A review of three decades of research on the invasive kelp Undaria pinnatifida in Australasia: An assessment of its success, impacts and status as one of the world's worst invaders

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A B S T R A C T

Marine invasive macroalgae can have severe local-scale impacts on ecological communities. The kelp Undaria pinnatifida is one of the most successful marine invasive species worldwide, and is widely regarded as one of the worst. Here, we review research on Undaria in Australasia, where the kelp is established throughout much of New Zealand and south-eastern Australia. The presence of Undaria for at least three decades in these locations makes Australasia one of the longest-invaded bioregions globally, and a valuable case study for considering Undaria's invasion success and associated impacts. In Australasia, Undaria has primarily invaded open spaces, turf communities, and gaps in native canopies within a relatively narrow elevation band on rocky shores. Despite its high biomass, Undaria has relatively few direct impacts on native species, and can increase community-wide attributes such as primary productivity and the provision of biogenic habitat. Therefore, Australasian Undaria research provides an example of a decoupling between the success and impact of an invasive species. Undaria will most likely continue to spread along thousands of kilometres of rocky coastline in temperate Australasia, due to its tolerance to large variations in temperature, ability to exploit disturbances to local communities, and the continued transfer among regions via vessel movements and aquaculture activities. However, the spread of Undaria remains difficult to manage as eradication is challenging and seldom successful. Therefore, understanding potential invasion pathways, maintaining native canopy-forming species that limit Undaria success, and effectively managing anthropogenic vectors of Undaria spread, should be key management priorities.

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1. Introduction

Biological invasions are a significant threat to native biodiversity and the ecological services it provides. The rate of biological invasions has increased throughout the world and many high profile invaders have been implicated in structural and functional changes in recipient ecosystems (Crooks, 2002; Thomsen et al., 2008; Maggi et al., 2015). In recent years, many species of introduced macroalgae have become conspicuous components of coastal ecosystems, where they can have a wide range of impacts on local communities, ecosystem function and ecosystem services (Thomsen et al., 2016b).

One of the most successful and purportedly problematic macro-algal invaders is the laminarian kelp, Undaria pinnatifida (Harvey) Suringar (hereafter Undaria). Undaria has been included as one of nine marine species in a list of the world's 100 worst invasive species (Lowe et al., 2000), and in Europe was rated as one of the top 10 worst invasive species (Gallardo, 2014) and the third most hazardous of 113 macroalgal introductions (Nyberg and Wallentinus, 2005).

Undaria is native to Russia and Asia, with large populations in China, Japan and North Korea, and is extensively cultivated to provide a highly prized food resource (e.g., Chaoyuan and Jianxin, 1997; Morita et al., 2003; Skripitsova et al., 2004; Na et al., 2016). As a result of its commercial importance, Undaria has been widely studied, with aspects of its early life history, genetics and chemical composition receiving particular attention (Lee et al., 2004; Prabhasankar et al., 2009; Wang et al., 2009). However, Undaria has also become one of the most widely distributed invasive marine macroalgae worldwide, having established in extensive areas in the NE Atlantic, SW Atlantic, NE Pacific, SE Pacific, SW Pacific and the Mediterranean and North Seas.

In the light of the continuing spread of Undaria into native communities, and its increasing encroachment onto port and aquaculture facilities (Dellatorre et al., 2014; Heiser et al., 2014; James et al., 2014; Minchin and Nunn, 2014; Pereyra et al., 2015; Atalah et al., 2016b), it is useful to assess the scientific findings with respect to the kelp’s invasiveness, impacts and management. Here, we focus on Australasia (Australia and New Zealand), where Undaria was observed for the first time three decades ago, making this part of the world one of Undaria's longest-invaded bioregions globally (Fig. 1). Australasia is also the most studied bioregion with respect to Undaria’s dispersal (Forrest et al., 2000; Sliwa et al., 2006; Russell et al., 2008; James and Shears, 2016a), population biology (Schaufele et al., 2005; Primo et al., 2010; Schiel and Thompson, 2012; James and Shears, 2016b), ecological interactions (Forrest and Taylor, 2002; Valentine and Johnson, 2004; 2005; Thompson and Schiel, 2012), and management (Hewitt et al., 2005; Forrest and Hopkins, 2013), reflecting concerns regarding the impacts of this species on the area’s unique and diverse native marine biota (Battershill et al., 1998). Additionally, the high connectivity of coastal areas by anthropogenic activities (e.g., vessel movements) within Australia and New Zealand means there is potential for Undaria to invade vast areas of coast in the future (Hayden et al., 2009). Therefore, research in Australasia provides unique insight into Undaria's role as an invasive species, and an opportunity to critically evaluate its reputation as being among the world’s worst invaders.

More specifically, we collate, summarise and review peer-reviewed research on Undaria in New Zealand and Australia, drawing on literature from other invaded regions where doing so leads to greater insight. We highlight factors that drive Undaria’s invasion success, the types of impacts it causes, its future invasion potential, and associated research gaps. We also consider management successes and failures of Undaria. In total, our review includes 50 published journal articles and 6 unpublished post-graduate theses specific to Undaria in Australasia, focusing on content that was electronically available following searches on Google Scholar, SCOPUS and Web of Science (S1). The review is not exhaustive in terms of the grey literature on Undaria, and does not necessarily include published research in which Undaria was not the sole focus.

2. Establishment and spread of Undaria in Australasia

2.1. Discovery and vectors of initial introduction

Undaria was first discovered in Australasia in Wellington, New Zealand, in 1987, and in Tasmania, Australia, in 1988 (Figs. 1 and 2). However, the arrival time in each location was likely several years earlier, given the extensive populations documented in the first reports of its occurrence (Hay and Luckens, 1987; Sanderson, 1990). For example, the Tasmanian population already extended over 10 km of coastline (Sanderson, 1990), while, in Wellington Harbour, thousands of sporophores were recorded over 7–8 km (Hay and Luckens, 1987). International shipping and fishing vessels are considered to be the likely vectors of initial introduction; for example, mature sporophores were found on recently-arrived ocean-going vessels in the early stages of the invasion in New Zealand (Hay, 1990). However, there have been multiple subsequent introductions to Australasia (Stuart et al., 1999; Wotton et al., 2004; Uwai et al., 2006). In the southern South Island of New Zealand (e.g., Lyttelton, Timaru and Oamaru Harbours), genetic variation among populations suggests that, before 2005, there had been at least eight different introductions from source populations in continental Asia and northern Japan (Uwai et al., 2006). Interestingly, genetic analyses appear to confirm initial hypotheses on the origins of Undaria into different regions of New Zealand that were based on morphological comparisons (Hay and Villouta, 1993; Campbell and Burridge, 1998). In Australia, invaded sites showed little haplotype variation, indicating a lower number of successful introductions (Voisin et al., 2005; Uwai et al., 2006).

