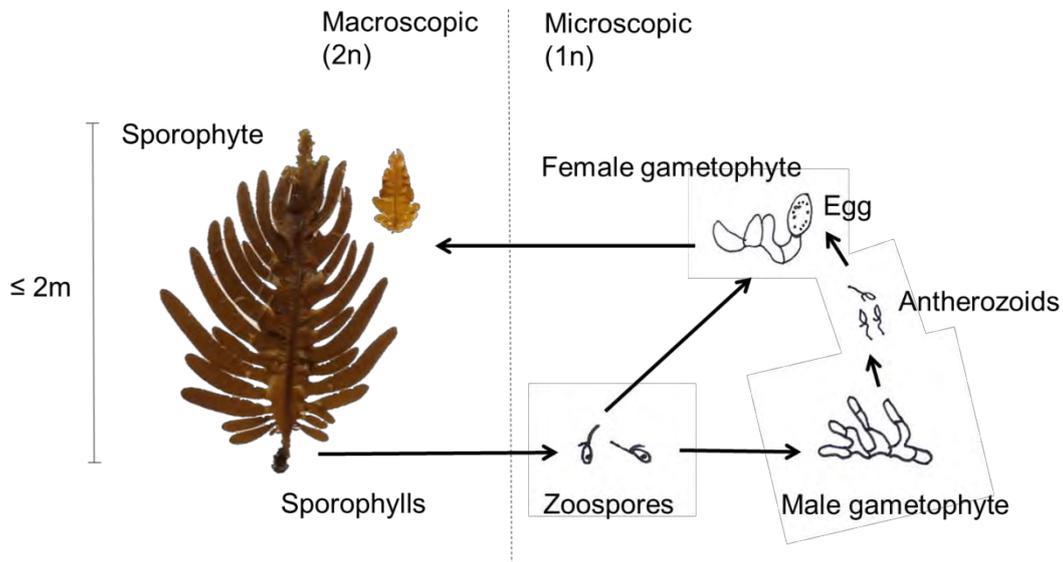


Fig. 1

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).

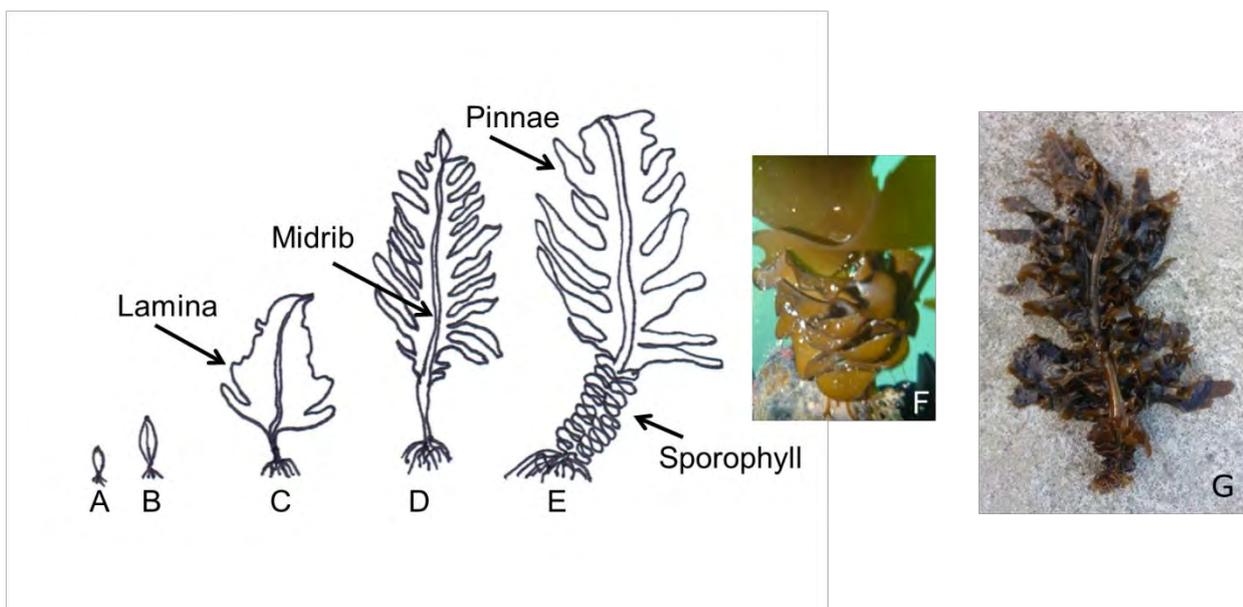


Fig. 2

Undaria growth stages and morphological features: juvenile sporophyte with lanceolated lamina and lacking a midrib (<math><10cm</math>) (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 ($\leq 2m$ 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 mature sporophyte with pinnately divided lamina and well developed sporophyll (G). Diagram adapted from National Introduced Marine Pest Information System [NIMPIS] (2011). Photographs taken by the author; sporophytes from Coromandel Harbour, Hauraki Gulf, Northern New Zealand.

Undaria has a typically weedy life history. The sporophyte phase lives for around 6-9 months, often growing to around two metres during this time. Thallus growth rates of ~10-30 mm day⁻¹ are common (Yoshikawa *et al.* 2001; Thornber *et al.* 2004; Hewitt *et al.* 2005; Schaffelke *et al.* 2005; Schiel and Thompson 2012). Sporophytes can reach maturity in 40-50 days and release up to 700 million zoospores (Campbell and Burrige 1998; Forrest *et al.* 2000; Schiel and Thompson 2012). *Undaria* has a particularly hardy gametophyte phase. Gametophytes may enter a dormancy phase and remain viable for several years until conditions become suitable for growth and this stage is particularly difficult to detect, control or eradicate (Thornber *et al.* 2004; Hewitt *et al.* 2005). *Undaria* sporophytes display phenotypic plasticity and the existence of different morphological forms also aids in its ability to tolerate a wide range of environmental conditions (Stuart 1997; Hunt *et al.* 2009; Shibneva and Skriptsova 2012).

Undaria possesses a set of attributes common to highly invasive species (Lockwood *et al.* 2007). It can occupy a broad ecological niche, including being tolerant to a wide range of temperatures (James *et al.* 2015). Suitable habitats encompass a variety of conditions and substrates, varying from highly modified and sheltered sites to the open coast on natural reefs (Saito 1975; Fletcher and Manfredi 1995). *Undaria* has an extensive vertical distribution, from the intertidal zone down to 25 m in suitably clear water (Russell *et al.* 2008; Miller and Engle 2009).

In addition, *Undaria* is easily transported and spread (Hay and Luckens, 1987; Hunt *et al.* 2009); including being spread by overland (human mediated) transfers as *Undaria* gametophytes and sporophytes can survive time out of the water (Hay 1990). Mechanisms of spread are covered in Section 3.

Summary of invasive attributes for *Undaria*

- Dense (monospecific) growth patterns
- Rapid growth rate
- Early maturation of sporophytes
- High fecundity/reproductive output
- Hardy microscopic gametophyte phase
- Morphological plasticity
- Variable lifecycle and growth strategies
- Colonises a range of substrata
- Broad temperature tolerance
- Wide depth distribution
- Easily spread and transported

3 SITES AFFECTED BY *UNDARIA* INVASION

3.1 Global range

Due to its propensity for spread via human mediated vectors (Hay and Luckens 1987; Hunt *et al.* 2009). *Undaria* has successfully colonised over fourteen countries outside its' native range, including sites in Great Britain, Atlantic and Mediterranean Europe, The Americas, Australia and New Zealand (James *et al.* 2015; Fig. 3).

