Undaria pinnatifida: a case study to highlight challenges in marine invasion ecology and management

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Abstract

Marine invasion ecology and management has progressed significantly over the last 30 years although many knowledge gaps and challenges remain. The kelp *Undaria pinnatifida*, or 'Wakame', has a global non-native range and is considered one of the world's 'worst' invasive species. Since its first recorded introduction in 1971 numerous studies have been conducted on its ecology, invasive characteristics and impacts, yet a general consensus on the best approach to its management has not yet been reached. Here, we synthesise current understanding of this highly invasive species, and adopt *Undaria* as a case study to highlight challenges in wider marine invasion ecology and management. Invasive species such as *Undaria* are likely to continue to spread and become conspicuous, prominent components of coastal marine communities. While in many cases marine invasive species have detectable deleterious impacts on recipient communities, in many others their influence is often limited and location specific. Although not yet conclusive, *Undaria* may cause some ecological impact, but it does not appear to drive ecosystem change in most invaded regions. Targeted management actions have also had minimal success. Further research is needed before well considered, evidence based management decisions can be made. However, if *Undaria* was to become officially unmanaged in parts of its non-native range, the presence of a highly-productive, habitat former with commercial value and a broad ecological niche, could have significant economic and even environmental benefit. How science and policy reacts to the continued invasion of *Undaria* may influence how similar marine invasive species are handled in the future.

Keywords: Invasive, non-indigenous, marine, ecology, management, *Undaria*, Wakame

1. Introduction

Globalisation is causing an ever-increasing number of species to be accidentally or intentionally introduced to areas outside of their native range (Perrings et al., 2010). Estimates include over 50,000 non-indigenous species (NIS) in the USA (Pimentel et al., 2005) and over 11,000 in Europe (DAISIE, 2009). This prolific exchange of species, coupled with extinctions and reduced biodiversity driven by anthropogenic environmental change, may be causing a progression towards homogenisation of the world's flora and fauna (McKinney and Lockwood, 1999). Those NIS which establish, spread and proliferate without the direct aid of humans are known as 'invasive species' (Richardson et al., 2011). Invasive species are considered one of the major drivers of global biodiversity decline (along with changes in climate, land and seabed use, atmospheric CO_2 and nitrogen deposition; Sala et al., 2000). Invasive species can also cause major economic loss to a variety of industries, including agriculture, forestry, aquaculture, construction, transport, utilities and tourism, as well as affecting human health (Williams et al., 2010). There is also significant costs associated with research, management and control. An estimate of total economic cost considering all of these aspects amounts to \$120 billion and £1.7 billion per year in the USA and UK respectively (Pimentel et al., 2005; Williams et al., 2010).

Due to the inherent connectivity within the marine environment, NIS are particularly prevalent and difficult to manage (Eno et al., 1997; Ruiz et al., 1997). In six heavily used ports in the USA, Australia and New Zealand, a new NIS was estimated to establish every 85 weeks; with the fastest rate of introduction every 32 weeks in San Francisco Bay (Hewitt, 2003). Over 250 marine NIS have been identified in Australia (Hewitt, 2003), 150 in New Zealand (Cranfield et al., 1998), 90 in the UK (Minchin et al., 2013) and over 200 in San Francisco Bay (USA) alone (Cohen and Carlton, 1998). The major vector of introduction is commercial shipping, followed by aquaculture, canals and aquarium trade (Molnar et al., 2008). Controls on introduction vectors are logistically the most efficient point to inhibit NIS establishment (Bax et al., 2001). However, due to the international, commercial and public nature of vectors, introductions are unlikely to be completely contained (Hulme, 2006). Once introduced, rapid-response management may allow eradication at a relatively low control cost (Anderson, 2005; Beric and MacIsaac, 2015), but early recognition of a marine NIS before it establishes is also problematic. Many species have microscopic life stages and are found in inconspicuous and often inaccessible habitats. The incomplete taxonomy and historical records that are apparent for many marine families, means that once recognised newly identified species will often be cryptogenic. It can often take considerable time for accurate identification and status of a newly identified species to be determined, requiring a wide range of genetic, ecological and biochemical techniques, further delaying potential rapid-response management.

Identifying specific characteristics that predispose a species to being invasive is challenging. Invasive species are generally considered to have high phenotypic or genetic plasticity and a broad ecological niche in order to survive introduction, establishment and spread in a non-native range (Newsome and Noble, 1986; Williamson and Fitter, 1996; Kolar and Lodge, 2001; Zenni et al., 2014). They are often described to have opportunistic life-histories, including high fecundity, growth rate and recruitment, however there are also successful invasive species with more competitive life-history traits (Duyck et al., 2007; Valentine et al., 2007). The probability of invasion increases with the number of individuals released or reproducing, the number of introduction events, and proximity to existing populations (Kolar and Lodge, 2001; Lockwood et al., 2005). Resource availability, such as light, food and physical space, is also a key factor which can influence the vulnerability of a recipient community to invasion (Levine and D'Antonio, 1999; Stachowicz et al., 2002).

Quantifying the ecological impacts of an invasive species is also complex. Differences in recipient communities, resource availability, environmental abiotic factors and attributes of the invasive species itself, can all create site-specific impacts. Factors such as abundance and geographical range of the invasive species may influence impacts in all cases (Parker et al., 1999), while other factors such as morphological, behavioural or even chemical characteristics of the invasive species are more species specific (Thomsen et al., 2011).

Invasive marine macroalgae (seaweeds) may function as ecosystem engineers that are able to modify the environment and alter recipient communities and, as such, have the potential to cause significant ecological and socio-economic impacts (Williams and Smith, 2007; Thomsen et al., 2009; Dijkstra et al., 2017). Overall there are thought to be approximately 350 different seaweed NIS accounting for around 20-30% of all marine NIS (Schaffelke and Hewitt, 2007; Thomsen et al., 2016). The cold-temperate kelp *Undaria pinnatifida* (Figure 1) is one of only two seaweeds (along with *Caulerpa taxifolia*) included in the Invasive Species Specialist Group list of the 100 most invasive species of the world (Lowe et al., 2000). Native to cold temperate areas of the North-west Pacific (the coastlines of Japan, Korea, Russia and China) the adventive kelp *Undaria pinnatifida* (Harvey) Suringar, 1873 (Phaecophycae, Laminariales), or 'Wakame' has a worldwide non-native range (Figure 2). First identified as an invasive species on the Mediterranean coast of France in the 1970s (Perez et al., 1981), *Undaria pinnatifida* (hereafter referred to as *Undaria*) is now established on the coastlines of 13 countries across 4 continents (James et al., 2015). The design of efficient and effective NIS management requires a clear understanding of a species physiology, invasion dynamics and ecological impacts. Due to its global distribution and status as an invasive species for over 30 years, *Undaria* is a useful case study to highlight both successes and failures in our handling and understanding of marine NIS.

2. *Undaria pinnatifida*

2.1. Biology, physiology and native ecology

In its native North-east Asia, *Undaria* is a winter annual species that inhabits rocky substrates from the low intertidal to 18 m depth, and is widespread at depths of 1-3 m (Saito, 1975; Koh and Shin, 1990; Skriptsova et al., 2004). It is also a major species for seaweed mariculture in China, Japan and Korea (Yamanaka and Akiyama, 1993), with total world yield in 2013 exceeding 2 million tonnes fresh weight (FAO FishStat). Sporophytes can grow up to 1 - 1.7 cm per day, reach 1.3 - 2 m in length and have a maximum lifespan of around 6 - 8 months (Castric-Fey et al., 1999; Choi et al., 2007; Dean and Hurd, 2007). They form large divided pinnate fronds and distinctive ruffled reproductive sporophylls (Figure 1). As with all kelps, *Undaria* has a heteromorphic life cycle, with large macroscopic diploid sporophytes that produce microscopic zoospores from reproductive sporophylls. The spores develop into microscopic dioecious haploid gametophytes, which, on maturation produce motile sperm that fertilise the sessile egg and a new sporophyte will start to grow *in situ* of the female gametophyte (Dayton, 1985). Sporophylls develop over several months and mature sequentially from the base upwards (Saito, 1975; Schaffelke et al., 2005). Zoospores are released over approximately 20 - 40 days at densities of $0.13 \times 10^5 - 12 \times 10^5$ spores per cm^2 of sporophyll per hour; amounting to $1 \times 10^8 - 7 \times 10^8$ spores over the lifetime of a sporophyte (Saito, 1975; Schaffelke et al., 2005; Primo et al., 2010; Schiel and Thompson, 2012). Once released spores typically move at around $0.13 - 0.33\ mm\ s^{-1}$ for 5 - 6 hours, but may remain motile for up to 3 days. Fixing ability starts to be reduced within a few hours, although viability can last over 10 days (Suto, 1952; Saito, 1975; Hay and Luckens, 1987; Forrest et al., 2000). Due to the low motility and vitality of the zoospores, settlement is strongly correlated to distance from mature sporophytes, and dispersal may be limited to as little as 0.2 - 10 meters from a spore release point (Suto, 1952; Forrest et al., 2000; Schiel and Thompson, 2012). Larger dispersal distances are thought to be facilitated by the drifting of entire sporophytes, which may remain viable for much longer periods. Overall, it has been estimated that maximum spore-mediated dispersal rates for populations are in the order of $10 - 200$ m yr^{-1}, while sporophyte drift may allow maximum dispersal rates of $1 - 10$ km yr^{-1} (Forrest et al., 2000; Sliwa et al., 2006; Russell et al., 2008).