2.2. Ongoing human-mediated spread

Anthropogenic vectors, including commercial shipping, fishing
and recreational vessels, and the transfer of aquaculture stock and equipment, are strongly implicated in the spread of *Undaria* among regions in Australasia (Hay, 1990; Sanderson, 1990; Floerl et al., 2004; Forrest, 2016). The occurrence of *Undaria* in ports, harbours and aquaculture regions, and genetic data that show close relationships among distant sites, indicate that anthropogenic vectors have facilitated the spread of *Undaria* far beyond that achievable by natural dispersal mechanisms (Hay and Luckens, 1987; Forrest et al., 2000; Sliwa et al., 2006; Uwai et al., 2006). The occurrence of *Undaria* on a variety of vessels, including a tug, a ferry and fishing boats, was documented early in the invasion timeline (Hay, 1990). Regional dispersal by vessel movements...
appears to have been particularly important in the upper South Island and the North Island of New Zealand, where only one haplotype was found prior to 2005 in all of six invaded sites that were sampled (Uwai et al., 2006). In addition, this same haplotype was present in Port Phillip Bay, indicating that inter-regional transfer was taking place up to ten years after the discovery of Undaria in Australasia (Campbell and Burridge, 1998).

Undaria continues to spread to new regions both in Australasia and worldwide (Dellatorre et al., 2014; James et al., 2014; Minchin and Nunn, 2014; Ministry for Primary Industries, 2017). As hubs of vessel activity (e.g., ports, marinas) and aquaculture have become increasingly colonised by Undaria, so has the kelp’s association with human transport vectors. For example, during monitoring conducted in several southern New Zealand ports in 1998–2001, Undaria was encountered on 31–50% of commercial and recreational vessels, (Forrest and Hopkins, 2013). Consequently, Undaria is being transported into remote and often pristine coastal regions to which it would be unable to spread via natural dispersal. For example, in 2010 Undaria was detected in the vicinity of an isolated vessel mooring in New Zealand’s Fiordland region, a remote area of high biodiversity value. An ongoing effort to eradicate the population was recently set-back by the discovery of Undaria at a second mooring area a few kilometres away from the initial incursion (Fiordland Marine Guardians, 2017). These Australasian examples clearly highlight that understanding the pathways of anthropogenic vectors is of primary importance when assessing the likely spread of Undaria, and indeed any invasive macroalga. To this end, studies of genetic variation (e.g., Voisin et al., 2005; Uwai et al., 2006) offer valuable insight into patterns of spread over more traditional morphological comparisons, due to the high morphological plasticity of Undaria (Stuart et al., 1999; Sherman et al., 2016).

2.3. Rate and mechanisms of natural dispersal and spread

The rate of local-scale spread of Undaria from founding populations in Australasia has been highly variable among regions. In Timaru, New Zealand, Undaria achieved only a 1-km expansion onto the open coast despite a proliﬁc 20-year tenure within the harbour (Hay and Villouta, 1993; Russell et al., 2008). In that location, the range of Undaria was likely constrained by unconsolidated gravel substrata that dominate the coastline, preventing colonisation (Russell et al., 2008). The most dramatic spread from a founding population has been in Tasmania where Undaria increased its range by around ten kilometres per year along the eastern coast, to occupy 320 km of coastline in 2002 (Shepherd, 2013). However, it is difﬁcult to calculate rates of secondary spread with certainty, as it is not possible to distinguish whether new areas are colonised through natural dispersal alone (drift of reproductive sporophytes or microscopic propagules; see below), or whether rates of spread have been enhanced by anthropogenic vectors (Forrest et al., 2000; Sherman et al., 2016).

The mechanisms underlying the spread of Undaria in natural environments likely include interactions among local hydrodynamic conditions, propagule pressure, substratum type, and structure of the local assemblages (Forrest et al., 2000; Sliwa et al., 2006; Russell et al., 2008; Schiel and Thompson, 2012; James and Shears, 2016a). Dispersal from asexual reproduction of the sporophytes is estimated to be small (1–100 m), and depends on mortality of the spores, current velocity and direction, dilution of spores in the water column, and availability of settlement substrata (Forrest et al., 2000; Schiel and Thompson, 2012). Local-scale spread can be increased by one to two orders of magnitude by
the drift of unattached sporophytes, or by sporophytes attached to unstable substrata such as cobbles that are transported by wave-action and water currents (Schaffelke et al., 2005; Sliwa et al., 2006). Such variation in modes of dispersal allows Undaria to make episodic range expansions across a range of spatial scales (Sliwa et al., 2006; Forrest et al., 2009). The resulting founding populations may occur in intertidal pools (Russell et al., 2008) or result from a step-wise or episodic progression in the shallow subtidal (Forrest et al., 2000; Schiel and Thompson, 2012). Given that Undaria is negatively buoyant, the success of subtidal drift is likely to vary among sites due to variations in water depth, currents, nearshore topography and habitat availability. In southern New Zealand for example, Undaria can dominate the algal assemblage on rocky shores in certain locations, yet comprise only 9–20% of stranded wrack on adjacent sandy beaches (Jiménez et al., 2015a). Hence, it is likely to be the case that some of the detached Undaria is transported offshore, although this possibility has not been tested in Australasia and remains a significant research gap (Table 1, also see section 4.4).

3. Factors affecting the invasion success of Undaria

3.1. Life-cycle characteristics

Biological traits such as a high reproductive output, fast growth, early and rapid maturation, and ability to delay development for extended periods in unfavourable conditions, have allowed Undaria to become a highly successful invader in Australasia (Campbell, 1999; Schaffelke et al., 2005; Dean and Hurd, 2007; Schiel and Thompson, 2012). Undaria has an annual, heteromorphic life-cycle characterised by alternating macroscopic sporophytes (longevity = 5–7 months) and microscopic gametophytes and sporingles (Saito, 1975). The development of the meiospore to dioecious gametophytes, zygotes and embryonic sporophytes (c. 1 mm in length) can take three weeks, but all stages can delay or exhibit reduced development when resources are limited (Thompson, 2004; Morellissen et al., 2013). Indeed, initial pulses of autumn recruitment are typically derived from microscopic sporlings or gametophytes that have survived over summer (c. 5 – 7-months) (Thompson, 2004; Schiel and Thompson, 2012; Morellissen et al., 2013). It is unknown exactly how long the different microscopic life-stages can persist, although recruitment from such stages has been observed to take place for up to 2.5-years (Hewitt et al., 2005). The capacity to delay development, coupled with a massive reproductive output (1.2 million spores per cm² of tissue and up to 700 million per individual), gives Undaria significant potential to persist microscopically in invaded locations (Schiel and Thompson, 2012). Under favourable conditions, Undaria can grow at 15 mm per day, allowing it to occupy space quickly, and become reproductive within one to three months after recruitment (Schaffelke et al., 2005; Primo et al., 2010; Schiel and Thompson, 2012).