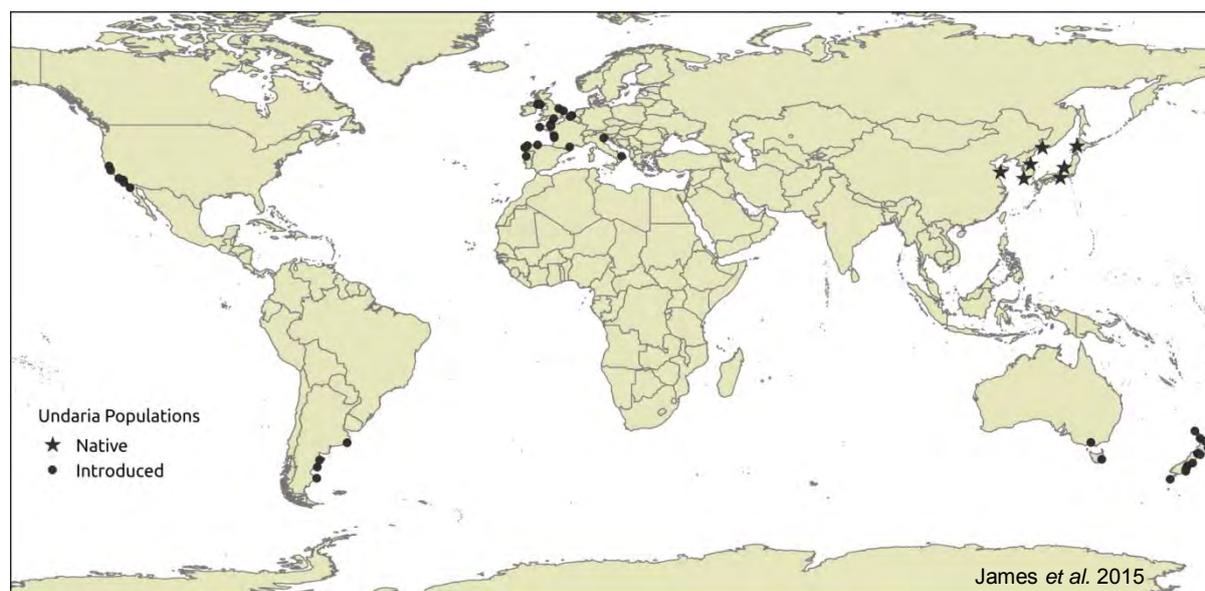


Fig. 3

Locations of native (star) and known introduced (circle) *Undaria* populations around the world.

The broad temperature tolerance of *Undaria* has allowed it to colonise a range of locations, from cold and warm temperate regions to sites influenced by sub-tropical currents, around the world. *Undaria* is now present at sites covering the length of New Zealand (James *et al.* 2014). *Undaria* can establish in regions with maximum temperatures of 13.5–29.5 °C and minimum temperatures of 0.1–15.5 °C, therefore extensive areas of the world's coastline have temperature regimes suitable for *Undaria* colonisation and are potentially at risk from invasion (James *et al.* 2015). The specific temperature requirements for the microscopic stages of development determine the annual presence of *Undaria*. Locations where summer water temperatures do not exceed 20 °C, such as the lower North Island and the South Island of New Zealand can support year round populations, whereas annual populations occur where summer temperatures exceed 20 °C, such as in the Hauraki Gulf, northern New Zealand (James and Shears 2016a).

3.2 Establishment at sites of introduction

Undaria can invade a diversity of environments, from artificial structures such as marinas, wharves and mussel farms to rocky reefs, cobbles and boulders (Minchin and Nunn 2014; Russell *et al.* 2008; Raffo *et al.* 2009; James and Shears 2016b). However, invasive *Undaria* populations often display a predilection for settlement on artificial structures, this most likely relates to spread via human mediated vectors as well as the provision of structures *Undaria* can easily colonise (Fletcher and Manfredi 1995; Floc'h *et al.* 1991; Floc'h *et al.* 1996; Voisin *et al.* 2005; Minchin and Nunn 2014). At natural coastal sites, *Undaria* commonly initially establishes in the intertidal and shallow subtidal zones where native canopy-forming species are absent or sparse (Russell *et al.* 2008; Fig. 4). Restricted light availability, such as via shading from native species, can inhibit recruitment of *Undaria* (Kohtio 2008). *Undaria* can often be found growing in association with turfing algae (coralline turf, such as *Corallina officianalis*) and small filamentous algal species (Casas *et al.* 2004, 2008; Johnson *et al.* 2004; Thompson and Schiel 2012; James and Shears 2013, 2016b; Fig. 5).

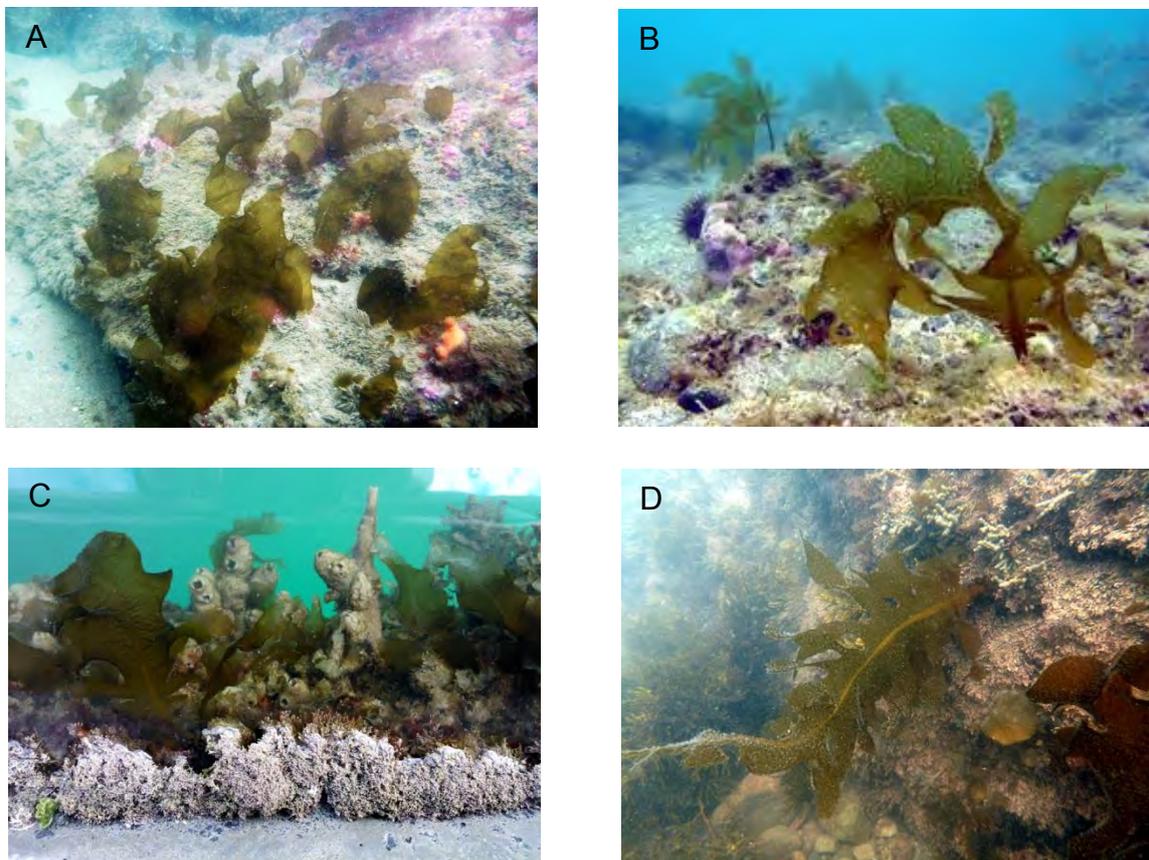


Fig. 4

Examples of sites where *Undaria* initially establishes: Juvenile *Undaria* sporophytes growing on coralline turf at Meola Reef (subtidal), Waitemata Harbour (A). Adult *Undaria* sporophytes growing on coralline turf on inshore reefs at Katherine Bay (subtidal), Great Barrier Island (B). Juvenile *Undaria* growing on coralline turf on the edge of a pontoon at the Westhaven Marina in the Waitemata Harbour (C). Juvenile *Undaria* growing on coralline turf on a rocky reef at Waitataramoa Bay (intertidal), Coromandel Harbour (D). All sites are in the Hauraki Gulf, Northern New Zealand. Photographs A and B taken by R. Hughes, photographs C and D taken by the author.