In most of its native range *Undaria* sporophyte recruitment occurs in winter, becomes reproductive in spring and goes through widespread senescence during summer, leaving only the microscopic gametophyte life stages which persist through autumn (Saito, 1975; Koh and Shin, 1990). Temperature is the key environmental factor which determines this annual population dynamic (Figure 3; Saito, 1975). *Undaria*'s native range has average monthly sea surface temperatures from -0.6°C to 16.8°C in the coldest months, and 23°C to 29.5°C in the warmest months (Skriptsova et al., 2004; Dellatorre et al., 2014; Watanabe et al., 2014; James and Shears, 2016b). The ability to tolerate this large annual range is due to the survival of microscopic gametophyte and sporophyte stages which can persist at temperatures between -1 and 30°C (Saito, 1975; Morita et al., 2003a). Sporophyte growth has a slightly more restricted temperature range of 0 - 27°C; optimum growth rate is site-specific, however tends to fall within 5 - 20°C, and senescence may be induced by exposure to temperatures at or above 24°C (Saito, 1975; Morita et al., 2003b; Skriptsova et al., 2004; Henkel and Hofmann, 2008; Bollen et al., 2016; James and Shears, 2016a). The reproductive sporophylls can be present between 5 - 27°C, and when mature, spore release and settlement occurs between approximately 11 - 25°C (Saito, 1975; Skriptsova et al., 2004; Thornber et al., 2004; James and Shears, 2016b). Although sporophytes may develop 15 - 20 days after spore settlement, under certain temperature, light or competitive regimes, gametophytes may grow vegetatively and remain viable for up to 2 years, thus creating an expanding seed-bank from previous generations in the understory (Pang and Wu, 1996; Thornber et al., 2004; Choi et al., 2005). The remaining life-stages are the most temperature specific and therefore drive the strict annual life-cycle in its native range (Figure

3). Gametophyte growth is optimum between 15-20°C, while gametogensis and fertilisation is optimum between 10-15 °C (Saito, 1975; Morita et al., 2003a; Henkel and Hofmann, 2008).

Although less defined than the influence of temperature, many abiotic factors can affect the growth and distribution of *Undaria*, including salinity, light, day length, nutrients and wave exposure. *Undaria* is predominantly found in fully saline conditions, with mean salinities below 27 psu generally limiting its range (Saito, 1975; Floc'h et al., 1991; Watanabe et al., 2014). However, laboratory based experiments have shown that zoospore attachment may occour at salinities as low as 19 psu, while gametophytes and sporophytes may survive at salinities as low as 6 psu (although below 16 psu sporophytes may start to become damaged) (Saito, 1975; Peteiro and Sanchez, 2012; Bollen et al., 2016). *Undaria* is viable over a wide range of light regimes; however, changes in irradiance and day-length will influence the rate of recruitment, growth and photosynthesis in both gametophyte and sporophyte stages (Pang and Luning, 2004; Choi et al., 2005; Baez et al., 2010; Morelissen et al., 2013). Although seasonal and site-specific, optimal growth occurs around $40-120\ \mu mol\ m^{-2}\ s^{-1}$, light saturation point for photosynthesis (I_k) can be reached around $100-500\ \mu mol\ m^{-2}\ s^{-1}$, while the light compensation point (I_c; when no net photosynthesis occurs), may be reached between $17- < 5\ \mu mol\ m^{-2}\ s^{-1}$ (Saito, 1975; Matsuyama, 1983; Campbell et al., 1999; Morelissen et al., 2013; Watanabe et al., 2014). Although requiring irradiance above approximately 3 $\mu mol\ m^{-2}\ s^{-1}$ for growth and maturation (Saito, 1975), the gametophyte is able to survive in complete darkness, in a latent phase, for at least 7 months (Kim and Nam, 1997); while zoospore settlement may not be affected by light regime at all (Morelissen et al., 2013).

When compared to perennial or summer annual Laminarians, *Undaria* has a comparatively low rate of nutrient uptake and nitrate storage, and therefore a close association between seawater and tissue nitrate (Dean and Hurd, 2007). This means that growth of sporophyte and gametophyte stages are positively related to nutrient concentration (Pang and Wu, 1996; Dean and Hurd, 2007; Gao et al., 2013; Morelissen et al., 2013). Zoospore settlement, however, is not considered to be influenced by nutrient concentration and therefore any inhibition of recruitment by nutrient limitation would occour at the gametophyte or sporophyte stage (Morelissen et al., 2013). Increased water motion can enhance nutrient uptake in kelps (Gerard, 1982), which is highlighted by rope based mariculture of *Undaria* being more efficient in moderately exposed sites with water velocities of up to $15 - 30\ cm\ s^{-1}$ when compared to sheltered sites of $5 - 12\ cm\ s^{-1}$ (Nanba et al., 2011; Peteiro and Freire, 2011; Peteiro et al., 2016). Within natural environments *Undaria* is found at highest abundance in moderately-sheltered to moderately-exposed open coasts or bays near the open sea (Saito, 1975; Floc'h et al., 1996; Russell et al., 2008). Due to the thin fragile nature of the sporophyte frond, *Undaria* is limited in highly exposed shores (Choi et al., 2007), although can still be found in low intertidal pools or lower subtidal areas, which have more shelter from wave action at exposed sites (Russell et al., 2008). Periods of low water motion are needed for high natural recruitment, with spore adhesion optimal at water velocities of $3\ cm\ s^{-1}$ (Arakawa and Morinaga, 1994). Under certain conditions spores may completely fail to adhere at flows $\geq 14\ cm\ s^{-1}$ (Saito, 1975), however in some cases no inhibition of adhesion rate may occur until flow rates reach over $16\ cm\ s^{-1}$, and spores may still adhere, albeit at a greatly reduced rate, at flows over $25\ cm\ s^{-1}$ (Arakawa and Morinaga, 1994; Pang and Shan, 2008).

Overall *Undaria* has a high growth rate, large reproductive output, high phenotypic plasticity and a relatively wide physiological niche. These factors are often considered characteristic of successful invasive species (Newsome and Noble, 1986; Williamson and Fitter, 1996). On the other hand, *Undaria* exhibits low natural dispersal ability, and its ecophysiological niche is not as broad as some other highly invasive marine macroalgae (Nyberg and Wallentinus, 2005). As such, it could be thought of as a low risk for widespread colonisation, however its invasion history demonstrates it to be a very successful invader.

