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*

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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 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 understorey 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).
**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. 1**

**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 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.

**Fig. 2**
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 Burridge 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.

<table>
<thead>
<tr>
<th>Summary of invasive attributes for Undaria</th>
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<tbody>
<tr>
<td>- Dense (monospecific) growth patterns</td>
</tr>
<tr>
<td>- Rapid growth rate</td>
</tr>
<tr>
<td>- Early maturation of sporophytes</td>
</tr>
<tr>
<td>- High fecundity/reproductive output</td>
</tr>
<tr>
<td>- Hardy microscopic gametophyte phase</td>
</tr>
<tr>
<td>- Morphological plasticity</td>
</tr>
<tr>
<td>- Variable lifecycle and growth strategies</td>
</tr>
<tr>
<td>- Colonises a range of substrata</td>
</tr>
<tr>
<td>- Broad temperature tolerance</td>
</tr>
<tr>
<td>- Wide depth distribution</td>
</tr>
<tr>
<td>- Easily spread and transported</td>
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</tbody>
</table>
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 officinalis*) 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).

![Image A](image1.png)

![Image B](image2.png)

![Image C](image3.png)

![Image D](image4.png)

**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; Shubneva and Skriptsova 2012). Once established Undaria can spread into more diverse range of sites, this is discussed in Section 4.

<table>
<thead>
<tr>
<th>Summary of common sites for Undaria establishment</th>
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<tbody>
<tr>
<td>• Artificial structures</td>
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<tr>
<td>• Natural hard substrate (e.g. reef, rocks or boulders)</td>
</tr>
<tr>
<td>• Intertidal or shallow subtidal areas</td>
</tr>
<tr>
<td>• Sites where native canopy-forming species are absent or sparse</td>
</tr>
<tr>
<td>• Sites with low to moderate wave exposure</td>
</tr>
<tr>
<td>• Areas with cover of geniculate coralline or small filamentous algal species</td>
</tr>
<tr>
<td>• Sites where light, space and nutrient availability are not limiting factors</td>
</tr>
</tbody>
</table>
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](image)

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 ~50 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 (Morelsson *et al.* 2013).
<table>
<thead>
<tr>
<th>Summary of mechanisms and associated ranges of spread for <em>Undaria</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>• Hull fouling: local to international distances, including crossing the equator</td>
</tr>
<tr>
<td>• Aquaculture transfers: local to international distances (including overland transfers of wet material)</td>
</tr>
<tr>
<td>• Saltation: around $100 - 400\ m\ yr^{-1}$</td>
</tr>
<tr>
<td>• Drifting detached sporophytes or sporophylls: Unknown</td>
</tr>
<tr>
<td>• Spore dispersal: up to $100\ m - 1\ km\ yr^{-1}$</td>
</tr>
</tbody>
</table>
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 Antartica* 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 Burridge 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).

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*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 Rhodymenia 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 affects 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; Ingoyen 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 *Ophioplucus 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).

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**Macrofaunal assemblages found in association with Undaria habitat can be different from those associated with un-invaded sites. Undaria 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.
Undaria is 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 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.
REFERENCES


Bader C (1998). The ecology of the butterfish Odax pullus around the Kaikoura Peninsula. (MSc Thesis), University of Canterbury, Christchurch.


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

<table>
<thead>
<tr>
<th>Reference</th>
<th>Method</th>
<th>Country</th>
<th>Region/location</th>
<th>Summary</th>
<th>Impact</th>
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</thead>
<tbody>
<tr>
<td>Hay and Luckens 1987</td>
<td>Survey</td>
<td>New Zealand</td>
<td>Wellington Harbour, North Island.</td>
<td>Dense <em>Undaria</em> populations in Wellington Harbour on artificial and natural substrate.</td>
<td>CC, SM</td>
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<tr>
<td>Sanderson 1990</td>
<td>Survey</td>
<td>Australia</td>
<td>Triabunna to Rheban, Tasmania.</td>
<td><em>Undaria</em> was established extensively across areas devoid of native canopy-forming species such as urchin barrens.</td>
<td>SM, CC</td>
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<tr>
<td>Castric-Fey <em>et al.</em> 1993</td>
<td>Survey</td>
<td>France</td>
<td>St Malo, Brittany.</td>
<td>Dense <em>Undaria</em> populations found on natural substrate.</td>
<td>SM, CC</td>
</tr>
<tr>
<td>Hay and Villouta 1993</td>
<td>Survey</td>
<td>New Zealand</td>
<td>Wellington, Timaru and Oamaru, South Island.</td>
<td>Dense <em>Undaria</em> populations dominating the low intertidal and shallow subtidal zone. Some populations taking over sites where small fleshey algae were previously dominant or present and excluding these natives.</td>
<td>SM, CC</td>
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<tr>
<td>Brown and Lamare 1994</td>
<td>Survey</td>
<td>New Zealand</td>
<td>Timaru, South Island.</td>
<td><em>Undaria</em> 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.</td>
<td>SM, CC</td>
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<tr>
<td>Floc’h <em>et al.</em> 1996</td>
<td>Experiment (Canopy removal with reproductive <em>Undaria</em> material introduced)</td>
<td>France</td>
<td>Island of Ushant, Brittany.</td>
<td><em>Undaria</em> prefers artificial structures (mussel farms) and may not be a threat to native areas. <em>Undaria</em> recruitment occurred better in the <em>Himanthalia</em> zone than amongst native canopy forming species.</td>
<td>CC, 0</td>
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<tr>
<td>Campbell and Burridge 1998</td>
<td>Survey</td>
<td>Australia</td>
<td>Port Phillip Bay, Victoria.</td>
<td>Dense <em>Undaria</em> populations on hard or at least semi-consolidated substrate. Extensive colonisation and prolific growth observed. <em>Undaria</em> may compete with and perhaps displace dominant macroalgal species found in this region.</td>
<td>SM, CC</td>
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<tr>
<td>Curiel <em>et al.</em> 1998</td>
<td>Observation, Survey (comp)</td>
<td>Italy</td>
<td>Lagoon of Venice</td>
<td>Quickly colonised hard substrata and may compete with native species. Decrease in understory species beneath 100% <em>Undaria</em> cover.</td>
<td>SM, CC</td>
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</table>
At all marinas surveyed, *Undaria* was the dominant fouling alga on the majority of pontoon floats, growing to a large size. *Undaria* is tolerant of a much wider range of environmental conditions than native algae and can therefore colonise sheltered substrata not covered by native species.

The effects of *Undaria* are additive rather than substitutive. No detectable effect on native algal assemblage.

Dense populations dominating substrate, on a seasonal basis. Possibility of competition with native species. In particular *Ulva rigida*, *Enteromorpha spp.*, *Antithamnion pectinatum*, *Chondrocanthus acicularis* in shallow areas and *Rhodymenia ardissonii* in deeper waters.

The effects of *Undaria* are additive rather than substitutive. No detectable effect on native algal assemblage. No evidence of displacement of native macrofaunal or macroalgal species.

High density *Undaria* growth following removal of native canopy.

The removal of *Undaria* from invaded sites resulted in a significant increase of native seaweed richness and diversity.

High density *Undaria* growth following dieback of native canopy. *Undaria* was rare or absent from control areas.

*Undaria* can out-compete native species in a marina environment: two kelp species, *Laminaria digitata* and *Laminaria saccharina*.
Casas et al. 2008  
Survey,  
Experiment (Undaria removal)  
Argentina  
Nuevo Gulf, northern Patagonia.  
Densely distributed Undaria population including amongst native algal species. Dense populations (up to 159 indiv/m2) growing on rocky seabed. Constant recruitment through the year.

Russell et al. 2008  
Survey  
New Zealand  
Major ports and harbours, South Island.  
Undaria prevalent at intertidal and subtidal sites including amongst native algal species. Undaria populations dominant within deeper subtidal zones replacing or covering Desmarestia ligulata and understorey species. Dense Undaria populations on artificial structures and natural substrate. High densities at some localities amongst the large bull kelp species Durvillaea antarctica and D. willana.

Teso et al. 2009  
Observations,  
Experiment (feeding assay)  
Argentina  
Nuevo Gulf, northern Patagonia.  
Feeding assays with the sea urchins Arbacia dufresnii and Pseudechinus magellanicus and the gastropod Tegula patagonica confirmed that these species feed on Undaria. But not to such an extent that they would control the growth or spread of Undaria.