Undaria will grow on rocks and debris (such as tyres, wood or rope) while it will not grow on adjoining areas of soft sediment or sand (Floc'h *et al.* 1991; Hewitt *et al.* 2005; Russell *et al.* 2008; Merreta *et al.* 2012; Fig. 5); zoospores settle more effectively on rocky substrate than on soft or sandy areas where they may not persist (Hewitt *et al.* 2005). Although it is most often found establishing in the intertidal or shallow subtidal zone, *Undaria* can establish at sites as deep as 25 m when water clarity, and hence light availability, is adequate (Miller and Engle 2009). Sites where light is restricted, such as in highly turbid conditions, can result in reduced size and density of sporophytes (James *et al.* 2016a; Curiel *et al.* 2001). As well as light availability, wave action can influence *Undaria* population density and growth. Sporophyte size and overall biomass are often higher at sites exposed to greater wave action (Castric-Fey 1999; Nanba *et al.* 2011; Peteiro and Freire 2011; Shibneva and Skriptsova 2012). Once established *Undaria* can spread into more diverse range of sites, this is discussed in Section 4.

Summary of common sites for *Undaria* establishment

- Artificial structures
- Natural hard substrate (e.g. reef, rocks or boulders)
- Intertidal or shallow subtidal areas
- Sites where native canopy-forming species are absent or sparse
- Sites with low to moderate wave exposure
- Areas with cover of geniculate coralline or small filamentous algal species
- Sites where light, space and nutrient availability are not limiting factors

3.3 Mechanisms of spread and invasion patterns

Spread from founding populations occurs in a variety of ways. *Undaria* does not naturally spread long distances via spore dispersal (Forrest *et al.* 2000; Grulois *et al.* 2011; Schiel and Thompson 2012) as spores only tend to travel 100 m or so from the parent sporophytes (Forrest *et al.* 2000). Spread primarily occurs via drifting reproductive material (Forrest *et al.* 2000) and human mediated vectors (Verlaque 2007). Spread by drifting material can occur by saltation, when a living *Undaria* sporophyte attached to a small pebble, shell or other loose material is carried along the seafloor with currents or tidal surges (Forrest *et al.* 2000; Sliwa *et al.* 2006; Primo *et al.* 2010; Grulois *et al.* 2011; James *et al.* 2014) or via detached sporophytes or reproductive material (Forrest *et al.* 2001). Human mediated vectors commonly include hull fouling, on recreational and commercial vessels, and transfers of aquaculture species and equipment (Floc'h *et al.* 1996; Hay 1990; Sinner *et al.* 2000; Neill *et al.* 2008; Russell *et al.* 2008; Hunt *et al.* 2009; Fig. 6).

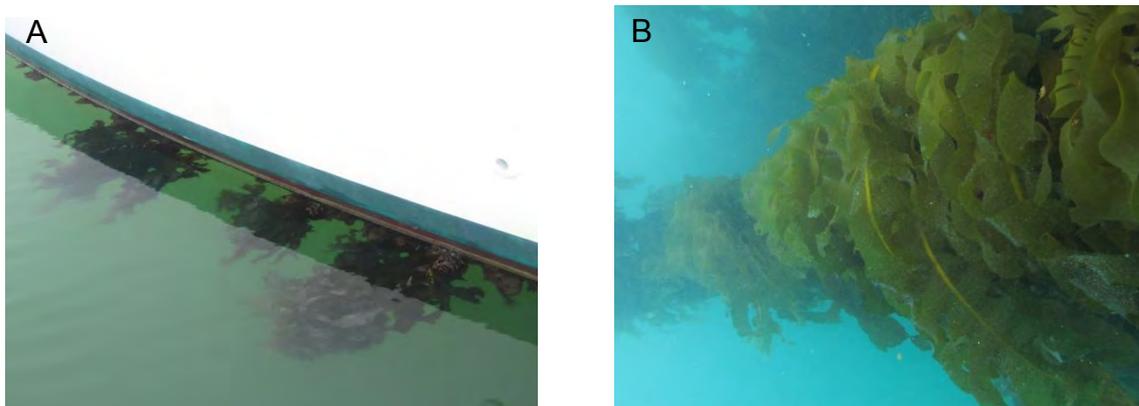


Fig. 5

Examples of human mediated vectors which can spread *Undaria* to new locations: *Undaria* growing on the hull of a recreational vessel berthed at the Westhaven Marina (A). *Undaria* fouling a mussel farm rope in the Coromandel Harbour (B). Both sites are in the Hauraki Gulf, northern New Zealand. Photographs taken by the author.

3.4 Rates of spread from founding populations

Currents and water-flow play a significant role in determining the range expansion of *Undaria* at individual sites (Forrest *et al.* 2001; Torres *et al.* 2004). Rates of spread for populations in southern New Zealand and Tasmania have been recorded at hundreds of metres to a few kilometres per year (Sanderson 1997; Brown 1999; Forrest *et al.* 2000; Russell *et al.* 2008). Dispersal of mature sporophytes via saltation in Tasmania resulted in spread rates of 50-170 m in six months (Sliwa *et al.* 2006). However, rates of spread from founding populations differ markedly across sites, for example, in Argentina, *Undaria* has spread along the coasts of San José and San Matías Gulfs at an average rate of $\sim 50 \text{ km yr}^{-1}$ (Dellatore *et al.* 2014). Rates of spread may be magnified in storms or strong currents (Sliwa *et al.* 2006).

Rates of spread are also dependent on site suitability (see section 3.2). If suitable substrate is available, the rate of invasion is likely to be most rapid in environments where light and nutrients are jointly abundant; such as where canopy-forming species are sparse or absent and anthropogenic nutrient additions occur (Morelison *et al.* 2013).

Summary of mechanisms and associated ranges of spread for *Undaria*

- Hull fouling: local to international distances, including crossing the equator
- Aquaculture transfers: local to international distances (including overland transfers of wet material)
- Saltation: around 100 - 400 m yr⁻¹
- Drifting detached sporophytes or sporophylls: Unknown
- Spore dispersal: up to 100 m - 1 km yr⁻¹

4 ECOLOGICAL IMPACTS FROM INVASION BY *UNDARIA*

Benthic macroalgae form the foundation of coastal food webs, contributing significantly to coastal productivity, providing habitat and food for benthic fauna, including invertebrates and fish. *Undaria* invasion changes the structure of the receiving ecosystem. The invasion of sites previously devoid of macroalgae, such as sites dominated by turfing algal species, changes habitat architecture. At these sites, invasion affects water movements, sediment accumulation, light penetration, nutrient dynamics as well as community composition and trophic interactions (Wallentinus and Nyberg 2007; Russell *et al.* 2008; South *et al.* 2015).

Quantitative data on how *Undaria* infestation affects the structure of receiving ecosystems, such as impacts on water movements, sediment accumulation and light penetration, are lacking from the literature. However, it is likely *Undaria* establishment modifies the environment in the same way as other canopy-forming macroalgal species. Macroalgal stands reduce current velocities, causing an increase in sedimentation and reducing turbidity (Kennelly 1989; Madsen *et al.* 2001).