2.2. Invasive characteristics

The primary vectors of introduction and long distance dispersion of *Undaria* were via fouling on the hulls of commercial vessels (Hay, 1990; Forrest et al., 2000; Silva et al., 2002), and accidental import with shellfish (Perez et al., 1981; Floc'h et al., 1991). *Undaria* was also intentionally introduced for cultivation into Brittany (France) in 1981 (Perez et al., 1981). As with most marine NIS, the initial introductions of *Undaria* therefore all occurred onto artificial substrates within anthropogenic habitats such as harbours, marinas, canals or modified embayments (e.g. Hay and Luckens, 1987; Floc'h et al., 1991; Fletcher and Farrell, 1999; Silva et al., 2002; Cremades et al., 2006; Zabin et al., 2009). Once established, widespread range expansion has been facilitated by human mediated transport to other anthropogenic habitats, largely from fouling on commercial and recreational vessels (Hay, 1990; Fletcher and Farrell, 1999; Russell et al., 2008; Zabin et al., 2009; Dellatorre et al., 2014; Minchin and Nunn, 2014; Kaplains et al., 2016). Once established in these anthropogenic or modified environments, *Undaria* can spread into natural habitats. Due to its requirement for attachment on hard substrates, it is predominantly found invading rocky reefs, however it can also be found more rarely to invade seagrass beds and mixed sediment communities (Floc'h et al., 1996; Farrell and Fletcher, 2006; Russell et al., 2008; James et al., 2014). In many parts of its non-native range *Undaria* populations have expanded, and under certain conditions can make up a significant proportion of canopy forming seaweeds. *Undaria*'s dominance is normally seasonal, spatially variable and mostly occurs on artificial substrates in anthropogenic habitats (Castric-Fey et al., 1993; Fletcher and Farrell, 1999; Curiel et al., 2001; Heiser et al., 2014; James and Shears, 2016a). It can, however, also be found as one of the dominant canopy forming seaweeds in natural habitats under certain competitive or environmental settings (Valentine and Johnson, 2003; Casas et al., 2004; Raffo et al., 2009; Thompson and Schiel, 2012; Heiser et al., 2014).

Due to the low natural dispersion rates of *Undaria*, local spread of populations tends to occur in a step-wise manner (Fletcher and Farrell, 1999). The rate of localised natural spread is therefore far lower than human mediated spread, with some populations having minimal range expansion for many years following their initial introduction. For example, in the UK it took over 7 years for *Undaria* to colonise a shoreline 200 m away from an established marina population (Farrell and Fletcher, 2006); in the USA many marina populations remain localised following introductions over 10 years ago (Kaplains et al., 2016); while in France it took 10 years for *Undaria* to be found outside of the enclosed lagoon to which it was first introduced (Floc'h et al., 1991). In New Zealand, population expansion seems to be dependent on the area in which it is found. In Timaru Harbour *Undaria* has extended less than 1 km from the harbour in over 20 years (Russell et al., 2008), in Marlborough Sound the range of *Undaria* has expanded by hundreds of meters a year (Forrest et al., 2000), in Moeraki Harbour expansion was around 1 km per year, while at Otago Harbour *Undaria* spread around 2 km per year along adjacent exposed coastlines outside the harbour (Russell et al., 2008). Considerably faster rates of spread have also been recorded in areas of Argentina and Australia. Within the San Jose Gulf (Argentina), only 4 years after its introduction, *Undaria* had spread across approximately 100 km of coastline (Dellatorre et al., 2014), and in certain parts of Tasmania local spread has been estimated to reach up to 10 km per year (Hewitt et al., 2005). Although the rate of range expansion is variable and site-specific, *Undaria* seems able to spread and proliferate without the direct aid of humans in all of its non-native range.

As previously discussed, temperature is the key environmental factor which determines the population dynamics of *Undaria* (Saito, 1975). Many parts of *Undaria*'s non-native range have smaller annual temperature variation than the majority of its native range, meaning thermal cues for its annual life history are lost and some macroscopic sprophytes can be present throughout the year (James et al., 2015, and references therein). Using both *in-situ* and satellite based temperature measures, it was estimated that where maximum summer sea-surface temperatures are less than or equal to 19.4°C *Undaria* sporophytes would be predicted to be present year round, whereas where temperature maxima is greater than or equal to 20.6°C an annual phenology could be expected (James et al., 2015).

Due to *Undaria* sporophytes living approximately 6 - 8 months, a recruitment period of four or more months, or multiple recruitment pulses per year could result in the year round presence of sporophytes (James et al., 2015). In Santa Barbara (California, USA) where average sea surface temperatures range from approximately 12°C to 19°C, the presence and growth of sporophytes occurs year round. There are two recruitment pulses, with a smaller autumn pulse at temperatures from 17°C to 21°C, and a larger winter recruitment when temperatures are 12°C to 17°C (Thornber et al., 2004). In this location, recruitment seems to be triggered by a fall in temperature below 15°C, with recruitment occurring around 8 weeks later (Thornber et al., 2004). A similar bi-annual recruitment has been recorded in New Zealand, with pulses in the autumn and spring (Hay and Villouta, 1993; Thompson and Schiel, 2012). In some areas, such as Brittany (France) and Patagonia (Argentina), sea surface temperatures reach over 15°C for only 3 - 4 months of the year. In these locations, although there are still seasonal pulses, some recruitment occurs year round (Castric-Fey et al., 1999; Casas et al., 2008; Martin and Bastida, 2008). The ability for *Undaria* to become one of the dominant canopy forming seaweeds and have a year round occurrence in parts of its non-native range, suggests that it could have significant ecological impacts on the recipient communities to which it invades.

2.3. Ecological impacts

Surveys examining the distribution of *Undaria* within mixed seaweed assemblages have identified that it occurs more commonly, or is found in higher abundance, where there is a lower density of native canopy species (e.g. Castric-Fey et al., 1993; Cremades et al., 2006; Russell et al., 2008; Heiser et al., 2014; De Leij et al., 2017, Table 1). Due to the lack of pre-invasion data, it could be argued that *Undaria* may have been the cause of this reduced native canopy. However, results indicate that *Undaria* is occupying substrates, depth ranges or anthropogenically stressed habitats where native canopy forming seaweeds are limited (e.g. Castric-Fey et al., 1993; Cremades et al., 2006; Russell et al., 2008; James and Shears, 2016b, Table 1). This is supported by an investigation where data on native kelp abundance was available before the *Undaria* invasion. This before-after control-impact (BACI) study showed that the introduction of *Undaria* led to no significant change in the abundance of native kelp species over three years (Forrest and Taylor, 2002).

In its native Japan and Korea, *Undaria* can act as a pioneer species, and is part of a natural successive colonisation process (Agatsuma et al., 1997; Kim et al., 2016). Where it has invaded, this pioneer-like trait is indicated by ecosystem stress or disturbance being key to *Undaria*'s recruitment into mixed canopy assemblages (Table 1). In some cases stress from eutrophic conditions have been shown to promote *Undaria* recruitment (Curiel et al., 2001; Carnell and Keough, 2014), while canopy disturbance is often a critical factor (Floc'h et al., 1996; Edgar et al., 2004; Valentine and Johnson, 2004; Martin and Bastida, 2008; Thompson and Schiel, 2012; South and Thomsen, 2016; De Leij et al., 2017). Experimental clearance of native kelp species within intertidal and subtidal environments in Australia and New Zealand caused *Undaria* to recruit into manipulated patches, while the following year *Undaria* declined and the native seaweeds started to recover (Valentine and Johnson, 2003; Thompson and Schiel, 2012).

Comparative studies have shown that *Undaria* harbours a distinct and reduced epifaunal and epifloral community when directly compared to native kelp species (Raffo et al., 2009; Arnold et al., 2016). However, as evidence suggests that *Undaria* is not able to displace native kelps, this does not indicate ecological impact in itself. Community wide impact studies suggest that the influence of *Undraia* is context specific (Table 1). In anthropogenic habitats *Undaria* may cause a decline in density and diversity of native understory and canopy flora and fauna (Curiel et al., 2001; Farrell and Fletcher, 2006). On natural rocky substrates in Patagonia, there is some evidence that *Undaria* can cause a reduction in diversity and richness of native macroalgae (Casas et al., 2004) and reduce fish abundance (Irigoyen et al., 2010), although this may be highly site-specific. Intertidal studies in New Zealand and Australia have described *Undaria*'s impacts on native biodiversity as transient (Table 1). For example, a two and half year study within intertidal reef habitats in New Zealand repeatedly removed *Undaria* from experimental patches. Measurement of various faunal and floral community indicators showed no long term effect of the presence of *Undaria* when compared to control sites (South et al., 2015). A similar result was found in a three year BACI study of an *Undaria* invasion into a sheltered embayment of New Zealand, with no evidence of significant ecological impacts on either macroalgae or sessile invertebrates (Forrest and Taylor, 2002).