3.2. Population biology

Undaria is an annual species in its native range, with a distinct hiatus when its macroscopic form is absent (Morita et al., 2003). In New Zealand, Undaria can have a modified phenology, being found at some sites year-round (Hay and Villouta, 1993; Schiel and Thompson, 2012; James et al., 2015), although in many of these sites it still exhibits an annually occurring period of low abundance and cover (Thompson and Schiel, 2012; James and Shears, 2016a). For example, year-round populations were found at Moeraki where the remnants of old individuals from the previous year overlapped with new recruits in the following year (Schiel and Thompson, 2012). In Wellington, a narrow band of reproductive adults was found on artificial substrata in February and March (late summer, 1991) when the majority of the previous cohort had senesced (Hay and Villouta, 1993). Similarly in the North Island, Undaria sporophytes with reproductive structures were found throughout the year on mussel farms in the Hauraki Gulf, but individuals were in very low abundance in late summer (mean ~ 0.5 m⁻²) (James and Shears, 2016a). It is likely that the shift of Undaria in New Zealand from a strictly annual species to one whose inter-annual cohorts overlap is due to the smaller, more favourable temperature range in New Zealand compared to its native range (Hay and Villouta, 1993; James and Shears, 2016b).

In addition to the occurrence of overlapping inter-annual populations, Undaria has been reported to produce biannual cohorts of recruits in parts of New Zealand (Schiel and Thompson, 2012). In Moeraki, pulses of recruits were observed in autumn and spring, with the spring recruitment occurring during senescence of the autumn cohort (Schiel and Thompson, 2012). In such situations, it is likely that the loss of conspecific canopy associated with Undaria senescence increases light availability and facilitates recruitment from gametophytes or juvenile sporophytes in the understory (Thompson and Schiel, 2012). In northern New Zealand, however, populations of Undaria in artificial habitats (marina jetty) have one annual cohort during a constricted growth period that more closely resembles the annual life-cycle of Undaria in its native range (James and Shears, 2016b).

The distinction between populations that have either a high, low, or fluctuating year-round cover is critical, because high year-round cover is likely to have a greater impact on the structure and function of the recipient assemblage than populations with intermittent periods of high and low cover. Indeed, it has been hypothesised that the lack of a persistent dense perennial cover is responsible for the relatively weak direct impact of Undaria on recipient communities in some locations (Thompson and Schiel, 2012; South et al., 2016; South and Thomsen, 2016). Multiple cohorts might enhance the invasion success of Undaria as they can increase temporal propagule pressure in invaded sites (Schiel and Thompson, 2012). It is also likely that the occurrence of two cohorts annually contributes to over-lapping inter-anual populations and a more sustained macroscopic presence of Undaria in invaded habitats. Further work at a greater number of invaded locations is needed to more broadly understand the persistence and population biology of Undaria in Australia and New Zealand. It is crucial that such studies report not only abundances of Undaria, but also include relevant population metrics such as cover, biomass and sporophyte size (Table 1).

3.3. Response to physical variables in the recipient environment

Undaria is able to tolerate wide variations in physical factors such as substratum conditions, water temperature, and wave climate (Hay, 1990; Russell et al., 2008; James et al., 2014, Fig. 3). A key factor in the initial success of an Undaria invasion is likely to be its ability to settle and develop to reproductive maturity on almost any hard substratum in the marine environment. For example, Undaria has been found attached to natural cobbles, bedrock, snail shells (including abalone), coraline algae, canopy forming algae and seagrass blades; as well as artificial surfaces including plastic buoys, metal boat hulls (and associated marine coatings), concrete wharf piling, steel cable, wooden pontoons, mooring ropes, and commercial mussel crops (Hay, 1990; Brown and Lamare, 1994; Campbell and Burridge, 1998; Wotton et al., 2004; Forrest and Blakemore, 2006; Sliwa et al., 2006; Thompson and Schiel, 2012). Ports, harbours, marinas and aquaculture sites offer extensive artificial substrata, including shallow floating structures (e.g.
<table>
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<th>Topic</th>
<th>Question</th>
<th>Rationale</th>
<th>Possible methods</th>
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<tbody>
<tr>
<td>Dispersal</td>
<td>Does Undaria continue to be introduced to already invaded areas via human vectors?</td>
<td>Gauging whether the transfer of Undaria from natal realms and among already invaded regions continues remains a considerable research gap that has implications for population resilience (due to increased genetic diversity); the potential for Undaria to expand its range, and the likely efficacy of eradication programmes.</td>
<td>Genetic analyses of haplotype variation.</td>
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<tr>
<td>Dispersal</td>
<td>What are the relative importance of natural and human mechanisms of dispersal in episodic range expansions?</td>
<td>Natural dispersal mechanisms (e.g., drifting sporophytes) are often considered to be more important than human mediated spread (e.g., thalli attached to boat hulls) in open coast situations. However, this has never been shown to be the case.</td>
<td>Modelling of relative dispersal among natural and human mechanisms of spread. Vessel movement and fouling surveys. Detailed benthic surveys within and across years.</td>
</tr>
<tr>
<td>Dispersal/trophic effects</td>
<td>What is the fate of sunken Undaria biomass and how does it affect trophic subsidies and patterns of dispersal?</td>
<td>Undaria is negatively buoyant and sunken drifting plants could be an important dispersal mode. Furthermore sunken Undaria biomass could subsidise benthic detritivore communities, especially since this has been observed on intertidal beaches where Undaria biomass was relatively low.</td>
<td>Subtidal surveys in the vicinity of Undaria beds. Stable isotope studies. Hydrological modelling of potential pathways.</td>
</tr>
<tr>
<td>Distribution</td>
<td>What is the abundance of Undaria at increasing water depth?</td>
<td>The abundance of Undaria at depths greater than 6 (NZ) or 12 (Australia) metres has not been reported and is critical if the impact of this species is to be understood.</td>
<td>Structured surveys of Undaria cover and density and recipient assemblages across depth gradients.</td>
</tr>
<tr>
<td>Distribution</td>
<td>What factors determine the vertical distribution of Undaria in the subtidal? Is this due to light limitation, negative interactions with native species (e.g., grazing and competition) or other factors?</td>
<td>The distribution of Undaria appears to be depth-limited.</td>
<td>Correlative studies of Undaria and abiotic variables such as light availability, turbidity, nutrients and native assemblages. Experiments to manipulate light availability, nutrients and grazer density in recipient habitats.</td>
</tr>
<tr>
<td>Distribution</td>
<td>What factors determine the vertical distribution of Undaria in the intertidal? Is this due to desiccation, negative interactions with native species or other factors?</td>
<td>Undaria does not generally occur above low water neap in Australasia.</td>
<td>Transplant experiments, grazer exclusion experiments.</td>
</tr>
<tr>
<td>Competition</td>
<td>Do early life-stages of Undaria and native species compete for resources such as nutrients, space and light?</td>
<td>Competition among early life stages of native algae and Undaria has not been studied in any detail.</td>
<td>Factorial laboratory experiments, out-plants of Undaria and native gametophytes, sporophytes and sporelings among cohorts.</td>
</tr>
<tr>
<td>Phenology</td>
<td>What are the percent cover, density, biomass, demography, and reproductive phenology of year round populations of Undaria in natural assemblages?</td>
<td>Year-round populations have been reported in some studies, however, ecologically relevant metrics (in particular, cover and biomass) that might mediate impacts, are infrequently recorded. A full understanding of the temporal presence of Undaria remains evasive.</td>
<td>Assessments of reproductive outputs, viability, fitness and longevity of meiospores, gametophytes and sporophytes among cohorts.</td>
</tr>
<tr>
<td>Phenology and demography</td>
<td>Does recruitment occur from newly released spores, or from extant gametophytes or sporelings (from the previous cohort) in areas that have two cohorts annually?</td>
<td>The occurrence of two cohorts annually is an ecologically important demographic change that could be due to favourable environments for early life stages (e.g. increased longevity of sporelings) or adults (i.e., a second reproductive adult cohort per year).</td>
<td>Assessments of reproductive outputs, viability, fitness and longevity of meiospores, gametophytes and sporophytes among cohorts.</td>
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<tr>
<td>Impact</td>
<td>How does the ecological impact of Undaria vary among habitats (e.g., mussel beds, Macrocystis pyrifera forests, Ecklonia radiata stands)?</td>
<td>The impacts of Undaria have only been tested in a few habitats.</td>
<td>Undaria removal or addition experiments. Correlation studies.</td>
</tr>
<tr>
<td>Impact</td>
<td>Are impacts of Undaria density dependent?</td>
<td>No study has used more than 2 levels (0) of Undaria density/cover and tested for linearity of effects. The responses of relatively few variables (e.g., cover, density, productivity) have been studied for Undaria. However, Undaria could impact less easily (or frequently) measured variables such as the reproductive out-put, growth and sub-lethal physiological responses of native species.</td>
<td>Manipulative experiments quantifying a wider range of response variables.</td>
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<td>Impact</td>
<td>Does Undaria have sub-lethal, cryptic or delayed impacts on the recipient environment?</td>
<td>Undaria is a high value seaweed that is now harvested or actively cultured in some areas of Australasia. By contrast, scientific research, and control and eradication are costly activities. There are likely to be many economic costs and benefits associated with the advent of Undaria.</td>
<td>Socio-economic impact analysis.</td>
</tr>
<tr>
<td>Impact/trophic effects</td>
<td>What are the socio-economic impacts of Undaria in Australasia?</td>
<td>Undaria is purported to have negative impacts on important taxa in the recipient community (e.g., other canopy-forming algae), but this has not been shown, potentially due to a lack of base line data and the difficulty in studying the invasion process as it occurs.</td>
<td>Modelling of food-web networks.</td>
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<td>Impact/trophic effects</td>
<td>How does Undaria affect food-web structure?</td>
<td>Native species consume Undaria differentially therefore this could modify food-web structure. Undaria can displace native species, but their ecology is often poorly understood - to gauge the effects of Undaria relevant contrasts must be made.</td>
<td>Targeted surveys, epifaunal sampling and assessments of primary productivity.</td>
</tr>
<tr>
<td>Impact/trophic effects</td>
<td>How does primary production and epifaunal assemblages of Undaria compare to the species it has been shown to displace (e.g., Colpomenia sinuosa)?</td>
<td>Undaria can displace native species, but their ecology is often poorly understood - to gauge the effects of Undaria relevant contrasts must be made.</td>
<td>Targeted surveys, epifaunal sampling and assessments of primary productivity.</td>
</tr>
<tr>
<td>Spread, mechanisms of invasion and impact</td>
<td>How does Undaria colonise and impact new areas?</td>
<td>Undaria is purported to have negative impacts on important taxa in the recipient community (e.g., other canopy-forming algae), but this has not been shown, potentially due to a lack of base line data and the difficulty in studying the invasion process as it occurs.</td>
<td>Establish baseline surveys in areas that have the potential to be invaded. Use Before After Control Impact (BACI) analysis or manipulative experiments to assess impacts.</td>
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</table>
Undaria has thrived in artificial coastal habitats within which it can spread largely unimpeded (Hay, 1990). In Wellington Harbour for example, Undaria spread among coastal infrastructure over 4 km in 1-year (Hay, 1990). In port and harbour locations, invasive species such as Undaria can make use of the extensive hard substrata as “stepping stones” to further their spread and population development (Fiori et al., 2009; Bulleri and Chapman, 2010). These stable and extensive populations can serve as sources of propagules for introductions into distant sites (i.e., by human-mediated spread), and conceivably can put intense propagule pressure on adjacent native communities (Ruiz et al., 2009; Simkanin et al., 2012; Forrest and Hopkins, 2013).

The tolerance of Undaria to wide variations in temperature is one of the attributes that has allowed it to become a successful invader, and makes it likely that Undaria will continue to expand its range throughout uninvaded temperate zones in Australasia (James et al., 2015). Indeed, based on its maximum and minimum thermal limits (13.5–29.5 °C and 0.1–15.5 °C, respectively) across latitudes in its native range (Sanderson, 1990; James et al., 2015), Undaria has the potential to colonise much of the southern Australian coastline from Cape Leeuwin in the south-west to Woolongong in the southeast of Australia, and the entire mainland of New Zealand as well as Stewart Island, the Chatham Islands (both already invaded) and the southern sub-Antarctic islands (Snares Island is already invaded, Fig. 1). Furthermore, future water temperature and pH scenarios anticipated in New Zealand are unlikely to affect population viability and ongoing spread, as Undaria meiospore and gametophyte development and germination are not expected to be adversely affected (Leal et al., 2016, 2017).

There are many aspects of the ecology of Undaria that remain little-studied or unclear (Table 1). For example, from limited studies, Undaria appears to be highly competitive for nutrients, especially in its juvenile period during winter when nitrate is available in relatively high concentrations (Campbell, 1999; Dean and Hurd, 2007). Similarly, Undaria gametophytes, zygotes and sporelings benefit from elevated nutrients, although this can depend on irradiance levels (Morelissen et al., 2013). The geographical limits resulting from light availability, and salinity, wave-exposure, and their interactions with depth, are uncertain, partly due to contradictions among results from laboratory studies and the reported distribution of Undaria.

Undaria has a lower saturated light requirement and compensation points, and greater photosynthetic efficiency than several native Australasian laminarian and fucoid algae (Campbell et al., 1999; Tait et al., 2015). However, the native species can be dominant to depths of 15 and > 40 m in New Zealand (Schiel, 1990) and Australia (Sanderson, 1997), respectively. In New Zealand, for example, the abundance of Undaria below six metres depth has not been quantified, despite anecdotal observations about its occurrence in deeper waters (Hay and Luckens, 1987; Dean and Hurd, 2007). The limited evidence about Undaria distribution along depth gradients, suggests that Undaria peaks in abundance just below the intertidal zone (to 4 m) and thereafter declines with depth (Brown and Lamare, 1994; Russell et al., 2008; Richards et al., 2011). Similarly, most Australasian studies have focused on

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**Fig. 3.** Overview of local environmental conditions that control invasion success of Undaria pinnatifida. Blue = facilitation, Red = inhibition. Interactions between the local conditions (e.g., resources, facilitators and enemies) are important. For example, Undaria might not be successful <4 m depth because of combined effects of light limitation and dominance of large perennial canopy forms. Citations from experimental (italics) and correlative (underlined) studies are given. Image credits: Integration and Application Network, University of Maryland Centre for Environmental Science (ian.umces.edu/imagelibrary/). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
populations of *Undaria* in shallow water (0–6 m, Edgar et al., 2004; Hewitt et al., 2005; Jiménez, 2015) with the exception of two studies done on Tasmanian reefs (7–12 m, Valentine and Johnson, 2003; Valentine and Johnson, 2005) and in which the cover of *Undaria* was low relative to other studies from shallower water (Jiménez et al., 2015a; South et al., 2016). If *Undaria* does have reduced abundance at depth this could be explained by light limitation during its early life history. For example, gametophyte development is stunted at low levels of irradiance (below 10 μmol quanta m-2 s-1), although gametophytes and embryonic sporophytes can grow vegetatively in such low light environments until conditions favour photosynthetic growth (Morelissen et al., 2013). Overall, the reasons for the apparent reduced abundance of *Undaria* at depth are unclear (Table 1). As well as reduced physiological performance in low light conditions, other limiting factors could include competition with native canopy-formers, increased grazing pressure, less substratum availability and increased stress from sedimentation (Valentine and Johnson, 2005; Thompson and Schiel, 2012; Geange et al., 2014).

At the upper extent of *Undaria*’s vertical distribution, intertidal populations do not typically occur higher on the shore than the low water neap tide mark (Forrest and Taylor, 2002; South et al., 2016), meaning *Undaria* does not inhabit the neap tide to mid-shore zone that is often occupied by native algal species such as *Hormosira banksii* and *Cystophora torulosa* (Lilley and Schiel, 2006). We expect that desiccation likely constrains the neap tide upper limit of *Undaria*, although we are not aware of any studies that have experimentally investigated this or alternative mechanisms, such as competition with intertidal algae or grazing by invertebrates (Table 1). Overall, a vertical distribution in which *Undaria* typically occurs in a narrow band from neap low tide to 4 m subtidal, mirrors that in its native range (Morita et al., 2003).

Patterns in the geographic distribution of *Undaria* suggest that it is limited by excessive wave action and low salinity. For example, *Undaria* has not been reported from the exposed west coast of New Zealand, where significant wave heights between seven and eight metres are not uncommon (National Institute of Water and Atmosphere, 2017). However, *Undaria* has invaded wave exposed regions of south eastern (Russell et al., 2008) and north eastern (James and Shears, 2016a) New Zealand. Such a discontinuity among east and west coasts could reflect greater and more consistent significant wave height on the west coast, or variations in anthropogenic or biological factors. For example, north-eastern populations of *Undaria* in exposed locations appear to be associated with urchin barrens (James and Shears, 2016b). It is unknown whether *Undaria* has the ability to establish on exposed coasts in deeper subtidal habitats that are less affected by wave energy, and where other factors such as low-light conditions are not limiting. Furthermore, optimal hydrodynamic conditions for *Undaria* have not been assessed and remain a considerable research gap (Table 1). With respect to salinity, *Undaria* has not been reported from estuarine locations in Australasia, contrasting its distribution in the UK (Fletcher and Farrell, 1998). The absence of *Undaria* from estuarine locations is surprising given the ability of zoospores to germinate in salinities as low as 8 S0 (Bite, 2001), and because adult tissues remain photosynthetically viable down to 6 S0 (Bollen et al., 2016). However, the distribution of *Undaria* in low salinity environments is possibly limited by differences in tolerance among different life stages of *Undaria* (Peteiro and Sánchez, 2012), smothering by sediment (Geange et al., 2014), or factors discussed above such as light-limitation (Morelissen et al., 2013).

### 3.4. Biological interactions and physical disturbances

Surprisingly, little is known about the role of biological disturbances and grazing pressure on *Undaria* abundance (Thompson, 2004; Valentine and Johnson, 2005, Fig. 3). In southern New Zealand, recruitment of *Undaria* was similar among plots where grazers had been excluded with cages and open controls, despite the fact that a common grazer (*Lunella smaragda*) reduced sporulating abundances in laboratory experiments (Thompson, 2004). By contrast, *Undaria* was the only canopy-forming macro-alga to inhabit sea urchin (*Heliocidaris erythrogramma*) barrens in Tasmania regardless of whether the sea urchins were excluded or not, suggesting indirect facilitation from urchins on *Undaria* abundance by inhibition of native competitive canopy forming species (Valentine and Johnson, 2005). The advent of *Undaria* on urchin barrens has also been noted in north-eastern New Zealand (James and Shears, 2016a). By contrast with the limited knowledge of grazer effects, the role of physical disturbance in facilitating invasion of native assemblages by *Undaria* has received considerable attention in Australasia. Studies have typically shown high recruitment into areas where native canopy-formers have been removed by single pulse disturbances (Valentine & Johnson 2003, 2004, 2005; Thompson and Schiel, 2012; Carnell and Keough, 2014; South and Thomsen, 2016). This outcome is likely a response to increased light and decreased physical abrasion by wind and the absence of native canopy-formers (Valentine and Johnson, 2003; 2004; Thompson and Schiel, 2012; Morelissen et al., 2013). Positive effects of canopy loss on *Undaria* recruitment were shown to be consistent across clearings of different sizes (0.01, 0.0625, 0.25 m2) and regardless of whether the canopy is inter- or intraspecific (Thompson and Schiel, 2012). However, *Undaria* does not appear to be able to maintain its cover, and in one study was replaced by the initial canopy-former over five months to a year (Thompson and Schiel, 2012), and in another study by mixed communities in which *Undaria* became a subordinate species over 1- to 2-years (Valentine and Johnson, 2003). Thus, it appears that *Undaria* is competitively inferior to many native canopy-forming species over longer-term stable conditions (Valentine and Johnson, 2003; Schiel and Thompson, 2012). A consistent result emerging from these experiments is that the presence of a dense bed of intact native canopy-forming algae greatly reduces the local-scale invasion success of *Undaria*. Furthermore, the ability of dense stands of native canopy-forming macroalgae to resist invasion by *Undaria* appears to be consistent among geographic regions, and variations in the identity of native species (Raffo et al., 2009; De Leij et al., 2017).

The majority of experimental studies that have tested for the effects of disturbance on *Undaria* recruitment have focused on disturbance to stands of native canopy-forming algae, and have simulated disturbances by removing the canopy in order to mimic events such as storms, grazing or die-back. However, habitats on temperate reefs commonly vary from those dominated by canopy-forming macroalgae, to low-lying assemblages that are characterised by coralline algae (Dayton et al., 1984) or invertebrates such as mussels (Menge et al., 2007). Low-lying assemblages dominated by coralline algae are readily invaded by *Undaria*, and experimental disturbance to these assemblages does not increase *Undaria* recruitment (Schiel and Thompson, 2012; Thompson and Schiel, 2012; Morelissen et al., 2016). For example, the removal of entire low-lying assemblages of predominantly coralline turf and other small algae had no effect on the number of *Undaria* recruits compared to intact control plots, indicating that *Undaria* does not require disturbance to invade low-lying intertidal assemblages (Morelissen et al., 2016). Indeed, *Undaria* appears to be facilitated by geniculate coralline algae, likely due to a reduction of desiccation stress and grazing pressure (Thompson, 2004; Thompson and Schiel, 2012). By contrast, coralline turfs can inhibit the
recruitment of native canopy-forming algae that do not attach to the turf or the sediment within its matrix (Schiel et al., 2006; Bellgrove et al., 2010; Alestra et al., 2014), and which could otherwise outcompete Undaria (Valentine and Johnson, 2003). Therefore, coralline turfs can facilitate invasion by Undaria through direct and indirect pathways (Thompson, 2004; Thompson and Schiel, 2012).

Furthermore, disturbance to stands of native canopy-forming algae can facilitate coralline and other turf-forming algae that can in turn prevent re-colonisation by the native species, providing a mechanistic explanation for the continued presence of Undaria in some locations (Valentine and Johnson, 2005).

Importantly, areas lacking high cover of native canopy-forming macroalgae can maintain dense populations of Undaria, with mature Undaria sporophytes providing a supply of propagules to canopy understoress that allow the invader to exploit canopy loss (Schiel and Thompson, 2012). Given the wide variety of substrata and assemblages to which Undaria can recruit, a key niche seems to be any space lacking large native perennial canopy-formers. Given the patchy nature of many coastal assemblages it is likely that there are many vacant niches in space and time that can be filled by this invader, which is an important consideration for managers undertaking site-specific risk analysis of the invasion threat (Russell et al., 2008; Schiel and Thomsen, 2012). Indeed, the ability of Undaria to fill vacant space has become prescient on the Kaikoura coast of New Zealand, where a 7.8 magnitude earthquake caused massive uplift (1–6 m over 100 km) of reefs on November 14, 2016. This uplift resulted in the almost complete die-off of dense forests of intertidal and subtidal algae in which Undaria had only occurred in small, isolated, populations (South and Thomsen, unpubl. data and pers. obs.). It is highly possible that Undaria will benefit from losses of native canopy-formers, expanding its range to become an abundant species on the Kaikoura coast. Furthermore, it is also possible to envision accelerated invasion success along much of the uninverted coastline of Australasia, in the event that native canopies shift to turf-dominated assemblages due to stressors such as moving urchin fronts (Ling et al., 2009), heatwaves (Wernberg et al., 2013), ocean warming (Connell and Russell, 2010) and acidification (Connell et al., 2013), urbanisation (Benedetti-Cecchi et al., 2001; Gorman and Connell, 2009), and eutrophication (Airoldi, 1998; Bellgrove et al., 2010).

4. Impact of Undaria on structure and function of recipient assemblages

4.1. Taxa-specific impacts

The most important questions regarding the impact of invasive species are whether they simply follow ecological change or exploit vacant niches (‘passenger’), are a direct cause of ecological change (‘driver’), or whether this role changes over time (‘passenger-turned-driver’) (Didham et al., 2005; MacDougall and Turkinson, 2005; Bulleri et al., 2010; Bauer, 2012). In Australasia, the impacts of Undaria on native species have been determined via experiments that have either removed native canopy-forming algae (Valentine and Johnson, 2003; Edgar et al., 2004; Thompson and Schiel, 2012; Carnell and Keough, 2014), the invader itself (Valentine and Johnson, 2005; Morelli et al., 2012; South et al., 2016), natives and the invader (South and Thomsen, 2016), or have used mesurative Before-After Control-Impact (BACI) experimental designs (Forrest and Taylor, 2002) to infer its effects.

That have experimentally tested the competitive ability of Undaria to invade intact stands of native canopy-formers indicate that it does not ‘drive’ change, because un-manipulated canopies were generally not invaded and canopy-formers were able to reconcile areas despite the presence of Undaria (Valentine and Johnson, 2003; Edgar et al., 2004; Thompson and Schiel, 2012; South and Thomsen, 2016). Furthermore, invader-removal studies suggest that Undaria does not reduce the abundance of canopy-forming seaweeds (Valentine and Johnson, 2005; South et al., 2016; South and Thomsen, 2016). For example, native canopy formers did not colonise plots that were kept free of Undaria for over 2-years in southern New Zealand, and native recruits were similar among plots with and without Undaria following experimental removals of the native canopy (South et al., 2016; South and Thomsen, 2016). The results from experimental studies are supported by BACI analyses done across four sites over three years in Lyttelton Harbour, New Zealand that suggested Undaria did not negatively affect local assemblages, rather it became most abundant under conditions that simultaneously favoured native macroalgae (Forrest and Taylor, 2002). However, in Victoria, Australia, Undaria reduced the size of re-colonising Ecklonia radiata recruits, but only when simultaneously exposed to elevated nutrient levels, suggesting that Undaria might be capable of causing long-term changes to invaded assemblages (Carnell and Keough, 2014). Still, the impact of Undaria on recruitment of native perennial canopy forming species in Australasia appears to be weaker than that of other large invasive algae such as Codium fragile ssp. tomentosoides (Lavin et al., 2002; Scheibling and Gagnon, 2006) and Sargassum muticum (Ambrose and Nelson, 1982; Stæhr et al., 2000; Britton-Simmons, 2004).

There is, however, increasing evidence that Undaria can inhibit smaller seasonal or opportunistic native species (Valentine and Johnson, 2005; South et al., 2016; South and Thomsen, 2016). For example, invading Undaria reduced the cover of the seasonal alga Colpomenia sinuosa (Phaeophyceae, Ectocarpales) compared to experimental plots where Undaria had been removed (South and Thomsen, 2016). Similarly, filamentous algae were inhibited by Undaria on subtidal urchin barrens in Tasmania, suggesting that Undaria can be a ‘passenger-turned driver’ of change (Valentine and Johnson, 2005; Bulleri et al., 2010). In addition, established stands of Undaria occasionally displaced the seasonal alga Lophothamnion hirtum (Rhodophyceae, Ceramiales) during a 2.5-year Undaria removal experiment (South et al., 2016).

Taken in concert, these results highlight that negative impacts only occurred when Undaria cover was greatest (i.e., in spring – early summer), and did not persist within and between years (Valentine and Johnson, 2005; South et al., 2016). Therefore, the direct effects of Undaria are space, time and taxon-specific, and might be of greater importance when the recipient assemblage is dominated by small taxa with temporally variable distributions that match that of Undaria. Still, we caution against strong inferences about the impact of Undaria, as direct effects have only been tested with manipulative experiments in five published studies worldwide (Casas et al., 2004; Valentine and Johnson, 2005; Irigoien et al., 2011a; South et al., 2016; South and Thomsen, 2016), and the context dependency of its impact remains poorly understood (Thomsen et al., 2011). Furthermore, these five removal experiments are potentially biased because the removals necessarily took place at an already invaded site, which may already have been affected by the invader (or another independent factor, e.g., elevated nutrients) prior to the experiment (Didham et al., 2005; Bulleri et al., 2010). Similarly, small-scale removal experiments do not account for possible functional impacts (e.g., due to detrital production) from the Undaria adjacent to cleared plots. Accordingly, removing the invader could, in contrast to the true initial invasion effects, have little measurable effect (Bulleri et al., 2010). It is therefore necessary that future research takes steps to incorporate factors that decouple the causes and effects of Undaria invasion (e.g., Bulleri et al., 2010; Mulas and Bertocci, 2016; South and Thomsen, 2016).
4.2. Impacts on native communities

Reported impacts of *Undaria* on community metrics such as species richness, evenness, or diversity have generally been neutral, regardless of the trophic level studied. For example, no impact on the richness, diversity or community structure of large mobile invertebrates (>5 mm) was detected over 2.5-years at Moeraki, New Zealand (South et al., 2016). Direct negative effects of *Undaria* on algal assemblages appear to be few and tend to reflect reductions in ephemeral algae (see earlier discussion in this section), rather than widespread structural change (South et al., 2016; South and Thomsen, 2016). However, effects on algae may also be facilitative; an increased richness of small native macroalgae in the low intertidal of Lyttelton Harbour was associated with increased *Undaria* cover or abundance, possibly because the *Undaria* canopy provided shelter from desiccation, or alternatively because *Undaria* and the small native taxa had similar habitat requirements (Forrest and Taylor, 2002).

4.3. Impacts on primary production and biochemical cycles

The establishment of large populations of *Undaria* can substantially increase net primary production and the capture of nutrients on invaded reefs during its macroscopic period (Dean and Hurd, 2007; Tait et al., 2015; South et al., 2016). For example, *Undaria* doubled net primary production and contributed an additional 140.5 and 2.66 g m$^{-2}$ of Carbon and Nitrogen (dry weights), respectively, to a low-lying assemblage in southern New Zealand (South et al., 2016). *Undaria* thalli erode from the apices of the laminae (from 0.24 ± 0.07 to 0.79 ± 0.2 cm d $^{-1}$) until only sporophylls and holdfasts remain at the end of their life (Dean and Hurd, 2007). Therefore, nutrients stored in the entire thallus are slowly redistributed into the water column and likely modify local biochemical cycles and food webs, especially when *Undaria* occurs in high abundance (Dean and Hurd, 2007; South et al., 2016).

*Undaria* is atypical compared to native canopy-forming algae in Australasia due to its annual life history, fast growth and the timing of its development during the cooler parts of the year (Campbell et al., 1999; Dean and Hurd, 2007; Schiel and Thompson, 2012). Photosynthetic rates are greatest in winter and spring during growth, and lower in summer during senescence, with the alga having mean photosynthetic maxima over these two periods of 38.14 mg O$_2$ g $^{-1}$ dw $h^{-1}$ and 15.90 mg O$_2$ g $^{-1}$ dw $h^{-1}$, respectively (Campbell et al., 1999). Maximum values of oxygen production of *Undaria* can be ten times greater than that of other laminarians (Campbell et al., 1999). Rather, it seems likely that *Undaria* has a facilitative effect on invertebrate abundances, through the provision of additional resources, that could have cascading implications for local food-web structures (Schmidt and Scheibling, 2006). Some native taxa such as abalone (*Haliotis iris*), amphipods (*Aora typica*) and turbonid snails (*Cookia sulcata* and *Lunella smaragda*) consume *Undaria* readily (Thompson, 2004; Jiménez et al., 2015b, Fig. 2), although the common epifaunal isopod *Badedoeta elongata* rejected it as a food source in feeding trials (Jiménez et al., 2015b). On the other hand, little is known about the epifaunal communities associated with algal species that are displaced by *Undaria* (e.g. filamentous algae and *Lophothamnion hirtum*, Valentine and Johnson, 2005, South et al., 2016; respectively). Therefore, the impact of *Undaria* on food-webs is likely to be complex, with many areas of uncertainties that warrant further investigation (Table 1).

The export of kelp detritus can be an important trophic subsidy across ecosystems (Wernberg et al., 2006; Vanderklift and Wernberg, 2008; Krumhansl and Scheibling, 2012b). Invasive macroalgae can modify such subsidies and, consequently, local assemblages of detritivores (*Krumhansl and Scheibling, 2012a*) and possibly filter-feeders. As noted in Section 2.3, it is possible that much of the negatively buoyant *Undaria* biomass detached from heavily-infested shores in southern New Zealand is exported to deeper waters offshore. Indeed, sunken *Undaria* biomass can reduce subtidal reef complexity by filling cracks and crevices sufficiently enough to reduce habitat for reef fish in Argentina (Jiménez et al., 2011b). However, the detritivore communities associated with subtidal detritus from *Undaria* have not been studied in Australasia or elsewhere (Table 1). Where *Undaria* does get washed ashore it can provide a considerable trophic subsidy...
(Jiménez et al., 2017). For example, the talitrid amphipod *Bel- lorchestia quoyana* consumes *Undaria* at similar rates to other algae that are commonly stranded on sandy beaches (Jiménez et al., 2017). It therefore seems likely that *Undaria* represents a significant addition to coastal food-webs. However, more research is warranted to determine the extent and scale of trophic provisioning associated with this invader (Table 1).

Overall, the impacts of *Undaria* are not well understood due to a deficit of studies, but it seems likely that its advent has modified patterns of biogenic habitat provision and trophic subsidies locally and across ecosystems, despite its seeming inability to displace many native taxa. However, it should be noted that research has focused on a relatively small number of response variables, whereas impacts might be restricted to less easily quantified responses. These include reproductive capacity (Lyons and Scheibling, 2007), growth (Carnell and Keough, 2014) and sub-lethal stress (Terlizzi et al., 2011), all of which could compromise the resilience of coastal ecological communities and therefore warrant further research (Table 1).

5. Eradication and sustained control of established populations

A number of *Undaria* eradication or sustained population control attempts have been undertaken in Australasia, which have varied in both their effort and efficacy. Generally the experiences to date support the need to manage pathways of *Undaria* spread as a first priority, on the basis that management post-establishment is difficult, expensive and seldom successful. In fact, successful eradications of marine invasive species generally required a sustained and intensive effort, and it often appears to be atypical circumstances that make eradication tractable (Willan et al., 2000; Wotton et al., 2004; Hopkins et al., 2011). In the case of *Undaria*, this situation was exemplified by the successful hot water treatment of the infected hull of a fishing vessel that sank at Chatham Island (Fig. 1); a remote locality 700 km to the east of mainland New Zealand (Wotton et al., 2004). This eradication effort was successful because: (a) the vessel was already known to have *Undaria* on the hull (Stuart, 2004), hence the response was rapid; (b) the criteria (temperature and exposure time) for effective *Undaria* heat treatment were known; (c) the area was isolated and surrounded by sand, with the vessel hull representing a discrete and ‘treatable’ surface compared with more complex natural and artificial marine habitats; and (d) the risk of imminent reinvasion was low, with the nearest stable established *Undaria* populations on mainland New Zealand.

By contrast, other attempts to eradicate *Undaria* from port and harbours having a range of natural seabed and artificial habitats have all failed. The most comprehensive and sustained programmes to date have been the ongoing effort in the Fiordland region of south-western New Zealand (also see Section 2.2) and a regional scale programme undertaken in the far south of New Zealand during 1997–2004 (Forrest and Hopkins, 2013). Although the latter programme failed to eradicate *Undaria*, it did demonstrate that through sustained and intensive control, employing a range of measures (e.g., physical removal, chemical treatments), *Undaria* populations could be contained, and the infestation of vessels in managed areas could be reduced to near-zero (Hunt et al., 2009; Forrest and Hopkins, 2013). It also developed initial proof of concept for a range of marine pest control methods that are now routinely implemented operationally, at least in New Zealand (Coutts and Forrest, 2007; Piola et al., 2009a; Hopkins et al., 2010, 2016; Piola and Hopkins, 2012; Atalah et al., 2016a; Hopkins et al., 2016).

The failure to eradicate *Undaria*, even when significant resources are directed to this goal, largely reflects the challenges presented by the kelp’s life-history characteristics (Hewitt et al., 2005; Forrest et al., 2009; Forrest and Hopkins, 2013). The rapid growth of *Undaria*, whereby sporophytes can reach maturity within less than 2-months after recruitment, means that manual removal needs to be regular (typically monthly). This situation, combined with the apparent persistence of *Undaria*’s benthic gametophyte life-stage (Hewitt et al., 2005), means that managed zones that are clear of visible *Undaria* need to be rechecked monthly for at least 3-years after the last sporophyte has been detected. However, detection can be difficult, especially in the presence of native canopy-forming algae whose juvenile life-stages are superficially similar in colour and morphology to *Undaria*. The failure to detect even a single sporophyte, which subsequently matures, can lead to the re-establishment of the population and undermine years of previous effort. To overcome such barriers, the more recent and ongoing attempt to eradicate *Undaria* from Fiordland involved the trans-plant of ~30,000–35,000 seaurchins (*Evechinus chloroticus*) into the primary control zone. This approach artificially created urchin barrens, which were expected to not only eliminate *Undaria*, but by removing the native macroalgal cover, also made it easier for divers to detect new *Undaria* recruits (Atalah et al., 2019).

Perhaps the most significant impediment to successful eradication arises due to *Undaria*’s multiple dispersal strategies. Although sporophore dispersal is limited (see section 2.3), dispersal-modes such as sporophyte drift can lead to episodic leaps in *Undaria* distribution across scales of kilometres. Due to *Undaria*’s strong association with human transport vectors, this situation can be compounded in localities having a complex network of anthropogenic vector activity (Floerl et al., 2009), particularly where vessels move into remote coastal areas outside main vessel hubs. These different mechanisms and scales of dispersal make it difficult to define surveillance boundaries for ongoing population delimitation. In fact, the ultimate reason for failure of the 1997–2004 management programme was that, despite monthly removals from the primary management area, a well-established *Undaria* population was detected in the wider managed region, in a vessel hub that was checked only infrequently (Forrest and Hopkins, 2013).

Similarly, at the time of writing, the future of the Fiordland eradication programme is in doubt, following the detection of another infested site (a vessel mooring and surrounding seabed) a few kilometres from the primary control zone. Hence, in both of these examples, eradication success appears to have been compromised by anthropogenic vectors, most likely vessels. This situation highlights the fundamental importance of effectively managing these risk pathways, in order to support the management of established *Undaria* populations (Fiordland Marine Guardians, 2017). Partly in response to the recent incursions of *Undaria* into Fiordland, vessel operators are now required to obtain a “Clean Vessel Pass” before going to that region, as part of a Marine Regional Pathway Management Plan developed by the regional authority (Environment Southland, 2017).

While regular antifouling remains one of the best strategies for reducing *Undaria* and other biofouling on vessels (Piola et al., 2009a; Floerl et al., 2016), the need for a more comprehensive toolbox has seen considerable research effort on tools to reduce or eliminate *Undaria* and other risk species that are associated with anthropogenic transport vectors. It is beyond our present scope to detail these, but examples include: encapsulation-based sterilisation methods for vessel hulls (Coutts and Forrest, 2007; Atalah et al., 2016a), which are needed on the basis that antifouling is not completely effective; chemical or heat treatments for internal recesses and pipework on vessels (Piola and Hopkins, 2012); and treatments for aquaculture equipment and seed-stock (Forrest and
6. Conclusions

Undaria is often considered to be one of the world’s worst invasive species. It is a species that, due to its large and conspicuous sporophyte stage, can have a dramatic appearance at high population densities in heavily invaded locations. However, the Australasian situation shows that, while Undaria can be highly successful at invading a wide range of coastal assemblages, evidence for direct adverse impacts is scant. This situation contrasts certain other invasive macroalgae that can have dramatic ecological effects (Ambrose and Nelson, 1982; Stehr et al., 2000; Scheibling and Gagnon, 2006; Bulleri et al., 2010), even when they are in relatively low abundance (Bulleri et al., 2017). Such a decoupling of invasion success and impact suggests that perhaps Undaria does not merit the world’s worst invasive status that has been attributed to it, and which has become propagated through the scientific literature in the absence of research documenting actual ecological effects. Despite this situation, there remain many knowledge gaps concerning the invasion ecology of Undaria, but many of these are likely to be highly complex and related to its additive effects on system-wide attributes, such as provision of biogenic habitat, net primary production, nutrient cycling and cross-system subsidies (Dean and Hurd, 2007; Jiménez, 2015; Tait et al., 2015; Thomsen et al., 2016a; South et al., 2016; Jiménez et al., 2017).

Insights from the Australasian scientific research on the mechanisms underlying the spread of Undaria, its invasion biology and impacts are highly applicable to research and management in other regions where this species has become invasive. Furthermore, synthesis of research on Undaria from Australasia and other regions of the world suggest some emerging generalities. In particular, these include the significant human-mediated spread of Undaria (Fletcher and Manfredi, 1995; Pereyra et al., 2015), its proliferation on artificial coastal structures (Curiel et al., 2002; Minchin and Nunn, 2014), the eventual and sometimes dramatic population expansions into native communities (Casas and Piriz, 1996; Fletcher and Farrell, 1998; Heiser et al., 2014; Pereyra et al., 2014), and the inability to compete with native canopy-forming macroalgae (Valentine and Johnson, 2003; Raffo et al., 2009; De Leij et al., 2017).

In addition, many unique insights have arisen from Undaria research in Australasia, most notably concerning facilitation by native taxa such as coralline algae and sea urchins, and the efficacy and applicability of control and eradication programmes. By contrast, there are some important aspects of the Undaria invasion in Australasia that have received little attention; these include potential socio-economic factors such as costs that might occur due to eradication programmes, and benefits that might arise from exploiting Undaria’s commercial value (Table 1).

In the 30 years since Undaria was first recorded in Australasia, it has spread to occupy vast tracts of coastline. Still, there remain expansive uninvaded rocky coastal habitats within the possible range of Undaria, a situation that is mirrored in other parts of the world where this alga is invasive (Sanderson, 1990; James et al., 2015). For reasons described herein, it can be expected that Undaria will continue to expand its range, and it is highly unlikely that eradication or population control based on existing tools will have any widespread effectiveness. Perhaps at best, intensive multi-faceted management (e.g., targeted population control in key vector hubs, strict regulations on vessel and gear biofouling, and immediate, intensive eradication responses when incursions are discovered) might reduce the risk of Undaria establishing in pristine or high value sites. Even more ambitious would be the effective management of anthropogenic stressors with the potential to cause declines in canopy-forming species across broad geographic scales, making native communities more susceptible to invasion.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.marenvres.2017.09.015.

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