In addition to structural changes, the presence of a kelp canopy acts to exclude or facilitate particular species, for example *Ecklonia radiata* can exclude sessile invertebrate species and promote the growth of encrusting coralline algae (Connell 2003), and understory assemblages differ among monospecific canopies of different types and mixed algal stands (Irving *et al.* 2004). Overall, impacts from invasion may be more pronounced at sites previously devoid of canopy-forming species (Forrest and Taylor 2002).

As mentioned in Section 2, studies on *Undaria* are compiled in Appendix I, this information is used to produce an overview of known impacts from invasion. Although not disparate, impacts *Undaria* has on different functional groups within invaded communities are discussed separately below.

4.1 Impacts on native canopy-forming algal species

As outlined in Section 3, *Undaria* frequently initially invades sites where native canopy-forming species are sparse or absent. The general absence or low abundance of *Undaria* amongst large native seaweeds at many sites 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; Carnell and Keough 2014) likely demonstrates a low competitive ability amongst dense populations of canopy-forming macroalgae which limit space and light availability for *Undaria* recruits (Castric-Fey *et al.* 1993; Floc'h *et al.* 1996; Grulois *et al.* 2011; Schiel and Thompson 2012).

However, *Undaria* can coexist with native canopy-forming species (e.g. Schiel and Thompson 2012). Establishment amongst native canopy-forming species can occur as *Undaria* populations proliferate and it spreads from populations which have initially colonised shallower sites, free from canopy-forming species, in close proximity (Fletcher and Farrell 2006; Russell *et al.* 2008) and particularly at sites where the native canopy is sparse or patchy. This includes sites where the native canopy is disturbed, such as where native species are removed by wave action, sand scour, urchin grazing or native kelp die-back (Hay 1990; Floc'h *et al.* 1996; Sanderson 1997; Valentine and Johnson 2003, 2004; Thompson and Schiel 2012). *Undaria* can spread amongst native canopy-forming species without disturbance if space and light are not limiting factors (Russell *et al.* 2008; Raffo *et al.* 2009; South *et al.* 2015; Morelissen 2014). This may occur quickly following establishment, or once *Undaria* has been established for long enough to overcome a lag phase of several years (Russell *et al.* 2008).

Undaria coexists with native populations of *Macrocystis pyrifera* in Nuevo Gulf, Argentina (Raffo *et al.* 2009), and in southern New Zealand it can occur amongst *Sargassum sinclairii*, *Cystophora spp*, *Desmarestia ligulata*, *Macrocystis pyrifera*, *Lessonia variegata*, *Marginariella boryana*, *Durvillaea Antarctica* and *D. willana* (Hay and Villouta 1993; Russell *et al.* 2008; South *et al.* 2015). In St Malo, France it can coexist with *Laminaria hyperborea*, *Laminaria digitata* and *Saccorhiza polyschides* (Castric-Fey *et al.* 1993).

In these circumstances, when *Undaria* inter-mingles with native canopy-forming species, it commonly represents an addition to native macroalgal canopy as opposed to a dominating force which acts to displace or out-compete native species. Impacts on native canopy-forming species may not be evident (Schiel and Thompson 2012) at all, or may be ephemeral due to the annual growth pattern of *Undaria*; i.e. native species may re-colonise cleared sites relatively quickly (Valentine and Johnson 2003; Thompson and Schiel 2012). Surveys in Argentina and Australia found *Undaria* was not displacing native macroalgae even when it was present as part of the native macroalgal canopy (Casas and Piriz 1996; Valentine and Johnson 2005; Raffo *et al.* 2009). Two before-after control-impact (BACI) studies which investigated *Undaria* impact on native canopy-forming species in southern New Zealand found no detectable effects on native algal assemblages following *Undaria* invasion into shallow subtidal algal communities (Wear and Gardener 1999 -cited in Sinner *et al.* 2000; Forrest and Taylor 2002). Similarly, the response of native algal assemblages to removal of *Undaria* at intertidal sites in the Wellington region revealed no significant effect of *Undaria* on the algal community composition (Morelissen *et al.* 2016).

However, once *Undaria* has been established at a site for many years, it may successfully spread to occupy deeper sites and a broader range of habitats, such as occurs in the Otago region, southern New Zealand (Russell *et al.* 2008). There has been some speculation that *Undaria* may be able to compete with some species of fucales in southern New Zealand once *Undaria* populations have been established for many years and reached high densities (Hay and Luckens 1987; Brown and Lamare 1994; Parsons 1995). Likewise, At deeper subtidal (>3–10 m) sites *Undaria* populations in southern New Zealand, in sheltered areas, growing amongst *Macrocystis pyrifera* may compete with *Ecklonia radiata* and *Landsburgia quercifolia* (Russell *et al.* 2008) and surveys in France have shown how *Undaria* competes with *Saccorhiza polyschides* (Castric-Fey *et al.* 1993).

Whilst *Undaria* may not be able to easily invade dense intact canopy-forming macroalgal communities, at modified coastal sites, such as harbours which also have increased nutrient inputs, *Undaria* can have a competitive advantage over native algal species (Campbell and Burrige 1998; Curiel *et al.* 2001; Torres *et al.* 2004; Sliwa *et al.* 2006; Sfrisco and Facca 2013; Carnell and Keough 2014). *Undaria* can out-compete native species, including canopy-forming species on artificial substrata such as marina and wharf structures (Curiel *et al.* 1998; Curiel *et al.* 2001; Farrell and Fletcher 2006).

Undaria is an opportunistic 'fugitive' species which occupies areas where cover of native canopy-forming species is sparse or absent. *Undaria* does not commonly displace native canopy-forming species in intact native communities where light and space are limiting factors. However, *Undaria* can coexist amongst canopy-forming algal communities and comprise a significant addition to algal density and cover as it occupies gaps amongst native species. *Undaria* can out-compete native canopy-forming species in some circumstances, including on artificial structures and in modified coastal environments and those affected by nutrient enrichment.

4.2 Impacts on understory algal species

Shifts in understory community structure occur when composition and density of canopy-forming species changes. Canopy-forming algae can reduce recruitment of sub-canopy algal species through shading and physical abrasion by the canopy (Connell 2003).

Observations from sites where *Undaria* forms dense stands suggest it can shade out smaller understory algal species (Curiel *et al.* 2001; Sanderson and Barret 1989; Silva *et al.* 2002; Russell *et al.* 2008; Hunt *et al.* 2009). In Wellington Harbour for example, where the native flora comprises relatively small foliose and filamentous red algae, and green seaweeds, such as *Ulva* and *Codium* species, shading by *Undaria* may exclude these smaller seaweeds (Hay and Villouta 1993). An *Undaria* removal experiment in the lagoon of Venice, Italy, found dense *Undaria* populations dominating substrate, on a seasonal basis, and concluded the possibility of competition with smaller native species: in particular *Ulva rigida*, *Enteromorpha* spp., *Antithamnion pectinatum*, *Chondrocanthus acicularis* in shallow areas and *Rhodomyenia ardissoni* in deeper waters. Likewise, an *Undaria* removal experiment in southern New Zealand recorded effects, although transient, on abundances of *Lophothamnion hirtum* and *Leathesia difformisa* which were reduced at sites covered by *Undaria* (South *et al.* 2015). Such effects have also been observed in Monterey Harbour, California where biomass of the red seaweed *Prionitis lanceolata* was significantly lower within *Undaria* habitat as opposed to sites where no *Undaria* was present (Hooton-Kaufman 2012) and in Nuevo Gulf, Argentina where areas dominated by *Codium vermilara* and other small algal species underwent a significant reduction in richness of native algal species once invaded by *Undaria* (Casas *et al.* 2004).

Undaria can reduce both the abundance and diversity of understory algal species. Effects on some species may be transient in areas where *Undaria* has a distinct annual growth cycle.

4.3 Impacts on carbon flow and primary productivity

At sites devoid of native canopy-forming species *Undaria* can form dense monospecific stands which form 100% cover on areas of suitable substrate (Curiel *et al.* 1998). At sites where *Undaria* grows amongst native canopy-forming species it can comprise a significant addition to the canopy (South *et al.* 2015). In southern New Zealand *Undaria* can be one of the most abundant single species on subtidal reefs, surveys in the Otago region found *Undaria* was contributing on average 43% to the total density of the algal communities and sometimes up to 75% of the canopy cover during its peak season in early summer (Jimenez *et al.* 2015a).

Sites with dense populations of *Undaria* experience substantial increases in production through both *in situ* and exported biomass (Sfriso and Facca 2013). The presence of *Undaria* amongst native macroalgae in southern New Zealand more than doubled net primary production of recipient communities during its annual peak in abundance; late winter to early summer (South *et al.* 2015). The role of *Undaria* in fixing carbon is vitally important to local food chains. In addition, *Undaria* populations release organic matter through both erosion and due to mortality during the senescent season (Yoshikawa *et al.* 2001; Tait *et al.* 2015). The erosion of *Undaria* thalli contributes nitrogen-rich material to the ecosystem, potentially in much larger amounts as compared to native perennial species (Tait *et al.* 2015). Large *Undaria* populations can therefore impact on local food chains through carbon fixing and through nutrient additions from eroded thalli, which are incorporated into the food chain by various consumers, including bacteria, filter feeders, and carnivores (Yoshikawa *et al.* 2001; Jimenez *et al.* 2015b). Because *Undaria* often comprises an addition to native macroalgal assemblages, as opposed to a replacement (Forrest and Taylor 2002; Thompson and Schiel 2012;

Valentine and Johnson 2005), invasion can result in a net gain in carbon production and export from invaded systems (South *et al.* 2015; Tait *et al.* 2015). Such an increase in primary productivity can have significant bottom-up effects on invaded ecosystems as outlined in following sections.

Undaria invasion can result in significant increases in carbon production and export.

4.4 Impacts on epifauna

Small mobile invertebrates, crustaceans such as amphipods or isopods, polychaetes and gastropods, associated with macroalgae are important as they use the host macroalgae as a habitat, and sometimes as food. Epifaunal species are responsible for 80% of the flux of materials through animals on rocky reefs, linking primary production to fish and other large consumers (e.g. Taylor 1998).

Field-based surveys have determined how 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.* 2016). This means a shift towards *Undaria* dominated reefs could result in different epibiotic assemblages and lower local biodiversity (Arnold *et al.* 2016). The significance of such differences in epifaunal assemblages and how these changes could affect higher trophic levels remain unknown.

Epibiotic assemblages found in association with *Undaria* are different and less diverse in comparison to those found on native macroalgae.

4.5 Impacts on macrofauna

The biogenic habitat structure provided by macroalgae affects higher trophic levels. Kelps can exclude invertebrates from the understory or act to facilitate their presence through the provision of habitat and or food. Several studies have identified how *Undaria* invasion can change native macrofaunal presence and composition.

Unlike the other large high profile invasive algae; *C. taxifolia*, *C. fragile* and *S. muticum* (Schaffelke and Hewitt 2007), which can provide a less attractive food source to herbivores and a less attractive habitat for local fauna relative to native macroalgae (Gollan and Wright 2006; Davidson *et al.* 2015 and references therein), *Undaria* can provide a preferable or equally palatable food source and habitat for some species; including urchins, crabs, gastropods and fish (Floc'h *et al.* 1991; Castric-Fey *et al.* 1993; Bader 1998; Thornber *et al.* 2004; Teso *et al.* 2009; Irigoyen *et al.* 2011a; Hooton-Kaufman 2012; Atalah *et al.* 2013; Jiménez 2015b).

Feeding assays conducted in New Zealand have determined how the gastropods *Cookia sulcata* and *Haliotis iris* consumed *Undaria* at rates comparable to most of the six native macroalgae offered to them (Jimenez *et al.* 2015b). Feeding assays with species from the Nuevo Gulf, Argentina found the sea urchins *Arbacia dufresnii* and *Pseudechinus magellanicus* and the gastropod *Tegula patagonica* feed on *Undaria* (Teso *et al.* 2009). Field studies from southern New Zealand have shown how the urchin *Evechinus chloroticus* can consume large amounts of *Undaria* (Atalah *et al.* 2013) and observations from northern New Zealand have indicated the gastropod *Lunella smaragdus* consumes *Undaria*; particularly as it senesces during summer (James and Shears 2016b). In California, surveys

observed extensive grazing on *Undaria* populations by native herbivores, predominately the kelp crab *Pugettia producta* (Thornber *et al.* 2004). Analysis of stomach contents of Butterfish fish, *Odax pullus*, in southern New Zealand has confirmed its consumption of *Undaria* (Bader 1998).

The provision of extra food and habitat by *Undaria* may lead to higher numbers of macrofauna being present amongst *Undaria* habitat as compared to non-*Undaria* habitat. Surveys in Monterey Harbour, California observed up to eleven fish species, representing adult and juvenile life stages, associating with a single *Undaria* sporophyte, and overall it was found that disproportionately more fish species utilise *Undaria* habitat as compared to other available habitat (Hooton-Kaufman 2012). Surveys in Nuevo Gulf, Argentina found abundance of two species of crustaceans *Coenophthalmus tridentatus* and *Nauticaris magellanica*, the urchin *Arbacia dufresnii*, one species of nemertina and several species of polychaetes was higher in *Undaria* habitat when compared to sites where *Undaria* was removed (Irigoyen *et al.* 2011a). In addition, some species were found only in association with *Undaria*. The shrimp *Nauticaris magellanica* was found associated to the holdfasts and sporophylls and the crab *Coenophthalmus tridentatus* was associated with *Undaria* thalli (Irigoyen *et al.* 2011a). Conversely, changes in habitat structure from *Undaria* invasion can also act to exclude species, such as in Argentina where reefs covered by *Undaria* had reduced numbers of some reef fish as compared to un-invaded sites (Irigoyen *et al.* 2011b).

Whilst *Undaria* invasion may change the diversity or abundance of some macrofaunal species, some species may not be affected by *Undaria* presence. Experiments in Nuevo Gulf, found no significant difference in numbers of the crustacean *Leucippa pentagona*, the mussel *Aulacomya atra atra* (recruits and adults), the limpet *Fissurella radiosa tixierae*, the gastropod *Tegula patagonica* (which is known to feed on *Undaria*), the brittle star *Ophioplocus janarii* and the chitons *Chaetopleura isabellei* and *Plaxiphora aurata aurata* between sites with *Undaria* present or where *Undaria* was removed (Irigoyen *et al.* 2011a). A comparative study in southern New Zealand found no difference in the abundance of primary and secondary settlers of four mussel (*Mytilid*) species, or the diversity of mobile invertebrate assemblages between sites where *Undaria* was present or absent (T. Alestra pers comm) and a BACI study in southern New Zealand found no evidence that *Undaria* infestation altered macrofaunal assemblages (Forrest and Taylor 2002).

Undaria invasion can have varying effects on the presence and the abundance of associated macrofaunal species, the provision 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). A further consequence on macrofaunal communities is related to the winter annual growth pattern of *Undaria* at many sites of invasion, resulting in a temporally variable supply of resources. For example, if macrofauna increase within *Undaria* habitat during its growth season, this could result in a lack of food or habitat for increased numbers of associated species 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).