The distribution, ecological impact and invasion dynamics of *Undaria* seem to indicate that it is predominantly acting as a passenger of ecosystem change - filling an empty niche or benefiting from resource availability which is temporarily released by ecosystem stress and having a limited impact on recipient communities (Didham et al., 2005; MacDougall and Turkington, 2005; Bauer, 2012). There is, however, some evidence that *Undaria* may be driving ecosystem change in certain environments. In a study by Carnell and Keough (2014), *Undaria* required native canopy disturbance to recruit and grow in high abundance, however under nutrient enhancement, the presence of *Undaria* seemed to limit the recovery of native canopies. In other examples, the native canopy has not inhibited *Undaria* recruitment (Farrell and Fletcher, 2006; Morelissen et al., 2016), and removal or die back of *Undaria* has led to recovery of native macroalgae (Curiel et al., 2001; Casas et al., 2004).

One way in which *Undaria* may be able to drive ecosystem change in the long term is due to its year round presence in some of its non-native range (Hay and Villouta, 1993; Fletcher and Farrell, 1999; Casas et al., 2008; James and Shears, 2016b). Many larger native canopy forming seaweeds are perennial, living up to 10 years, with seasonal growth, reproductive and senescence stages. If *Undaria* is able to recruit in multiple pulses throughout the year onto available substrate left open by the natural die back of native species it may be able to slowly monopolize space, increasing in density and excluding native seaweeds. Due to the long life time of some native species, significant increases in the density and distribution of *Undaria* may not be seen for many decades in the absence of wider ecosystem disturbance. Long term monitoring and manipulations of *Undaria* invaded communities would be needed in order to demonstrate the potential of this interaction.

It has been suggested that *Undaria* could have facilitative impacts within certain invaded communities, by proving trophic or habitat subsidy (Suarez-Jimenez et al., 2017; Jimenez et al., 2015; Irigoyen et al., 2011; Cecere et al., 2000). For example, in a low complexity limestone plateau, benthic macrofaunal richness and diversity was higher where *Undaria* was present (Irigoyen et al., 2011). Similarly, within a highly polluted and low diversity enclosed basin of the Ionian Sea the presence of *Undaria* was observed to have a positive ecological function, by increasing benthic primary production and providing food and biogenic habitat for other organisms (Cecere et al., 2000). Further research is needed to better elucidate the net impact (i.e. negative and facilitative) of *Undaria* across a range of invaded ecosystems. To date, the majority of studies have been carried out in the southwest Pacific, yet current evidence suggests that *Undaria* impacts are context specific. A key knowledge gap relates to the impacts of *Undaria* in other invaded regions, such as the northwest Atlantic and northeast Pacific. Future research should also include an emphasis on manipulative and BACI studies, as well as long term monitoring activities and comparative work across large spatial scales, in order to causally determine the effects of *Undaria* within invaded ecosystems.

2.4. Management

Management frameworks designed to control the abundance and spread of *Undaria* could only be found for two of the countries to which it has been introduced (Table 2). These are largely generic, with measures applicable to wider NIS introductions. For example, the key measures recommended for managing *Undaria* in New Zealand include: surveillance and response to new infestations in high-value areas, vector monitoring and control, prohibition of intentional release, controls on ballast water discharge, improved research, education and public awareness (Sinner et al., 2000). Although not necessarily a requirement, none of these measures will reduce localised natural spread or abundance of *Undaria*.

Eradication using heat treatment has been successful where an isolated population occurred on a wrecked trawler in the Chatham islands, New Zealand (Wotton et al., 2004). Removal of all sporophytes over a 15 month period led to the long term eradication of *Undaria* from the site and inhibited its spread to natural substrates. Even at this small scale, eradication cost around $0.4 million (NZD). Eradication from longer established populations in natural environments has not yet been successful. A management trial in Tasmania, removed *Undaria* monthly from a 800 m^2 area of rocky reef. Although there was a significant reduction in sporophyte abundance, eradication was not achieved, with sporophytes present at each subsequent visit (Hewitt et al., 2005). Experimental manipulations carried out in New Zealand and Italy, whereby small (0.5 m^2) areas of *Undaria* dominated rocky substrate were scraped clean, also saw fresh recruitment within one year (Curiel et al., 2001; Thompson and Schiel, 2012).

As previously discussed, many studies have shown that *Undaria* requires a level of ecosystem stress or disturbance to recruit and spread in mixed seaweed canopies. Reducing, mitigating, or preventing anthropogenic disturbance to native canopies has therefore been suggested as a management option to prevent the spread, and limit the abundance of *Undaria* (Valentine and Johnson, 2003). However, where *Undaria* has already established at high densities, or if it is acting as a 'back-seat driver' - suppressing native species once recruited (Bauer, 2012), maintaining native canopies alone is unlikely to be effective (Valentine and Johnson, 2003).

The management options available to directly target the local spread and abundance of

Undaria are unclear. Where *Undaria* can be found in multiple locations and at high abundance within natural environments it seems unlikely that eradication would be feasible. This is generally accepted by environmental managers, with widespread eradication of *Undaria* not currently being considered in any country to which it has been introduced (Table 2). Due to the importance of artificial or anthropogenic environments in the establishment of *Undaria* and its relatively low natural dispersal rates, control of new or isolated populations should be plausible. Monitoring of harbors, marinas, ports, high-value natural areas and natural boundaries, with rapid response eradication to any new sightings could greatly reduce wide-scale spread of *Undaria* and therefore the ecological impacts it may have on natural habitats (Forrest et al., 2009). In New Zealand, *Undaria* is currently absent from the west coast of the South Island, and large areas of the North Island's west coast. In April 2010 a mature sporophyte was found within Sunday Cove, Fiordland World Heritage Area, on the west coast of the South Island (ES, 2016). Since that time, dive based surveys and removal of *Undaria* have been carried out every 4-5 weeks at a cost over $1 million (NZD). Six years after the commencement of the program occasional young individuals are still found, however it is still the aim of managers to entirely eradicate *Undaria* from the area (ES, 2016).

In many regions where *Undaria* is now accepted (i.e. eradication is no longer being considered), commercial farming and wild harvest is being developed. Mariculture expanded across Brittany, after *Undaria*'s initial introduction in 1981, with 9 sites established into the early 1990s (Castric-Fey et al., 1993). Cultivation and mariculture has also been carried out on the Galician coast of Spain since the late 1990s, and is continuing to develop along the North coast (Perez-Cirera et al., 1997; Peteiro et al., 2016). In 2010 The Ministry for Primary Industries (New Zealand) introduced a revised policy for the commercial use of *Undaria* which approved its wild harvest from artificial substrates or when cast ashore in selected areas. It also approved mariculture in three heavily infested areas, but prohibited harvest from natural substrates unless part of a designated control program (MAF, 2010). The rationale behind the prohibition of harvest from natural substrates was that "it could disturb or remove native canopy species leading to a proliferation of *Undaria*", while "harvesting when taken as part of a control programme is allowed as any risks associated with harvest will be outweighed by reduced *Undaria* in localised areas" (MAF, 2010). It may be possible that one of the remaining options to reduce the abundance and local spread of *Undaria* where eradication is no longer feasible, would be through the legalisation of commercial wild harvest from natural substrates. Strict biosecurity would have to be implemented to avoid its spread, and harvesting practises would need to minimise damage to native canopies - such as through a licensing system for hand harvesting only in specific areas. Timings of harvest would also have to be carefully considered, as removal or thinning of the *Undaria* canopy can result in a strong positive response of conspecific recruitment, and increased growth rate of the remaining stock (Thompson and Schiel, 2012; Gao et al., 2014). However, removal before maturation could greatly reduce spore and seed-bank densities, and would perhaps limit the abundance and spread of *Undaria* over time.