Raffo et al. 2009  
Survey (Comp)  
Argentina  
Nuevo Gulf  
No evidence of interspecific competition with Macrocystis pyrifera. Density and diversity of the fauna associated with the holdfast was different to that on M. pyrifera.

Irigoyen et al. 2011a  
Experiment (Undaria removal)  
Argentina  
Nuevo Gulf  
Species richness and diversity were higher in plots covered by Undaria than when Undaria was removed. Species associated with Undaria habitat were different from those found in non-Undaria habitat.

Irigoyen et al. 2011b  
Survey (Comp)  
Argentina  
Nuevo Gulf  
Underwater visual census found fish abundance decreased markedly in low-relief reefs that had been covered by Undaria.

Schiel and Thompson 2012  
Survey  
New Zealand  
Moeraki and Lyttelton, South Island.  
The effects of Undaria are additive rather than substitutive. Undaria recruited to patches in the native canopies and habitats unsuited to most of the dominant fucoids. No evidence that Undaria overgrows other species or affects them through shading.

Thompson and Schiel 2012  
Experiment (Native canopy removal)  
New Zealand  
Lyttelton, South Island  
Undaria recruitment in the subtidal zone was facilitated by native canopy removal and the presence of coralline turf (Corallina officinalis). Carpophyllum maschalocarpum reclaimed sites of Undaria invasive over the following year.
<table>
<thead>
<tr>
<th>Study</th>
<th>Year</th>
<th>Study Type</th>
<th>Location</th>
<th>Key Findings</th>
<th>Authors</th>
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<tr>
<td>Hooton-Kaufman 2012</td>
<td>USA</td>
<td>Survey (Comp)</td>
<td>Monterey Harbour,</td>
<td>In all months when fishes were present they used <em>Undaria</em> habitat</td>
<td>HT, CC</td>
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<td>California.</td>
<td>disproportionately more than other available habitat. Biomass of the red alga</td>
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<td><em>Prionitis lanceolata</em> was significantly higher in non-<em>Undaria</em> habitat. All</td>
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<td>other algal species showed no statistical difference in biomass between the</td>
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<td>two habitat types.</td>
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<td>Carnell and Keough 2014</td>
<td>Australia</td>
<td>Experiment (native</td>
<td>Port Phillip Bay,</td>
<td>Recruitment of <em>Undaria</em> to removal plots. Low competitive ability amongst</td>
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<td>canopy removal and</td>
<td>Victoria</td>
<td><em>Ecklonia radiata</em> in the absence of added or excess nutrients. But proliferation</td>
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<td>additional nutrient)</td>
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<td>of <em>Undaria</em> in the canopy removal and nutrient-addition treatment negatively</td>
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<td>Tait et al. 2015</td>
<td>New Zealand</td>
<td>Experiment (<em>In situ</em></td>
<td>Moeraki peninsula,</td>
<td>High biomass turnover associated with the annual life history of <em>Undaria</em>. Has</td>
<td>CC, HT</td>
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<td></td>
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<td>photorespirometry)</td>
<td>South Island</td>
<td>the potential to increase carbon export to surrounding ecosystems compared to</td>
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<td>Arnold et al. 2015</td>
<td>England</td>
<td>Survey</td>
<td>Plymouth Sound</td>
<td><em>Undaria</em> forms a dominant and conspicuous component of communities on</td>
<td>CC, HT</td>
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<td>natural substrata. <em>Undaria</em> supported a structurally dissimilar and less</td>
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<td>diverse epibiotic assemblage than the native perennial kelp species.</td>
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<tr>
<td>Jiménez et al. 2014</td>
<td>New Zealand</td>
<td>Experiment (laboratory feeding assay)</td>
<td>University of Otago, South Island.</td>
<td>All of the grazers tested (the amphipod <em>Aora typica</em>, the isopod <em>Batedotea elongata</em> and the gastropods <em>Cookia sulcata</em> and <em>Haliotis iris</em>) ate <em>Undaria</em> at rates comparable to most of the six native macroalgae offered, except for <em>B. elongata</em>, which barely consumed it. <em>Undaria</em> invasion has the potential to contribute organic matter to the local food web and may alter existing trophic relationships.</td>
<td>HT</td>
</tr>
<tr>
<td>Jiménez et al. 2015a</td>
<td>New Zealand</td>
<td>Survey</td>
<td>Otago, South Island.</td>
<td><em>Undaria</em> has the potential to influence carbon fluxes and faunal communities in</td>
<td>HT</td>
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<td>subtidal food webs, but that such effects are unlikely to be transferred across</td>
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<td>coastal habitats.</td>
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<td>South et al. 2015</td>
<td>New Zealand</td>
<td>Survey, Experiment</td>
<td>Moeraki Peninsula,</td>
<td>The effects of <em>Undaria</em> are additive rather than substitutive; it did not displace</td>
<td>CC, HT, 0</td>
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<td></td>
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<td>(press removal)</td>
<td>South Island</td>
<td>native species but did provide biogenic habitat, biomass and significant inputs of</td>
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<td>carbon to the reef system. May represent a net gain to communities and</td>
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<td>ecosystems.</td>
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<tr>
<td>Moreisson et al. 2016</td>
<td>Survey, Experiment (native canopy removal and Undaria removal)</td>
<td>New Zealand Wellington Harbour, North Island.</td>
<td>No consistent differences in native algal community composition between locations, despite higher <em>Undaria</em> 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 <em>Undaria</em> are additive rather than substitutive; removal of <em>Undaria</em> did not change native intertidal assemblage structure in either harbour or south coast sites.</td>
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</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Reference</th>
<th>Comments</th>
<th>Summary</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parsons 1995</td>
<td>Review of New Zealand literature on <em>Undaria</em>.</td>
<td>It is believed that <em>Undaria</em> will become part of the natural community and will not displace any other species completely.</td>
</tr>
<tr>
<td>Dean 1999</td>
<td>Review of New Zealand and international literature on <em>Undaria</em>.</td>
<td>Less competitive than New Zealand seaweeds, no effects on understory, effects may occur due to grazing pressure on natives post <em>Undaria</em> season.</td>
</tr>
<tr>
<td>Sinner <em>et al.</em> 2000</td>
<td>Review of New Zealand and international literature on <em>Undaria</em>.</td>
<td>Long term impact of <em>Undaria</em> within and beyond stands of established sporophytes are unknown.</td>
</tr>
<tr>
<td>Nyberg and Wallentinus 2005</td>
<td>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.</td>
<td><em>Undaria</em> ranked in the top five risk species. Identified as one of the most hazardous species in Europe. <em>Undaria</em> 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.</td>
</tr>
<tr>
<td>Schaffelke and Hewitt 2007</td>
<td>Review of New Zealand and international literature for impacts from invasive seaweeds.</td>
<td>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.</td>
</tr>
<tr>
<td>Williams and Smith 2007</td>
<td>A Global review of the distribution, taxonomy and impacts of introduced seaweeds. Cited six papers on <em>Undaria</em>: Forrest and Taylor 2002, Valentine and Johnson 2005, Casas <em>et al.</em> 2004, Edgar <em>et al.</em> 2004, Valentine and Johnson 2003, Farrell and Fletcher 2006.</td>
<td>Native seaweeds can act to resist (three cases cited) or facilitate (one case cited) invasion by <em>Undaria</em>. 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.</td>
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<tr>
<td>McLaughlan <em>et al.</em> 2014</td>
<td>An assessment for impacts from Europe's top 10 invasive species. Cited three papers from Argentina for impacts on ecosystem services by <em>Undaria</em>: Casas <em>et al.</em> 2004; Irigoyen <em>et al.</em> 2011a, 2011b.</td>
<td><em>Undaria</em> 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. <em>Undaria</em> may reduce native seaweed diversity and reduce habitat for reef fishes by physically obstructing refuges. <em>Undaria</em> impedes light penetration resulting in &quot;bottom-up&quot; effects. Annual die-back may cause fish and other animals to move to nearby areas.</td>
</tr>
</tbody>
</table>
Davidson et al. 2015

An update to the 2007 review of the impacts of introduced macroalgae (Schatellke 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.

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.

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.

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.