Macrofaunal assemblages found in association with <i>Undaria</i> habitat can be different from those associated with un-invaded sites. <i>Undaria</i> provides food and habitat for many species including urchins, crabs, gastropods and fish.

Summary of ecological impacts from *Undaria* invasion

- Changes the biogenic structure and function of benthic sites
- Substantially modifies sites previously devoid of native canopy-forming species
- Increases carbon production and export
- Modifies canopy-forming algal community composition; can comprise a significant addition to canopy cover
- Can compete with and exclude some native canopy-forming species at certain sites (e.g. deeper sites, artificial structures, modified sites which are affected by nutrient enrichment)
- Can reduce the presence and diversity of understory algal species
- Changes the presence and diversity of epibiotic assemblages
- Can alter macrofaunal species abundance and diversity (including urchins, crabs, gastropods and fish)
- May increase grazing pressure on native macroalgae due to a lack of food or habitat for increased numbers of associated grazers outside the *Undaria* growth season

5 ISSUES UNDERSTANDING IMPACTS FROM *UNDARIA* INVASION

Whilst there is evidence that increases in food and habitat availability from *Undaria* invasion can modify community composition and alter trophic interactions, mechanisms underlying such changes are complex and difficult to quantify (e.g. Schaffelke and Hewitt 2007). Invasion impacts vary spatially and temporally and separating changes caused by *Undaria* invasion from natural variation, over space and time, is a challenging task (Forrest and Taylor 2002). Previous studies have often been conducted over small scales and timeframes in the field and manipulative field studies are generally characterised by few replicates and high variability. These types of studies may not detect weak or unexpected effects (Thomsen *et al.* 2009) and make it difficult to rely on the extrapolation of results to wider scales. In addition, because *Undaria* has a variable growth cycle, studies which include the full annual cycle may show smaller effects as compared to studies which focus on the main period of *Undaria* abundance (which can vary depending on water temperature regimes).

Overall, there remains a paucity of field studies to identify specific impacts of macroalgal invasions on native communities (e.g. Schaffelke and Hewitt 2007; Williams and Smith 2007; McLaughlan *et al.* 2014; Davidson *et al.* 2015). The complexities around studying invasion impacts from *Undaria* present a challenge with regards to quantifying and mitigating impacts from invasion and for many sites a lack of baseline information, such as detailed site surveys prior to invasion, precludes a robust understanding of the impacts from *Undaria* invasion. Studies which are one-off surveys or compare invaded and un-invaded sites with no baseline data cannot always be reliably used as evidence for impacts because results may reflect natural variation. Ideally, a before–after control–impact framework would be used most often for studying invasions (Forrest and Taylor 2002). However, because of the time consuming and expensive nature of such studies, along with the fact that there is no guarantee the before–after impact site will be invaded, or be invaded to the extent that provides adequate impact information, this approach is rare.

Only recently have studies begun to emerge which aim to understand specific impacts, such as impacts on associated species abundance or diversity, and those which address ecosystem level effects. While it is recognised that changes in net primary production could have cascading impacts on ecosystem functioning, data around these interactions remains scarce (Yoshikawa *et al.* 2001; South *et al.* 2015; Jiménez *et al.* 2015a). Feeding assays conducted in laboratories illustrate how *Undaria* can provide a food source for native species but do not allow an understanding of the extent to which these species may utilise *Undaria* as a food source in the natural environment. Field based studies reporting how native species consume *Undaria* are limited.

Understanding ecological impacts from *Undaria* invasion requires quantitative information. Further research is needed in the form of empirical and manipulative experiments, including investigating community-level interactions, such as food web impacts from changes to primary production. Studies must encompass a variety of environments and extend over pluriannual timeframes.

6 DISCUSSION

Undaria is a prolific macroalgal invader and the ecological implications of *Undaria* invasion in New Zealand are considerable. *Undaria* can re-engineer habitats, where it grows in monospecific stands, which in no way resemble the native community in structure or function. *Undaria* has the potential to invade sites around the entire coast of New Zealand (James *et al.* 2015; James *et al.* 2016a) and to alter native communities significantly at these sites.

Suitable coastal sites, such as reef areas free of native canopy-forming species and generally at shallow depth ranges, can support *Undaria* at densities of up to 200 sporophytes m⁻² and form standing crops with biomass in excess of 10 kg m⁻² (Hay and Villouta 1993; Brown and Lamare 1994; Brown 1999; Sinner *et al.* 2000). At sites where native canopy-forming species are present, *Undaria* can intermingle to form a substantial component of macroalgal assemblages; such as occurs at sites on the east coast of the South Island (Russell *et al.* 2008; South *et al.* 2015; Jimenez *et al.* 2015b).

When *Undaria* grows at such densities, in monospecific or mixed stands, it makes a significant but inconsistent contribution of food and habitat to intertidal and subtidal reefs (Jimenez *et al.* 2014; South *et al.* 2015). There is evidence to suggest *Undaria* invasion can cause changes to native community composition at all trophic levels. As well as increasing primary productivity, it can reduce the abundance and diversity of understory algal assemblages, out-compete some native canopy-forming species and affect the abundance and composition of associated epibionts and macrofauna: including gastropods, crabs, urchins and fish. The on-flow effects from *Undaria* invasion, such as potentially increasing numbers of mobile invertebrates and fish, are site and species specific and may be more pronounced at sites where native canopy-forming macroalgae are naturally absent.

6.1 Impacts of *Undaria* invasion on social and cultural values

While this review concentrates on ecological impacts from invasion, it is also true that *Undaria* can substantially alter the natural character, ecological and intrinsic values of sites once it becomes established, areas popular for marine recreational activities can suffer visual impacts, for divers and snorkelers, at the height of the *Undaria* growth season (Irigoyen 2011b). Tourism values may be impacted if *Undaria* invades popular diving or snorkelling areas (Henkel and Hofmann 2008; Raffo *et al.* 2009). Changes to commercial and recreational values of reef systems may also occur if *Undaria* causes changes to fish and gastropod communities (Irigoyen *et al.* 2011a, b). In New Zealand *Undaria* infestation can ultimately damage the cultural values and mauri of infested sites (Hunt *et al.* 2009).

6.2 How climate change could influence *Undaria* invasion

Whilst *Undaria* invasion poses a current risk to intact native ecosystems, additional impacts may occur in combination with climate change. Responses of invasive species to climate change, and the interactions of climate change with other stressors, may differ from the responses of native species and will further alter ecological impacts from invasive species (Hellmann *et al.* 2008). 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 (Lüning and Neushul 1978; Kain 1979; Lüning 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). 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).

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 a 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 (Wernberg *et al.* 2010). It is therefore 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 species such as *Undaria* which have higher temperature tolerances and more adaptable life cycles.

6.3 Conclusions and recommendations

Undaria invasion can modify intertidal and subtidal communities, impacts can occur across all trophic levels. However, it is challenging to obtain quantitative information on ecological impacts from *Undaria* invasions and impact assessments cannot keep up with rates of introduction and spread of *Undaria* to new locations. Further research is needed to determine more site and species specific impacts from *Undaria* invasion.

Nevertheless, enough evidence is available to warrant real concern over *Undaria* invasion and the subsequent ecological impacts on native communities. The presence and impacts from *Undaria* invasion undermine efforts to conserve biodiversity and representative native ecosystems in particular. Furthermore, future interactions between environmental stressors such as high levels of modification, eutrophication, and ocean warming may give *Undaria* a significant advantage over native species as community resilience is lowered. It may therefore be prudent to rely on qualitative, theoretical risk assessments, such as those based on expert opinion and modelling (see Campbell and Hewitt 2013), to provide timely information to decision-makers on risks posed by *Undaria* invasion.

The set of attributes which make *Undaria* one of the most invasive species in the world, and a current lack of tools or methods to control or eradicate *Undaria* post invasion (e.g. Forrest and Blakemore 2006), 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*.

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Appendix I: Summary of literature on *Undaria* invasion with reported impacts

Reference	Method	Country	Region/location	Summary	Impact
Hay and Luckens 1987	Survey	New Zealand	Wellington Harbour, North Island.	Dense <i>Undaria</i> populations in Wellington Harbour on artificial and natural substrate.	CC, SM
Sanderson 1990	Survey	Australia	Triabunna to Rheban, Tasmania.	<i>Undaria</i> was established extensively across areas devoid of native canopy-forming species such as urchin barrens.	SM, CC
Castric-Fey <i>et al.</i> 1993	Survey	France	St Malo, Brittany.	Dense <i>Undaria</i> populations found on natural substrate.	SM, CC
Hay and Villouta 1993	Survey	New Zealand	Wellington, Timaru and Oamaru, South Island.	Dense <i>Undaria</i> populations dominating the low intertidal and shallow subtidal zone. Some populations taking over sites where small fleshy algae were previously dominant or present and excluding these natives.	SM, CC
Brown and Lamare 1994	Survey	New Zealand	Timaru, South Island.	<i>Undaria</i> populations abundant in open spaces, disturbed sites and on cobbled areas. Low abundance amongst large brown algal species. Opportunist species but may compete with Sargassum, Cystophora and Carpophyllum spp.	SM, CC
Floc'h <i>et al.</i> 1996	Experiment (Canopy removal with reproductive <i>Undaria</i> material introduced)	France	Island of Ushant, Brittany.	<i>Undaria</i> prefers artificial structures (mussel farms) and may not be a threat to native areas. <i>Undaria</i> recruitment occurred better in the <i>Himanthalia</i> zone than amongst native canopy forming species.	CC, 0
Campbell and Burrige 1998	Survey	Australia	Port Philip Bay, Victoria.	Dense <i>Undaria</i> populations on hard or at least semi-consolidated substrate. Extensive colonisation and prolific growth observed. <i>Undaria</i> may compete with and perhaps displace dominant macroalgal species found in this region.	SM, CC
Curiel <i>et al.</i> 1998	Observation, Survey (comp)	Italy	Lagoon of Venice	Quickly colonised hard substrata and may compete with native species. Decrease in understory species beneath 100% <i>Undaria</i> cover.	SM, CC

Fletcher and Farrell 1999	Survey (artificial structures)	England	Solent region (Harbours/Marinas)	At all marinas surveyed, <i>Undaria</i> was the dominant fouling alga on the majority of pontoon floats, growing to a large size. <i>Undaria</i> is tolerant of a much wider range of environmental conditions than native algae and can therefore colonise sheltered substrata not covered by native species.	CC, SM
Wear and Gardener 1999 (cited in Sinner et al 2000)	Survey (BACI)	New Zealand	Wellington Harbour, North Island	The effects of <i>Undaria</i> are additive rather than substitutive. No detectable effect on native algal assemblage.	CC, 0
Curiel <i>et al.</i> 2001	Survey (comp), Experiment (<i>Undaria</i> removal)	Italy	Lagoon of Venice, Adriatic Sea.	Dense populations dominating substrate, on a seasonal basis. Possibility of competition with native species. In particular <i>Ulva rigida</i> , <i>Enteromorpha spp.</i> , <i>Antithamnion pectinatum</i> , <i>Chondrocanthus acicularis</i> in shallow areas and <i>Rhodymenia ardissoni</i> in deeper waters.	CC, SM
Forrest and Taylor 2002	Survey (BACI)	New Zealand	Lyttelton Harbour, South Island.	The effects of <i>Undaria</i> are additive rather than substitutive. No detectable effect on native algal assemblage. No evidence of displacement of native macrofaunal or macroalgal species.	CC, 0
Valentine and Johnson 2003	Experiment (native canopy removal)	Australia	East coast, Tasmania.	High density <i>Undaria</i> growth following removal of native canopy.	SM, CC
Casas <i>et al.</i> 2004	Experiment (<i>Undaria</i> removal)	Argentina	Nuevo Gulf, northern Patagonia.	The removal of <i>Undaria</i> from invaded sites resulted in a significant increase of native seaweed richness and diversity.	CC
Edgar <i>et al.</i> 2004	Experiment (native canopy removal)	Australia	East coast, Tasmania.	High density <i>Undaria</i> growth following removal of native canopy.	CC, SM
Stuart 2004	Literature review, Observations	New Zealand	South coast, South Island.	Review covered background but impacts suggested were based on the authors observations. <i>Undaria</i> can exclude understory species. Furoid species may be displaced and exclusion of canopy forming species is possible.	CC, SM
Valentine and Johnson 2004	Survey (Comp)	Australia	East coast, Tasmania.	High density <i>Undaria</i> growth following dieback of native canopy. <i>Undaria</i> was rare or absent from control areas.	CC, SM
Farrell and Fletcher 2006	Experiment (algal removal, marina)	England	Torquay Marina, Devon.	<i>Undaria</i> can out-compete native species in a marina environment: two kelp species, <i>Laminaria digitata</i> and <i>Laminaria saccharina</i> .	SM, CC

Casas <i>et al.</i> 2008	Survey, Experiment (<i>Undaria</i> removal)	Argentina	Nuevo Gulf, northern Patagonia.	Densely distributed <i>Undaria</i> population including amongst native algal species. Dense populations (up to 159 indiv/m ²) growing on rocky seabed. Constant recruitment through the year.	SM, CC
Russell <i>et al.</i> 2008	Survey	New Zealand	Major ports and harbours, South Island.	<i>Undaria</i> prevalent at intertidal and subtidal sites including amongst native algal species. <i>Undaria</i> populations dominant within deeper subtidal zones replacing or covering <i>Desmarestia ligulata</i> and understory species. Dense <i>Undaria</i> populations on artificial structures and natural substrate. High densities at some localities amongst the large bull kelp species <i>Durvillaea antarctica</i> and <i>D. willana</i> .	SM, CC
Teso <i>et al.</i> 2009	Observations, Experiment (feeding assay)	Argentina	Nuevo Gulf, northern Patagonia.	Feeding assays with the sea urchins <i>Arbacia dufresnii</i> and <i>Pseudechinus magellanicus</i> and the gastropod <i>Tegula patagonica</i> confirmed that these species feed on <i>Undaria</i> . But not to such an extent that they would control the growth or spread of <i>Undaria</i> .	HT, CC
Raffo <i>et al.</i> 2009	Survey (Comp)	Argentina	Nuevo Gulf	No evidence of interspecific competition with <i>Macrocystis pyrifera</i> . Density and diversity of the fauna associated with the holdfast was different to that on <i>M. pyrifera</i> .	CC, HT
Irigoyen <i>et al.</i> 2011a	Experiment (<i>Undaria</i> removal)	Argentina	Nuevo Gulf	Species richness and diversity were higher in plots covered by <i>Undaria</i> than when <i>Undaria</i> was removed. Species associated with <i>Undaria</i> habitat were different from those found in non- <i>Undaria</i> habitat.	HT, CC
Irigoyen <i>et al.</i> 2011b	Survey (Comp)	Argentina	Nuevo Gulf	Underwater visual census found fish abundance decreased markedly in low-relief reefs that had been covered by <i>Undaria</i> .	HT, CC
Schiel and Thompson 2012	Survey	New Zealand	Moeraki and Lyttelton, South Island.	The effects of <i>Undaria</i> are additive rather than substitutive. <i>Undaria</i> recruited to patches in the native canopies and habitats unsuited to most of the dominant fucoids. No evidence that <i>Undaria</i> overgrows other species or affects them through shading.	CC
Thompson and Schiel 2012	Experiment (Native canopy removal)	New Zealand	Lyttelton, South Island	<i>Undaria</i> recruitment in the subtidal zone was facilitated by native canopy removal and the presence of coralline turf (<i>Coralline officinalis</i>). <i>Carpophyllum maschalocarpum</i> reclaimed sites of <i>Undaria</i> invasive over the following year.	CC

Hooton-Kaufman 2012	Survey (Comp)	USA	Monterey Harbour, California.	In all months when fishes were present they used <i>Undaria</i> habitat disproportionately more than other available habitat. Biomass of the red alga <i>Prionitis lanceolata</i> was significantly higher in non- <i>Undaria</i> habitat. All other algal species showed no statistical difference in biomass between the two habitat types.	HT, CC
Carnell and Keough 2014	Experiment (native canopy removal and additional nutrient)	Australia	Port Phillip Bay, Victoria	Recruitment of <i>Undaria</i> to removal plots. Low competitive ability amongst <i>Ecklonia radiata</i> in the absence of added or excess nutrients. But proliferation of <i>Undaria</i> in the canopy removal and nutrient-addition treatment negatively influenced the recovery of <i>Ecklonia</i> .	SM, CC
Tait <i>et al.</i> 2015	Experiment (<i>In situ</i> photorespirometry)	New Zealand	Moeraki peninsula, South Island	High biomass turnover associated with the annual life history of <i>Undaria</i> . Has the potential to increase carbon export to surrounding ecosystems compared to perennial fucoid species.	CC, HT
Arnold <i>et al.</i> 2015	Survey	England	Plymouth Sound	<i>Undaria</i> forms a dominant and conspicuous component of communities on natural substrata. <i>Undaria</i> supported a structurally dissimilar and less diverse epibiotic assemblage than the native perennial kelp species.	CC, HT
Jiménez <i>et al.</i> 2014	Experiment (laboratory feeding assay)	New Zealand	University of Otago, South Island.	All of the grazers tested (the amphipod <i>Aora typica</i> , the isopod <i>Batedotea elongata</i> and the gastropods <i>Cookia sulcata</i> and <i>Haliotis iris</i>) ate <i>Undaria</i> at rates comparable to most of the six native macroalgae offered, except for <i>B. elongata</i> , which barely consumed it. <i>Undaria</i> invasion has the potential to contribute organic matter to the local food web and may alter existing trophic relationships.	HT
Jiménez <i>et al.</i> 2015a	Survey	New Zealand	Otago, South Island.	<i>Undaria</i> has the potential to influence carbon fluxes and faunal communities in subtidal food webs, but that such effects are unlikely to be transferred across coastal habitats.	HT
South <i>et al.</i> 2015	Survey, Experiment (press removal)	New Zealand	Moeraki Peninsula, South Island.	The effects of <i>Undaria</i> are additive rather than substitutive; it did not displace native species but did provide biogenic habitat, biomass and significant inputs of carbon to the reef system. May represent a net gain to communities and ecosystems.	CC, HT, 0

Morelison <i>et al.</i> 2016	Survey, Experiment (native canopy removal and <i>Undaria</i> removal)	New Zealand	Wellington Harbour, North Island.	No consistent differences in native algal community composition between locations, despite higher <i>Undaria</i> cover at one site. Physical disturbance of the native algal assemblage is not a key requirement for this kelp to invade and establish in new areas in the low intertidal zone. The effects of <i>Undaria</i> are additive rather than substitutive; removal of <i>Undaria</i> did not change native intertidal assemblage structure in either harbour or south coast sites.	CC, 0
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Impacts listed are CC = Changes to community composition, SM = Space monopolisation, HT = effects on higher trophic levels. 0 = Studies which found no effect on native canopy-forming algae.

Appendix II: Summary of previous literature reviews which include impacts from *Undaria* invasion

Reference	Comments	Summary
Parsons 1995	Review of New Zealand literature on <i>Undaria</i> .	It is believed that <i>Undaria</i> will become part of the natural community and will not displace any other species completely.
Dean 1999	Review of New Zealand and international literature on <i>Undaria</i> .	Less competitive than New Zealand seaweeds, no effects on understory, effects may occur due to grazing pressure on natives post <i>Undaria</i> season.
Sinner <i>et al.</i> 2000	Review of New Zealand and international literature on <i>Undaria</i> .	Long term impact of <i>Undaria</i> within and beyond stands of established sporophytes are unknown.
Nyberg and Wallentinus 2005	Species traits which facilitate introduction and predominance were quantitatively ranked using interval arithmetic to search for common patterns among 113 marine macroalgae introduced in Europe. Three main categories were used: dispersal, establishment and ecological impact.	<i>Undaria</i> ranked in the top five risk species. Identified as one of the most hazardous species in Europe. <i>Undaria</i> was given a high impact score in this study based on size, morphology, habitat effects (including abundance and possibility to suppress other species), and life span.
Schaffelke and Hewitt 2007	Review of New Zealand and international literature for impacts from invasive seaweeds.	Unable to find sufficient substantial quantitative information about the impacts of alien seaweeds to detect common patterns. A number of studies which have shown significant ecological impacts, but do not identify the underlying mechanisms. Invasion impacts may be specific to the invaded system or the period of time since establishment and/or past disturbance.
Williams and Smith 2007	A Global review of the distribution, taxonomy and impacts of introduced seaweeds. Cited six papers on <i>Undaria</i> : Forrest and Taylor 2002, Valentine and Johnson 2005, Casas <i>et al.</i> 2004, Edgar <i>et al.</i> 2004, Valentine and Johnson 2003, Farrell and Fletcher 2006.	Native seaweeds can act to resist (three cases cited) or facilitate (one case cited) invasion by <i>Undaria</i> . Manipulative community-level field studies in combination with modelling are needed to identify not only the impacts of introduced seaweeds on native communities but also the factors that influence invasibility for a more integrative understanding of invasive seaweed ecology.
McLaughlan <i>et al.</i> 2014	An assessment for impacts from Europe's top 10 invasive species. Cited three papers from Argentina for impacts on ecosystem services by <i>Undaria</i> : Casas <i>et al.</i> 2004; Irigoyen <i>et al.</i> 2011a, 2011b.	<i>Undaria</i> could potentially produce a bottom-up effect on local food chains by increasing abundance of prey for a wide variety of predators, from invertebrates to marine mammals. <i>Undaria</i> may reduce native seaweed diversity and reduce habitat for reef fishes by physically obstructing refuges. <i>Undaria</i> impedes light penetration resulting in "bottom-up" effects. Annual die-back may cause fish and other animals to move to nearby areas.

Davidson *et al.* 2015 An update to the 2007 review of the impacts of introduced macroalgae (Schaffelke and Hewitt 2007). Aimed to find patterns of impacts, to examine whether certain species were more likely to cause significant impacts, and to identify mechanisms contributing to the observed impacts. Cites five papers on *Undaria*: Farrell and Fletcher, Irigoyen 2011a, b; Raffo 2009; Carnell and Keough 2014.

Petrocelli *et al.* 2015 Aims to take stock of the situation regarding the distribution and impact of three of the most spread invasive seaweeds around the world: *Codium fragile*, *Gracilaria vermiculophylla* and *Undaria pinnatifida*.

Undaria causes changes to competitive relationships in the recipient habitat via space monopolization and changed community composition. This study outlined a critical knowledge gap as the authors were unable to find comparable quantitative information about ramifications of macroalgal introductions, information in this updated review was still considered too sparse to identify general patterns and mechanisms of impact from invasive macroalgae.

Scarcity of pluriannual studies in the field to assess actual negative or positive impacts on native communities is evident. Most studies were carried out in the laboratory or in mesocosms, and the reported impact was only a speculative extrapolation of results.