Decisions taken by environmental managers on whether to manage *Undaria* within a given jurisdiction should be made on a case-by-case basis. Where *Undaria* has recently arrived, or has a restricted range, it is likely that there will be a better chance of successful control or eradication. However, due to the widespread global distribution of *Undaria*, re-introduction is probable without the implementation of thorough biosecurity. The native community into which *Undaria* is introduced may also strongly influence the decisions of environmental managers. The invasion of *Undaria* is likely to have greater ecological impact in areas where there are no functionally similar native species. Whereas, in communities which are dominated by native canopy-forming macroalgae, *Undaria* may have limited impact on the community as a whole, and act as a passenger of ecosystem change. Economics and the maintenance of ecosystem services will also be factors that influence the decisions made by environmental managers. Although not covered as part of this review *Undaria* can act as fouling pest to industries such as aquaculture, shipping and recreational boating (Hay, 1990; Zabin et al., 2009; Minchin and Nunn, 2014; James and Shears, 2016a). The overall economic impacts of this interaction are poorly understood, but as has been noted above, *Undaria* could also have economic benefit through the development of an *Undaria* mariculture industry. Careful consideration and further research is needed on a site-specific basis. Clearly, the risks, costs, impacts and benefits of all options, including potential management or eradication and possible acceptance, should be considered when developing management plans for *Undaria*.

3. Lessons learnt for wider marine invasion ecology

3.1. Predicting invaders and reacting to NIS

Although our understanding of marine NIS has greatly increased, *Undaria* is a useful case study to demonstrate that current capacity to predict the invasion dynamics of many marine NIS, and their interactions and impacts within native communities, remains limited. Once introduced, most NIS would not be expected to establish or become invasive (Lodge, 1993; Williamson and Fitter, 1996). Where invasion does occur, the time from initial introduction to when a species becomes invasive is highly variable. In some cases this "lag-time" may last decades, with little-to-no proliferation of NIS populations for a considerable time after introduction (Crooks, 2005). This is highlighted by the invasion history of *Undaria*, which has exhibited a wide range of expansion rates following introduction into different regions. Predicting which NIS are likely to become invasive can therefore be challenging. Species traits are often used to predict which NIS may become invasive (Newsome and Noble, 1986; Williamson and Fitter, 1996), although this approach has limitations (Kolar and Lodge, 2001; Nyberg and Wallentinus, 2005; Duyck et al., 2007).

Undaria was considered to be an acceptable species for intentional introduction into France for mariculture purposes in 1981 (Perez et al., 1981). A better understanding of a species ecology and physiology is required before intentional introductions are conducted. However, when adventive species arrive unexpectedly, the necessity for rapid response management negates this consideration. A failure to react to new introductions could have major consequences. As marine invasive species can cause significant damage to the environment and economy, and due to the complex nature of species invasions, a precautionary principle should be adopted to minimise the rate of any new introductions (Grosholz, 2002; Bax et al., 2003; Molnar et al., 2008).

3.2. Ecological impacts

For some marine invasive species, deleterious ecological impacts can be substantial and easy to detect. Introduced voracious predators such as the northern Pacific seastar, *Asterias amurensis*, in Tasmania (Ross et al., 2003), the Lionfish, *Pterois volitans*, in the tropical Atlantic (Green et al., 2012) and the North American mud crab *Rhithropanopeus harrisii* in the Baltic Sea (Jormalainen et al., 2016), prey on wide range of native species and proliferate in the absence of native predators. In these examples clear community-wide impacts can be identified. Similarly, when invasive species greatly alter nutrient pathways, trophic interactions or habitat structure, impacts at the community and ecosystem level are easily detectable (Crooks, 2002; Simberloff, 2011). For example, colonial ascidians of the genus *Didemnum* have overgrown large areas of hard substrates, particularly in the Netherlands and USA. These 'mats' can greatly alter the physical habitat, cause mortality through smothering of sessile flora and fauna and have major deleterious impact on wider ecosystem functioning with socioeconomic consequences (Bullard et al., 2007; Gittenberger, 2007). The invasion of *Undaria* highlights that in many other cases ecological impacts are far harder to quantify, and may vary considerably between locations and recipient communities. For these species, justifying costly eradication attempts may be challenging. However, as marine invasive species spread to new regions, decisions will have to be made on potential rapid response management before site-specific impact studies can be carried out.

Invasive species, including *Undaria*, can also have facilitative impacts on the recipient community (Rodriguez, 2006; Irigoyen et al., 2011; Dijkstra et al., 2017). The invasion of bivalve molluscs onto soft sediments, such as *Musculista senhousia* and *Crassostrea gigas*, is a useful example of facilitation by a marine invasive on multiple levels. They provide complex habitats which can greatly increase infaunal and epifaunal abundance, increase organic content in sediment to the benefit of associated organisms, and can act as a trophic subsidy to predatory invertebrate and vertebrate species (Crooks and Khim, 1999; Escapa et al., 2004; Padilla, 2010). In order to understand the overall ecological impact a marine invasive species has on the recipient community, both deleterious and facilitative effects must be considered. Intrinsically the facilitation of one species is likely to occur at the expense of others, due to changes in competition or predation. In fact for both *Musculista senhousia* and *Crassostrea gigas*, where high densities are found, a reduction in the abundance of functionally similar native species is often recorded (Creese et al., 1997; Crooks and Khim, 1999; Padilla, 2010). In many cases, unequivocal evidence of significant ecological impact of an invasive species on recipient communities will be difficult to attain. Prioritisation of management actions will be influenced by the perceived impacts of marine invasive species, in terms of their threat to conservation and the maintenance of ecosystem services across different regions, as well as their direct socioeconomic impacts.

3.3. Management

Managing marine NIS is expensive and time consuming, while eradication may be impossible once a species is established and widespread (Hulme, 2006). There are examples of successful rapid response eradication of invasive species in the marine environment. The seaweed *Caulerpa taxifolia* was first identified in the USA in 2000 (Jousson et al., 2000). A rapid response only 17 days after its first discovery allowed the successful implementation of a 5 year eradication program using containment and chemical treatment, at a cost of around $7.5 million (USD)

(Anderson, 2005). However, as shown by *Undaria*, once a marine NIS is established, proliferation and spread may be inevitable due to the natural or engineered connectivity of many water-bodies. As population size increases the costs of control also increase, while attempting eradication of established populations would require significant resources and effort, and may ultimately be unsuccessful (Hobbs and Humphries, 1995). A pertinent example of a marine invasive species where targeted management was deemed to be inappropriate is the macroalgae *Sargassum muticum* or 'Japanese wireweed' in Europe. After its introduction into the UK in 1973, *Sargassum* spread across much of Europe's northeast Atlantic and Mediterranean coastlines. A variety of impact studies have been carried out in different parts of its non-native range with varying results. Some studies found it to alter the recipient community to which it was introduced (Viejo, 1997; Staehr et al., 2000; Harries et al., 2007), however other long-term studies recorded limited effects from the invasive species (Sanchez and Fernandez, 2005; Olabarria et al., 2009). Although attempts at management were made (Critchley et al., 1986), due to its widespread distribution, uncertainties in the level of its ecological impact, as well as the costs and difficulties in its control, *Sargassum* now has no targeted management across most of Europe.

As with many other invasive species *Undaria* has a largely opportunistic life-strategy, taking advantage of resource availability in order to establish and spread (Gurevitch and Padilla, 2004). These species are sometimes considered "passengers" - promoted and maintained due to the presence of ecosystem stress or disturbance but not in themselves the cause of ecosystem change. (MacDougall and Turkington, 2005). A potential management option for these species is not to directly target the species itself, but instead to manage the causes of ecosystem stress or disturbance, with the ultimate aim of restoring, maintaining or even promoting the diversity, integrity and biotic resistance of recipient communities to invaders. Managing long term global-scale stressors such as climate change will be challenging but crucial given the known interactions between climate and the spread of NIS (Occhipinti-Ambrogi, 2007). On a local-to-regional scale, however, managing stressors such as coastal inputs of sediments and nutrients and physical disturbances from resource extraction, fishing activities and coastal development may allow some biotic resistance to be maintained. While designing and prioritising targeted management options for invasive species is of significant importance, especially for those that are considered of high risk or highly damaging, it is also clear that attention should be given to preserving the integrity, diversity and resistance of native communities through maintaining good overall environmental status. This has been shown for *Undaria*, as its abundance and spread is limited by the presence of diverse, native macroalgae canopies (e.g. Castric-Fey et al., 1993; Valentine and Johnson, 2003, 2004; Russell et al., 2008; De Leij et al., 2017).

As marine NIS continue to spread and extend their non-native ranges, decisions will be made on the necessity and feasibility of managing new incursions. Although a precautionary principle should be applied, it is unrealistic to assume that management and control of all species can be achieved due to the widespread establishment of many marine invasive species. Difficult choices will have to be made regarding which species should be targeted, with some potentially becoming an accepted part of the local biota. These decisions must be made on a case-by-case basis using the best information available, and will depend on a variety of factors including the likely effectiveness, practicality, risk and cost of management options, as well as negative and positive ecological and socioeconomic impacts of a given species.

3.4. Accepting NIS

Many NIS have been established in their non-native range for a considerable time, and are now considered part of the natural biota in different regions across the world with major economic benefit and even cultural importance (Ewel et al., 1999; Davis et al., 2011). These species frequently occur in high abundance and over a wide distribution, and could therefore be classed as invasive. Due to the historic nature of species introductions, the widespread acceptance of certain NIS or invasive species is particularly common in the terrestrial environment.

The vast majority of the world's agricultural and horticultural species are NIS where they are grown. Many freshwater fish species have also been historically introduced for farming and sports fishing purposes and are treated essentially as part of the natural biota in many regions (Copp et al., 2005; Gozlan, 2008; Eustice, 2014).

In the marine environment there is a tendency for all NIS to be classed as damaging invasives, however many species have been established outside their native range for many decades, with little-to-no reported impacts. Although further intentional spread may be restricted, few have targeted management plans aiming to reduce their abundance, and are in practise, treated the same as native species. An example of a marine species where perceptions are changing is the Pacific Oyster, *Crassostrea gigas*. The oyster has been intentionally introduced from Asia for farming across the world since the late 1800s. Although initially believed unable to reproduce in the lower sea temperatures around the cold-temperate Pacific and Atlantic coasts, wild populations have established in most introduced regions. In some cases, this species is considered as a damaging invasive, with management being developed, or enforced to reduce its spread (NSW, 1994; Guy and Roberts, 2010). However, in many parts of the USA and France, where introductions occurred in the 1920s and 1960s respectively, they are now being seen as part of the natural biota, and are targeted by both wild capture fisheries and aquaculture using seeded bottom culture techniques (Feldman et al., 2000; Cognie et al., 2006; Buestel et al., 2009).

Although somewhat contentious, in certain cases invasive species could be considered to have benefits to nature conservation (Schlaepfer et al., 2011, 2012; Vitule et al., 2012). This may occur if the invasive species (1) has considerable facilitative and minimal deleterious impacts on native species; (2) acts as a catalyst for restoration of native habitats; (3) functionally replaces a limited or extinct native species; (4) facilitates a species of high conservation value; or (5) acts as a biocontrol agent (Schlaepfer et al., 2011). These benefits are again more commonly identified in the terrestrial environment due to the historical and often intentional nature of introductions (e.g. Morrison et al., 1998; Lugo, 2004). *Crassostrea gigas* may be another pertinent example relating to the marine environment. In many parts of Europe and America native oysters have been over harvested and are considered endangered. It has been suggested that the spread of the invasive Pacific Oyster may have conservation benefit, functionally replacing the native species, providing habitat, a trophic subsidy and increased biofiltration; while also providing an exploitable resource, reducing further harvesting pressure on the native homolog (Shpigel and Blaylock, 1991; Paalvast et al., 2012).

As previously stated, some marine invasive species, such as voracious predators, or those with perennial life-cycles and more competitive life-history traits, can have major detrimental ecological impact. Many of these species also have minimal facilitative impacts and may lack any societal benefits. These species are unlikely to be accepted and may require prolonged management or control. *Undaria*, however, is a large primary producer, which may provide a trophic and habitat subsidy to native communities within some systems. Although more site-specific research is needed, in many cases it has also been recorded as having minimal deleterious impact on native species. There is also commercial potential, with both wild harvest and rope based mariculture conducted in parts of *Undaria*'s non-native range (Castric-Fey et al., 1993; Perez-Cirera et al., 1997; MAF, 2010; Peteiro et al., 2016). In areas where likelihood of controlling *Undaria* is low due to widespread established populations, and context specific studies show limited ecological impact, it may be that *Undaria* becomes one of few marine invasive species accepted as part of the local biota, with the potential for further development as a commercial resource.

4. Conclusions

There are many challenges facing the future of marine invasion ecology. Total prevention of introductions of new NIS is highly unlikely, while management or eradication is extremely costly and often infeasible. Invasive species are likely to continue their spread and become conspicuous and prominent components of coastal marine communities. In many cases marine invasive species have clearly detectable deleterious impacts on recipient communities, however, in many others their influence is often limited and site-specific. *Undaria* has now been established for over 40 years in some of its non-native range. In these areas, rapid response or eradication is no longer an option and the need for any targeted management should be considered. Although not yet conclusive, *Undaria* seems to have minimal ecological impacts in most invaded locations and does not appear to be a 'driver' of ecosystem change in most contexts. If this is shown to be the case, it may be more beneficial to target management effort towards the causes of ecosystem stress that reduce native biotic resistance and allow *Undaria* to proliferate, rather than attempting to exclude the species itself. Further research is needed before well considered, evidence-based management decisions can be made on a case-by-case basis. However, if *Undaria* was to become officially 'unmanaged' in parts of its non-native range and accepted as a component of the native flora, the presence of a habitat forming, primary producer with a broad ecological niche and potential commercial value, may deliver significant economic and even environmental benefit. How science and policy reacts to the continued spread and proliferation of *Undaria* may influence how similar marine invasive species are handled in the future.

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6. Author contributions

G.E. is the primary author and produced the majority of the content of this review. D.A.S. was involved throughout the process from first draft to final manuscript; including conception, composition, critical review and final approval for submission.

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Figure legends

Figure 1: Different developmental stages of *Undaria pinnatifida* sporophytes (A-D). *Undaria pinnatifida* can be found growing in the subtidal and intertidal, as well as on natural and artificial substrates (E-G).

Figure 2: Approximate distribution of *Undaria pinnatifida.* Global map: Green = native range, red = non-native range. Regional maps: Each point represents a distinct location but does not indicate precise position or entire extent. See Table S1 for more information and references.

Figure 3: Thermal tolerances of the different life-stages of *Undaria pinnatifida.* Lighter colours = life-stage possible but may be limited. See in text for references

Table 1: Summary of studies on *Undaria pinnatifida* for which inference could be made to its competitive ability with functionally similar species and its impact on recipient communities. Substrate: RR = Rocky reef, RP = Rock plateau, Art = Artificial (SW = Sea wall, M = Marina pontoon or buoys). Method: Obs = Observational survey, Rem = Manipulative removal experiment, CI = Control-impact, BACI = Before-after control-impact. Competitive ability: red = competitively superior to functional similar native species, orange = competitively equal or unaffected, green = competitively inferior or opportunistic. Impact on community: red = detrimental, orange = no significant change, green = facilitative.

Reference	Location	Substrate	Description of response variable	Duration (months)	Method	Summary	Competitve ability	Impact on community
Carnell and Keough (2014)	SW Pacific (Victoria, Australia)	RR	Kelp density and biomass	6	Rem	Recruitment of *Undaria* where native kelp removed and nutrients added. Presence of *Undaria* reduced the recovery of native kelp.		
Casas et al. (2004)	SW Atlantic (Patagonia, Argentina)	RR	Macroalgal community	8	Rem	Higher abundance, richness and diversity of native algal species after removal of *Undaria*, compared to unmanipulated control sites.		
Castric-Fey et al. (1993)	NE Atlantic (Brittany, France)	RR	Kelp density and biomass	<1	Obs	Higher abundance of *Undaria* where native kelps are limited due to depth or substrate.		
Cremades et al. (2006)	NE Atlantic (Galicia, Spain)	RR	Macroalgal community	5	Obs	Higher abundance of *Undaria* where native canopy is limited due to depth, substrate or anthropogenic stressors.		
Curiel et al. (2001)	N Mediterranean (Veneto, Italy)	Art(SW)	Macroalgal density and biomass	26	Rem, Obs	Decline in native macroalgal density when *Undaria* was present in high densities. Presence of *Undaria* caused decline in understory algae.		
De Leij et al. (2017)	NE Atlantic (Devon, UK)	RR	Kelp density and biomass	4	Rem, Obs	*Undaria* density and biomass limited in the presence of native canopy-dominant kelps. Removal of native kelp increased recruitment of *Undaria*.		
Edgar et al. (2004)	SW Pacific (Tasmania, Australia)	RR	Macrofaunal and macroalgal community	12	Rem	Native canopy removal led to significant recruitment of *Undaria* compared to unmanipulated control patches, however, recovery to near control levels at end of study. No significant difference on associated fauna and flora.		
Farrell and Fletcher (2006)	NE Atlantic (Devon, UK)	Art(M)	Kelp density. Coarse understory flora and fauna metrics.	48	Rem, Obs	Removal of native kelp had no significant effect on *Undaria* recruitment. Over time abundance of *Undaria* increased in both removal and control areas, coupled with native kelp reduction. Differences in associated flora and fauna due to presence of *Undaria*.		
Floc'h et al. (1996)	NE Atlantic (Brittany, France)	RR, Art(Rope)	*Undaria* abundance	12	Rem, Obs	Laying of *Undaria* sporophylls led to recruitment into exposed areas where canopy removed, but not where canopy was intact. No *Undaria* present at any site one year after manipulation.		
Forrest and Taylor (2002)	SW Pacific (Canterbury, New Zealand)	RR	Macroalgal and macofaunal community	30	CI, BACI	No evidence for displacement of native canopy by *Undaria*. No significant contrasts indicating displacement of macrofauna or algal species, or changes in species assemblage due to the presence of *Undaria*.		
Heiser et al. (2014)	NE Atlantic (Devon, UK)	RR, Art(M, SW)	Kelp density	2	Obs	Highest abundance of *Undaria* in marinas and at sites where native canopy forming kelps were low in abundance.		
Irigoyen et al. (2010)	SW Atlantic (Patagonia, Argentina)	RR,RP	Fish abundance	5	CI	*Undaria* reduced abundance of fish in low-relief reefs by obstructing access to shelters when it became dislodged and settles on the reef.		

Reference	Location	Substrate	Description of response variable	Duration (months)	Method	Summary	Competitive ability	Impact on community
Irigoyen et al. (2011)	SW Atlantic (Patagonia, Argentina)	RP	Macrofaunal diversity	8	Rem	Presence of *Undaria* associated with increased macrofaunal richness, diversity and abundance, when compared to *Undaria* excluded areas.		
James and Shears (2016b)	SW Pacific (Waikato, New Zealand)	RR, Art(Rope)	*Undaria* abundance. Coarse metric of native algal community.	30	Obs	*Undaria* found in high abundance on ropes in mussel farms. In adjacent reef habitats *Undaria* found predominantly in areas lacking a native canopy.		
Martin and Bastida (2008)	SW Atlantic (Patagonia, Argentina)	RR, RP	Kelp density	13	Rem, Obs	*Undaria* abundance limited in the presence of native kelp. Removal of native kelp increased recruitment of *Undaria*.		
Morelissen et al. (2016)	SW Pacific (Wellington, New Zealand)	RR	*Undaria* abundance	12	Rem	Removal of native canopy did not effect *Undaria* recruitment compared to intact, or partially disturbed canopies. Species composition of algal community developing after disturbance also had no relationship with *Undaria* recruitment.		
Raffo et al. (2009)	SW Atlantic (Patagonia, Argentina)	RR	Kelp density and biomass	<1	CI, Obs	Presence of *Undaria* had no effect on native *Macrocystis* density or growth. Presence of *Macrocystis* had no effect on *Undaria* density or growth.		
Russell et al. (2008)	SW Pacific (Otago, New Zealand)	RR	Macroalgal community	2	Obs	*Undaria* predominantly found where native kelps are limited (due to depth or substrate), as well as within inherently patchy habitats in areas lacking canopy.		
South et al. (2015)	SW Pacific (Otago, New Zealand)	RR, RP	Macroalgal and macofaunal community	30	Rem	No significant effects of *Undaria* removal on diversity and abundance of native algae and invertebrates.		
South and Thomsen (2016)	SW Pacific (Canterbury, New Zealand)	RR	Macroalgal and macofaunal community	6	Rem, CI	Removal of native canopy increased recruitment of *Undaria*. Negative correlation between native canopy cover and *Undaria*. *Undaria* exclusion had little effect on recipient community, with a transient reduction in only one ephemeral native alga.		
Thompson and Schiel (2012)	SW Pacific (Canterbury, New Zealand)	RR, RP	Macroalgal density	12	Rem	Removal of native canopies significantly increased recruitment of *Undaria*. In all areas native canopy started to recover within 1 year. The smaller the disturbance area, the faster native canopy recovery occurred.		
Valentine and Johnson (2003)	SW Pacific (Tasmania, Australia)	RR	Macroalgal community. Coarse macrofauna density metric.	24	Rem	Removal of native algal canopy promoted *Undaria* recruitment. Following initial recruitment of *Undaria*, abundance declined over time associated with a substantial recovery of native canopy forming species.		
Valentine and Johnson (2004)	SW Pacific (Tasmania, Australia)	RR	Macroalgal density. Coarse macrofauna density metric.	22	CI	Natural dieback of native canopy led to high recruitment of *Undaria*, compared to little or no recruitment of *Undaria* in areas with intact canopies.		
Valentine and Johnson (2005)	SW Pacific (Tasmania, Australia)	RR	*Undaria* density. Coarse metric of native algal community.	30	Rem	Removal of *Undaria* had limited effects on native algae after one year. The following year, there was no evidence that any algal group responded to the removal of the *Undaria* canopy.		

Table 2: Status and management of *Undaria pinnatifida* within its non-native range

Country	First recorded	Population status	Dedicated management plan	Summary of known management	Management aim	References
France	1971	Common in natural and anthropogenic habitats across current range. Active mariculture.	None found	Mariculture limited to areas with already developed infrastructure and high *Undaria* abundance. Mariculture under strict control to prevent potential ecological impacts and further spread.	Inhibit range expansion	Antoine et al. (2012); Castric-Fey et al. (1993)
New Zealand	1987	Common in natural and anthropogenic habitats across current range. Active mariculture.	Sinner et al. (2000)	Surveillance and response to new infestations in high-value areas, vector monitoring and control, prohibition of intentional release, controls on ballast water discharge, improved research, education and public awareness.	Inhibit range expansion	Russell et al. (2008); James et al. (2014)
Spain	1988	Common in natural and anthropogenic habitats across current range. Active mariculture.	None found	*Undaria* not included as an invasive or potentially invasive species within invasive alien species legislation.	Unmanaged	Baez et al. (2010); BOE (2013)
Australia	1988	Common in natural and anthropogenic habitats across current range	NSPMMPI (2015)	Reduce spread to high value areas, possible commercial harvest with tight biosecurity, modify drydock timing to minimise sporophyte development, maintain integrity of native canopy algae, ballast water management, monitoring.	Inhibit range expansion	Valentine and Johnson (2004); Primo et al. (2010)
Italy	1992	Largely confined to heavily modified environments and on artificial substrates.	None found	None found	None found	Cecere et al. (2000); Curiel et al. (2001)
UK & ROI	1994	Confined to anthropogenic habitats in many locations. Common in natural habitats in parts of the south English and Welsh coast.	None found	None found	None found	Heiser et al. (2014); Minchin and Nunn (2014); Wood et al. (2015)
Portugal	1999	Found at only one marina and one natural reef site.	None found	None found	None found	Veiga et al. (2014)
Belgium	1999	Uncertain. Likely to be predominantly in ports across current range.	None found	None found	None found	Leliaert et al. (2000); VLIZ (2011)
Holland	1999	Predominantly in anthropogenic habitats in the Wadden Sea. In natural and anthropogenic habitats in Oosterschelde.	None found	Recommendations for a national coordinated management plan.	Inhibit range expansion	Gittenberger and Stegenga (2013); Verbrugge et al. (2015)
USA	2000	Largely confined to anthropogenic habitats (Only two records on natural reef in 2001)	None found	Academic and citizen science led research and removal from marinas in California.	Inhibit range expansion	Kaplains et al. (2016)
Argentina	2000	Common in natural and anthropogenic habitats across current range	None found	Manual removal of macroscopic sporophytes and a regular monitoring program to track and eventually prevent its dispersal within one province.	Inhibit range expansion	Dellatorre et al. (2014)
Mexico	2003	Isolated island population on natural reef	None found	None found	None found	Aguilar-Rosas et al. (2004)

Figure 1:

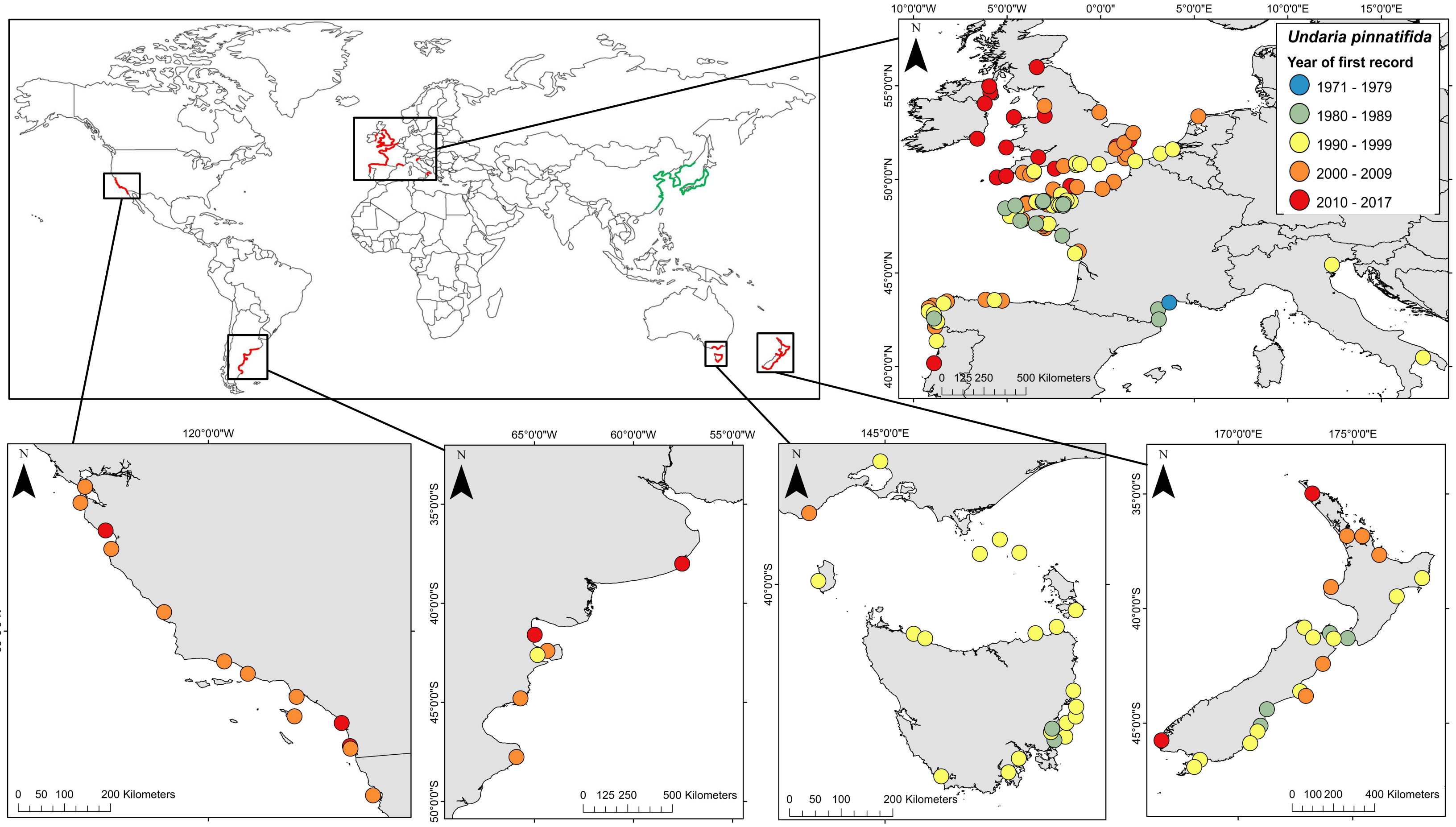
Undaria pinnatifida
Year of first record
1971 - 1979
1980 - 1989
1990 - 1999
2000 - 2009
2010 - 2017
10°0'0"W
5°0'0"W
0°0'0"
5°0'0"E
10°0'0"E
15°0'0"E
55°0'0"N
50°0'0"N
45°0'0"N
40°0'0"N
0 125 250 500 Kilometers
120°0'0"W
35°0'0"N
0 50 100 200 Kilometers
65°0'0"W
60°0'0"W
55°0'0"W
35°0'0"S
40°0'0"S
45°0'0"S
50°0'0"S
0 125 250 500 Kilometers
145°0'0"E
40°0'0"S
0 50 100 200 Kilometers
170°0'0"E
175°0'0"E
35°0'0"S
40°0'0"S
45°0'0"S
0 100 200 400 Kilometers
N

Figure 2:

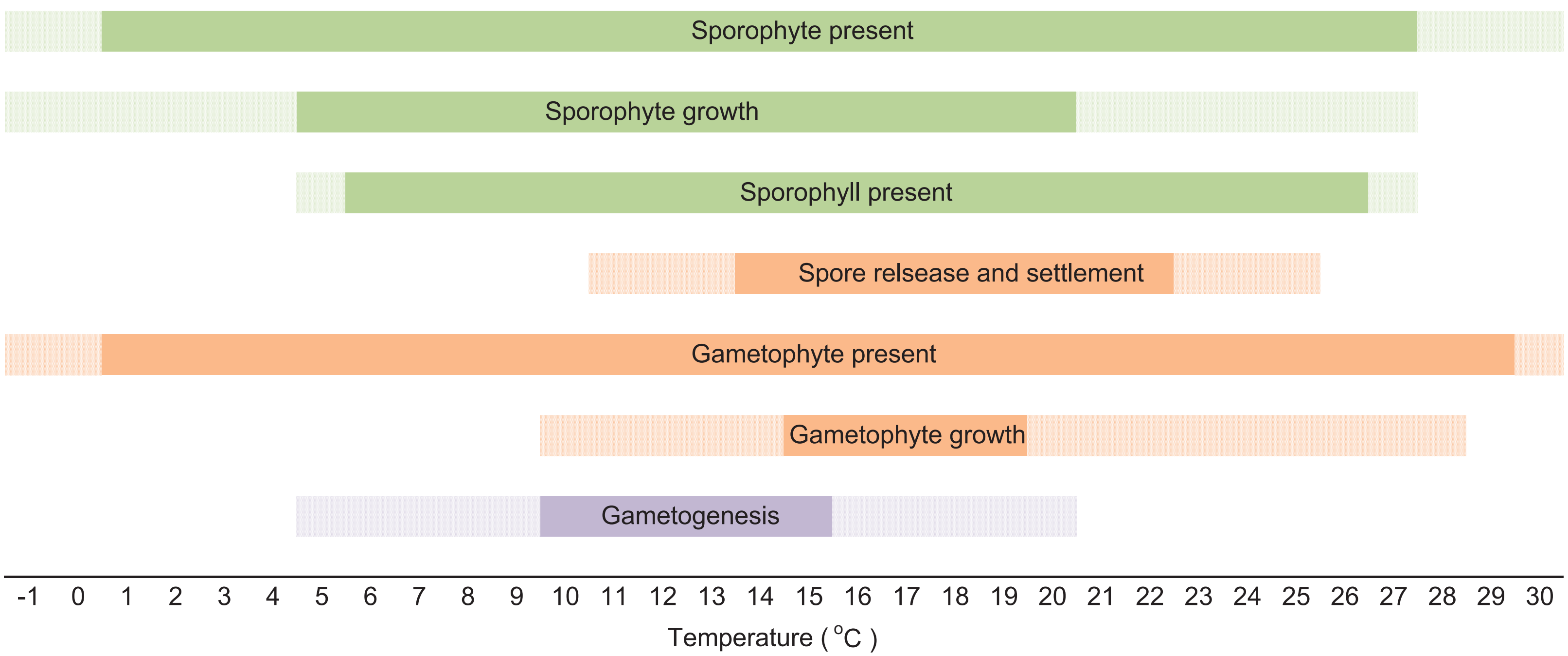
Sporophyte present
Sporophyte growth
Sporophyll present
Spore relsease and settlement
Gametophyte present
Gametophyte growth
Gametogenesis
-1 0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30
Temperature (°C)

Figure 3: