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MARINE BIOLOGICAL ASSOCIATION OF THE UK
&
UNIVERSITY OF SOUTHAMPTON

The ecology, impact and management feasibility of the invasive kelp *Undaria pinnatifida* in the UK.

by

Graham Epstein

A thesis submitted in partial fulfillment for the
degree of Doctor of Philosophy

in the
Faculty of Natural and Environmental Sciences
School of Ocean and Earth Science
Marine Biology and Ecology Group

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MARINE BIOLOGICAL ASSOCIATION OF THE UK
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ABSTRACT

Faculty of Natural and Environmental Sciences
School of Ocean and Earth Science
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Doctor of Philosophy

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Supervised by Dr. Dan A. Smale , Prof. Stephen J. Hawkins & Prof. Colin Brownlee

The invasive kelp *Undaria pinnatifida* has a global non-native range and is considered one of the "world's worst invasive species". It has been present in the UK for at least 25 years; however given its status, there remains a dearth of information regarding its ecology, impacts and management feasibility. A variety of surveys and manipulative techniques were implemented in rocky reefs and marinas of the southwest UK to better support the design and prioritisation of management, and to advance ecological understanding of marine invasive species more generally. This thesis consistently highlighted that marinas are paramount to the successful spread, proliferation and reproductive fitness of *Undaria.* Excluding or limiting its abundance in marinas may, therefore, restrict the likelihood of its spread to new regions and its proliferation to surrounding natural habitats. Management feasibility, however, was considered to be low, due to targeted removal measures in marinas altering recruitment patterns and even promoting total recruitment, and the high inter-habitat and inter-annual variation recorded in *Undaria* population dynamics. Within natural rocky reef habitats, *Undaria* was absent or found in low abundance in areas of high wave exposure, high desiccation stress, and where there was high abundance of the native perennial *Laminaria* spp.. *Undaria* is therefore likely to be restricted in the potential range into which it can proliferate. Where *Undaria* had invaded rocky reef communities, there was a consistent and significant impact upon the native annual canopy-forming macroalgae *S. polyschides.* The overall ecosystem impact of *Undaria* on rocky reef communities of the UK, however, is likely to be small, with no consistent impacts identified for any other macroalgal species, including the canopy dominant *Laminaria* spp.. There are cases where targeted management of *Undaria* may be proportionate and feasible; however, in many locations around the UK, *Undaria* is likely to remain unmanaged and will become an accepted part of the biota. 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.

Contents

List of Figures

List of Tables

Research Thesis: Declaration of Authorship

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Title of thesis:	The ecology, impact and management feasibility of the invasive kelp *Undaria pinnatifida* in the UK

I declare that this thesis and the work presented in it are my own and has been generated by me as the result of my own original research.

I confirm that:

1. This work was done wholly or mainly while in candidature for a research degree at this University;
2. Where any part of this thesis has previously been submitted for a degree or any other qualification at this University or any other institution, this has been clearly stated;
3. Where I have consulted the published work of others, this is always clearly attributed;
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6. Where the thesis is based on work done by myself jointly with others, I have made clear exactly what was done by others and what I have contributed myself;
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Epstein, G. and Smale, D.A. (2017a) '*Undaria pinnatifida*: A case study to highlight challenges in marine invasion ecology and management', Ecology and Evolution, 7(20), pp. 8624–8642.

Epstein, G. and Smale, D.A. (2017b) 'Environmental and ecological factors influencing the spillover of the non-native kelp, *Undaria pinnatifida*, from marinas into natural rocky reef communities', Biological Invasions, 20(4), pp. 1049-1072.

Epstein, G., Hawkins, S.J. and Smale, D.A. (2018) 'Removal treatments alter the recruitment dynamics of a global marine invader - Implications for management feasibility', Marine Environmental Research, 140, pp. 322-331.

Epstein, G. and Smale, D.A. (2018) 'Between-habitat variability in the population dynamics of a global marine invader may drive management uncertainty', Marine Pollution Bulletin, 137, pp. 488-500.

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Chapter 1

Introduction

This chapter led to the publication of:

- **Epstein, G.** & Smale D. A. (2017) *Undaria pinnatifida*: A case study to highlight challenges in marine invasion ecology and management. *Ecology and Evolution*, 7, 8624—8642.

1.1 Opening remarks

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; Seebens *et al.*, 2017). Estimates include over 50,000 non-native species 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). Between 1970 and 2012 global vertebrate species populations are estimated to have declined by 52% (WWF, 2014) and marine populations by 49% (WWF, 2015). Invasive species are considered one of the major drivers of this biodiversity decline (along with changes in climate, habitat loss, nitrogen deposition and over-exploitation) (Sala *et al.*, 2000). Invasive species can also impact a range of socioeconomic sectors, including agriculture, forestry, aquaculture, construction, transport, utilities, tourism and human health (Williams *et al.*, 2010). There are also significant costs associated with their 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).

Over 90 marine non-native species are known to occur on the coastlines of the UK (Minchin *et al.*, 2013). Although there are various awareness raising programs, monitoring surveys and legislative instruments in place to reduce the rate of introductions and spread of marine non-natives, there are currently no targeted species-specific management or eradication proposals (GBNNSS, 2015; 2018). A recent prioritisation process carried out as part of the EU Marine Strategy Framework Directive (MSFD) highlighted the non-native kelp, *Undaria pinnatifida*, as an important species to be monitored as to indicate that "non-indigenous species introduced by human activities are at levels that do not adversely alter the ecosystems" (Stebbing *et al.*, 2015). However, we currently know very little about the abundance, spread, ecology or impact of *Undaria*, particularly within natural coastal habitats in the UK. Further research is needed to underpin evidence-based decisions on what should be considered "levels that do not adversely alter ecosystems" and how these levels should be maintained. There are also opportunities to employ *Undaria* as a model species to improve our understanding on the ecology of marine non-native species more generally, and to highlight the challenges in defining their impact and management feasibility.

This review chapter summarises the broader issues around non-native species introductions and highlights the difficulties in identifying, measuring and categorising the ecological impacts of marine non-native species. It also discusses the complexities in determining management priorities, and challenges in designing efficient and effective management practises in the marine environment. Finally, current evidence regarding the biology, physiology, ecology and management of *Undaria* is critically reviewed. The chapter concludes with the aims and rationale of the thesis.

1.2 Terms and concepts

Nomenclature within invasion ecology is highly debated; even the definition of "invasive" remains contested. The International Union for Conservation of Nature (IUCN) describes invasive species as "animals, plants or other organisms introduced by man into places out of their natural range of distribution, where they become established and disperse, generating a negative impact on the local ecosystem and species." (IUCN, 2000). However, there are many calls within primary and secondary literature for the impacts of non-native species, and how they are perceived, not to be included in the definition of "invasive" itself (Daehler, 2001; Occhipinti-Ambrogi and Galil, 2004; Falk-Petersen *et al.*, 2006; Ricciardi and Cohen, 2007; Blackburn *et al.*, 2011; Richardson *et al.*, 2011). This is primarily due to the idea that impact, which is difficult to measure and can be subjective, should be considered separately from the classification of an invasive species. It is also recognised that strict definitions may not be appropriate to all stakeholders and a level of flexibility may be necessary depending on the context in which certain terms are used (Hodges, 2008; Heger *et al.*, 2013). Although not part of a consensus Richardson *et al.* (2011) provided an up-to-date compendium of terminology; these definitions have been adopted and applied throughout the current thesis. To prevent ambiguity, some more frequently used terms are outlined here:

Native species: A species which has evolved in a given geographical area or has arrived through natural means without the direct aid of humans (including through range expansion - see Richardson *et al.* (2011) for definition of this term). The locations to which this applies is termed a species native range.

Non-native species (NNS): A species whose existence within a given region is directly mediated by human actions that have allowed it to overcome biogeographical barriers. The locations to which this applies is referred to as a species non-native range.

Cryptogenic species: A species whose origin, or means of arrival, is not known or uncertain

Introduction: The intentional or accidental movement of a species by human activities to an area outside its native range.

Recipient community: The species which are present in a location where a non-native has been introduced.

Vector: The physical means or agent by which a species has been introduced to a new region.

Established: Those non-native species whose reproduction and persistence does not depend on further human intervention or introductions from a native population.

Propagule pressure: The number of individuals introduced or released into a single location. Initial introductions always occur through human activities, but further propagule pressure can be caused by natural spread and reproduction of established non-native species.

Invasive non-native species (INNS): An established non-native species which proliferates and spreads without the direct aid of humans. It should be noted that all invasive species are non-native species, however a non-native species is not always invasive.

Impact: synonym of ‘effect’, or ‘change’. No implicit negative or positive association applied.

Once introduced, most NNS would not be expected to establish or become successful invaders (Lodge, 1993; Williamson and Fitter, 1996a). 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 no or negligible proliferation of the NNS for a considerable time after introduction (Crooks, 2005). To facilitate their introduction, establishment and proliferation into a non-native range, INNS are generally considered to have a level of phenotypic or genetic plasticity and a broad ecological niche (Williamson and Fitter, 1996b; Kolar and Lodge, 2001; Zenni *et al.*, 2014). However, identifying specific characteristics that predispose a species to being, or becoming, invasive is highly challenging (Newsome and Noble, 1986; Williamson and Fitter, 1996b; Kolar and Lodge, 2001; Nyberg and Wallentinus, 2005). While INNS are often described as having opportunistic life-histories, including high fecundity, growth rate and recruitment, a considerable number of successful INNS have 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 (Lockwood *et al.*, 2005; Simberloff, 2009). 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.*, 2002a; Arenas *et al.*, 2006; Britton-Simmons and Abbott, 2008).

NNS can cause significant damage to the environment and economy, and due to the complex nature of species invasions a precautionary principle should be applied with any new introductions minimised. A failure to react to new introductions and control established NNS could be considered as management decisions in themselves. However, due to the sheer number of NNS already established, it is unrealistic to assume that management and control of all species can be targeted. Separating NNS and INNS with negligible ecological impacts from those that cause damage or pose significant risk to native communities allows for some prioritisation for control (McGeoch *et al.*, 2016).

1.3 Marine non-natives

Due to the inherent connectivity within the marine environment, NNS are particularly prevalent and difficult to manage (Eno *et al.*, 1997; Ruiz *et al.*, 1997). For example, in six heavily used ports in the USA, Australia and New Zealand, a new NNS 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 NNS have been identified in Australia (Hewitt, 2003), 150 in New Zealand (Cranfield *et al.*, 1998), 90 in the UK (Minchin *et al.*, 2017) and over 200 in San Francisco Bay (USA) alone (Cohen and Carlton, 1998). The most common taxonomic groups of NNS to become established are crustaceans, molluscs and algae (Molnar *et al.*, 2008; Minchin *et al.*, 2013). While the most heavily invaded areas are the temperate North Atlantic, temperate North Pacific and Eastern Indo-Pacific (Molnar *et al.*, 2008).

The major vector of introduction is commercial shipping (through ballast and hull fouling); followed by aquaculture (intentional release for stock enhancement, movement of equipment and the trade of food or stock), canals (through locks due to water motion or active swimming) and aquarium trade (accidental or intentional release) (Molnar *et* *al.*, 2008). Other vectors include drilling platforms, recreational boating, research activities and floating debris (Bax *et al.*, 2003). Anthropogenic or artificial habitats such as harbours, marinas, canals or modified embayments are often key to the establishment of marine NNS (Ruiz *et al.*, 2009). Artificial substrates such as piers, pontoons, buoys, seawalls, breakwaters and aquaculture equipment are generally found in more highly polluted, low salinity, sediment loaded or nutrient enriched environments, due to being located in areas of intensified human activity. This distinct physical and biological environment provides a habitat to which many native species are not adapted and can therefore harbour a distinct and depauperate assemblage (Glasby *et al.*, 2005; Bulleri and Chapman, 2010). These environments also coincide with major introduction pathways, which in combination with the reduced competition from native species, increases the chance of NNS establishment (Bax *et al.*, 2003).

1.4 Ecological impacts of non-native species

Quantifying the ecological impacts of a NNS is highly complex. Differences in recipient communities, resource availability, environmental abiotic factors and attributes of the NNS, can all create site-specific impacts. Factors such as abundance and range of the NNS may influence impact in all cases (Parker *et al.*, 1999), while other factors such as morphological, behavioural or even chemical characteristics of the NNS are more species specific (Thomsen *et al.*, 2011a). Invasion impact frameworks aim to design a mechanistic approach to quantify impacts and explain variation among investigations, species and locations. They generally consider some aspect of abundance and range of the NNS, and a measure of per capita effect (Parker *et al.*, 1999; Thiele *et al.*, 2010; Thomsen *et al.*, 2011a). A framework developed by Thomsen *et al.* (2011a) recommended that to truly partition and quantify per capita effect of a specific NNS, it would be necessary to carry out manipulations of the identity and abundance of NNS, recipient communities, resource availability and abiotic conditions, with a minimum of two levels per manipulation and a control. While it is highly unlikely that such thorough experimentation will be possible on the vast majority of NNS, it does highlight the complexity of their ecological impacts.

Deleterious ecological impact can be measured on multiple levels of organisation within the recipient community. The clearest interaction is direct competition with a single, functionally similar native species. A notable example is the introduction of smooth cordgrass, *Spartina alterniflora*, into the UK. Once introduced the species hybridised with the native cordgrass, *Spartina maritima*, to form the species *Spartina anglica.* This hybrid has been spread worldwide and has caused widespread mortality of native homologs (Doody, 1984; An *et al.*, 2007; Strong and Ayres, 2009). Another example includes the gastropod *Batillaria attramentaria* which directly competes with the native American snail *Cerithidea californica* and has been shown to reduce survival, growth and reproduction of the native species (Byers *et al.*, 2002). Introduced veracious predators such as the northern Pacific seastar, *Asterias amurensis*, in Tasmania (Ross *et al.*, 2003), the Lionfish, *Pterois volitans*, in the tropical Atlantic and the Mediterranean (Green *et al.*, 2012; Azzurro and Bariche, 2017), and the green crab *Carcinus maenas* in North America (Grosholz *et al.*, 2000), prey on wide range of native species and proliferate in the absence of native predators. In these examples community-wide deleterious impacts can be clearly identified. For some species, impacts can manifest at the ecosystem scale, due to alterations in nutrient pathways, trophic interactions or habitat structure (Crooks, 2002; Wallentinus and Nyberg, 2007; 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). Whereas in San Francisco Bay the introduction of the Asian clam *Poramocorbula amurensis* has significantly impacted nutrient pathways. Extremely high abundances of this filter-feeding clam have altered local nutrient levels and caused early cessation of the spring phytoplankton bloom, which, in turn, has a deleterious bottom up effect on benthic and pelagic food-webs within the bay (Cloern, 1996).

NNS can also have facilitative impacts on the recipient community. Facilitation can occur through creation or replacement of habitat, trophic subsidy provision or competitive and predatory release (Rodriguez, 2006; Wallentinus and Nyberg, 2007; Schlaepfer *et al.*, 2011). Rodriguez (2006) divides NNS facilitation into three scenarios: Novel - whereby a unique attribute is supplied by the NNS, providing a new exploitable resource; Substitutive - whereby the NNS functionally replaces a native species acting as a surrogate resource; and Indirect - when an NNS species reduces a native competitor or predator causing associated native species abundance to increase. The invasion of bivalve molluscs onto soft sediments, such as *Musculista senhousia* and *Crassostrea gigas* (now *Magallana gigas,* however referred to as *Crassostrea gigas* hereafter), is a pertinent example of facilitation by a marine NNS on multiple levels. They provide complex habitats which can greatly increase infaunal and epifaunal abundance, increase organic content in sediments which may benefit both flora and fauna, and can act as a trophic subsidy to predatory invertebrate and vertebrate species (Crooks, 1998; Crooks and Khim, 1999; Escapa *et al.*, 2004; Padilla, 2010). Intuitively, the facilitation of one species is likely to occur at the expense of others, due to changes in competition or predation. Indeed, where *Musculista senhousia* and *Crassostrea gigas* are found at high densities, reduced abundances of functionally similar native species has been recorded (Creese *et al.*, 1997; Crooks and Khim, 1999; Padilla, 2010). It is also possible for NNS to facilitate the recruitment and spread of other NNS. This process, known as 'invasion meltdown', could drive further invasions, potentially leading to an additive increase in overall impact (Simberloff and Von Holle, 1999; Simberloff, 2006).

To fully understand the ecological impact a marine NNS has upon recipient communities, both deleterious and facilitative effects need to be considered. It must be noted, however, that 'facilitation effects' are not synonymous with 'positive effects'. In terms of nature conservation, any impact of an NNS, be it deleterious or facilitative could be considered detrimental due to alteration of the native communities and natural habitats.

1.5 Benefits of non-native species

Many NNS are now considered part of the natural biota in different regions across the world with minimal environmental impact, 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 INNS. Due to the historic nature of species introductions, the widespread acceptance of certain NNS or INNS is particularly common in the terrestrial environment. The vast majority of the world's agricultural and horticultural species are non-native where they are grown, including some of the most common tree species in the UK (including Stika spruce, sweet and horse chestnut, apple and pear). Many freshwater fish species have also been historically introduced for farming and sports fishing purposes. The rainbow trout, *Oncorhynchus mykiss*, and common carp, *Cyprinus carpio*, are native to areas of Asia and are now widespread across the Americas, Europe and Australia. Although control on their transport and release is still enforced in some countries (Cambray, 2003; Fausch, 2008; Vilizzi *et al.*, 2015) across many parts of Europe they are treated essentially as part of the natural biota (Copp *et al.*, 2005; Gozlan, 2008; Eustice, 2014).

In the marine environment there is a tendency for all NNS to be classed as damaging. However, many species have been established outside their native range for many decades. Although further intentional spread may be restricted, few have targeted management plans aiming to reduce their abundance, and are in practice, treated the same as native species. In the UK, of the 90 marine NNS identified, only one (*Didemnum vexillum*) is currently listed as being under development for an "Invasive Species Action Plan" on the GB non-native species secretariat website (GBNNSS, 2018). 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. Although initially believed unable to reproduce outside its native range, *C. gigas* is now established in most introduced regions. In some cases, this species is considered as a damaging INNS, with management actions 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 with wild capture fisheries and aquaculture using seeded bottom culture techniques (Grizel and Heral, 1991; Feldman *et al.*, 2000; Cognie *et al.*, 2006; Buestel *et al.*, 2009).

Although somewhat contentious, in certain cases NNS could be considered to have benefits to nature conservation (Schlaepfer *et al.*, 2011; 2012; Vitule *et al.*, 2012). This may occur if the NNS: (i) exerts strong facilitation and minimal deleterious impact on native species; (ii) acts as a catalyst for restoration of native habitats; (iii) functionally replaces a limited or extinct native species; (iv) facilitates a species of high conservation value; or (v) acts as a biocontrol agent (Schlaepfer *et al.*, 2011). These benefits have been 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* is an example that could apply to the marine environment. It has been suggested that the spread of the invasive Pacific oyster may have conservation benefit by functionally replacing lost native species, providing habitat, increasing biofiltration, serving as a trophic subsidy and providing an exploitable resource, reducing further harvesting pressure on the native homolog (Shpigel and Blaylock, 1991; Paalvast *et al.*, 2012).

Possible beneficial effects of marine NNS should also be considered in any management prioritisation process. As global biodiversity decline continues in response to multiple anthropogenic pressures, NNS are predicted to proliferate and in some cases dominate over functionally similar native species (Dukes and Mooney, 1999; Stachowicz *et al.*, 2002b; Occhipinti-Ambrogi, 2007). In this case, those NNS with desirable facilitative impacts, or even nature conservation benefits, may become increasingly important, acting as surrogates for endangered or extinct native species and possibly mitigating biodiversity decline (Rodriguez, 2006; Schlaepfer *et al.*, 2011).

1.6 Driver-passenger model

All marine habitats are affected by a wide range of biotic and abiotic stressors, each of which can individually, or in combination, contribute to changes in community structure. It can therefore be difficult to separate the effects of different stressors and determine their contribution to ecosystem change. General correlations between increasing abundance of NNS and declines in recipient communities are not sufficient to determine causation, and therefore some means of partitioning the effects is needed. NNS are often described as opportunistic, taking advantage of resource availability in order to establish and spread (Gurevitch and Padilla, 2004). It could be argued that truly opportunistic species could not, in themselves, be a major cause of ecosystem change. They have low competitive ability, requiring a level of ecological stress such as physical disturbance or eutrophication in order to colonise space left open by more competitive species (Stearns, 1976). If the stressor is removed opportunists are often progressively out-competed by competitively superior species, reducing their abundance and persistence within the stressed region. If an NNS was truly opportunistic, they would be considered “passengers” - promoted and maintained due to the presence of ecosystem stressors but not in themselves the cause of ecosystem change (Figure 1.1). If, however, NNS out-compete or overgrow subordinate native species causing them to be limited or excluded in the absence of wider ecological stress, they would be “driving” ecosystem change (Figure 1.1) (Didham *et al.*, 2005; MacDougall and Turkington, 2005).

A study by MacDougall and Turkington (2005) was the first to attempt to quantify where an NNS sat within this driver-passenger model. They hypothesised that when an NNS was reduced or excluded from a given area, if the species was acting as a driver of ecosystem change, a direct increase in abundance and richness of native species would occur. If, however, there was no recovery of native biota, the NNS would not be the main limiting factor - suggesting the passenger scenario (Figure 1.1). Over a three year treatment period, the abundance of two invasive perennial grasses were reduced, excluded or left as a control in grass dominated patches of Oak woodland. Over half of the resident species showed no change or decreased in abundance within both treatments, including functionally similar native species (native perennial grasses), which would be expected to directly compete with the NNS (MacDougall and Turkington, 2005). As some native species did significantly increase in abundance (predominantly understory species), it indicates that the presence of the NNS does to some extent limit native species growth. This experiment showed that the driver-passenger model is clearly scalar, with high dependence on both the NNS and the recipient community in which it is found (Didham *et al.*, 2005; Bauer, 2012).

Due to the scalar nature of the driver-passenger model many species will not be easily categorised. Bauer (2012) suggested that a third term of “back-seat driver” could be applied. In these cases a NNS will be facilitated by ecosystem stressors, recruiting and dominating when native communities are suppressed. However, once established, the NNS will maintain suppression, or cause further declines in abundance of native species (Figure 1.1). In this back-seat driver scenario, the abundance of the NNS should independently explain some of the declines in native species; while the interaction between NNS and other ecosystem stressors would need to be investigated to understand the full effect. Removal experiments would therefore be expected to find inconsistent or partial recovery of native species in the absence, or reduced abundance, of the NNS (Figure 1.1).

Experimental manipulations of *Caulerpa racemosa* invaded seaweed communities in the Mediterranean are a good example of such findings (Bulleri *et al.*, 2010). *Caulerpa racemosa* establishment is generally dependent on disruption of the native macroalgal assemblage, and removal of the invader from degraded sites did not promote recovery of native canopies (Bulleri *et al.*, 2010). This suggests the passenger model; however, the presence of the NNS enhanced sediment cover and algal turf abundance, which in turn suppressed native erect algae. The NNS was therefore considered to be preventing the recovery of native populations of canopy forming macroalgae, by maintaining the ecosystem in an alternate stable state (Bulleri *et al.*, 2010) - thus matching the back-seat driver model (Bauer, 2012).

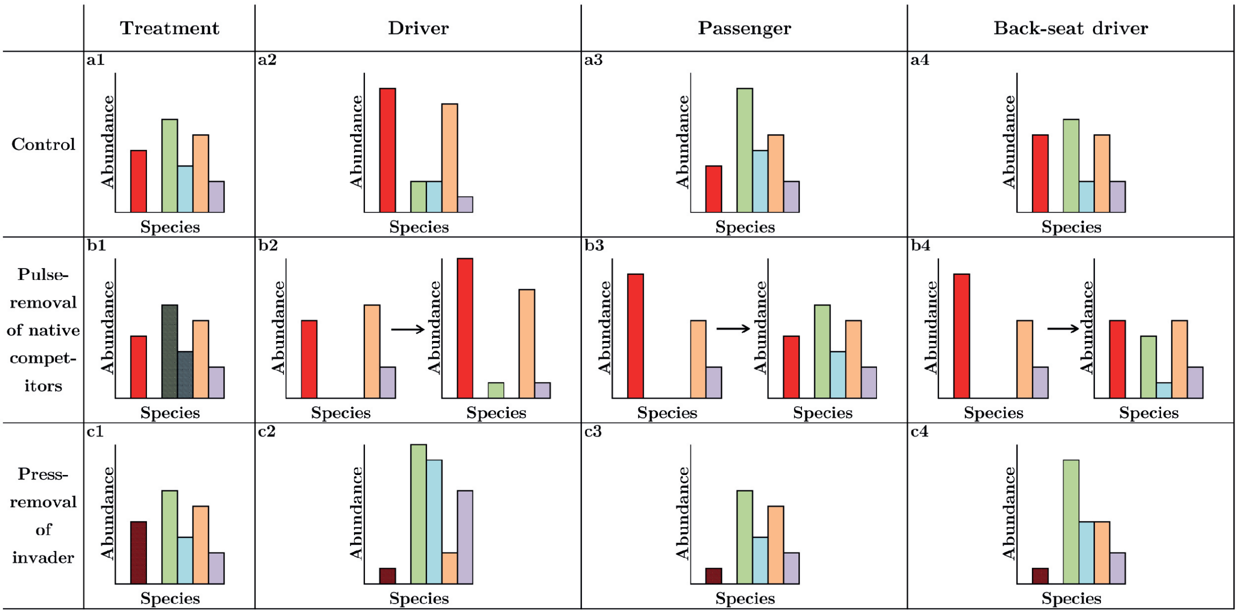


FIGURE 1.1: Graphical representation of predicted changes in community under different experimental treatments within the driver-passenger model. Red = invasive species; pastel colours = recipient native community. In an un-manipulated monitoring scenario (a1-4), in the long term, assuming the absence of wider ecological stress, an invasive species which is acting as a driver would be predicted to increase in abundance, out-competing or overgrowing subordinate native species causing them to be limited or excluded - the invasive species may also have facilitative impacts on some native species (a2). In a passenger scenario, the invasive species is expected to be progressively out-competed by competitively superior native species (a3). As a back-seat driver, invasive species may slowly increase in abundance while maintaining suppression, or causing further declines in abundance of native species (a4). Ecological stressors causing disturbance or removal of competitors (b1 - indicated by dark shading), would be expected to lead to an initial increase in abundance of an invasive species in all driver, passenger and back-seat driver scenarios (b1-4). This response is likely to be much larger in the passenger and back-seat driver scenarios due to their need for ecosystem stress to recruit and dominate (b3-4). Over time (indicated by arrow), in the driver scenario further increases in abundance of the invader and impact (suppression or facilitation) on native species would be predicted (b2); in the passenger scenario, eventual recovery to a pre-perturbed state could be expected (b3); whereas in the back-seat driver model there would be mixed results with some long term suppression or further impacts on native species (b4). Long term exclusion, or removal, of the invader (c1-4-indicated by dark shading) would be expected to cause recovery of native community in the driver scenario (c2), little to no change if the invader is a passenger (c3), and inconsistent or partial recovery of native community in the back-seat driver scenario (c4).

A level of understanding on the drivers of ecosystem change can have a major influence on designing the most effective and efficient management measures. For species that act as back-seat drivers, removal of the NNS and restoration of ecosystem properties may be required to allow recovery of the recipient community. Whereas for a NNS primarily acting as a passenger of change, management which directly targets the species is likely to be inefficient. Targeting the cause of ecosystem stress will benefit the ecosystem as a whole and reduce the recruitment and spread of the passenger NNS. Managing long-term stressors such as changes in climate or habitat degradation are, however, unlikely to be a viable control option for NNS considered to be of any significant risk. Therefore, for an NNS that drives ecosystem change to any extent, or acts as a back-seat driver, management options may be confined to the NNS themselves.

1.7 Management

Managing marine NNS is expensive and time consuming, while eradication may be impossible once a species is established and widespread. The only way to preclude impact is to prevent introduction through the control of vectors (Thresher and Kuris, 2004). Controls on shipping, aquaculture, aquarium trade and industrial equipment are logistically the most efficient point to inhibit NNS establishment (Bax *et al.*, 2001; Hewitt *et al.*, 2007; Keller *et al.*, 2011). However, due to the international, commercial and public nature of some vectors, introductions are unlikely to be completely prevented (Hulme, 2006). Once introduced, rapid-response management may allow eradication at a relatively low control cost (Anderson *et al.*, 2005; Lodge *et al.*, 2006; Beric and MacIsaac, 2015) (Figure 1.2). However, early recognition of an introduced marine NNS before it establishes is also challenging due to the presence of microscopic life stages in many species and the inaccessibility of many marine environments. Moreover, due to taxonomic uncertainties and a scarcity of historical records for many marine taxa, newly recorded species will often be classed as cryptogenic. It can often take considerable time for the correct identification and status of a newly recorded species to be determined, requiring a wide range of molecular and taxonomic techniques, further delaying potential rapid-response management

There are examples of successful rapid response eradication in the marine environment. The seaweed *Caulerpa taxifolia* was first identified as an invasive in 1984 in the Mediterranean (Meinesz and Hesse, 1991) but was also found in the USA and Australia in 2000 (Jousson *et al.*, 2000; Millar, 2004). In the USA, a rapid response just 17 days after its first discovery in Agua Hedionda Lagoon and Huntington Harbour, led to the successful implementation of a 5 year eradication programme using containment and chemical treatment, at a cost of around $7.5 million (USD) (Anderson, 2005). Since this eradication, there has been no reintroduction of *Caulerpa taxifolia* and it remains absent from the coasts of the USA.

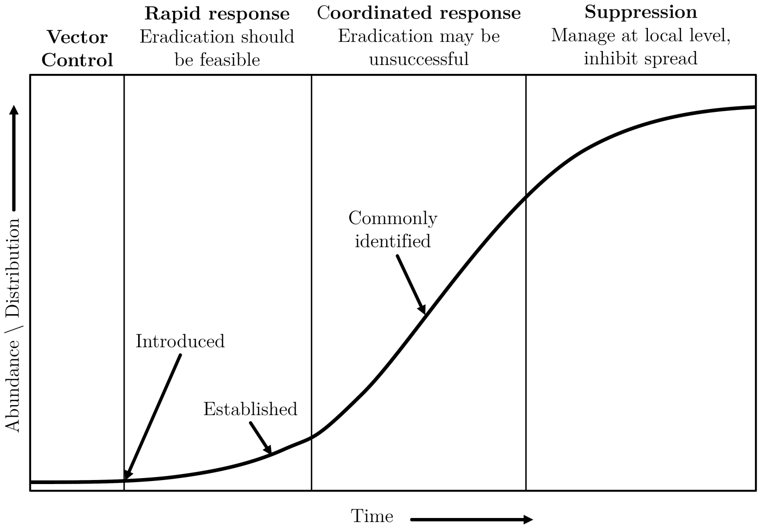


Figure 1.2: Invasion curve representing phases of non-native species management options and associated control costs as abundance and distribution of a non-native increases over time.

Once a marine NNS is established, however, an increase in abundance and spatial extent may be inevitable due to the natural or engineered connectivity of many water-bodies. As abundance increases the costs of control also increase, while attempting eradication would require intense coordinated effort and may ultimately be unsuccessful (Hobbs and Humphries, 1995) (Figure 1.2). The carpet sea squirt, *Didemnum vexillum* is a pertinent example of such a management attempt. Eradication programmes were implemented within harbours and marinas of Holyhead, Wales (Kleeman, 2009; Holt and Cordingley, 2011) and Shakespeare Bay, New Zealand (Coutts and Forrest, 2007). Both used a smothering treatment whereby infected areas were wrapped to reduce water flow and cause mortality from anoxia. There was a large reduction in local abundance, including total mortality at some sites, however in both instances, a year following cessation of treatment the population had recovered to pre-treatment levels. The costs of eradication attempts were around £0.3-0.4 million (GBP), and had little to no effect on the long term population dynamics of the INNS (Coutts and Forrest, 2007; Kleeman, 2009).

If eradication is unsuccessful or deemed infeasible due to the abundance or distribution of the NNS, localised controls or attempted inhibition of spread are the only remaining management options (Critchley *et al.*, 1986; Coutts and Forrest, 2007; Forrest *et al.*, 2009; Kleeman, 2009). Due to this being the most challenging and costly control point (Figure 1.2), it is of the utmost importance to have detailed information on the distribution and abundance of an NNS, the detrimental or beneficial impacts it may have on recipient communities, and whether it is driving ecosystem change, in order to be able to effectively prioritise management (Byers *et al.*, 2002; McGeoch *et al.*, 2016).

1.8 *Undaria pinnatifida*

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 introduced range (Figure 1.3). First identified on the Mediterranean coast of France in 1971 (Perez *et al.*, 1981), *Undaria pinnatifida* (hereafter referred to as *Undaria*) is now established on the coastlines of New Zealand (Hay and Luckens, 1987; Hay, 1990), Australia (Sanderson, 1990; Campbell and Burridge, 1998), Northern France (Castric-Fey *et al.*, 1993), Spain (Salinas *et al.*, 1996), Italy (Cecere *et al.*, 2000; Curiel *et al.*, 2001), United Kingdom (Fletcher and Manfredi, 1995), Republic of Ireland (Kraan, 2016) Portugal (Veiga *et al.*, 2014), Belgium (Leliaert *et al.*, 2000), Netherlands (Stegenga, 1999), Argentina (Casas and Piriz, 1996), Mexico (Aguilar-Rosas *et al.*, 2004) and the USA (Silva *et al.*, 2002).

Non-native seaweeds are ecosystem engineers able to cause significant economic and ecological impacts (Schaffelke *et al.*, 2006; Williams and Smith, 2007). Worldwide there are thought to be approximately 350 different seaweed NNS accounting for around 20%–30% of all marine NNS (Schaffelke and Hewitt, 2007; Thomsen *et al.*, 2016). Clear quantitative evidence of their ecological impacts is, however, generally lacking. *Undaria* is considered one of the 100 worst INNS in the world, and the second worst invasive seaweed (Lowe et al., 2000), and is therefore clearly thought to be of significant risk to the natural environment.

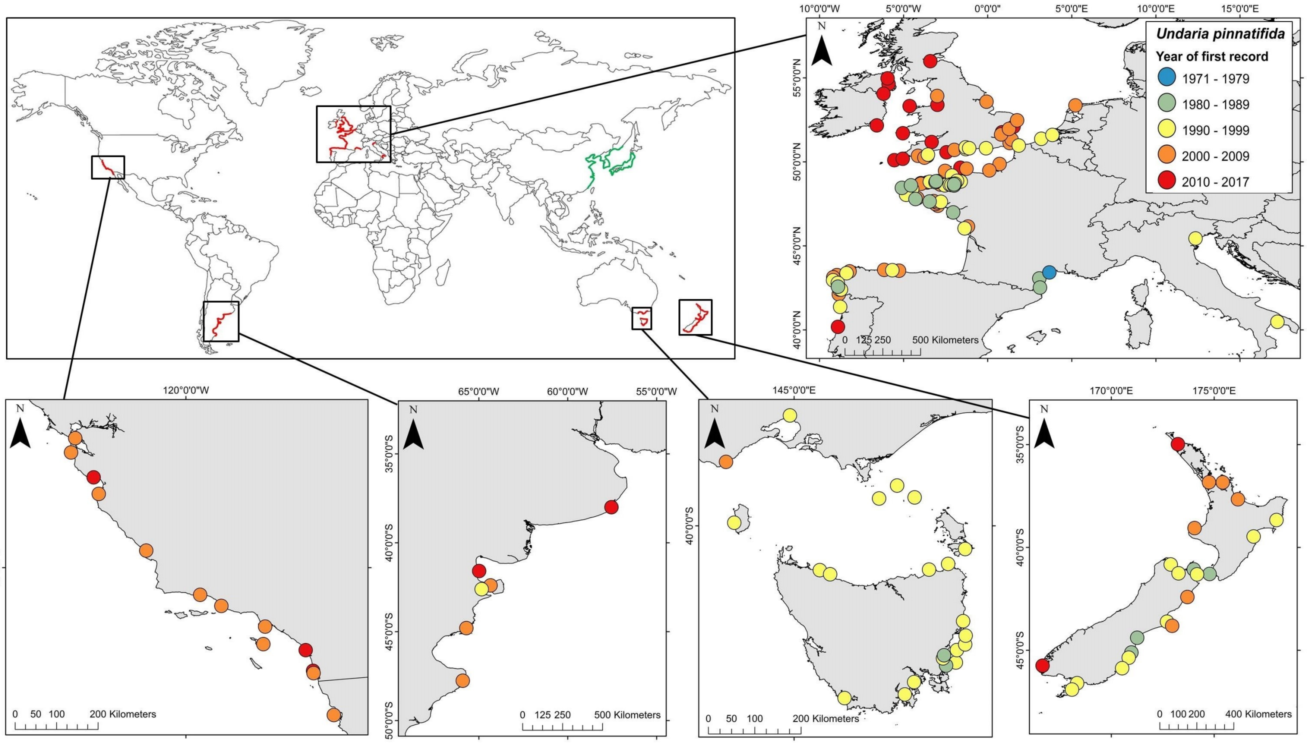


FIGURE 1.3: Approximate distribution of *Undaria pinnatifida*. Global map: Green = native range, red = non-native range. Regional maps: Each point represents a distinct location but does not indicate precise position or entire extent. See Table A.1 for more information and references.

1.8.1 Biology, physiology and native ecology

In its native North-west Pacific, *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.*, 1999b; Choi *et al.*, 2007; Dean and Hurd, 2007). They form large divided pinnate fronds and distinctive ruffled reproductive sporophylls (Figure 1.4). 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).

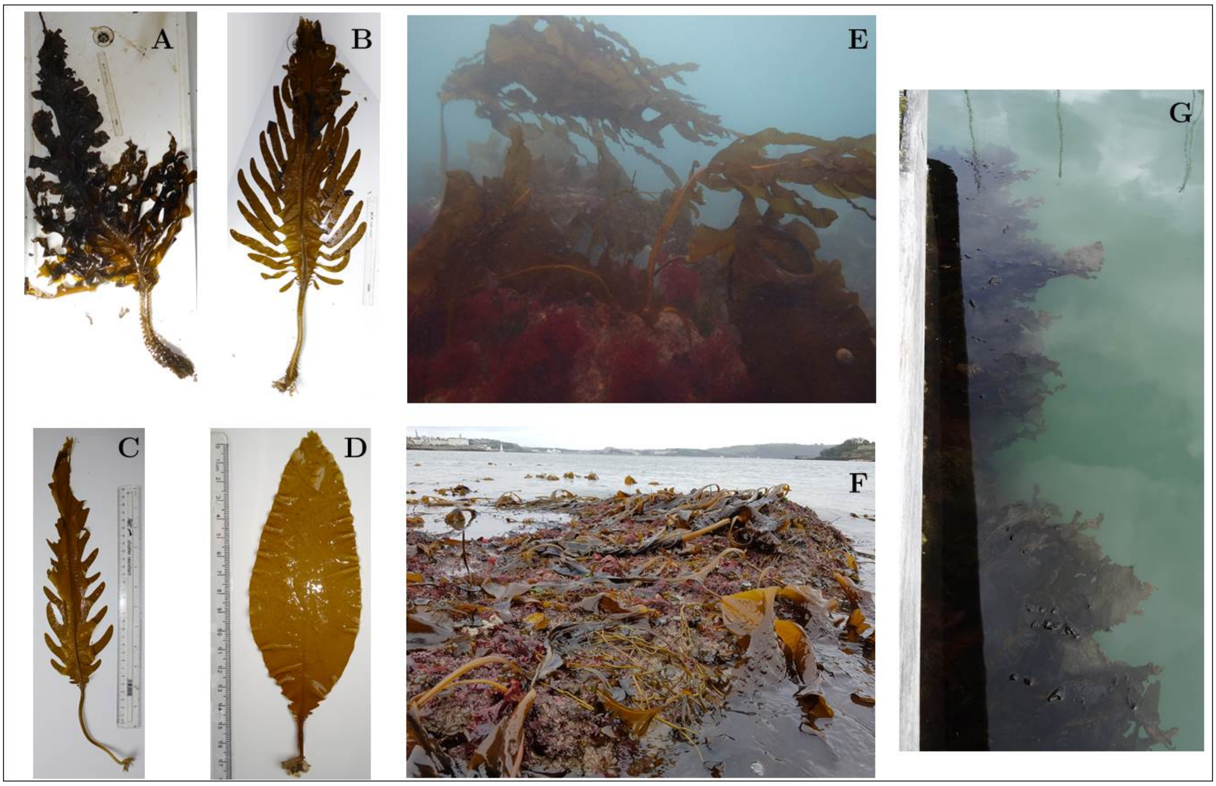


Figure 1.4: Different developmental stages of *Undaria pinnatifida* sporophytes (A-D). *Undaria pinnatifida* can be found growing in the subtidal and intertidal, as well as on natural and artificial substrates (E-G).

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 1.5) (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 *et al.*, 2015). 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°C and 30°C (Saito, 1975; Morita *et al.*, 2003b; 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; James *et al.*, 2015; Bollen *et al.*, 2016). 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 1.5). Gametophyte growth is optimum between 15 - 20°C, while gametogenesis and fertilisation is optimum between 10 - 15°C (Saito, 1975; Morita *et al.*, 2003a; Henkel and Hofmann, 2008).

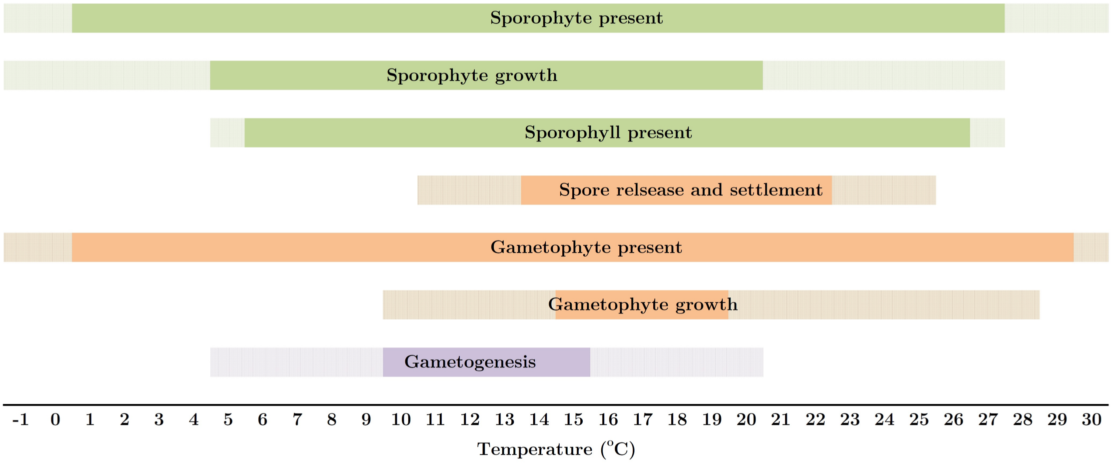


FIGURE 1.5: Thermal tolerances of the various life-stages of *Undaria pinnatifida*. Lighter colours = life-stage possible but may be limited. See in text for references

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 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 occur at salinities as low as 19 , while gametophytes and sporophytes may survive at salinities as low as 6 (although below 16 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 Lüning, 2004; Choi *et al.*, 2005; Baez *et al.*, 2010; Morelissen *et al.*, 2013). Although seasonal and site-specific, optimal growth occurs around 40 - 120 μmol m^{-2} s^{-1}, light saturation point for photosynthesis (I_k) can be reached around 100 - 500 μmol m^{-2} s^{-1}, while the light compensation point (I_c; when no net photosynthesis occurs), may be reached between 17 - <5 μmol 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 μmol 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 strongly 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 occur 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 lamina, *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 INNS (Newsome and Noble, 1986; Williamson and Fitter, 1996b). 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 INNS.

1.8.2 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 NNS, 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; Kaplanis *et al.*, 2016). In most parts of its non-native range *Undaria* has also 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; Curiel *et al.*, 2001; Farrell and Fletcher, 2006; Heiser *et al.*, 2014; James and Shears, 2016a; b). 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 (Kaplanis *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 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 sporophytes 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 for a maximum of 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.*, 1999a; 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.

1.8.3 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) (Table 1.1). 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, 2016a) (Table 1.1). 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 recruitment of *Undaria* into mixed canopy assemblages (Table 1.1). 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; Valentine and Johnson, 2003; Edgar *et al.*, 2004; Martin and Bastida, 2008; Thompson and Schiel, 2012; South and Thomsen, 2016). 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 *Undaria* is context specific (Table 1.1). In artificial 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 1.1). 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).

TABLE 1.1: Summary of studies on *Undaria pinnatifida* for which tentative 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*.	🟩	🟧

Reference	Location	Substrate	Description of response variable	Duration (months)	Method	Summary	Competitive ability	Impact on community
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.		🟥
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.	🟩	🟧

Reference	Location	Substrate	Description of response variable	Duration (months)	Method	Summary	Competitive ability	Impact on community
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.	🟩	🟧

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 span 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 providing trophic or habitat subsidy (Cecere *et al.*, 2000; Irigoyen *et al.*, 2011; Suárez-Jiménez *et al.*, 2015b; Suárez-Jiménez *et al.*, 2017). 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. deleterious 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 varying spatial scales, in order to causally determine the effects of *Undaria* within invaded ecosystems.

1.8.4 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 1.2). These are largely generic, with measures applicable to wider NNS 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 an 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). Management within New Zealand between 1997 and 2009 targeted specific areas of artificial and natural substrates in order to limit the further spread of *Undaria* (Forrest and Hopkins, 2013). Prolonged removal led to a large reduction in density on artificial port structures (1-5% of pre-managed density) and vessel infestation rates (31-56% of vessels infected in unmanaged ports, 0.06-1.3% infected in managed ports). Although this sustained regional-scale management effort was successful in limiting local populations, reintroduction and wider-scale spread still occurred (Forrest and Hopkins, 2013).

Since 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 become 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 1.2). 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 harbours, 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 (Environment Southland, 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 (Environment Southland, 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.

Table 1.2: Status and management of *Undaria pinnatifida* within its non-native range

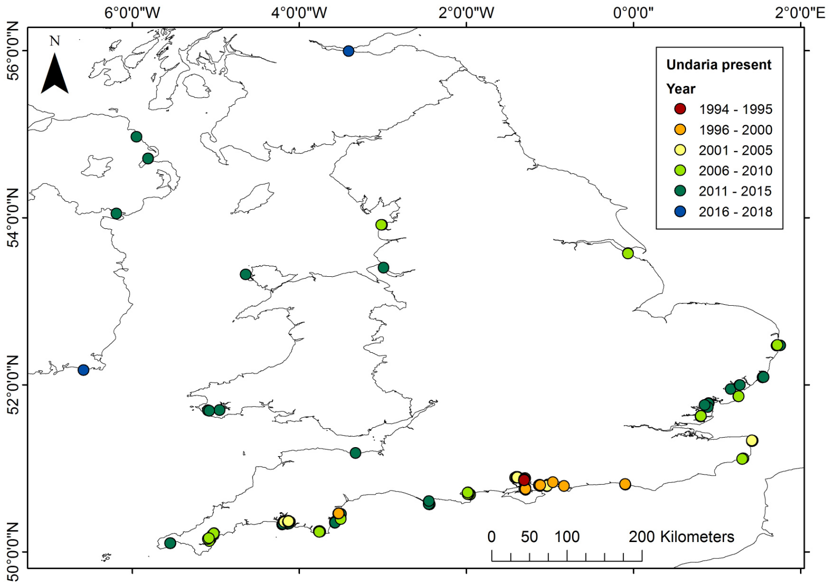
Country	First recorded	Population status	Dedicated management plan	Summary of known management	Management aim	References
France	1971	Common in natural and artificial habitats across current range. Active mariculture.	None found	Mariculture limited to areas with already developed infrastructure and high *Undaria* abundance. Mariculture under strict control to prevent potential ecological impacts and further spread.	Inhibit range expansion	Antoine *et al.*, 2012; Castric-Fey, Girard and Lhardyhalos, 1993
New Zealand	1987	Common in natural and artificial habitats across current range. Active mariculture.	Sinner, Forrest and Taylor, 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 artificial 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 artificial habitats across current range	NSPMMPI, 2015	Reduce spread to high value areas, possible commercial harvest with tight biosecurity, modify dry-dock timing to minimise sporophyte development, maintain integrity of native canopy algae, ballast water management, monitoring.	Inhibit range expansion	Valentine and Johnson, 2004; Primo, Hewitt and Campbell, 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 artificial 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 artificial habitats in the Wadden Sea. In natural and artificial 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 artificial 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	Kaplanis, Harris and Smith, 2016
Argentina	2000	Common in natural and artificial 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

Decisions taken by environmental or conservation 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*.

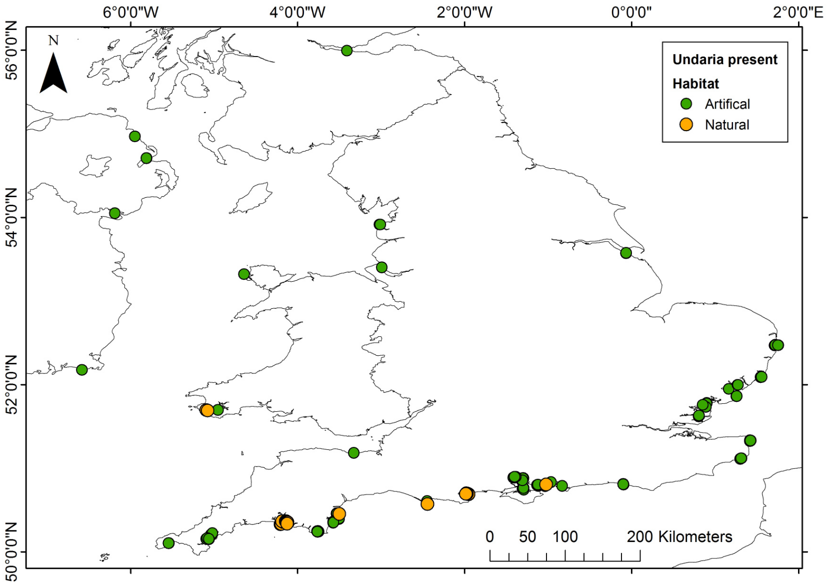
1.9 UK context

The first occurrence of *Undaria* in the UK was recorded in 1994 on floating marina pontoons in the Hamble Estuary (Fletcher and Manfredi, 1995) (Figure 1.6). Due to the large volume of cross-channel traffic into the Hamble, introduction is thought to have occurred from plants attached to small boats travelling from Brittany where *Undaria* populations had been established since the 1980s (Fletcher and Manfredi, 1995; Fletcher and Farrell, 1999). Although all individuals were removed following this initial UK sighting, a high-frequency long term eradication program was not introduced and some plants appeared to have already reproduced. It is therefore unsurprising that eradication was unsuccessful and *Undaria* increased in abundance (Farrell, 2003). By 1999 *Undaria* had expanded to marinas across the Hamble, and had been recorded along the south coast at Portsmouth, Cowes, Chichester and Torquay - all within marinas (Fletcher and Farrell, 1999; Farrell, 2003) (Figure 1.6).

Undaria can now be found across the south and east coast as far north as the Firth of Forth (Scotland), as well as on the west coast in areas of Pembrokeshire and Anglesey (Wales), Lancashire and Somerset (England), and the east coast of Ireland and Northern Ireland (NBN, 2017) (Figure 1.6). The vast majority of these records are from artificial habitats, largely marinas and harbours. Records from natural habitats are far fewer (as of 2016 approximately 53 out of 328 known records) and confined to the south coasts of Devon, Dorset, Hampshire and Pembrokeshire (NBN, 2018) (Figure 1.6). Given *Undaria*'s widespread distribution, this small number of sightings from natural habitats may indicate that it is largely confined to artificial substrates. It could, however, simply be under recorded in natural habitats due to lower sampling effort and challenges in accessing the low intertidal and shallow subtidal rocky reefs where it may most commonly be found.



(a) Time of initial *Undaria* record, 1994-2018.



(b) Habitat type in which *Undaria* was recorded, 1994-2018. Natural habitat records shown on top of artificial. Habitat type determined from record information gathered from National Biodiversity Network

Figure 1.6: UK records of *Undaria*, 1994-2018

Growth and population dynamics of *Undaria* were investigated on the initial population from the Hamble marina in 1996-1997 (Farrell, 2003). Macroscopic sporophytes could be found throughout the year, with the highest abundance in Spring, and a second smaller peak in abundance in Autumn. Juvenile sporophytes (less than 1 cm) could be found in February-April and September-October suggesting two recruitment pulses. These were also identified as the main growth periods, with the highest growth rate in March-April. Some mature plants (with sporophylls) could be found throughout the year; however mature plants had peak abundance during summer months (June-August), with a level of spore release estimated from around March/April-December. A smaller overwintering cohort was also identified with small plants tagged during August developing into mature plants by April (Farrell, 2003).

A long term manipulation investigating competition between *Undaria* and native kelps was carried out in 1996-2002 at Torquay marina (Farrell and Fletcher, 2006). Experimental patches were marked on areas of pontoons with high abundance of native kelps, but which lacked *Undaria*. Manipulated patches were cleared of all large brown macroalgae and compared to unmanipulated control patches. Across the 6 years of the study, there was no significant difference in the community found between the control and clearance patches. Over time, native kelps and green algae decreased across the study area with a significant increase in *Undaria* and the non-native ascidian *Styela clava*. It was therefore suggested that *Undaria* was slowly colonising marina pontoons in a stepwise fashion, out-competing the native canopy forming algal species. It was also observed that *Undaria* did not colonise the adjacent rocky shoreline throughout the duration of the study, and was therefore considered to have a low competitive ability with native kelps on the natural rocky shore (Farrell and Fletcher, 2006).

In the UK, the remaining studies on *Undaria* have been carried out since 2011 within Plymouth Sound (Heiser *et al.*, 2014; de Leij, 2015; Arnold *et al.*, 2016). In September 2011 Heiser *et al.* (2014) recorded *Undaria* across the Plymouth waterfront, as well as within the neighbouring bays of Barnpool and Mt Batten, on a variety of artificial and natural rocky substrates. The highest abundance was recorded at marinas, while across sites *Undaria* was significantly more abundant on vertical rather than horizontal substrates where native kelps were found in low abundance. Arnold *et al.* (2016) measured the abundance, biomass and biogenic habitat provision of *Undaria* compared to native kelps on natural rocky substrates at one subtidal site (Firestone Bay) for 5 time points between April and December 2014. *Undaria* was present in April, May, June and August surveys, but absent in December, with highest abundance and biomass in June. *Undaria* also harboured a distinct and less diverse assemblage of epifauna compared to *Laminaria ochroleuca* and *Saccharina latissima*, but similar to that of *Saccorhiza polyschides* (Arnold et al., 2016). At the same site in March - June 2015 de Leij (2015) carried out a canopy clearance experiment, which indicated that the native kelp canopy has a significant inhibitive effect on *Undaria* within natural substrates, with higher abundance and percent cover in cleared patches when compared to un-manipulated areas. This trend was supported by surveys which showed that the abundance and biomass of *Undaria* was negatively correlated to native kelp abundance at two sites in July 2015 (de Leij, 2015).

Although there is a growing body of information on the ecology and invasion dynamics of *Undaria* in the UK, there are still significant knowledge gaps which would need to be filled in order to make clear evidence-based management decisions.

1.10 Rationale, overall aims and objectives of thesis

This thesis aims to improve current understanding of the ecology, impacts and management feasibility of *Undaria* in UK coastal environments. Survey and monitoring of macroalgal communities will aim to identify the invasion and population dynamics of *Undaria* in the UK; including exploring abiotic and biotic factors that affect its spread, abundance and distribution within natural and artificial habitats. More targeted manipulations have been used to understand the potential for ecological impact on various recipient communities and consider the feasibility of potential management measures. The specific objectives of each chapter are outlined below.

The first data chapter (Chapter 2) describes an in-situ survey conducted across the southwest of the UK, which aims to identify environmental and ecological factors which may influence *Undaria* distribution-abundance patterns. This study also investigates the potential for spillover of *Undaria* populations from artificial habitats (marinas) to natural habitats (rocky reefs).

Chapter 3 compares the population structure, reproductive capacity and morphology of *Undaria* between three habitat types in the same locality. The aim is to examine between-habitat variability in population dynamics, while also considering how such variability patterns may influence invasion dynamics and potential management.

The next chapter (Chapter 4) is a manipulative study, whereby experimental monthly removals of *Undaria* are implemented in marinas to investigate the influence of management interventions on recruitment dynamics. The aim of this study is to improve current understanding of *Undaria* recruitment patterns but predominantly to consider how the results may have implications for management feasibility.

Using a variety of survey and manipulation techniques, Chapter 5 aims to ascertain whether *Undaria* is coexisting or competing with functionally similar native species. Heavily invaded canopy-forming macroalgae communities are studied across three habitat types. The results are considered within the context of contemporary coexistence theory, which provides a framework for classifying invasive species impact by considering niche and fitness differences between species.

The last data chapter (Chapter 6) describes a long term intertidal press-removal, whereby *Undaria* is serially removed from experimental patches of reef in order to quantify the impact of *Undaria* on invaded intertidal macroalgal communities. A variety of ecological and biochemical response variables are quantified, in order to determine both lethal and sub-lethal effects of *Undaria* on native species.

Finally, Chapter 7 provides a brief overview and synthesis of the project to frame the research in a broader context, and considers the principal knowledge gaps and challenges relating to *Undaria* and other marine INNS.

Chapter 2

Environmental and ecological drivers of distribution

This chapter was published as:

- **Epstein, G.** & Smale D. A. (2017) Environmental and ecological factors influencing the spillover of the non-native kelp, *Undaria pinnatifida*, from marinas into natural rocky reef communities. *Biological Invasions* 20(4), 1049—1072

2.1 Introduction

Artificial structures are strongly associated with the colonisation of marine non-native species (NNS) (Glasby *et al.*, 2007; Ruiz *et al.*, 2009; Bulleri and Chapman, 2010). Seawalls, pontoons, buoys and aquaculture equipment are generally found in more nutrient enriched, low salinity, sediment loaded or polluted environments, as a result of being located in areas of intensified human activity. This distinct physical and biological environment provides a habitat to which many native species are not adapted and can therefore harbour a distinct assemblage (Glasby *et al.*, 2007; Ruiz *et al.*, 2009; Bulleri and Chapman, 2010). These environments also coincide with major introduction pathways and therefore often support a high propagule pressure of NNS (Bax *et al.*, 2003).

Recreational boating is now recognised as one of the major vectors and introduction pathways of NNS, which may be transported via hull fouling or within ballast and bilge water (Clarke Murray *et al.*, 2011; Zabin, 2014; Airoldi *et al.*, 2015; Fletcher *et al.*, 2017). Floating pontoons within harbours and marinas have therefore been identified as key habitats for NNS and are now the focus of numerous monitoring and assessment programs (e.g. Connell, 2001; Arenas *et al.*, 2006; Glasby *et al.*, 2007; Bishop *et al.*, 2015; Foster *et al.*, 2016). This has led to many new records of NNS originating from marina habitats over the last two decades (e.g. Fletcher and Manfredi, 1995; Arenas *et al.*, 2006; Ryland *et al.*, 2014). Although this may be because of increased sampling effort, the abundance and richness of NNS is also considerably higher within marinas when compared to adjacent natural hard-bottom habitats (Connell, 2001; Glasby *et al.*, 2007; Dafforn *et al.*, 2012; Airoldi *et al.*, 2015). This would suggest that marinas act as 'strongholds' for NNS.

Species which were initially recorded in marinas can now be found in a variety of natural habitats, albeit normally at lower abundances (e.g. Minchin and Duggan, 1988; Connell, 2001; Farrell and Fletcher, 2006; Ryland *et al.*, 2009; Dafforn *et al.*, 2012). The interconnected nature of the marine environment makes it hard to definitively link the spread of species from artificial structures to natural coastal habitats. However, as marinas generally comprise large areas of artificial substrate with high abundances of NNS, they can facilitate the development of substantial propagule pressure (Arenas *et al.*, 2006; Glasby *et al.*, 2007; Foster *et al.*, 2016). The proximity of many of these marinas to natural hard-bottom substrates means the 'spillover' of NNS from marinas to nearby natural habitats is highly likely in many systems.

The ability to separate NNS with negligible ecological impacts from those that pose significant risk to native communities is critically important for biodiversity conservation and effective management of natural resources (Blackburn *et al.*, 2014; Jeschke *et al.*, 2014). This is because of the need to prioritise management and control of the large number of marine NNS already established globally (Bax *et al.*, 2003; Molnar *et al.*, 2008; Minchin *et al.*, 2013). The abundance and range of NNS are generally considered as key aspects of impact assessments (Parker *et al.*, 1999; Thomsen *et al.*, 2011). However, due to their 'conservation value', the ecological impact of NNS in natural habitats is generally considered as greater to that of NNS on artificial structures (Kueffer and Daehler, 2009). Although many other factors will influence the overall effect an NNS has on native communities, understanding processes driving the abundances, distributions and rates of transfer of NNS within natural habitats is paramount.

There are thought to be approximately 350 species of non-native marine macroalgae worldwide and at least 17 in the UK, accounting for 20-30% of all marine NNS (Schaffelke *et al.*, 2006; Minchin *et al.*, 2013; Thomsen *et al.*, 2016). Marine macroalgae can function as ecosystem engineers with the potential to cause significant economic and ecological impacts (Schaffelke and Hewitt, 2007; Williams and Smith, 2007; Thomsen *et al.*, 2009). The cold-temperate kelp *Undaria pinnatifida* is one of only two marine macroalgae (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). *Undaria pinnatifida* (hereafter referred to as *Undaria*) is native to the northwest Pacific, where it inhabits rocky coastlines of Japan, Korea, Russia and China (Saito, 1975; Koh and Shin, 1990; Skriptsova *et al.*, 2004). It is also a major species for seaweed mariculture, and is predominantly grown using longline ropes (Yamanaka and Akiyama, 1993; Peteiro *et* *al.*, 2016). As a NNS *Undaria* can now be found in many parts of the northeast and southwest Atlantic, southwest and east Pacific, and the Tasman Sea (James *et al.*, 2015).

The impact of *Undaria* on recipient communities is thought to be highly variable and site-specific. Current evidence indicates that in the majority of cases *Undaria* seems to act as a passenger of ecosystem-change, requiring a level of disturbance or high resource availability in order to establish and proliferate, while having minimal impact on native communities (Forrest and Taylor, 2002; Valentine and Johnson, 2005; South *et al.*, 2015; South and Thomsen, 2016). However, there is evidence that in some settings *Undaria* may impact macroalgal, invertebrate and fish communities (Farrell, 2003; Casas *et al.*, 2004; Irigoyen *et al.*, 2010; Irigoyen *et al.*, 2011; Carnell and Keough, 2014). More research is needed to better understand the range of impacts *Undaria* may have on recipient communities; there is a clear need for long-term manipulative studies that incorporate a range of responses at the individual, population and community level.

The initial introduction of *Undaria* outside of its native range was via accidental import with shellfish into French Mediterranean coastlines in 1971 (Perez *et al.*, 1981; Floc'h *et al.*, 1991), followed by intentional introductions for cultivation into Brittany in 1981 (Perez *et al.*, 1981). Accidental or intentional introductions for farming were initially the primary vector of transport in the northeast Atlantic (Voisin *et al.*, 2005; Peteiro *et al.*, 2016). However, over time and across other regions, long distance dispersal of *Undaria* was predominantly thought to be via fouling on the hulls of commercial vessels (Hay, 1990; Forrest *et al.*, 2000; Silva *et al.*, 2002; Voisin *et al.*, 2005). Within certain regions, *Undaria* is strongly associated with aquaculture infrastructure and secondary spread is thought to have occurred between aquaculture sites (James and Shears, 2016a). In the north east Atlantic secondary spread and range expansions are thought to have been facilitated by fouling on recreational vessels and transport to nearby ports and marinas (Fletcher and Farrell, 1999; Veiga *et al.*, 2014; Zabin, 2014; Kaplanis *et al.*, 2016).

In its non-native range, *Undaria* is characterised by its prevalence on artificial rather than natural substrates (Floc'h *et al.*, 1996; Fletcher and Farrell, 1999; Cremades *et al.*, 2006; Russell *et al.*, 2008; Veiga *et al.*, 2014; Kaplanis *et al.*, 2016). Many of the records of *Undaria* therefore originate from ports, marinas and aquaculture sites (Hay and Luckens, 1987; Fletcher and Manfredi, 1995; Silva *et al.*, 2002; Meretta *et al.*, 2012; Kraan, 2016). Both marinas and aquaculture sites contain artificial substrates which are held at a constant shallow depth, providing ideal light conditions for the growth of *Undaria* (Fletcher and Farrell, 1999; Cremades *et al.*, 2006; Grulois *et al.*, 2011; Minchin and Nunn, 2014; James and Shears, 2016). As a non-native, *Undaria* can also be found in a variety of natural habitats including seagrass beds and mixed sediment communities, although it is most commonly found on rocky reef (Hewitt *et al.*, 2005; Martin and Bastida, 2008; Russell *et al.*, 2008; Dellatorre *et al.*, 2014; Minchin and Nunn, 2014). Due to its low natural dispersal ability, following introduction into a non-native region, the natural spread of *Undaria* can be relatively slow (Floc'h *et al.*, 1991; Farrell and

Fletcher, 2006; Kaplanis *et al.*, 2016). However, in many cases it has been suggested that the presence of *Undaria* in natural habitats is linked to source populations in nearby artificial habitats (Floc'h *et al.*, 1996; Farrell and Fletcher, 2006; Russell *et al.*, 2008; Grulois *et al.*, 2011; James and Shears, 2016a).

In the UK *Undaria* was first recorded in 1994, attached to floating marina pontoons in Port Hamble (Fletcher and Manfredi, 1995). By 1999, *Undaria* had spread to other marinas and harbours along the south coast of England (Farrell and Fletcher, 2006). Currently, although the majority of records still originate from southern England, the species has been recorded on the south, east and west coasts of England, on the east coast of Northern Ireland and the Republic of Ireland, and in Scotland at Queensferry (Figure 2.1). In the vast majority of locations these records are from artificial structures, primarily marina and harbour pontoons (Fletcher and Farrell, 1999; Heiser *et al.*, 2014; Minchin and Nunn, 2014; Kraan, 2016; NBN, 2017). Despite its widespread distribution, *Undaria* has been recorded on natural substrates in relatively few areas of the UK (Fletcher and Farrell, 1999; Farrell and Fletcher, 2006; Heiser *et al.*, 2014; NBN, 2017). This may be because it is largely confined to artificial habitats, or it could be generally under-recorded in shallow natural habitats that are more difficult to sample.

Here, the southwest UK is used as a case region, to investigate links between *Undaria* distribution-abundance patterns in artificial habitats and those observed within natural rocky reef habitats. Attributes of both the marina and coastal sites are quantified to identify factors which may influence the distribution and abundance of *Undaria* on natural rocky reefs. The overall objectives of the study were: i) to determine whether *Undaria* is largely confined to artificial habitats or whether it has spread to natural rocky reef; ii) to quantify ecological and environmental factors that may influence the spread of *Undaria* into natural habitats and explicitly link them with observed distribution-abundance patterns; and iii) to consider how these findings may influence the design of appropriate management responses.

2.2 Materials and methods

2.2.1 Survey locations

Records of *Undaria* on the south coast of Devon and Cornwall were obtained from the National Biodiversity Network Gateway (NBN, 2016). These were largely confined to marina environments, with relatively few records of *Undaria* from natural rocky reef habitats (see Farrell and Fletcher, 2006; Heiser *et al.*, 2014 for further details). Based on existing records five locations were chosen for survey; Torbay, Dartmouth, Salcombe, Plymouth Sound and Newlyn (Figure 2.1). Of these, two are designated as protected areas due to their high conservation value; Plymouth Sound (Special Area of

Conservation) and Salcombe Estuary (Special Site of Scientific Interest). All surveys were completed during summer (June-August) as this is the season when the main recruitment and growth periods of *Undaria* would be expected to have ended, and therefore the populations should be at a plateau; however it would also be the start of the main annual senescence (Heiser *et al.*, 2014; Minchin and Nunn, 2014; Arnold *et al.*, 2016; Murphy *et al.*, 2017). Temporal variation in recruitment, growth and senescence stages between locations may have had an influence on overall abundance, biomass or cover estimates. However, long-term sampling across all locations would be needed to remove any temporal influence, which falls outside the scope of the current study. The 2.5 month restricted summer survey period was therefore considered to be an appropriate design for this survey, with similar time periods being used for other studies of *Undaria* within the UK (Farrell, 2003; Heiser *et al.*, 2014; Minchin and Nunn, 2014; Arnold *et al.*, 2016; De Leij *et al.*, 2017; Minchin *et al.*, 2017).

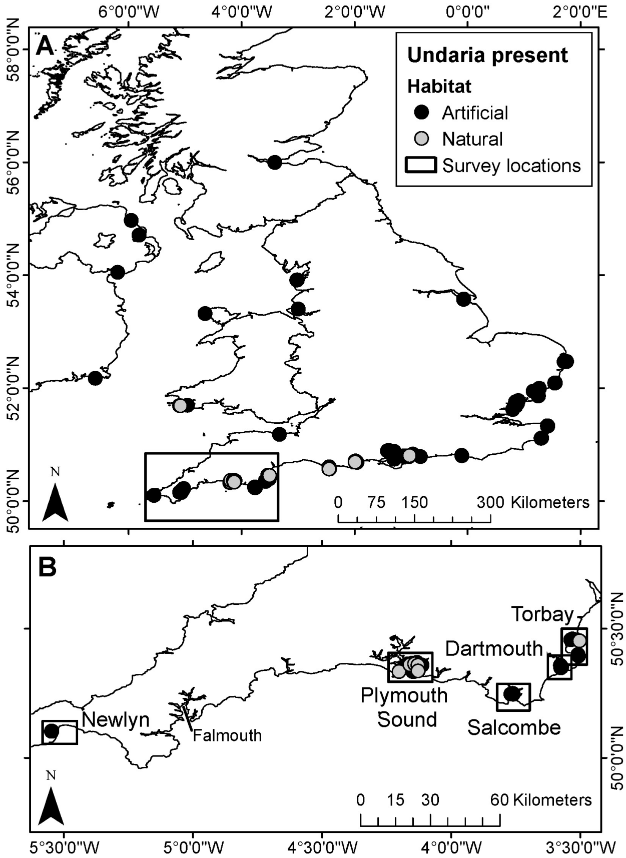


FIGURE 2.1: (A) Records of *Undaria* occurrence in the UK and Ireland (Kraan 2016; Minchin *et al.*, 2017; NBN 2016). Black box indicates survey region. (B) Locations selected for survey in the southwest UK survey region (black boxes). *Undaria* records are present around Falmouth, although not shown here as this location was not part of the current study. Within both maps records from natural habitats (grey points) shown on top of those from artificial habitats (black points). Habitat type was determined based on survey and site information from the original records.

2.2.2 Marina surveys

Marinas containing records of *Undaria* in NBN (2016) were visited during 13^{th} June -25^{th} August 2016. The same observer walked the full extent of the marina pontoons and gave a single categorical score for *Undaria* percent cover of submerged floats using a SACFOR scale (Superabundant [S > 80%], Abundant [A 40-79%], Common [C 20-39%], Frequent [F 10-19%], Occasional [O 5-9%], Rare [R 1-5%], None [N 0%]). The areal extent of each marina was calculated using Google aerial imagery © 2016, and a measure of *Undaria* propagule pressure for each marina was calculated by multiplying the median percent cover value from the SACFOR category by aerial extent. Values were summed for marinas within a given location to give an estimate of total marina propagule pressure (hereafter referred to as 'propagule pressure'). Although this is a relatively coarse proxy for propagule pressure (it was not feasible to collect more precise measures of spore density or recruitment density across such broad spatial scales), it is representative of the standing stock of mature sporophytes and no clear differences in the relative abundance of reproductively-active sporophytes were observed between marinas. Time of first record in each marina was also collected from NBN (2016).

The coverage of both native and non-native large brown macroalgae on marina pontoons can be highly spatially variable within a single marina. This is dependent on a variety of factors including aspect, shading, water depth, exposure, shielding from vessels and disturbance. Therefore, to get a comparative measure of abundance and biomass of *Undaria* at each marina, the area supporting the greatest coverage of brown macroalgae (assessed visually during the SACFOR search) was targeted for further high resolution sampling. This was typically the outermost pontoons nearest to the marina entrance, where there is little or no shielding from vessels, greater water depth and stronger water flow (Epstein pers obs). Within the selected area, 10 replicate 0.25 m^2 quadrats where haphazardly placed against the side of submerged floats. All *Undaria* were removed from the quadrat, enumerated, and the total biomass quantified (g FW). Values were averaged over the ten quadrats at each marina to yield comparable values of abundance and biomass.

2.2.3 Coastal surveys

Using ArcMap 10.3.1 the mean high water spring (MHWS) coastline of each location was divided into equal segments of 3.75 km in length. Those coastal segments closest to the marina sites identified above were selected first. A single survey site was haphazardly chosen within the segment based on shore access and presence of suitable rocky substrate - identified using Google aerial imagery © 2016 and by carrying out site visits. The first segment was generally seaward of each marina due to a lack of suitable rocky habitat on the estuary/river side of the artificial habitat. If a coastal segment contained no shore access, or there was a lack of suitable rocky substrate, it was removed from the study area and site selection continued to the adjacent segment. Survey sites closest to marinas were surveyed first, with each subsequent survey moving to the adjacent segment, therefore extending the range of the study area from the marina site. If two consecutive survey sites contained no *Undaria*, survey effort moved to the opposite side or shore from the marina. If two days of survey effort (3-4 sites) recorded no *Undaria* within a given location no further sites were sampled.

Surveys were completed by snorkel at low slack-tide during 2^{nd} July – 30^{th} August 2016. In order to maintain a similar tidal height on the substrate, large spring tides were avoided, leading to tidal heights of between 0.7 m and 2.0 m above chart datum at the time of survey. At each site, four 25 m transects were laid using a weighted line, each separated by approximately 25 m. Transects were placed haphazardly, but were stratified to areas of suitable rocky substrate within the intertidal/subtidal fringe zone, which was covered by ~0.5-1.5 m of water at the time of survey. Video of the macroalgal canopy along the transect was collected using a Panasonic Lumix FT5 waterproof camera fitted to an underwater tray and handle. A 65 cm scale was fixed to the front of the camera tray in order to maintain the video at an approximate set distance above the canopy, to standardise the area of observation (approximately 20 m^2 per transect). Both horizontal and vertical substrates were included in the video, dependent on the topography at a given site. For each transect the substrate was categorised by the percent contribution of bedrock, boulders ($>$ 500 mm), cobbles (60–500 mm), gravel ($5-59$ mm) and sand ($<$ 5 mm), which was estimated by eye. This was converted to a univariate measure of substrate stability using the formula:

$$Substrate\ stability = \%Bedrock + \frac{2 * \%Boulders}{3} + \frac{\%Cobbles}{3}$$

The percent canopy cover of *Undaria*, measured on a SACFOR scale, was also recorded *in situ* for each transect; this visual census incorporated macroalgal canopies ~2m each side of the transect line and therefore covered a greater area than the video transects. The geographic position of each transect was estimated by matching the time at the start and end of the video to a GPS track recorded from a Garmin etrex GPS, housed in a swim buoy attached to the surveyor (Figure 2.2).

Following the survey, each video transect was viewed twice. On the first view the video was played frame-by-frame and the number of *Undaria* (both entire and partial plants) were counted. If *Undaria* was found during the *in-situ* search, but was not counted within the video transect, a nominal value of 1 was given, to distinguish these transects from true absences. This resulted in two measures of *Undaria* for each transect: (i) the *in-situ* SACFOR measure at wider spatial scale but coarser resolution and (ii) the abundance measure at smaller spatial scales but finer resolution obtained from the video transects. On the second viewing of the video transects the percent canopy cover of other large brown canopy-forming macroalgae (*Laminaria* spp., *Saccorhiza polyschides*, *Saccharina latissima*, *Himanthalia elongata*, *Chorda filum*, *Sargassum muticum* and *Alaria esculenta*) was estimated on the SACFOR scale.

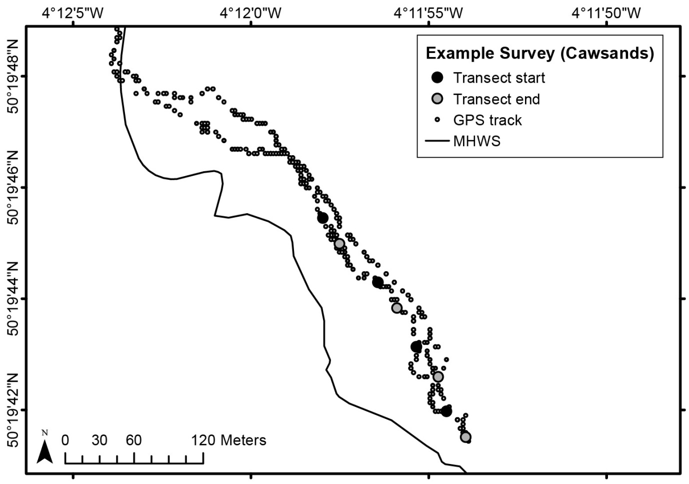


FIGURE 2.2: Example layout of survey at a coastal reef site. The geographic position of each transect (start - black, end - grey) was estimated by matching the time at the start and end of the video to a GPS track (small grey dots) recorded from a hand-held GPS, housed in a swim buoy attached to the surveyor

2.2.4 Other coastal site characteristics

The dispersal distance between each coastal survey site and the nearest marina was calculated in ArcMap 10.3.1. The primary method of natural dispersal of *Undaria* is from spores, which have low natural dispersal abilities (Saito, 1975; Forrest *et al.*, 2000; Schiel and Thompson, 2012). Long-distance drift of mature sporophytes is considered a potential secondary method of natural dispersion (Forrest *et al.*, 2000; Grulois *et al.*, 2011), which may create distinct dispersal distances. However, along-shore distance was considered the most appropriate measure of dispersal distance from marina to reef site, due to the low buoyancy of mature sporophytes, the predominance of spore mediated natural dispersion, and the likely correlation between along-shore distance and linear distance to marinas. Polylines were creating running from the centre of each study site along the MHWS shoreline to the nearest marina. Estuarine channels of less than 500 m in width were not considered as geographical barriers to *Undaria* dispersal (Forrest *et al.*, 2000; Russell *et al.*, 2008), and therefore a straight line was drawn across these points. Human mediated dispersal is highly stochastic, with both long and short distance vectors. This has the potential to influence connectivity between sites, however due to its high variation, estimating a true value is highly challenging, while calculating a proxy such as quantification of vessel movements in each location was unfeasible and falls outside the scope of the current study. The maximum abundance and biomass of *Undaria* at the nearest marina was also applied as a coastal site characteristic.

Local wave exposure was calculated by manually summing the distance to land from the centre of each study site for each of 18 radial points separated by 20°. The maximum radial distance was set as 200 km as this is approximately where the fetch is considered large enough for wave conditions to be fully developed for UK coastal locations (Burrows *et al.*, 2008). Distance at each radial point was calculated using a high resolution polyline of UK MHWS and will therefore be strongly influenced by small, site level topography and barriers. A lower resolution, "segment-level", measure of exposure was calculated from the Burrows *et al.* (2008) UK fetch model. Within this model the UK coastline is divided into 200 m scale grid cells and wave fetch is determined as the distance to the nearest land cell in 16 radial sectors, based on three resolutions of searches of the surrounding cells, up to a distance of 200 km (Burrows *et al.*, 2008). For each coastal cell the mean values of fetch with its two immediately adjacent cells is then calculated to create a measure of exposure (Burrows *et al.*, 2008). For the closest coastal cell to the centre of each study site, this final exposure value was used as a measurement of segment exposure.

2.2.5 Data analysis

Zero-skewed distribution and abundance data are frequently found in studies on rare or restricted-range species (Martin *et al.*, 2005). During this study, *Undaria* was absent in 57% of transects. Analysis was therefore carried out using zero-inflated models as the preponderance of zeros would cause high overdispersion within ordinary count models (Poisson and negative binomial). Zero-inflated models have commonly been used to identify environmental and ecological factors influencing the distribution-abundance patterns of rare or restricted-range aquatic species, including marine NNS (e.g. Fletcher *et al.*, 2013; Anton *et al.*, 2014; Hoogenboom *et al.*, 2015; Erhardt and Tiffan, 2016; Cambie *et al.*, 2017). Factors affecting the distribution and abundance of *Undaria* at coastal sites were assessed using zero-inflated negative binomial models (ZINB, Zuur *et al.*, 2009). A ZINB is a mixture model whereby zero values are modelled as coming from two parts. In the first instance, a binomial GLM models the probability of measuring a zero based on selected covariates and presence-absence of the response - hereafter referred to as the 'zero model' or π_i. The second part models remaining variation in zeros, and positive values with a negative binomial GLM - hereafter referred to as the 'count model' or μ_i (Zuur *et al.*, 2009). All models were run in R 3.2.2 (R Core Team, 2015) using the *zeroinfl* function from the *pscl* package (Zeileis *et al.*, 2008).

The two *Undaria* response variables, abundance counts from the video transects and SACFOR cover from *in situ* surveys (median value from the SACFOR category rounded to the nearest percent), were modelled separately. Predictor variables used to model the response included both ecological and environmental attributes of each site. Specifically, ecological descriptors were the percent cover of *Laminaria* spp., *S. latissima* and *S. polyschides* on natural reef; the abundance of *Undaria* at the nearest marina, and local marina propagule pressure; whereas substrate stability, distance to nearest marina and wave exposure described the environment. Percent cover of *Laminaria* spp., *S. latissima* and *S. polyschides* were calculated as the median value from the SACFOR category (expressed as a decimal value). On average these three species accounted for 91% of all brown macroalgal canopy (excluding *Undaria*), and were therefore considered to characterise the associated community as a whole. During the marina surveys it was noted that the annual senescence of the *Undaria* lamina had progressed at different rates at each marina. This could greatly influence the overall biomass and therefore 'biomass at nearest marina' was not used as a predictor variable. The holdfasts and stipes of plants generally stay attached to the substrate for some time following senescence of the blade, and therefore, abundance at nearest marina was considered a reliable descriptor. Time since first record in each location was not used as a predictor variable because the metric is (i) highly influenced by historic survey effort which is unequal between locations; (ii) unlikely to reflect the actual date of introduction due to lack of absence records in many cases; and (iii) likely to be highly related to the abundance at and propagule pressure from marinas.

Collinearity in predictor variables was tested using Pearson correlation coefficients and variance inflation factors (VIF) using the *pairs* and *corvif* functions (Zuur *et al.*, 2009). The need to transform variables before testing for collinearity was assessed graphically. No transformations were needed, and no collinearity was identified ($r \leq 0.6$, $VIF < 2.6$, for all variables).

Models were fitted using backward selection. Initially a full ZINB with all predictor variables included within both the zero and count models was constructed. The coefficient with the lowest significance value was dropped, and the model rerun. This was repeated until all coefficients within the model had a p value < 0.01. Each model was compared to the subsequent nested model using a likelihood ratio test using the *lrtest* function within the *lmtest* package (Zeileis and Hothorn, 2002). Second-order Akaikes information criterion (AICc) were calculated for all models using the AICc function in the *AICcmodavg* package (Mazerolle, 2016). Optimal models were selected based on both likelihood ratio tests and AICc values, however AICc values with a difference of less than 2 were not considered significant. The selection of a ZINB over a zero inflated Poisson model (ZIP; where remaining zeros and positive values are modelled with a Poisson distribution) was due to over-dispersion in the count portion of the data. This was justified using a likelihood ratio test at both full and optimal model stages.

Model validation was carried out using diagnostic plots. Pearson residuals were plotted against fitted values from the optimal ZINB model, and against each explanatory variable. Observed values of the response were plotted against fitted values from the optimal ZINB, and model fit was tested using a simple linear regression (Pineiro *et al.*, 2008). Relative importance of each coefficient was calculated as the percentage value of the z-statistic from the total absolute z-value for each portion of the optimal models.

To further examine the relationship between predictor and response variables, binomial models were constructed for *Undaria* presence-absence and each predictor variable selected in the optimal zero model; while negative binomial models were constructed for each predictor selected in the optimal count models and positive abundance and SACFOR data. This was carried out using the *glm* function from base R (R Core Team, 2015) and the *nb.glm* function from the *MASS* package (Venables and Ripley, 2002).

Mapping was carried out within ArcMap 10.3.1. The *dplyr* package (Wickham and Francois, 2015) was used for data manipulation and all graphs were created using *ggplot2* (Wickham, 2009).

2.3 Results

2.3.1 Marina surveys

Undaria was found at all thirteen marina sites surveyed (Figure 2.3). The highest percent cover was in Plymouth Sound, with *Undaria* scored as Superabundant within three marinas. It was also the location supporting the highest abundance (50.9 ± 7.9 per 0.25 m^2; mean ± SE) and biomass (2906.5 ± 413.6 g per 0.25 m^2) of *Undaria* within a marina. The lowest percent cover within a single marina was at Dartmouth where *Undaria* was scored as Occasional. The lowest abundance (2.8 ± 1.0 per 0.25 m^2) and biomass (270.4 ± 68.4 g per 0.25 m^2), was recorded at marinas in Dartmouth and Newlyn respectively.

Overall, Plymouth Sound marinas had the highest mean abundance and biomass of *Undaria*. It was also the location with the largest mean percent cover (calculated from the median values from the SACFOR scales), total aerial extent of marinas and propagule pressure (Figure 2.4). Torbay was the location with the earliest record of *Undaria* (1996), and had the second highest value for all factors (mean abundance, mean biomass, mean percent cover, total aerial extent of marinas and propagule pressure). Summary statistics for all locations are shown in Figure 2.4.

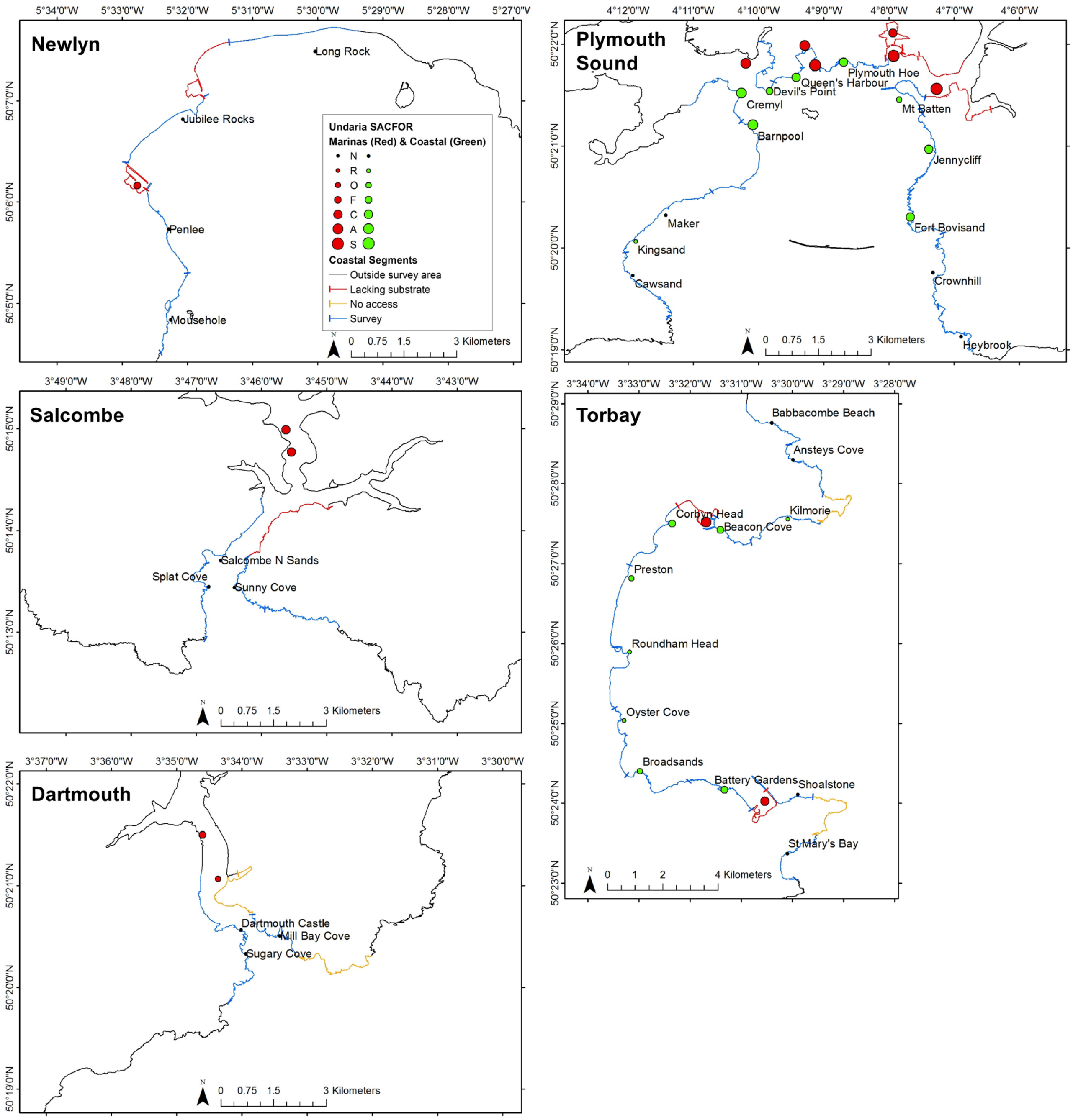


FIGURE 2.3: *Undaria* SACFOR at marina (red) and coastal (green) survey sites. Labels indicate the names of coastal survey sites. Where applicable *Undaria* absence is indicated by a black point. Ports which did not contain floating pontoons (such as north of Jubilee rocks, Newlyn) were not surveyed. Coastal segments are coloured to indicate where a survey was completed (blue), where no shore access was available (orange) and where natural rocky substrate was lacking and therefore no survey was carried out (red). Coastline which was outside of the scope of this survey is shown in black.

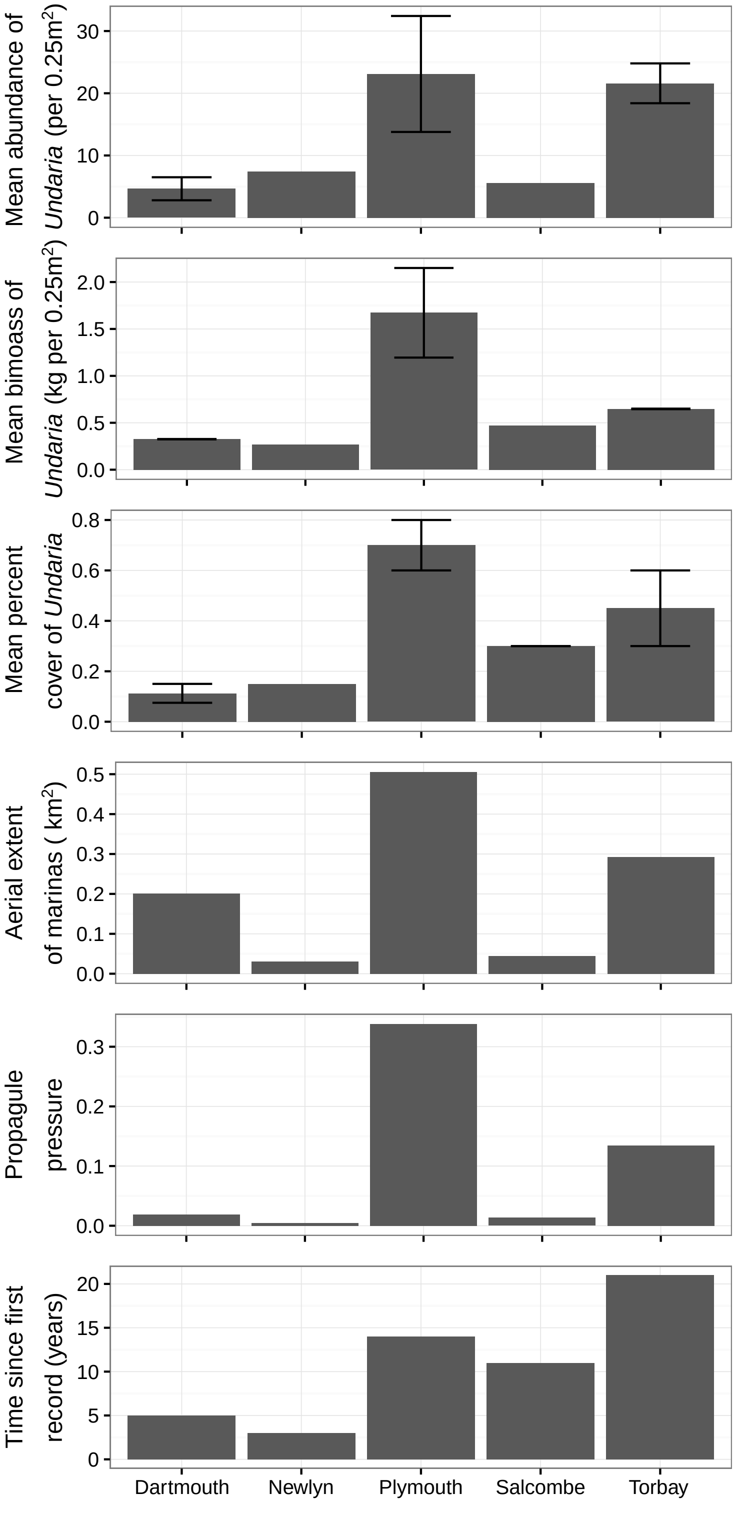


FIGURE 2.4: Attributes of surveyed marinas in each location. Abundance (inds. per 0.25 m^2), biomass (kg per 0.25 m^2) and percent cover (%) of *Undaria* calculated as a mean (±SE) of all surveyed marinas within a location (Salcombe and Newlyn only one marina surveyed). Aerial extent of marinas (km^2) and propagule pressure are a sum of all marinas, while time since first record is the earliest record for any marina within a given location.

2.3.2 Coastal surveys

Across all locations a total of 35 coastal sites were surveyed (13 sites in Plymouth, 12 in Torbay, 4 in Newlyn, 3 in Dartmouth and 3 in Salcombe). *Undaria* was found at only 17 sites and within 60 of 140 transects, all of which were in Plymouth Sound and Torbay (Figure 2.3). *Undaria* was not recorded at any coastal sites within Newlyn, Dartmouth or Salcombe (Figure 2.3). The range of site characteristics found in each location is shown in Table 2.1.

The structure of the associated brown macroalgal canopy varied considerably between sites, ranging from being entirely dominated by *Laminaria* spp. to comprising a far more mixed canopy of *Undaria*, *S. polyschides* and *S. latissima*. The average percent cover of each canopy-forming macroalgae at each site was calculated from the median values from the SACFOR categories at each transect and is shown in Figure 2.3 (*Undaria*) and Figure 2.5 (other canopy formers).

The abundance of *Undaria* (counted within the video transects) was highly correlated to the *in-situ* measure of *Undaria* percent cover (r = 0.93, calculated using the median values from the SACFOR category), however there was clear overlap in abundance values between different SACFOR categories (Figure 2.6). *Undaria* was recorded as Superabundant within two transects at Barnpool (Plymouth Sound), where the maximum abundance was also recorded (258 within a single video transect) and was recorded as Rare within ten transects across seven sites in Torbay and Plymouth.

Table 2.1: Range of site characteristics across each survey location

Location	Distance to nearest marina (km)		Site exposure (km)		Segment exposure (km)		Substrate stability (%)	
	Min	Max	Min	Max	Min	Max	Min	Max
Dartmouth	2.87	3.91	206.2	604.4	224.4	350.4	57	97
Newlyn	1.93	9.16	482.9	893.4	866.8	986.4	33	90
Plymouth	0.72	12.99	31.4	926.6	247.2	866.0	30	95
Salcombe	4.55	6.60	412.9	611.3	260.4	599.6	50	88
Torbay	0.99	13.09	38.7	803.2	490.0	1279.2	37	97

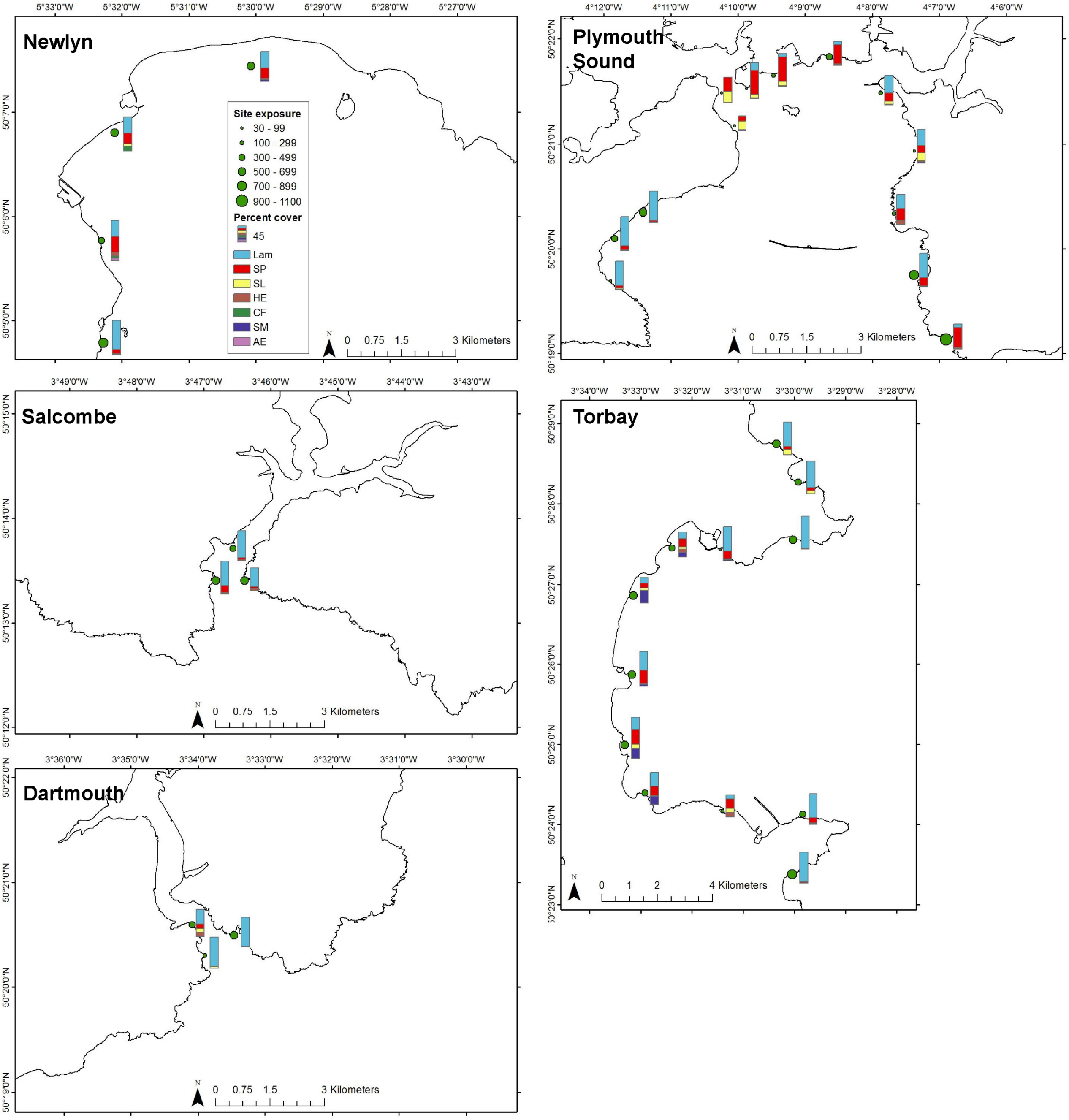


FIGURE 2.5: Site exposure (km) of each coastal survey site indicated by size of green point. The associated canopy community is shown to the right of each point as a stacked bar chart. Lam = *Laminaria* spp., SP = *Saccorhiza polyschides*, SL = *Saccharina latissima*, HE = *Himanthalia elongata*, CF = *Chorda filum*, SM = *Sargassum multicium*, AE = *Alaria esculenta*. Height of the bar is relative to percent cover of each species based on the SACFOR data.

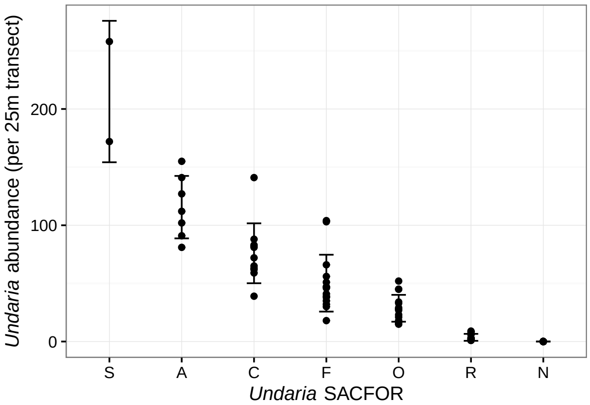


FIGURE 2.6: Relationship between *Undaria* SACFOR and abundance measured at each survey transect. Bars indicate the mean abundance±SD for each SACFOR category.

2.3.3 Factors affecting the abundance and distribution on coastal reef

Using the backwards selection process eleven ZINB models were constructed for both the *Undaria* abundance and SACFOR response variables (Table 2.2). The lowest AICc value for *Undaria* abundance was 620.6 (A6), however five different models had a ΔAICc of less than 2 (A4 to A8) and were therefore considered for optimal model selection. Likelihood ratio tests indicated that a significant term was not dropped in the backwards selection until A8, although its significance was negligible (pSP from π_i; χ^2 = 3.8517, df = 1, p = 0.050). A8 was therefore chosen as the optimal model (Table 2.3). For the SACFOR response variable the lowest AICc was 496.2 (S6), with 4 models ΔAICc less than 2 (S5 to S8). Likelihood ratio tests indicated that a significant term was not dropped from the model until S9 (Site exp from π_i; χ^2 = 5.4353, df = 1, p = 0.020) and therefore S8 was chosen to be the optimal model. All coefficients in both optimal models were statistically significant with p values < 0.025 (Table 2.3).

Simple linear regression of observed values against fitted values from the optimal models indicated a significant model fit for both *Undaria* abundance ($F_{(1,138)} = 586.7$, p $<2.2e^{-16}$, Adj-$R^2 = 0.81$) and SACFOR ($F_{(1,138)} = 554.7$, p $<2.2e^{-16}$, Adj-$R^2 = 0.80$). Justification of model type (ZINB over a ZIP), was confirmed using likelihood ratio tests at the full (A0 and S0) and optimal (A8 and S8) model stages (χ^2(A0) = 434.12, df = 1, p $<2.2e^{-16}$; χ^2(A8) = 551.85, df = 1, p $<2.2e^{-16}$; χ^2(S0) = 138.41, df = 1, p $<2.2e^{-16}$; χ^2(S8) = 166.62, df = 1, p $<2.2e^{-16}$).

The relative importance of each term from the optimal models (% z-value) suggests that distance to, and abundance at, the nearest marina had the most significant effect on the zero model for both *Undaria* abundance and SACFOR (Table 2.3). For the count model the percent cover of *Laminaria* spp. had the highest relative importance for both abundance and SACFOR variables (Table 2.3).

Table 2.2: ZINB backwards selection process. A0 and S0 are full models containing all variables in the count (μ_i) and zero (π_i) portions of the model. Dropped term indicates the variable dropped at each stage of the backwards selection, with the likelihood ratio test comparing the new model to the preceding model. Δ AICc = difference to the lowest AICc value for each model. Selected optimal models are indicated by an asterisk. Dist marina = distance to nearest marina (km), Abund marina = abundance at nearest marina (n 0.25 m^{-2}), Stability = substrate stability (%), Seg exp and Site exp = segment exposure and site exposure respectively (km), pSL and pSP = the percent cover of *Saccharina latissima* and *Saccorhiza polyschides* respectively (%), Prop pres = propagule pressure (km^2).

Model	Dropped term	df	AICc	Δ AICc	Likelihood ratio test
	Undaira abundance				
A0	None	21	631.0	10.4	
A1	Dist marina from μ_i	20	628.3	7.7	$\chi^2 = 0.0012$ (df = 1, p = 0.972)
A2	Abund marina from μ_i	19	626.2	5.6	$\chi^2 = 0.7155$ (df = 1, p = 0.398)
A3	Stability from π_i	18	624.4	3.8	$\chi^2 = 0.8392$ (df = 1, p = 0.360)
A4	Seg exp from π_i	17	622.5	1.9	$\chi^2 = 0.7318$ (df = 1, p = 0.392)
A5	pSL from μ_i	16	621.6	1.0	$\chi^2 = 1.7375$ (df = 1, p = 0.188)
A6	pSL from π_i	15	620.6	0.0	$\chi^2 = 1.4751$ (df = 1, p = 0.225)
A7	Seg exp from μ_i	14	621.0	0.4	$\chi^2 = 2.9855$ (df = 1, p = 0.084)
A8*	pSP from π_i	13	622.4	1.8	$\chi^2 = 3.8517$ (df = 1, p = 0.050)
A9	Prop pres from π_i	12	626.2	5.6	$\chi^2 = 6.2146$ (df = 1, p = 0.013)
A10	pSP from μ_i	11	628.5	7.9	$\chi^2 = 4.7247$ (df = 1, p = 0.030)
	Undaira SACFOR				
S0	None	21	508.6	12.4	
S1	Seg exp from μ_i	20	505.9	9.7	$\chi^2 = 0.0825$ (df = 1, p = 0.774)
S2	Abund marina from μ_i	19	503.4	7.2	$\chi^2 = 0.1655$ (df = 1, p = 0.684)
S3	pSL from μ_i	18	501.1	4.9	$\chi^2 = 0.3889$ (df = 1, p = 0.533)
S4	Stability from π_i	17	499.2	3.0	$\chi^2 = 0.7475$ (df = 1, p = 0.387)
S5	Seg exp from π_i	16	497.4	1.2	$\chi^2 = 0.8015$ (df = 1, p = 0.371)
S6	pSL from π_i	15	496.2	0.0	$\chi^2 = 1.3112$ (df = 1, p = 0.252)
S7	Dist marina from μ_i	14	496.5	0.3	$\chi^2 = 2.8843$ (df = 1, p = 0.089)
S8*	pLam from π_i	13	497.6	1.4	$\chi^2 = 3.4965$ (df = 1, p = 0.062)
S9	Site exp from π_i	12	500.6	4.4	$\chi^2 = 5.4353$ (df = 1, p = 0.020)
S10	pSP from π_i	11	501.0	4.8	$\chi^2 = 2.8707$ (df = 1, p = 0.090)

TABLE 2.3: Optimal ZINB models for *Undaria* abundance (A8) and SACFOR (S8). Dist marina = distance to nearest marina (km), Abund marina = abundance at nearest marina (n 0.25 m^{-2}), Stability = substrate stability (%), Site exp = site exposure (km), pLam and pSP = the percent cover of *Laminaria* spp. and *Saccorhiza polyschides* respectively (decimal %), Prop pres = propagule pressure (km^2), Log(θ) = link function between count (μ_i) and zero (π_i) portions of the model. % z-value = absolute z-value for a given term expressed as a percentage of total absolute z-values for that portion of the model.

Model term	Coefficent value (β)	SE	z-value	p-value	% z-value
Undaria Abundance (A8)					
μ_i					
Intercept (α)	2.719	0.503	5.41	<0.001	18.24
pLam	-2.618	0.424	-6.18	<0.001	20.84
pSP	-0.960	0.425	-2.26	0.024	7.62
Stability	0.026	0.006	4.06	<0.001	13.69
Site exp	-0.002	<0.001	-3.56	<0.001	12.00
Prop pres	3.502	1.004	3.49	<0.001	11.77
Log(θ)	0.994	0.212	4.70	<0.001	15.85
π_i					
Intercept (α)	0.621	2.383	0.26	0.794	1.70
pLam	5.243	1.696	3.09	0.002	20.26
Dist marina	0.497	0.145	3.43	<0.001	22.49
Abund marina	-0.357	0.094	-3.82	<0.001	25.05
Site exp	0.005	0.002	2.40	0.016	15.74
Prop pres	-11.552	5.136	-2.25	0.024	14.75
Undaria SACFOR (S8)					
μ_i					
Intercept (α)	2.321	0.453	5.13	<0.001	16.55
pLam	-2.696	0.427	-6.32	<0.001	20.40
pSP	-1.304	0.397	-3.29	0.001	10.61
Stability	0.020	0.006	3.22	0.001	10.41
Site exp	-0.002	0.000	-3.90	<0.001	12.60
Prop pres	3.390	0.931	3.64	<0.001	11.76
Log(θ)	1.322	0.241	5.48	<0.001	17.68
π_i					
Intercept (α)	5.443	2.495	2.18	0.029	12.78
pSP	-7.709	2.844	-2.71	0.007	15.89
Dist marina	0.609	0.170	3.59	<0.001	21.07
Abund marina	-0.453	0.120	-3.78	<0.001	22.13
Site exp	0.007	0.003	2.40	0.016	14.06
Prop pres	-13.437	5.599	-2.40	0.016	14.07

Scatterplots and binomial models of *Undaria* presence-absence data were used to further examine the relationship of each predictor variable selected in the optimal zero models (Figure 2.7). Individually, all factors significantly affected the probability of *Undaria* presence, with the percent cover of *Laminaria* spp. (β = -4.301, z = -5.74, p = 9.78e^{-09}), distance to nearest marina (β = -0.366, z = -5.06, p = 4.23e$^{-07)}$ and site exposure (β = -0.006, z = -5.81, p = 6.25e$^{-09)}$ all negatively related to *Undaria* presence; while the percent cover of *S. polyschides* (β = 4.042, z = 4.12, p = 3.75e$^{-05)}$, abundance at nearest marina (β = 0.138, z = 4.68, p = 2.90e$^{-06)}$ and propagule pressure (β = 7.708, z = 5.13, p = 2.87e$^{-07)}$ were all positively related to *Undaria* presence (Figure 2.7).

Negative binomial models of positive abundance data and individual variables selected in the count model of A8 indicated percent cover of *Laminaria* spp. (β = -1.743, z = -4.13, p = 3.66e$^{-05)}$ and site exposure (β = -0.003, z = -4.90, p = 9.37e$^{-07)}$ had a significant negative relationship with *Undaria* abundance; while propagule pressure (β = 5.247, z = 4.90, p = 9.68e$^{-07)}$ had a positive relationship (Figure 2.8). Individually, substrate stability (β = -0.004, z = -0.59, p = 0.556) and the percent cover of *S. polyschides* (β = -0.312, z = 0.55, p = 0.583) were not significantly related to *Undaria* abundance (Figure 2.8). The same predictor variables were selected in the count portion of the optimal SACFOR model (S8), and negative binomial models indicated the same relationships as for the abundance model (Figure 2.9) [(Percent cover of *Laminaria* spp. (β = -2.137, z = -5.37, p = 7.84e$^{-08)}$, site exposure (β = -0.003, z = -5.30, p = 1.19e$^{-07)}$, propagule pressure (β = 5.758, z = 5.66, p = 1.52e$^{-08)}$, substrate stability (β = -0.014, z = -1.92, p = 0.054), percent cover of *S. polyschides* (β = -0.607, z = -1.10, p = 0.272)].

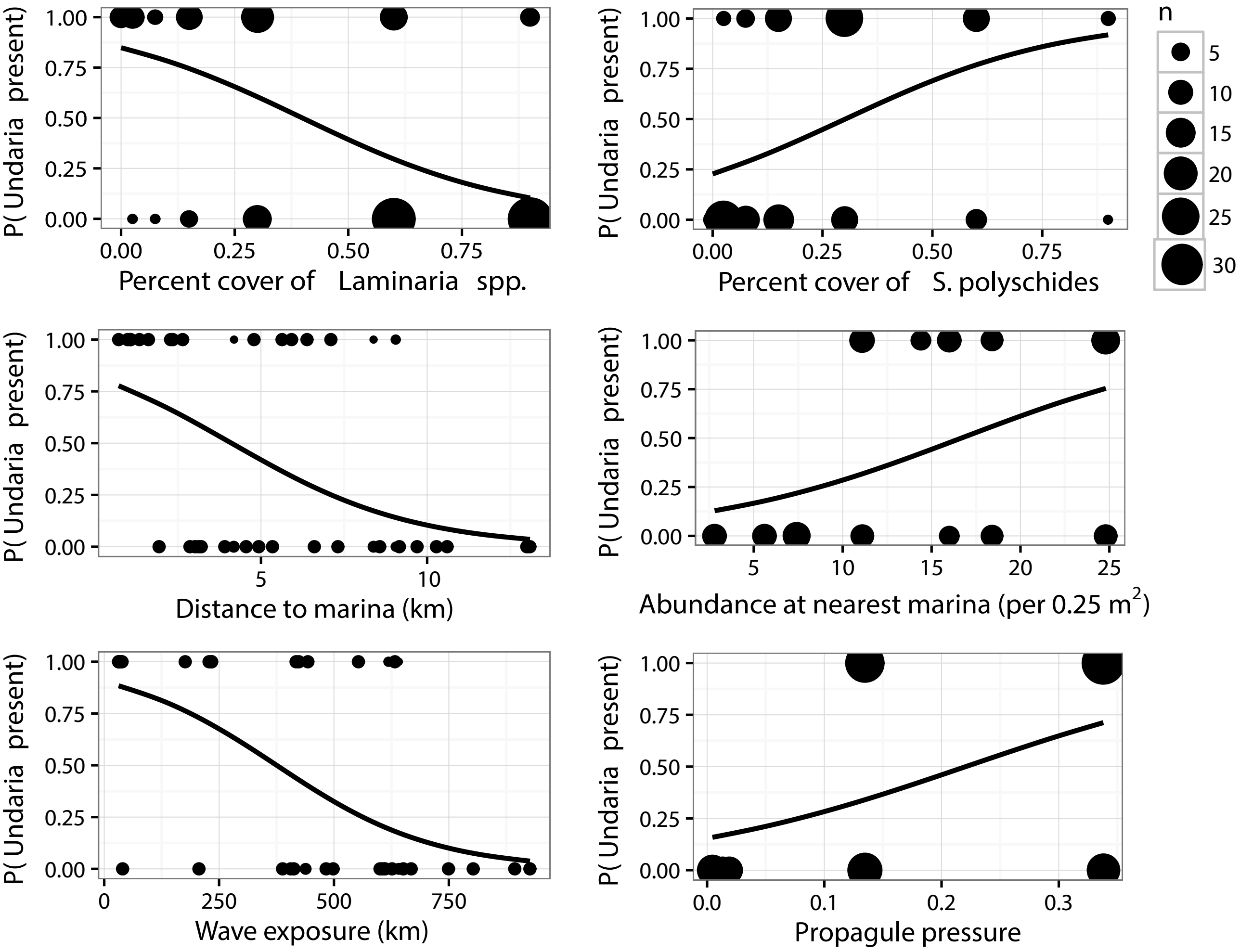


Figure 2.7: Relationship between key predictor variables selected in the zero portion of the optimal ZINB models (A8 and S8) and *Undaria* presence-absence. Size of points is equivalent to number of transects (n). Significance determined by binomial GLMs are indicated by plotted lines of fitted values for the probability of *Undaria* presence across the sampled range of the predictor.

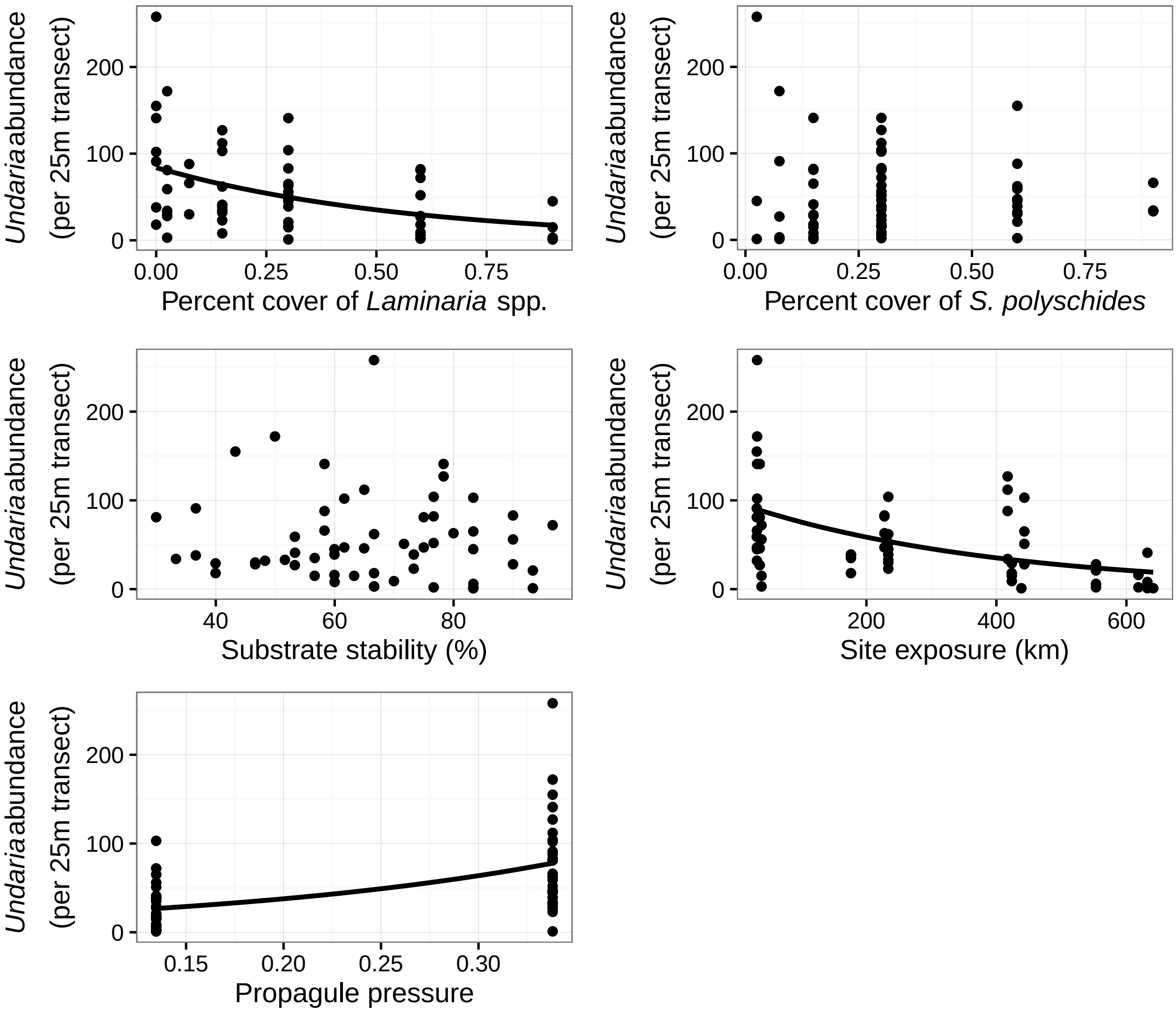


FIGURE 2.8: Relationship between key predictor variables selected in the count portion of the optimal ZINB model (A8) and *Undaria* abundance. Significance determined by negative binomial GLMs are indicated by plotted lines of fitted values for the abundance of *Undaria* across the sampled range of the predictor.

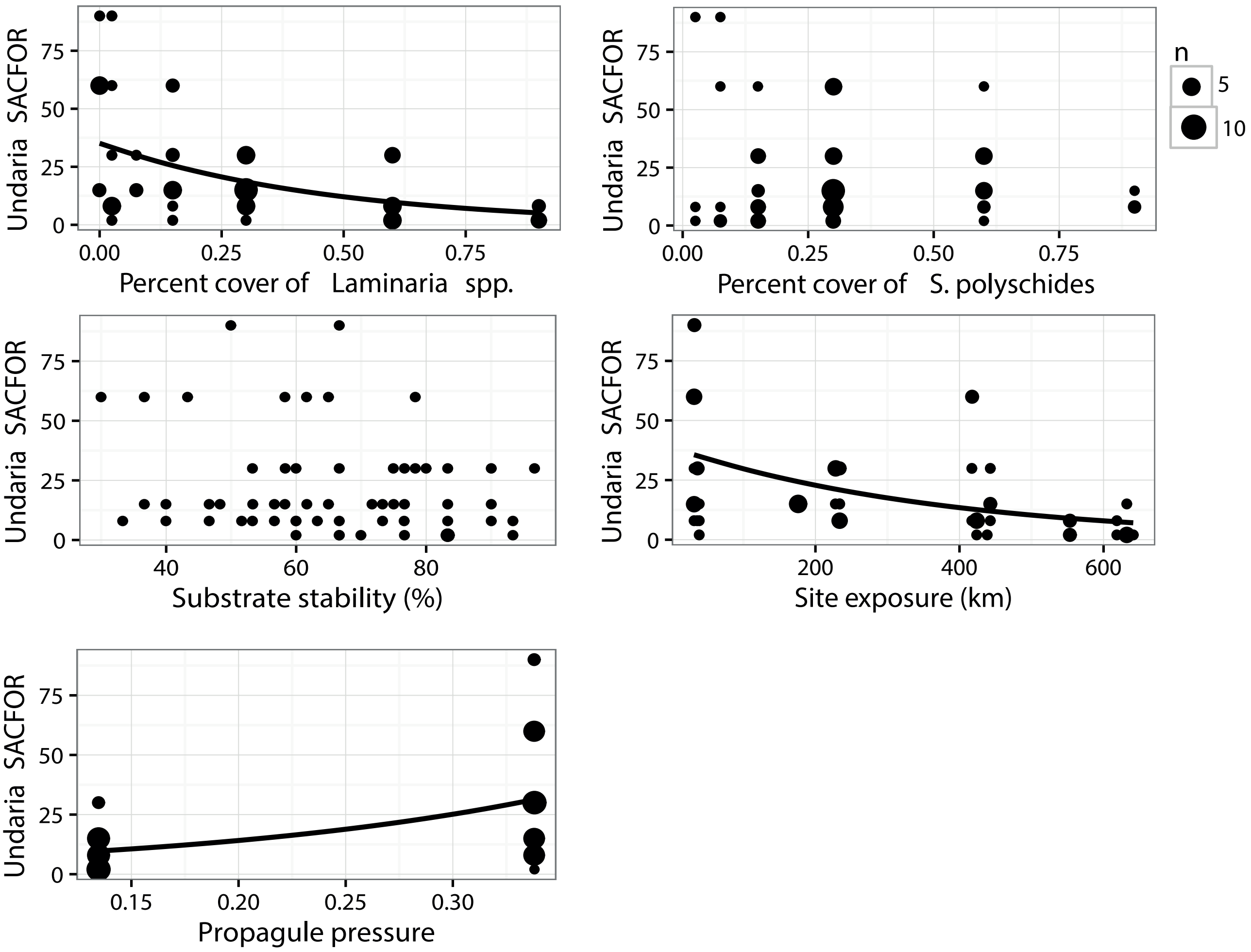


FIGURE 2.9: Relationship between key predictor variables selected in the count portion of the optimal ZINB model (S8) and *Undaria* SACFOR. Size of points is equivalent to number of transects (n). Significance determined by negative binomial GLMs are indicated by plotted lines of fitted values for *Undaria* SACFOR across the sampled range of the predictor.

2.4 Discussion

2.4.1 Invasion pathways

The northeast Atlantic is a hotspot of *Undaria* invasion, yet a knowledge gap remains regarding the details of its invasion gateways and pathways (Floc'h *et al.*, 1996; Fletcher and Farrell, 1999; Minchin and Nunn, 2014). Overall this study supports the hypothesis that artificial habitats facilitate a spillover and spread of *Undaria* to natural rocky reef (Floc'h *et al.*, 1996; Cremades *et al.*, 2006; Farrell and Fletcher, 2006; Russell *et al.*, 2008; James and Shears, 2016a). Although this had been suggested for *Undaria* in the northeast Atlantic (Floc'h *et al.*, 1996; Cremades *et al.*, 2006; Farrell and Fletcher, 2006; Grulois *et al.*, 2011), it had yet to be robustly examined across multiple locations. In the southwest UK it seems that marinas act as 'strongholds' for *Undaria* and in many cases the species is restricted to these habitats. Attributes of the marinas themselves, including their proximity to reef sites and the abundance and propagule pressure of *Undaria* they supported, had the strongest relationships with presence/absence patterns of *Undaria* within natural reef habitats. However, attributes of the recipient site, particularly the structure of the native macroalgal canopy and wave exposure, also strongly influenced the probability of *Undaria* occurrence. When *Undaria* was present, natural biotic and abiotic factors including the percent cover of *Laminaria* spp. and wave exposure had the largest impact on the abundance and cover of *Undaria*.

2.4.2 Marina habitats

Undaria is now a dominant fouling species in marinas across the southwest UK. This is unsurprising given its ability to proliferate on artificial substrates (Floc'h *et al.*, 1996; Fletcher and Farrell, 1999; Cremades *et al.*, 2006; Russell *et al.*, 2008; Veiga *et al.*, 2014; Kaplanis *et al.*, 2016) and its prevalence in UK marinas (Fletcher and Farrell, 1999; Heiser *et al.*, 2014; Kraan, 2016; NBN, 2017). Indeed, *Undaria* is now more abundant than native kelp species at most marinas surveyed during the current study (Epstein pers obs.). This observation would support disturbance experiments which indicate that *Undaria* may out-compete native seaweeds in artificial habitats, including marinas within the UK (Curiel *et al.*, 2001; Farrell and Fletcher, 2006). There was, however, high variation in the abundance, biomass and percent cover of *Undaria* between marinas in this study. This is likely to be based on a variety of biotic and abiotic factors including competition, disturbance, temperature and light (Farrell and Fletcher, 2006; Schiel and Thompson, 2012).

The widespread development of marinas across the UK is creating large surface areas of artificial hard substrate, which is held at a constant shallow depth in sheltered conditions; ideal for *Undaria* growth (Farrell and Fletcher, 2006; Minchin and Nunn, 2014;

Veiga *et al.*, 2014; Kaplanis *et al.*, 2016). Maximum areal extent of marinas within a given location was over 0.5 km^2 (Plymouth Sound), with Torbay (0.29 km^2) and Dartmouth (0.20 km^2) also having considerable total surface areas of marinas. The high abundance and spatial coverage of *Undaria* on these substrates creates considerable propagule pressure; and therefore some spillover of *Undaria* to nearby natural habitats could be expected. This study shows, however, that in many cases *Undaria* is confined to marina habitats. *Undaria* was recorded on natural rocky reef in only 2 of the 5 locations (i.e. 40%), 17 of 35 sites (49%), and 60 of 140 transects (43%). This confinement to marina or harbour environments is not uncommon for the species and is similar to non-native populations from other locations including the USA (Silva *et al.*, 2002; Kaplanis *et al.*, 2016) and Portugal (Veiga *et al.*, 2014). It has been suggested that *Undaria* may have a lower competitive ability in natural habitats, which may account for its confinement to artificial substrates in certain areas (Floc'h *et al.*, 1996; Curiel *et al.*, 2001; Forrest and Taylor, 2002; Valentine and Johnson, 2003; Edgar *et al.*, 2004; Farrell and Fletcher, 2006; Dellatorre *et al.*, 2014; De Leij *et al.*, 2017).

2.4.3 Rocky reef habitats

Where *Undaria* was present on natural substrates its abundance and percent cover was highly variable over relatively small spatial scales. In both Torbay and Plymouth Sound *Undaria* ranged from Superabundant/Abundant to Rare, with as few as 1 or 2 plants seen at some sites compared to well over 100 within a single transect at many others. As with findings from *Undaria* distribution studies in many other locations (Castric-Fey *et al.*, 1993; Cremades *et al.*, 2006; Martin and Bastida, 2008; Russell *et al.*, 2008), this suggests that when *Undaria* has colonised natural habitats there are a variety of factors which will influence its abundance and proliferation.

The two factors that had the strongest relationships with *Undaria* presence-absence at rocky reef sites were the distance to nearest marina and *Undaria* abundance at the nearest marina. For example, *Undaria* was not recorded at any sites >9.1 km away from the nearest marina, or where the nearest marina had an abundance of <11.1 individuals per 0.25m^2. These factors had a similar relationship to the abundance and cover of *Undaria* in natural habitats. Marina propagule pressure also had a significant relationship with *Undaria* presence-absence, abundance and percent cover. Indeed, *Undaria* was not recorded at any sites with propagule pressure under 0.13, and was more abundant and prominent within macroalgal canopies in locations with higher propagule pressure.

These patterns support the idea that the presence of *Undaria* on coastal reefs is heavily influenced by the build-up and eventual ‘spillover’ from artificial habitats. In many parts of its non-native range (New Zealand, Spain, France and the UK), the spillover from artificial to natural habitats has been suggested as an important mechanism in its invasion dynamics. This includes from harbours and marinas (Floc'h *et al.*, 1996; Cremades *et al.*, 2006; Farrell and Fletcher, 2006; Russell *et al.*, 2008), aquaculture sites (Cremades *et al.*, 2006; James and Shears, 2016a) and algal mariculture sites (Floc'h *et al.*, 1996). This study provides the first empirical evidence of spillover from artificial to natural habitats in the UK.

The spillover can, however, be a slow process. In the UK *Undaria* was present in a marina for 7 years before it was found on the adjacent rocky shoreline only 200 meters away (Farrell and Fletcher, 2006); while in a harbour of New Zealand *Undaria* was widespread in artificial habitats but took 9 years to spread to natural substrates (Russell *et al.*, 2008). The date of first record at a given marina is likely to give a poor estimate of true residence time, therefore this factor was not used in the statistical analysis of this study (see Methods section). Residence time is, however, likely to be a factor that influences the abundance and percent cover of *Undaria* at marinas, consequent propagule pressure at nearby reefs, and therefore its potential spillover. Within this survey the two locations with longest known introductions (Plymouth and Torbay) were the only two locations where *Undaria* was recorded on rocky-reef. The locations with shortest times since first record (Newlyn and Dartmouth, 3 and 5 years respectively) also had the lowest abundance, and one of the lowest percent covers at marinas. Over time, if the abundance and percent cover of *Undaria* increases at these sites, a spillover to reefs may become more likely. However, *Undaria* was absent along the rocky shoreline of Salcombe, despite the fact that it has persisted in the marina for at least 10 years, which may be due to other factors affecting overall propagule pressure, such as areal extent of marinas or the connectivity to nearby reef. Lag-time may be due to a slow build-up of propagule pressure in artificial habitats, eventually reaching a threshold which promotes spillover into natural habitats. In this study, the greater probability of occurrence, abundance and cover of *Undaria* at coastal sites in locations with higher marina propagule pressure lends support for this mechanism.

It should be noted that this survey specifically investigated marina populations, and a number of stratified rocky-reef sites around these marinas. There is potential for *Undaria* to be present on other artificial and natural substrates which were not included as part of this survey, which may therefore influence the distribution-abundance patterns of *Undaria* at the surveyed marina and reef sites. However, the survey design was considered appropriate to elucidate the link between marinas and the spread and distribution of *Undaria* at rocky-reef sites and was optimal given the constraints of the available time and resources. Further studies should investigate the influence of other artificial substrates on the spread of *Undaria.* Structures such as moorings, coastal defence, piers and bridges could act as important stepping-stones for further dispersal.

2.4.4 Species specific interactions

The structure of the native brown macroalgal canopy was strongly related to *Undaria* populations in natural reef habitats, as a lower coverage of *Laminaria* spp. was associated with a higher probability of occurrence and greater abundance and percent cover of *Undaria*. *Laminaria* spp. (i.e. *L. digitata*, *L. hyperborea* and *L. ochroleuca*) are the dominant canopy forming macroalgae along open rocky coastlines of the northeast Atlantic (Smale *et al.*, 2013). They are large, long-lived perennial macroalgae with high competitive ability (Bartsch *et al.*, 2008; Smale *et al.*, 2013). In comparison, *Undaria* is considered to be opportunistic, with a fast growth rate, a short annual life-cycle and high investment in reproductive output (Saito, 1975; Choi *et al.*, 2007; Schiel and Thompson, 2012). As such, it has been suggested that *Undaria* would be competitively inferior to *Laminaria* spp. in natural reef habitats of the UK (Fletcher and Farrell, 1999; Farrell and Fletcher, 2006; Heiser *et al.*, 2014; Minchin and Nunn, 2014; De Leij *et al.*, 2017). In its native Japan and Korea, *Undaria* functions as a pioneer species in many environments, typical of early successional stages (Agatsuma *et al.*, 1997; Kim *et al.*, 2016), and this opportunistic strategy is seemingly mirrored in many parts of its non-native range. Disturbance to native canopies is often key to the recruitment and proliferation of non-native *Undaria* (Valentine and Johnson, 2003; Thompson and Schiel, 2012; Carnell and Keough, 2014; De Leij *et al.*, 2017), and distributional studies in France, New Zealand, Argentina and the UK have shown that *Undaria* occurs more commonly and at higher abundance when native macroalgal canopies have less cover (Castric-Fey *et al.*, 1993; Martin and Bastida, 2008; Dellatorre *et al.*, 2014; Heiser *et al.*, 2014; Jiménez *et al.*, 2015; South and Thomsen, 2016; De Leij *et al.*, 2017). The results of this study support these findings across multiple sites and locations, with *Laminaria* spp. exerting a strong influence over *Undaria* presence-absence, abundance and percent cover. As the persistence of dense, intact *Laminaria* canopies may restrict the proliferation of *Undaria* in rocky reef habitats, preserving this biotic resistance by maintaining good environmental conditions could provide an additional management option to the direct control or exclusion of *Undaria*.

Undaria was, however, found in 16 transects where *Laminaria* spp. percent cover was recorded as Abundant (40-79%) or Superabundant (> 80%). In the majority of these transects *Undaria* was Rare or Occasional; however at three sites (Jennycliff, Fort Bovisand and Beacon Cove) *Undaria* was recorded as Common with an abundance of >70 sporophytes per 25 m transect. Although the native *Laminaria* canopy in the UK seems to have an inhibitive effect on *Undaria* (Farrell and Fletcher, 2006; De Leij *et al.*, 2017), these results indicate that in certain conditions they are able to co-exist at relatively high abundance and percent cover. These refugia among dense native canopies may allow *Undaria* to build up propagule pressure within natural substrates; removal or disturbance of the native canopy may therefore not be a proviso to *Undaria* presence or spread.

The relationship between *Undaria* and *S. polyschides* was less clear. In the ZINB model a higher coverage of *S. polyschides* was positively associated with occurrence of *Undaria*, but had a negative relationship with abundance and percent cover of *Undaria*. Further investigation showed a significant pattern of co-occurrence of the two species, but the negative relationship with abundance and cover of *Undaria* was less well defined. *Undaria* and *S. polyschides* are known to have a similar niche and life history (Norton and Burrows, 1969; Castric-Fey *et al.*, 1993; Yesson *et al.*, 2015). Both are annual kelps with peak recruitment in late winter to early spring, maximal growth and biomass in late spring, and senescence through autumn (Norton and Burrows, 1969; Floc'h *et al.*, 1991; Castric-Fey *et al.*, 1999a; Fletcher and Farrell, 1999). They are both opportunistic when compared to *Laminaria* spp., with high growth rates and reproductive outputs, and are both found at highest abundance and cover in the low intertidal-shallow subtidal fringe (Norton and Burrows, 1969; Floc'h *et al.*, 1991; Castric-Fey *et al.*, 1993; Floc'h *et al.*, 1996; Castric-Fey *et al.*, 1999b; Fletcher and Farrell, 1999). The positive relationship recorded between *Undaria* occurrence and *S. polyschides* cover may be indicative of overlapping niches. However, due to their similarities, the presence of direct competition between these species has previously been suggested (Castric-Fey *et al.*, 1993; Fletcher and Farrell, 1999; Farrell and Fletcher, 2006). This could be the cause of the negative relationship between *Undaria* abundance/cover and *S. polyschides* cover found within this study; perhaps with *Undaria* outcompeting *S. polyschides* under certain environmental conditions.

2.4.5 Influence of abiotic factors

Wave exposure was also an important determinant of *Undaria* presence-absence, abundance and percent cover in natural habitats as *Undaria* was not recorded at sites with total wave fetch >642 km, while abundance and cover was generally greater at more sheltered sites. Across its native and non-native range *Undaria* is generally found at highest abundance in 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 its lamina *Undaria* is susceptible to wave action and is generally absent from highly exposed shores (Choi *et al.*, 2007; Yesson *et al.*, 2015). Periods of low water motion are also needed for high natural recruitment, with spore adhesion optimal at low water velocities (Saito, 1975; Pang and Shan, 2008). This study showed that on coastal sites in the southwest UK *Undaria* is highly influenced by local scale differences in exposure and may be limited or excluded from some areas due to the lack of suitable rocky substrates in sheltered settings.

A similar study carried out in northern New Zealand investigated the association between *Undaria* in mussel farms (the key habitat for *Undaria* colonisation in that region) and adjacent rocky-reef (James and Shears, 2016a). Similar to this study, *Undaria* was more commonly found on artificial substrates where it also reached significantly higher abundance compared to natural reef sites. At natural reef sites *Undaria* was found at only 8 sites (compared to 33 mussel farm sites), and was most strongly related to distance from shore, mussel farm size and mean abundance at farms; *Undaria* was also most abundant at reef sites which were lacking native macroalgal canopies. This aligns closely with the current study, as distance to and abundance at marinas, and native competitors, were major factors influencing *Undaria* presence-abundance patterns at reef sites. Both studies therefore suggest the potential spillover effects from artificial habitat sources to natural substrates, while also recognising the influence of natural biotic factors. One discrepancy between the studies is the influence of wave exposure, which was not identified as a significant factor influencing reef populations in northern New Zealand (James and Shears, 2016a). The influence of wave exposure is likely to be hard to quantify, with very local scale variations able to alter recruitment success (Saito, 1975; Pang and Shan, 2008; Russell *et al.*, 2008). *Undaria* has also been recorded in wave exposed environments in southern New Zealand (Russell *et al.*, 2008), but is generally found in sheltered environments in its native range and across the northeast Atlantic (Saito, 1975; Cremades *et al.*, 2006; Yesson *et al.*, 2015; Peteiro *et al.*, 2016). This may be due to local scale differences in wave dynamics, other related biotic factors, or different quantification or ranges of wave exposure.

The growth, recruitment and life-history of *Undaria* is known to be influenced by other environmental factors including light, salinity, nutrients and temperature (Saito, 1975; Floc'h *et al.*, 1991; Gao *et al.*, 2013; James and Shears, 2016a; Murphy, Johnson and Viard, 2017). Although these factors may have affected the abundance and distribution of *Undaria* in this study, its wide physiological niche means that their influence is likely to be small. Within its non-native range *Undaria* is known to occur in high abundance from the open coast to more estuarine environments with lower salinity, higher sediment and nutrient loading (Floc'h *et al.*, 1991; Curiel *et al.*, 2001; Russell *et al.*, 2008). *Undaria* sporophytes are able to survive salinities down to 11 psu and light compensation point can occur as low as 17 - <5 μmol m^{-2} s^{-1} (Saito, 1975; Watanabe *et al.*, 2014). *Undaria* is also viable over a wide range of light regimes, with light compensation point of sporophytes reached between 17 and <5 μmol m^{-2} s^{-1} and the gametophyte requiring irradiances over just 3 μmol m^{-2} s^{-1} for growth and maturation (Saito, 1975; Campbell *et al.*, 1999; Watanabe *et al.*, 2014; Epstein and Smale, 2017), This study was also carried out over a latitudinal gradient of just 0.4° and within similar enclosed near-coast environments and, as such, did not encompass wide gradients in temperature, light and salinity. Studies conducted over larger spatial scales may identify temperature, light and salinity as important predictor variables for *Undaria* distribution patterns.

2.4.6 Spatial and temporal context

Although the patterns recorded in this study are highly likely to be associated with the physical and biological attributes of the environment, it should be noted that the findings are based on an observational survey, which is correlative in nature and cannot directly determine causation. Although challenging to implement, long-term monitoring and manipulative experiments would be needed to fully elucidate the influence of the biotic and abiotic factors on *Undaria* populations. Genetic methods may also be useful to identify the flow of individuals between habitats and locations. Such methods have been used to link *Undaria* populations from natural and artificial habitats in the Bay of St Malo (Brittany), for example (Grulois *et al.*, 2011). Previous manipulative studies have also indicated the inhibitive effect of native perennial canopies on the abundance and distribution of *Undaria* in various regions (e.g. Valentine and Johnson, 2003; Edgar *et al.*, 2004; Thompson and Schiel, 2012; South and Thomsen, 2016; De Leij *et al.*, 2017). However, further work, including long-term press-removals, disturbance experiments with long term monitoring and recruitment studies would yield a better understanding of the strength and direction of effects from the various biotic and abiotic factors identified in this survey. This is particularly needed in the northeast Atlantic where these types of studies are generally lacking.

2.4.7 Management perspective

Due to their conservation value and the variety of ecological goods and services they provide, managing the ecological impacts of NNS in natural habitats could be considered as a priority over artificial or anthropogenic environments (Kueffer and Daehler, 2009). Where *Undaria* is confined to artificial habitats management may be deemed a low priority. However, the results of this study suggest that limiting the abundance and propagule pressure of *Undaria* in artificial habitats may restrict the likelihood of its spread and proliferation into surrounding natural rocky reef communities. Once present in natural habitats, the management or eradication of *Undaria* is highly challenging and often infeasible (Curiel *et al.*, 2001; Hewitt *et al.*, 2005; Thompson and Schiel, 2012). Management could, therefore, be targeted to areas where *Undaria* is still confined to artificial habitats, but are considered at high risk of spillover to adjacent natural habitats.

Management within New Zealand between 1997 and 2009 targeted specific areas of artificial and natural substrates in order to limit the further spread of *Undaria* (Forrest and Hopkins, 2013). Prolonged removal led to a large reduction in density on artificial port structures (1-5% of pre-managed density) and vessel infestation rates (31-56% of vessels infected in unmanaged ports, 0.06-1.3% infected in managed ports). Although this sustained regional-scale management effort was successful in limiting local populations, reintroduction and wider-scale spread still occurred, therefore making the cost and effort of management attempts hard to justify (Forrest and Hopkins, 2013). In the current study, two of the survey locations (Plymouth Sound and Salcombe) are managed and protected under legal designations. In Plymouth Sound, *Undaria* is now a conspicuous component of native communities (Heiser *et al.*, 2014; Arnold *et al.*, 2016) and there is a pressing need to identify the level of ecological impact. Here, management actions aimed at reducing its abundance or spatial extent would likely be ineffective. In Salcombe, however, if *Undaria* is truly restricted to artificial habitats, management actions aimed at maintaining the biotic resistance of local native communities and limiting its abundance and propagule pressure within marinas could prove fruitful. This is likely to only be effective if accompanied by strict biosecurity (to avoid re-introduction) and long term commitments to management.

It is evident that NNS are now prevalent in the marine environment (Ruiz *et al.*, 1997; Bax *et al.*, 2003) and are often highly abundant in artificial habitats (Glasby *et al.*, 2007; Ruiz *et al.*, 2009; Bulleri and Chapman, 2010). The potential for artificial structures to facilitate the spread of marine NNS both geographically and across different habitats has been highlighted for other non-native flora and fauna (Bax *et al.*, 2003; Glasby *et al.*, 2007; Ruiz *et al.*, 2009; Bulleri and Chapman, 2010; Airoldi *et al.*, 2015). However, in many cases NNS remain constrained to these artificial habitats (Coutts and Forrest, 2007; Dafforn *et al.*, 2012; Airoldi *et al.*, 2015). The exact mechanisms behind why some marine NNS remain constrained in their distribution, while others readily proliferate across multiple habitat types and wide spatial scales will be challenging to define. As shown for *Undaria*, spread of a NNS is likely to be strongly influenced by variability in propagule pressure and habitat suitability. Due to the interconnected nature of the marine environment, the risk of spillover to natural substrates over various temporal scales is inevitable, unless management or eradication of the NNS is implemented. Identifying high risk areas, natural boundaries and factors affecting the spread and abundance of NNS in natural habitats is key to future management prioritisation (Forrest *et al.*, 2009). This study should allow better decisions to be made regarding the management of one of the most prolific invasive macroalgae in the UK.

Chapter 3

Between-habitat variability in population dynamics

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3.1 Introduction

The spread of invasive non-native species (INNS) is recognised as a major threat to global biodiversity and the provision of ecological goods and services. As well as ecological impacts, INNS have major socioeconomic implications, causing losses of \$120 billion per year in the USA alone (Pimentel *et al.*, 2005; Williams *et al.*, 2010; Early *et al.*, 2016). Biosecurity measures are of principle importance in preventing the establishment and subsequent impacts of invasive non-native species. However, as no combination of biosecurity measures is entirely effective, active management of INNS within their non-native range is often needed (Simberloff *et al.*, 2013; Early *et al.*, 2016; McGeoch *et al.*, 2016; Seebens *et al.*, 2017). At the outset of an invasion process, an INNS will generally have a limited geographical range, relatively low propagule pressure, and have completed few reproduction cycles. It is therefore widely accepted that rapid response greatly increases the likelihood of eradication or containment (Beric and MacIsaac, 2015; Early *et al.*, 2016). Rapid response measures require decisive action but relatively minimal understanding of the biology or ecology of an INNS (Simberloff, 2003). If an INNS is not removed, it is likely to increase its geographical range, population size and propagule pressure over time. Where this occurs, management activities may be constrained to limiting the size of populations or reducing their spread (Fraser *et al.*, 2006; Hulme, 2006;

Simberloff *et al.*, 2013). In these situations, information on the biology and ecology of an INNS is critical for effectively designing and implementing management measures (Sakai *et al.*, 2001; Simberloff, 2003).

Information on the population dynamics of INNS is also important to improve the wider understanding of general ecological processes, and to achieve a more holistic view of INNS management (Sakai *et al.*, 2001). Differing life-history and morphological traits can exert a strong influence on a species' invasiveness, spread and ecological impact within recipient communities (Williamson and Fitter, 1996b; Kolar and Lodge, 2001; Duyck *et al.*, 2007; Ricciardi and Cohen, 2007; Bauer, 2012). In some cases, information on the traits or behaviours of an INNS may be available from within its native range, which can be useful in determining management options. However, as INNS often exhibit high phenotypic or genetic plasticity, traits and attributes recorded in the native range may differ from those exhibited within a non-native range (Williamson and Fitter, 1996b; Kolar and Lodge, 2001; Zenni *et al.*, 2014). INNS can also be found in differing habitat types in their non-native range, where they are often associated with modified or artificial habitats, rather than natural habitats which may be more suitable in their native range (Glasby *et al.*, 2007; Airoldi *et al.*, 2015). As such, predicting an invader's traits based on its native ecology is problematic, and highlights the need for site-specific studies. Determining how the population biology of an INNS varies across regions or habitats should improve our understanding of potential impacts and, consequently, inform management decisions and design of efficient and effective control methods.

The invasive kelp, *Undaria pinnatifida* (hereafter referred to as *Undaria*), is one of the most widespread marine invaders, and can now be found in many parts of the northeast and southwest Atlantic, southwest and east Pacific, and the Tasman Sea (Epstein and Smale, 2017a). In its non-native range *Undaria* is predominantly recorded on artificial substrates, particularly floating structures within ports, marinas and aquaculture sites (Fletcher and Manfredi, 1995; Floc'h *et al.*, 1996; Cremades *et al.*, 2006; Veiga *et al.*, 2014; Kaplanis *et al.*, 2016; Epstein and Smale, 2017b). However, *Undaria* is also found in natural habitats throughout much of its non-native range, predominantly within shallow rocky reef habitats that are sheltered or moderately exposed to wave action (Fletcher and Farrell, 1999; Russell *et al.*, 2008; Dellatorre *et al.*, 2014; James and Shears, 2016a; Epstein and Smale, 2017b).

In its native range, *Undaria* is an over-wintering annual species found on rocky substrates from the low intertidal to 18 m depth (Saito, 1975). It is also a major mariculture species, primarily grown on seeded ropes held at shallow depths (Yamanaka and Akiyama, 1993). Due to its importance in mariculture, a considerable volume of research has been conducted on native populations to examine reproduction, morphology, physiology, chemical properties and population dynamics in both natural and artificial habitats (e.g. Matsuyama, 1983; Skriptsova *et al.*, 2004; Choi *et al.*, 2007; Nanba *et* *al.*, 2011; Shibneva *et al.*, 2013; Watanabe *et al.*, 2014). In its non-native range, several population studies have been conducted - primarily in Australasia but also in the USA and Argentina - either in natural or artificial habitats, but not both (Thornber *et al.*, 2004; Schaffelke *et al.*, 2005; Casas *et al.*, 2008; Primo *et al.*, 2010; Schiel and Thompson, 2012; James and Shears, 2016b). In the northeast Atlantic, where *Undaria* has been present since the early 1980s, understanding of its population dynamics remains severely limited (Castric-Fey *et al.*, 1999a; Cremades *et al.*, 2006; Murphy *et al.*, 2016; Murphy *et al.*, 2017). Furthermore, as *Undaria* is known to exhibit a relatively plastic life-history and morphology (Nanba *et al.*, 2011; Schiel and Thompson, 2012; Shibneva *et al.*, 2013; James *et al.*, 2015; James and Shears, 2016b), formal examinations of population-level variability between habitats types and environmental settings are needed to better understand its non-native biology and potential role within invaded systems. Any dissimilarity in population dynamics between habitats could mediate its impacts upon native flora and fauna and have important implications for management decisions.

Undaria was first recorded in the UK in 1994, attached to floating marina pontoons in Port Hamble (Fletcher and Manfredi, 1995), but can now be found across much of the UK, predominantly on artificial structures such as marina and harbour pontoons (Fletcher and Farrell, 1999; Heiser *et al.*, 2014; Minchin and Nunn, 2014; Kraan, 2016; Epstein and Smale, 2017b). In some areas *Undaria* has also been recorded on natural rocky substrates (Fletcher and Farrell, 1999; Heiser *et al.*, 2014; Arnold *et al.*, 2016; De Leij *et al.*, 2017; Epstein and Smale, 2017b). Although *Undaria* has been present in the UK for almost 25 years, there remains a dearth of information regarding its population dynamics, even though it is listed as a priority species for monitoring and surveillance as part of obligations to the Marine Strategy Framework Directive (Stebbing *et al.*, 2015). In this study, we examined spatiotemporal variability in population structure, reproductive activity and morphology of *Undaria* over 2 years at 9 sites, representing 3 habitat types: subtidal rocky reef, intertidal rocky reef and marina pontoons. The aim was to: (i) characterise spatiotemporal variability in the population structure of *Undaria* in its non-native range; (ii) determine the influence of habitat-type on the population dynamics and morphology of *Undaria*; (iii) consider how variability patterns may affect potential management. The over-arching objective was to adopt *Undaria* as a case study to examine how environmental setting may mediate population dynamics of marine INNS in general and, in turn, influence approaches to management.

3.2 Materials and methods

3.2.1 Site selection

Plymouth Sound is one of few areas in the UK where *Undaria* is widespread in both artificial and natural habitats (Epstein and Smale, 2017b). It was first recorded in 2003 within marinas and in 2011 on natural substrates (NBN, 2017). Due to the widespread distribution of *Undaria* (Heiser *et al.*, 2014; Arnold *et al.*, 2016; De Leij *et al.*, 2017; Epstein and Smale, 2017b), the extensive areas of intertidal and subtidal rocky-reef, as well as numerous marinas (Knights *et al.*, 2016), Plymouth Sound is an ideal location to conduct long-term studies on *Undaria* populations.

Selection of 9 long-term study sites (3 each of intertidal reef, subtidal reef and marinas) was carried out between 10th March and 5th April 2016. Sites were chosen based on the following criteria: (i) available safe access points; (ii) approval to conduct scientific work; (iii) widespread occurrence of *Undaria* (based on previous information or *in-situ* sightings); (iv) limited human disturbance; (v) similar substrate type within habitats; (vi) extensive suitable substrate ($\geq 40m^2$ in marinas, $\geq 100m^2$ in reef sites). During the site selection process, visual searches of the low intertidal zone were conducted across the Plymouth waterfront and at Mount Batten (Figure 3.1); subtidal searches were conducted at 7 sites across the same area by SCUBA; while site visits and discussions for permissions to work at marinas were conducted at 4 locations (Figure 3.1). Further local knowledge on suitability of sites and *Undaria* status were gained for both rocky reef (Smale, pers. comm.) and marinas (Wood, pers. comm.). Three marina and reef sites were selected across the Plymouth waterfront, with subtidal reef sites deeper and adjacent to intertidal reef sites (Figure 3.1).

The intertidal and subtidal rocky reef sites were all sheltered to moderately-sheltered from wave action and were characterised by extensive bedrock platforms interspersed with areas of larger boulders and compacted cobbles. The marina sites were distributed along the Plymouth waterfront all within sheltered, non-drying harbours, with similar concrete pontoon constructions (Figure 3.1). At reef sites, in order to aid relocation, permanent markers were placed at each site; a stainless steel screw and coloured markers were fixed to the shore at intertidal sites, and a large clump-weight with a sub-surface marker buoy was placed at each subtidal site. A light and temperature sensor (HOBO Temperature/Light weather-proof Pendant Data Logger 16k, Onset) was also deployed for the duration of the study, recording temperature (in degrees Celsius) and illuminance (lux) at 30min intervals. The loggers were attached to permanent markers at reef sites, or adjacent to the pontoons at marinas.

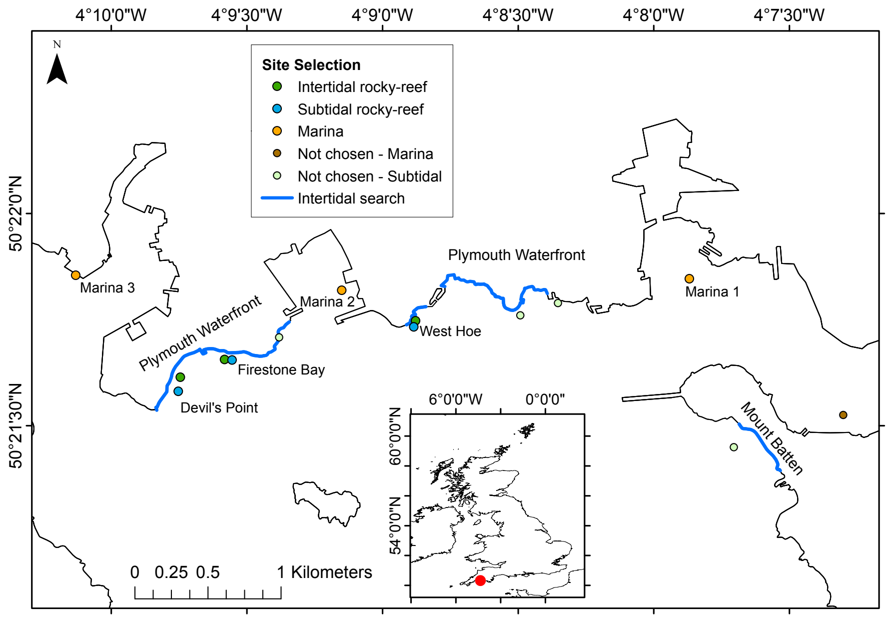

Figure 3.1: Study sites in Plymouth Sound (location of Plymouth within the UK shown as red point on inset map). Selection of 9 long-term study sites, 3 each of intertidal rocky-reef (large green points) subtidal rocky-reef (large blue points) and marinas (large orange points), was carried out in March-April 2016. This included visual searches of the low intertidal zone (blue line), subtidal searches (green points) and marina site visits (brown points).

3.2.2 Sampling and population structure

Sampling of *Undaria* populations was carried out every 3 months (March, June, September, December) from March 2016 to December 2017, with all 9 sites sampled within a 2-week period during each sampling event. As *Undaria* is predominantly found in the low intertidal to shallow subtidal zone of rocky-reefs (Saito, 1975; Fletcher and Farrell, 1999; Heiser *et al.*, 2014), subtidal sites were restricted to depths of 0.5 - 1.2 m below chart datum and intertidal sites to 0.3 - 1 m above chart datum. At each sampling event 10 x 0.25 m^2 haphazard quadrats (stratified to rocky substrate) were placed within an area of approximately 100 m^2 around the permanent marker at each site. Due to the large size of the sampling area it is highly unlikely that quadrats would have been placed in directly the same location over the 8 sampling events. All subtidal sites were sampled using SCUBA, and when the tidal range allowed intertidal sites were sampled on low-spring tides, otherwise all sampling was carried out by SCUBA.

Sampling within marinas was carried out on the vertical sides of floating pontoons, with the entire area being fully immersed at all times; the depth of the sampling area was therefore 0 - 0.4 m below the surface. During each sampling event, 10 x 0.25 m^2 haphazardly placed quadrats were positioned blindly against the pontoon surface. Sampling was restricted to approximately 40 m^2 of pontoon surface in the outer section of the marina based on substrate suitability, interactions with vessels and human disturbance. Due to the relatively limited area available for sampling, a note of the position of each quadrat was taken to avoid overlapping quadrat samples during the study.

All visible *Undaria* sporophytes were removed from each quadrat by gently prising the holdfast from the substrate, and were placed into collection bags and returned to the laboratory for further analysis. Most individuals could be identified to species by eye, however when needed, confirmation of the species as *Undaria* was carried out using light-microscopy and the presence of Yendo cells (Castric-Fey *et al.*, 1999b, Figure 3.2). For each quadrat the *Undaria* sporophytes were sorted into developmental stages (Figure 3.2, Table 3.1), based on a categorical classification system numbered from 0 to 5 (adapted from Casas *et al.*, 2008). The abundance and biomass of *Undaria* sporophytes categorised to each developmental stage was recorded for each quadrat separately.

3.2.3 Morphology

To quantify spatiotemporal variability in *Undaria* sporophyte morphology, up to 10 random sporophytes representing each developmental stage were randomly selected and retained from each site, during every sampling event. Attributes measured to the nearest 0.1 cm were: Stipe width (SW), stipe length (SL), lamina width (LW), lamina length (LL), sporophyll width (SPW) and sporophyll length (SPL) (Figure 3.3). Dependent on the developmental stage, different morphological attributes were recorded based on their presence and appropriateness for describing the morphology (developmental stage 0 & 1 = SW, SL, LW, LL; developmental stage 2, 3 & 4 = SL, LW, LL, SPW, SPL; developmental stage 5 = SW, SL, SPW, SPL).

TABLE 3.1: Description of *Undaria pinnatifida* developmental stages as shown in Figure 3.2. Classification adapted from Casas *et al.* (2008).

Developmental stage	Developmental category	Description
Stage 0	Recruit	No defined midrib or pinnate blade divisions. Identified as *Undaria* due to presence of Yendo cells (as shown in first image of Figure 3.2).
Stage 1	Recruit	Defined midrib and pinnate blade divisions, no sporophyll.
Stage 2	Mature	As stage 1 but with ruffled sporophyll which does not surround the stipe.
Stage 3	Mature	As stage 1 but with ruffled sporophyll surrounding the stipe.
Stage 4	Senescing	Decaying sporophyte identified by dark coloration of blade and sporophyll, and distinct morphology of blade.
Stage 5	Senescing	Blade completely lost; with or without sporophyll.

Figure 3.2: Developmental stages of *Undaria pinnatifida* sporophytes (adapted from Casas *et al.* 2008). Early-Mid-Late indicates growth towards the next developmental stage for comparative purposes; however this distinction was not recorded. Each box shows a single sporophyte with a magnified image of the sporophyll/stipe, except Stage 0 Early which shows two sporophytes and a magnified section of the outer part of the blade indicating the presence of Yendo cells (see Castric-Fey *et al.* 1999b). Table 3.1 describes each stage.

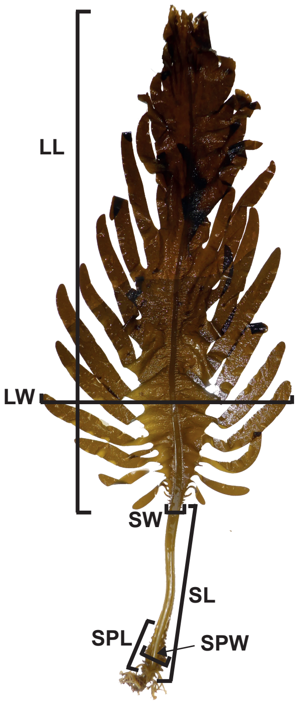

Figure 3.3: Morphological attributes measured for *Undaria pinnatifida* sporophytes (example shown is developmental stage 2). Attributes measured to the nearest 0.1 cm were: Stipe width (SW), stipe length (SL), lamina width (LW), lamina length (LL), sporophyll width (SPW) and sporophyll length (SPL).

3.2.4 Reproductive activity

Reproductive activity of *Undaria* populations was assessed using a standardised spore release method from a sample of mature sporophytes (method adapted from Schaffelke *et al.*, 2005). At each sampling event up to 10 random mature sporophytes (developmental stage 2 or 3, and SPW $>$ 2 cm) were selected from each site. Due to the seasonality of *Undaria* populations, 10 mature sporophytes were not always found across the 10 quadrats. Therefore, where mature sporophytes were found, the average sample size for each site was 7.7 sporophytes (ranging from 3-10 dependent on the sampling event). Where no reproductive sporophylls were found reproductive activity was assumed to be zero. As different parts of the sporophyll mature at different rates (Schaffelke *et al.*, 2005), 3 sub-samples of sporophyll tissue were taken from each sporophyte. Discs of 0.6 cm in diameter were punched from each sporophyll, one towards the top of the sporophyll, one from the middle and one from towards the bottom. Each disc was taken from the centre of the sporophyll lobe, and the total biomass of the three discs was recorded to the nearest 0.01 g. The remainder of the sporophyll was removed from the stipe and also weighed to the nearest 0.01 g. As a procedural control, 3 random samples of 0.6 cm diameter discs of non-reproductive blade tissue were also selected at each sampling event and site. All discs were wiped clean and patted dry using absorbent paper. They were then placed in individually labelled 2 ml eppendorf tubes and incubated overnight at 4°C in complete darkness. Following the incubation, 0.96 ml of room temperature 30 KDa filtered seawater was added to each tube to induce spore release, and was left for 1 hour. To end the spore release 0.04 ml of 10% formalin (diluted in filtered seawater) was then added to each tube and the sporophyll disc was removed using sterile forceps.

The number of spores within the 1 ml solution in each eppendorf was estimated using a BD Accuri C6© flow cytometer, using a 20 mW 488 nm solid state blue laser. *Undaria* zoospores are generally spherical, measuring approximately 4 μm in diameter upon release (Petrone *et al.*, 2011). Therefore, acquisition thresholds of forward light scatter (FSC; light scattered by particles at narrow angles in the same direction as the laser beam, recording a proxy of particle size) was set at 2,000, and red fluorescence (FL3; wavelength $>$ 670 nm) was set at 900. Based on previous experience these thresholds are considered appropriate for capturing autofluorescent picoplankton and small nanoplankton such as *Undaria* spores (van der Merwe *et al.*, 2014). A 30 μl subsample was analysed from each eppendorf at a flow rate of 66 μl/min and a core size of 22 μm. For each particle passing the laser, FL3 and side scatter (SSC; light scattered by particles at 90° to the direction of the laser beam, recording a proxy of particle size) values were recorded on logarithmic density plots generated using the BD Accuri CFlow© Plus software. These plots allowed for optimal distinction between instrument or water sample background noise and *Undaria* spores. Where spore release had occurred, a distinct "point cloud" could be identified on the density plots at values $>10^4$ FL3 and SSC (Figure 3.4), which is characteristic of autofluorescent phytoplankton of the size of *Undaria* spores (van der Merwe *et al.*, 2014). For each set of samples a single square electronic gate was drawn on the density plots around the point cloud to select the occurrence of spores. The number of particles within the gated region was then enumerated using the software. In order to remove further procedural noise, the average number of particles (rounded to the nearest whole spore) counted in the gated region of the three non-reproductive procedural control samples was subtracted from the count for each sporophyll sample (if the mean procedural count was greater than the number counted for a sample, the value was set as zero, not a negative value). Overall, this gave an estimate of the number of spores present in 30 μl of the solution in each eppendorf. Values were averaged for the 3 sub-samples of each sporophyll, and multiplied to gain two metrics of reproductive activity - number of spores released per cm^2 of sporophyll tissue, and total number of spores per sporophyll based on the percentage biomass of the 3 sporophyll discs from total sporophyll biomass.

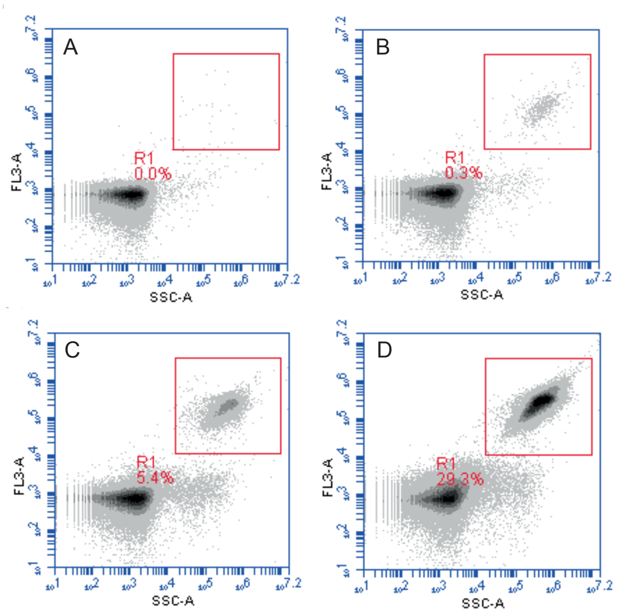

Figure 3.4: Example of flow cytometry density plots from a procedural control (A) and three sporophytes with varying reproductive activity (B-D). Side scatter (SSC-A; recording a proxy of particle size) is plotted against red fluorescence (FL3-A; wavelength > 670 nm). A single square electronic gate (red box) was drawn on density plots around the point cloud to select the occurrence of spores; its position was the same within each sample set.

3.2.5 Data Analysis

Mean abundance and biomass values for *Undaria* were generated for each site and sampling event (from n = 10 quadrats) prior to formal analysis. Reproductive activity was also averaged within site at each sampling event due to uneven sample sizes. Prior to statistical analysis all data were log transformed (log[x+1]) due to strong right-skewness and heterogeneity of variances. Using three-way ANOVA, values of abundance, biomass and reproductive activity were modelled as a function of "habitat" (categorical; 3 levels: Marina, Intertidal, Subtidal), "month" (categorical; 4 levels: March, June, September, December) and "year" (categorical; 2 levels: 2016, 2017). Optimal models were chosen using backward selection. A full model with all predictor variables and their interactions was constructed first, and model terms were serially excluded based on their complexity and their significance value (i.e. the coefficient with the highest complexity and lowest significance value was dropped and the model rerun). Terms were excluded until the next coefficient that would be dropped had a p value < 0.05. Each model was compared to the subsequent nested model using ANOVA to confirm that a significant term had not been excluded. Validation of the optimal model was carried out using diagnostic plots, and significant pairwise differences between habitats were tested using post hoc F-tests with Holm adjusted p-values.

Population structure was described by calculating the relative proportion of recruits, mature and senescing sporophytes within each site at every sampling event. Statistical differences in population structure were assessed using permutational ANOVA (PERMANOVA) on Bray-Curtis similarity matrices of untransformed proportion data (Anderson *et al.*, 2008; Clarke *et al.*, 2014). Using the same model design as above, a PERMANOVA was initially constructed using all coefficients and their interactions. Optimal model selection was carried out as above, until a coefficient with a p value >0.05 could not be dropped. Post hoc tests for the effect of individual habitats were carried out using pair-wise PERMANOVA, and similarity percentage breakdowns (SIMPER) were used to determine the principal contributors to the observed dissimilarity within significant pairwise contrasts.

Difference in morphology of *Undaria* between habitats was also assessed using multivariate techniques, with morphological attributes of individual plants treated as a multivariate response. For each developmental stage separately, morphological data were normalised (subtracting the mean and dividing by the standard deviation for each morphological attribute) in order to bring each attribute to comparable dimensionless scales. Resemblance matrices were constructed based on Euclidean distance, and the dissimilarity between habitats was visualised using threshold metric multidimensional scaling (tmMDS) on bootstrap averages with their 95% confidence regions. Statistical differences in morphology between habitats was assessed using PERMANOVA with Habitat (3 levels, fixed factor), and Site (6 levels, random factor nested within habitat) as the independent variables. Post hoc tests for the effect of individual habitat were carried out using pair-wise PERMANOVA.

All ANOVAs were constructed using the *lm* function from base R (R Core Team, 2017), and post hoc pairwise tests were carried out using the *testInteractions* function from the *phia* package (De Rosario-Martinez, 2015). All PERMANOVAs were run with 4999 permutations of residuals under a reduced model with Type 3 (partial) sums of squares. tmMDS plots were visualised using 50 restarts and a minimum stress of 0.01. Bootstrap averages were calculated with 100 bootstraps per group, with automatic selection of dimensions based on $\rho > 0.99$.

Univariate statistics were carried out in R 3.4.3 (R Core Team, 2017), multivariate statistics in PRIMER-e version 7 (Clarke *et al.*, 2014), data manipulation was carried out using *dplyr* (Wickham and Francois, 2015), graphs were created using *ggplot2* (Wickham, 2009) and mapping (Figure 3.1) was carried out within ArcMap 10.3.1. All mean values are presented ± Standard Error (SE).

3.3 Results

Undaria was recorded at all sites during every sampling event, with the exception of a single instance in the intertidal reef habitat at Firestone Bay, in December 2016. Maximum abundance and biomass values were both recorded on marina pontoons, with

50.9 *Undaria* per 0.25 m^2 recorded at marina 1 and 1.9 kg per 0.25 m^2 at marina 2, in June 2016. Across habitats, there was largely an annual cycle with abundance and biomass highest in June (11.0 ± 1.0 inds.0.25m^{-2} and 0.78 ± 0.06 kg.m^{-2})and lowest in December (2.7 ± 0.4 inds.0.25m^{-2} and 0.04 ± 0.01 kg.m^{-2}). There were, however, dissimilarities between habitats, with abundance and biomass generally highest within marinas and lowest on subtidal reefs (Figure 3.5). For both abundance and biomass there was significant Habitat*Month and Month*Year interactions indicating that the differences between habitats changed depending on month, and the monthly pattern differed between years (Table 3.2, Figure 3.5). Pairwise tests indicated that the abundance of *Undaria* was significantly higher in marinas when compared to subtidal reef habitats throughout the year, but only significantly higher than intertidal reef habitats in March and June. Intertidal reef habitats supported significantly higher abundances than subtidal habitats, but only in June and September (Table B.1). The significant difference in biomass between habitats was constrained to June, with marinas and intertidal reef greater than subtidal reef (Table B.1). Variation in monthly patterns between years was particularly distinct within reef habitats with higher abundance and biomass in March 2017, but lower in June and September 2017 when compared to the same months in 2016 (Figure 3.5).

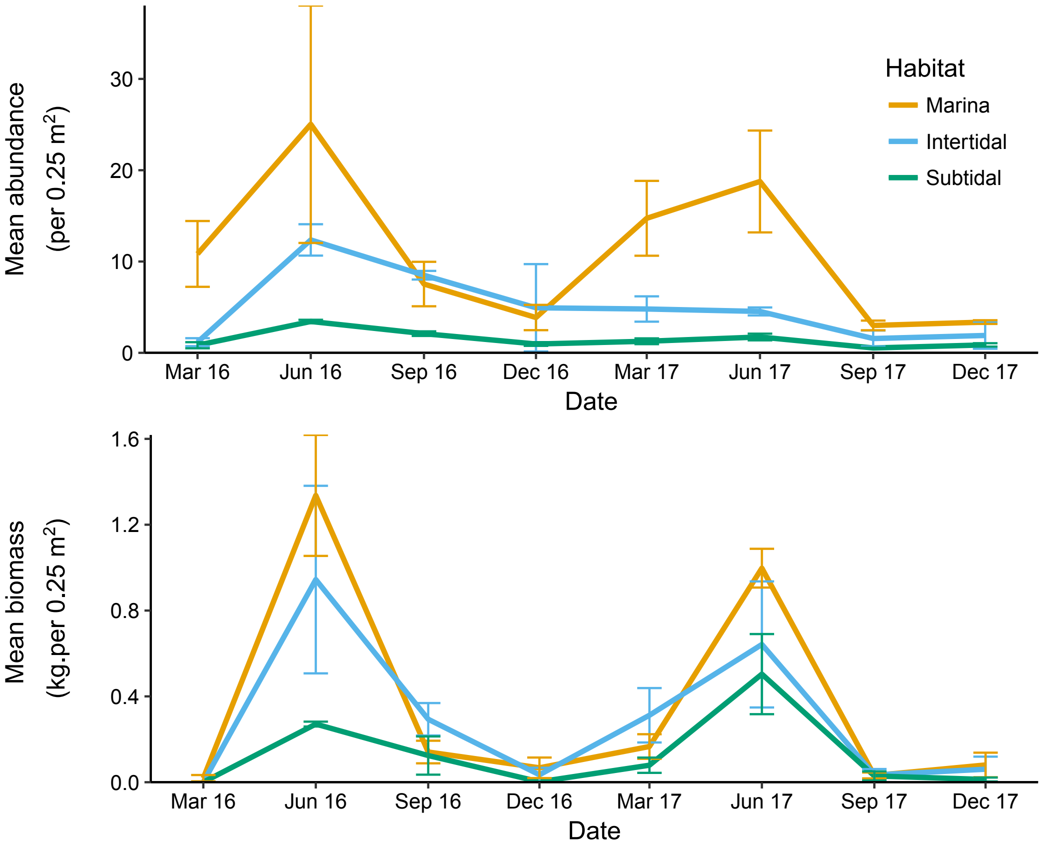

FIGURE 3.5: Mean abundance and biomass of *Undaria pinnatifida* (± standard error) found across the study period in each habitat (marina = orange, intertidal reef = blue, subtidal reef = green).

Table 3.2: Results from the optimal ANOVA models, testing for difference in the abundance and biomass [log(x+1)] of *Undaria pinnatifida* across the study period. The degrees of freedom (df), mean sum of squares (MS), F-value (F) and p-value (p) are shown for each coefficient. Significant coefficients shown in bold (α <0.05).

	Abundance				Biomass			
Coefficient	df	MS	F	p	df	MS	F	p
Habitat	**2**	**10.74**	**44.58**	**<0.001**	**2**	**0.13**	**7.64**	**0.001**
Month	**3**	**3.86**	**16.02**	**<0.001**	**3**	**0.99**	**57.87**	**<0.001**
Year	**1**	**1.12**	**4.66**	**0.035**	1	<0.01	0.01	0.931
Habitat*Month	**6**	**0.58**	**2.43**	**0.037**	**6**	**0.07**	**3.82**	**0.003**
Month*Year	**3**	**1.70**	**7.04**	**<0.001**	**3**	**0.07**	**3.95**	**0.013**

An overall annual cycle in terms of population structure was identified across habitats; peak recruitment was recorded in December and March (90 ± 4%, 89 ± 4% of sporophytes sampled were recruits in December and March respectively), mature sporophytes dominated in June (71% ± 4% of sporophytes mature in June), and senescence predominantly occurred in September (75 ± 7% of sporophytes senescing in September) (Figure 3.6). While the structure of populations on intertidal and subtidal reef habitats was similar across the study, the structure of populations on marina pontoons was distinct (Figure 3.6). Recruitment occurred over an extended period within marinas, with a higher proportion of recruits in June and September, outside of the main recruitment period. Populations in marinas were also generally more mixed, with a higher proportion of mature sporophytes in December and senescing sporophytes in June indicating more concurrent generations when compared to reef habitats (Figure 3.6). As recorded for abundance and biomass, the Habitat*Month and Month*Year interaction terms were also significant for population structure (Table 3.3). Pairwise tests between habitats indicated significant differences between marinas and intertidal reef habitats in March, June and September, and between marinas and subtidal reef habitats in June (Table B.2). This dissimilarity was predominantly due to more mixed populations of recruits, mature and senescing plants on marina pontoons when compared to the reef habitats (Table B.3). Comparing the proportion of individual developmental stages at each sampling event also indicated more mixed populations in marinas compared to intertidal and subtidal reef habitats (Figure 3.7; mean standard deviation: 0.044 in marinas, 0.067 subtidal, 0.075 intertidal). The significant Month*Year interaction was related to annual variation in population structure in March and June, with a higher proportion of mature sporophytes and a lower proportion of recruits in 2017 compared to 2016 (Figure 3.6). This dissimilarity occurred across all habitats but was more pronounced in intertidal and subtidal reef habitats than in marinas (Figure 3.6).

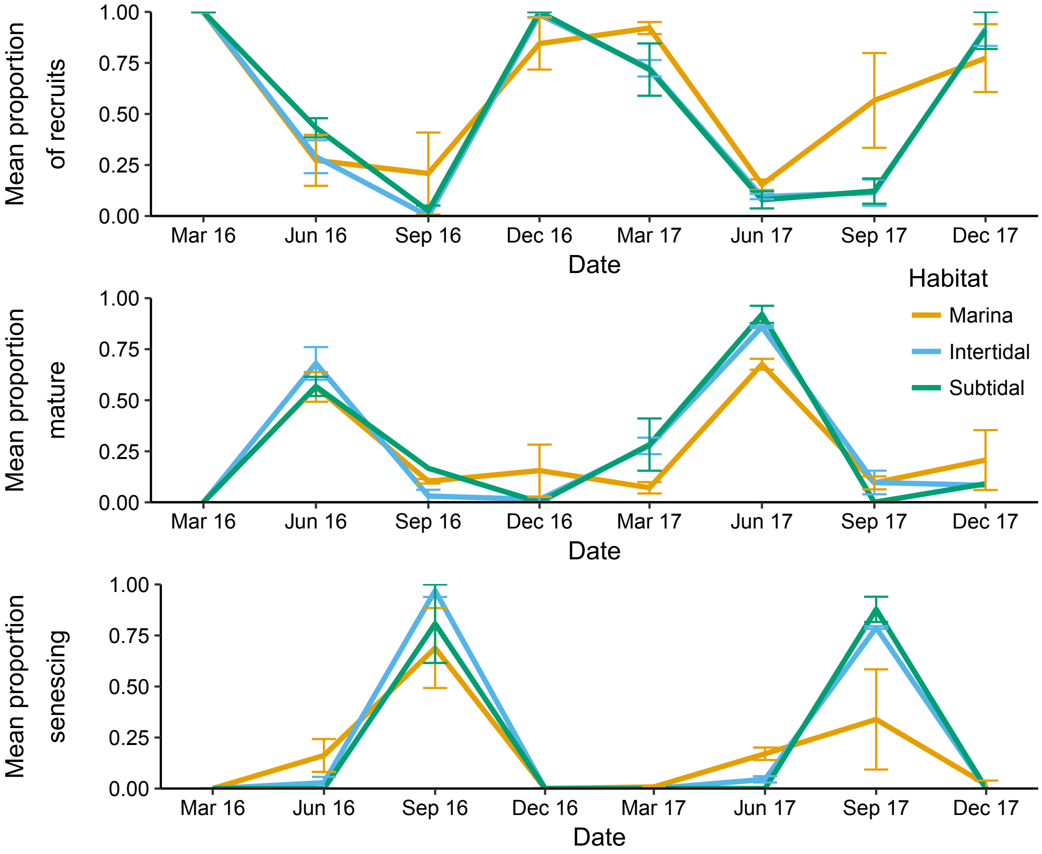

FIGURE 3.6: Mean proportion of recruits, mature and senescing sporophytes of *Undaria pinnatifida* (± standard error) found across the study period in each habitat (marina = orange, intertidal reef = blue, subtidal reef = green). Table 3.1 describes classification of sporophytes to each developmental category.

TABLE 3.3: Results from the optimal PERMANOVA model, testing for difference in population structure of *Undaria pinnatifida* across the study period. The degrees of freedom (df), mean sum of squares (MS), pseudo F-value (F) and p-value (p) are shown for each coefficient. Significant coefficients shown in bold (α <0.05).

Coefficient	df	MS	F	p
Habitat	2	572.1	1.79	0.159
Month	**3**	**38720.0**	**121.42**	**<0.001**
Year	**1**	**1786.1**	**5.60**	**0.008**
Habitat*Month	**6**	**1113.1**	**3.49**	**<0.001**
Month*Year	**3**	**1448.4**	**4.54**	**0.002**

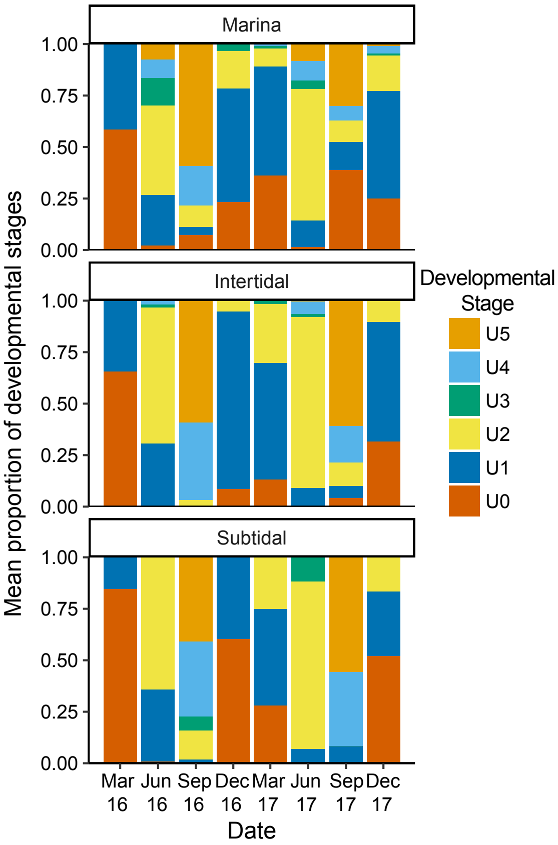

Figure 3.7: Proportion of each developmental stage of *Undaria pinnatifida* in each habitat across the study period (Stage 5 = orange, 4 = light blue, 3 = green, 2 = yellow, 1 = dark blue, 0 = red). Table 3.1 describes classification of sporophytes to each developmental stage.

Reproductive activity varied markedly between habitats and across sampling events. Where mature sporophytes were found, the lowest activity was recorded on subtidal reef in March 2017 (6.0 ± 4.0 x 10^2 spores.cm^{-2} hr^{-1} and 2.8 ± 2.6 x 10^4 spores.sporophyll^{-1} hr^{-1}) and the highest reproductive activity was recorded in marinas in June 2016 (6.7 ± 2.8 x 10^5 spores.cm^{-2}·hr^{-1} and 1.0 ± 0.6 x 10^8 spores.sporophyll^{-1}.hr^{-1}). Reproductive activity was generally highest on marina pontoons, followed by intertidal reef, and lowest on subtidal reef (Figure 3.8). At every sampling event, both reproductive activity metrics were higher in marinas than in reef habitats, with the exception of June 2017 (Figure 3.8). For both metrics there was a statistically significant overall effect due to Habitat and a significant Month*Year interaction (Table 3.4). Due to the high variability in the activity metrics, pairwise tests between individual habitats were only statistically significant between subtidal reef and marinas, however, the overall pattern of marinas > intertidal reef > subtidal reef remained (Table B.4). The significant Month*Year interaction indicates inter-annual variation in reproductive activity, which was most pronounced in March with higher activity in 2017 than 2016 (Figure 3.8).

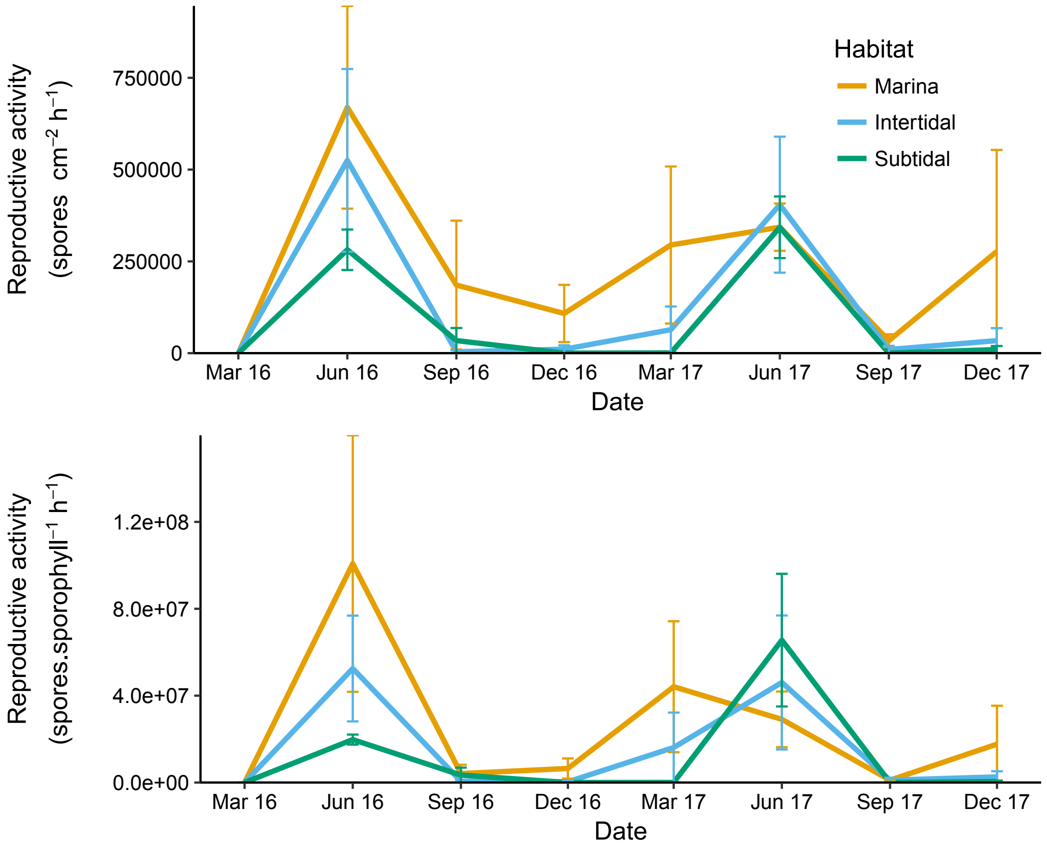

Figure 3.8: Mean reproductive activity of *Undaria pinnatifida* (± standard error) found across the study period in each habitat (marina = orange, intertidal reef = blue, subtidal reef = green). Two reproductive metrics are shown: spores per cm^2 of sporophyll tissue per hour, and total spores per sporophyll per hour

Table 3.4: Results from the optimal ANOVA models, testing for difference in two reproductive activity metrics [log(x+1)] of *Undaria pinnatifida* across the study period. The degrees of freedom (df), mean sum of squares (MS), F-value (F) and p-value (p) are shown for each coefficient. Significant coefficients shown in bold (α <0.05).

	Spores cm^{-2} h^{-1}				Spores sporophyll^{-1} h^{-1}			
Coefficient	df	MS	F	p	df	MS	F	p
Habitat	**2**	**70.72**	**4.05**	**0.022**	**2**	**111.75**	**3.41**	**0.039**
Month	**3**	**352.01**	**20.15**	**<0.001**	**3**	**632.43**	**19.29**	**<0.001**
Year	1	26.80	1.53	0.220	1	67.50	2.06	0.156
Month*Year	**3**	**72.12**	**4.13**	**0.010**	**3**	**151.41**	**4.62**	**0.006**

Morphology of *Undaria* sporophytes also differed between habitats at various developmental stages. Bootstrap averages and tmMDS highlighted lower variation in marina habitats when compared to reef habitats, indicated by the smaller 95% confidence area around the bootstrap mean across all developmental stages (Figure 3.9). Greatest dissimilarity in tmMDS was between sporophytes sampled in marinas and reef habitats, particularly in developmental stages 2, 4 and 5; with intertidal and subtidal reef habitats clustering closer on tmMDS (Figure 3.9). Statistically significant variation in morphology between habitats was found for all developmental stages except stage 0 sporophytes (Figure 3.9, Table B.5) In general, the morphological attributes measured showed that sporophytes were smallest in marinas, and largest on subtidal reef (except for stage 5) (Table B.6). Sporophytes from marinas were statistically distinct from those from subtidal reefs at every developmental stage, except stage 2, and from sporophytes from intertidal reefs at developmental stages 4 and 5 (Table B.6, Table B.7). There was no significant difference in sporophyte morphology between intertidal and subtidal reef habitats at any developmental stage (Table B.6, Table B.7).

3.4 Discussion

3.4.1 Population dynamics and management uncertainty

The population dynamics of INNS can greatly influence their success, spread and ecological impact, and can also affect the design and implementation of effective management measures (Williamson and Fitter, 1996b; Sakai *et al.*, 2001; Simberloff, 2003; Ricciardi and Cohen, 2007; Bauer, 2012). As such, information on spatiotemporal variability in population structure, reproduction and morphology can be used as evidence to prioritise, or deprioritise, management of a given species or introduction event (McGeoch *et al.*, 2016; Booy *et al.*, 2017; Epstein, 2017; Seebens *et al.*, 2017). Here, we have shown that information garnered from distinct habitats or environments cannot be generalised across the non-native range of a given INNS, even across small spatial scales. This study was conducted at sites < 3 km apart, yet population dynamics differed markedly between habitat-types. Although not considered here, similar variation in population dynamics can also occur over larger spatial scales within the non-native range of *Undaria* (Hay and Villouta, 1993; Schiel and Thompson, 2012; James *et al.*, 2015). This highlights the need for site-specific data when considering the ecology, impact and management of INNS. *Undaria* is one of the most cosmopolitan marine invaders, being found in almost every temperate region of the world (Epstein and Smale, 2017a) and is highly likely to continue its spread into un-invaded regions. A greater volume of data collected from a range of environmental contexts is needed to better predict its invasion dynamics, to inform management decisions and the design of effective containment, removal or eradication methods.

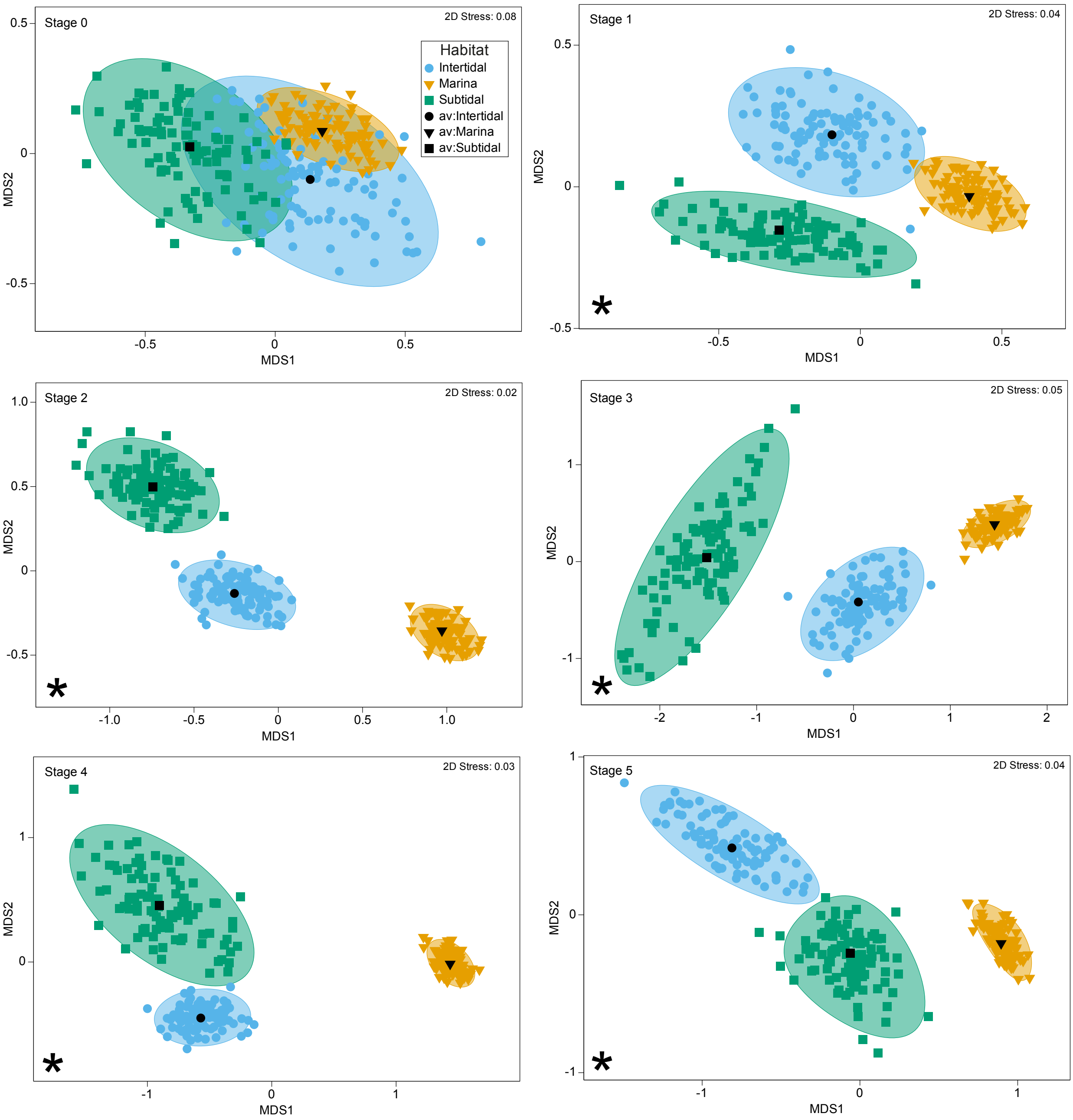

FIGURE 3.9: Threshold metric multi-dimensional scaling (tmMDS) plots of bootstrapped average morphological data within each habitat (orange triangle = marina, blue circle = intertidal reef, green square = subtidal reef). Each developmental stage was assessed separately. Circular areas indicate the 95% confidence region around the bootstrap average. Bootstrapping and tmMDS based on Euclidean distance matrices constructed from normalised data. Asterisks indicate significant difference between habitats based on PERMANOVA (Table B.5).

3.4.2 Contrast between artificial and natural habitats

Artificial structures in coastal marine environments are known to experience high propagule pressure of INNS, but low competition from native species, rendering them favourable habitats for the colonisation and proliferation of invaders (Glasby *et al.*, 2007; Dafforn *et al.*, 2012; Bishop *et al.*, 2015). Of the three habitats examined here, the abundance and biomass of *Undaria* was highest in marinas. This pattern is mirrored across its non-native range, with *Undaria* more widespread and abundant on artificial rather than natural substrates (Fletcher and Farrell, 1999; Veiga *et al.*, 2014; James and Shears, 2016a; Kaplanis *et al.*, 2016; Epstein and Smale, 2017b; South *et al.*, 2017).

The current study was able to highlight further differences in population dynamics between artificial and natural habitats. For example, we recorded an extended recruitment period and more concurrent generations in marinas when compared to reef habitats, indicated by higher proportions of recruits and mature individuals outside of the main recruitment/maturation periods. Year-round recruitment events, or multiple recruitment pulses per year, have been recorded for *Undaria* in other parts its non-native range, primarily within artificial habitats (Thornber *et al.*, 2004; Cremades *et al.*, 2006; Casas *et al.*, 2008; Primo *et al.*, 2010; James and Shears, 2016a; b). Similarly, studies conducted in artificial habitats have previously recorded the presence of mature individuals year-round (Hay and Villouta, 1993; Primo *et al.*, 2010; James and Shears, 2016a; b), whereas studies conducted in natural reef habitats have tended to report very low abundances or absences of mature plants during some months of the year (Hay and Villouta, 1993; Schaffelke *et al.*, 2005; Casas *et al.*, 2008; Schiel and Thompson, 2012; Arnold *et al.*, 2016; James and Shears, 2016a). The direct comparison between habitats conducted within the current study allows us to conclude that *Undaria* exhibits extended recruitment periods and more concurrent generations in marina habitats, when compared to natural reefs.

As the presence of a sporophyll is not necessarily a true indication of maturation of the sporophyte, reproductive activity was also measured within the current study. Reproductive activity in reef habitats predominantly occurred in only one of the quarterly sampling events (June), the same period where the highest proportion of mature sporophytes was recorded. Reproductive activity was significantly higher within the marina habitats, and was more sustained throughout the year. Previous studies have shown that at reef sites in Australasia reproductive activity is restricted to around 3-4 months or one season of the year (Schaffelke *et al.*, 2005; Schiel and Thompson, 2012), and that patterns of reproductive activity from some marinas can be more consistent throughout the year (Primo *et al.*, 2010); however these studies were conducted in different regions. The populations monitored in this study show that reproduction is higher and more consistent on marina pontoons than in reef habitats of the same locality. Overall, our formal cross-habitat comparison of population dynamics indicated that *Undaria* populations are significantly dissimilar between marinas and reef habitats, even within a single region. If this dissimilarity was found to be consistent across habitat types and regions, the higher reproduction, recruitment and concurrent generations are likely to be key factors influencing the success of *Undaria* in artificial habitats across its non-native range.

3.4.3 Variation on rocky reef

Some dissimilarity in population dynamics was also recorded between intertidal and subtidal reef habitats. Although populations were similar in structure in terms of the proportions of recruits, mature and senescing plants at each sampling event, intertidal reef habitats generally supported higher abundance and biomass than subtidal habitats. There is limited information on depth-related abundance patterns of *Undaria* in its non-native range. It can extend from the low intertidal zone to 12-18 m depth (Saito, 1975; Forrest and Taylor, 2002; Valentine and Johnson, 2003; Epstein and Smale, 2017a; South *et al.*, 2017), but is generally thought to peak in abundance in the intertidal-subtidal fringe and become less abundant with depth (Castric-Fey *et al.*, 1993; Hay and Villouta, 1993; Dean and Hurd, 2007; Russell *et al.*, 2008; South *et al.*, 2017). Our study provides empirical support for this as, on average, standing biomass within intertidal habitats was 4.5 ± 5.2 (SD) times greater than on subtidal reefs. This pattern was likely driven by a range of both biotic and abiotic factors that vary with habitat depth, such as competition from native species (e.g. Raffo *et al.*, 2009), light availability (e.g. Russell *et al.*, 2008) and physical disturbance (e.g. Valentine and Johnson, 2003).

Populations within both intertidal and subtidal reef habitats also exhibited high inter-annual variability in abundance, biomass and structure between the two survey years. At the start of this study (March 2016) we recorded very low abundance and little recruitment within reef habitats. Abundance increased sharply between March and June 2016, indicating that peak recruitment had occurred between these months. In December 2016, however, the next recruitment period had seemingly commenced, indicated by the significantly higher abundance of recruits sampled when compared to March 2016 and little to no increase in abundance between December and March 2017. This earlier seasonal cycle in 2017 was also indicated by the higher proportion of mature sporophytes in March and June 2017 when compared to 2016. Conversely, populations within marinas exhibited a more similar pattern between the survey years. It is likely that reef habitats are subjected to greater environmental variability (i.e. in temperature, light, nutrients, storm events), especially when compared to more sheltered and enclosed marinas, which may lead to high inter-annual variation in population structure. This high inter-annual variation is a major factor that may contribute to difficulties in designing effective and efficient control measures for *Undaria* once it spreads to natural substrates.

3.4.4 Morphological variation

Undaria is typically categorised into two growth forms based on the geographical variation in morphology observed in its native range. *Undaria* f. *typica* is characterised by shallow pinnate divisions on the blade, a short stipe and sporophylls confluent with the base of the blade; whereas *Undaria* f. *distans* has a longer stipe, deeper pinnate divisions and a blade distinct from the sporophylls (Yendo and Rlgakuhakushi, 1911; Okamura, 1915). Although the separation between these growth forms is thought to be largely driven by abiotic environmental factors (Castric-Fey *et al.*, 1993; Castric-Fey *et al.*, 1999b; Stuart *et al.*, 1999), especially water velocity (Nanba *et al.*, 2011), there is also evidence of genetic dissimilarity between certain forms (Niwa *et al.*, 2017). Within the current study, highest dissimilarity in morphology was recorded between sporophytes from marinas and reef habitats. Sporophytes on reef sites generally had longer stipes and wider blades, more typical of f. *distans.* Sporophytes in marinas not only had shorter stipes and narrow blades, but the sporophylls were often more developed, indicated by higher proportions of sporophytes at developmental stage 3 across the study period. Although not formally tested as part of this study, it was noted during the sampling process that sporophytes on marina pontoons often had shallow pinnate divisions on the blade and sporophylls confluent with the base of the blade (Epstein, pers. obs.); overall those sporophytes found in marinas were more typical of f. *typica.* It is highly likely that this variation in morphology is driven by dissimilarity in abiotic environmental factors between marinas and reef sites, particularly in relation to water velocity and exposure; however, genetic distinction between marina and reef populations cannot be discounted. Other factors that may drive the patterns in morphology found in this study may include both inter and intra specific competition, and differences in light intensity, nutrients and disturbance (Thompson and Schiel, 2012; Gao *et al.*, 2013; Sfriso and Facca, 2013; Carnell and Keough, 2014; Watanabe *et al.*, 2014).

3.4.5 Influence of biotic and abiotic factors

There are a number of biotic and abiotic factors which are likely to contribute to the variation in population dynamics and morphology of *Undaria* between habitats and between years. Temperature is often considered as the key driver of *Undaria* population dynamics (Saito, 1975; Thornber *et al.*, 2004; Gao *et al.*, 2013; James and Shears, 2016b; Murphy *et al.*, 2016). Here, average daily temperatures were largely similar between habitats and years, although marinas showed marginally more extremes, with warmer temperatures recorded during spring and summer, and colder temperatures in autumn and winter when compared to reef sites (Figure B.1). However, temperatures recorded within all habitats throughout the study were well within the thermal niche of *Undaria* throughout the year, and it is therefore unlikely that temperature was a key factor in driving the dissimilarities observed in this study (James *et al.*, 2015; James and

Shears, 2016b; Epstein and Smale, 2017a). During spring tides, intertidal reef habitats were exposed to much larger short-term fluctuations in temperatures (i.e. hourly variability) than both marinas and subtidal habitats (Figure B.2). Intertidal populations were, however, found at higher abundance and biomass than those on subtidal reefs and exhibited similar population dynamic patterns, so were not evidently impacted by greater short-term temperature variability. Light availability was also quantified within each habitat and, although seasonally variable, mean daytime illuminance was lowest on subtidal reef (Figure B.3, Figure B.4). Mean daytime illuminance in intertidal reef sites was skewed by sporadic high light intensities during exposure at low spring tides but, in general, light levels were higher and more consistent in marinas compared with intertidal reef habitats (Figure B.3, Figure B.4). As such, light availability may be one of the underlying causes of the observed between-habitat dissimilarity in the population structure of *Undaria.* Light intensity has previously been considered as a potential key driver of the success of *Undaria* within certain invaded communities and a factor limiting its distribution to larger depths (Valentine and Johnson, 2003; Russell *et al.*, 2008; De Leij *et al.*, 2017; South *et al.*, 2017).

Other factors which were not measured as part of this study but could also induce variation in population dynamics and morphology include inter- and intra- specific competition, wave exposure and nutrients. Inter-specific competition from functionally-similar brown macroalgae is likely to be lower on artificial substrates, when compared to reef sites (Connell, 2001; Farrell and Fletcher, 2006; Airoldi *et al.*, 2015; South *et al.*, 2017), which may allow *Undaria* to recruit, mature and reproduce more successfully in marinas. Inter-specific competition is also likely to vary across depth within reefs habitats, and has previously been identified as a potential factor limiting the depths at which *Undaria* can persist at high abundances (Castric-Fey *et al.*, 1993; Cremades *et al.*, 2006; Russell *et al.*, 2008; Raffo *et al.*, 2009). Intra-specific competition will, however, be higher within marinas and may result in the smaller and more stunted f. *typica* forms, which seem to have a higher investment in reproduction rather than growth of the stipe and blade. Marinas will also be inherently more sheltered and nutrient enriched than reef habitats (Rivero *et al.*, 2013; Foster *et al.*, 2016; Bax *et al.*, 2018). Growth of both *Undaria* gametophytes and sporophytes is positively related to nutrient concentration (Pang and Wu, 1996; Dean and Hurd, 2007; Morelissen *et al.*, 2013), and *Undaria* is thought to be negatively impacted by high wave exposure (Epstein and Smale, 2017b; South *et al.*, 2017). *Undaria* individuals also exhibit relatively slow nutrient uptake (Dean and Hurd, 2007) so that increased circulation by high water flow leads to increased growth rate, and overall larger sporophytes when compared to less tidal sites (Nanba *et al.*, 2011). These abiotic factors may, therefore, have led to the distinct population dynamics and morphology of *Undaria* in marinas.

Within its native range *Undaria* has a strictly annual life cycle, with a clear period in late summer/autumn where macroscopic sporophytes are absent due to unfavourably high water temperatures (Saito, 1975; Koh and Shin, 1990). While some degree of annularity was observed for the populations examined here, macroscopic sporophytes were still found at each site, during every sampling event, except for in one instance; while mature individuals were found in at least one site in each habitat throughout the year. In many parts of its non-native range (including the UK) the thermal cues for its strict annual life cycle are lost due to the temperate environmental conditions (James *et al.*, 2015). Indeed, it is this temperature regime that drives the more complex patterns in population dynamics recorded in this study, and allows *Undaria* sporophytes to be present year-round with overlapping generations.

3.4.6 Future perspectives for management

Our study confirms that marinas are of significant importance in the establishment potential of *Undaria*. Due to the interconnected nature of the marine environment, the population dynamics of *Undaria* within artificial habitats are likely to be paramount to its successful spread, proliferation and reproductive fitness across its non-native range. They should, therefore, be the principle target of future management actions. This study also showed that there can be significant variation in abundance, biomass and morphology of *Undaria* between habitats, which could greatly alter its ecological impacts (Thomsen *et al.*, 2011b; Blackburn *et al.*, 2014; Jeschke *et al.*, 2014). Previous studies on *Undaria* have identified varying levels of ecological impact dependent on the environment under investigation and response variables recorded (Epstein and Smale, 2017a; South *et al.*, 2017). Further research is needed to identify whether the ecological impact of *Undaria* varies considerably between habitats within a single introduced region, and how this may alter management prioritisation.

Designing efficient and effective control methods for an established INNS is dependent on having an adequate knowledge of its ecology and population biology (Sakai *et al.*, 2001). The results shown here highlight that generalisations cannot be made across invaded habitat types, making management highly complex. Site-specific data on the population dynamics and impact of INNS is needed to make truly objective evidence-based management decisions; however, developing an extensive evidence base requires considerable time and resources. Careful consideration is required into whether this would lead to beneficial management outcomes compared to less evidence-based but more rapid response actions (Beric and MacIsaac, 2015; Early *et al.*, 2016; McGeoch *et al.*, 2016). Data will not be available in every instance and management decisions will have to be made on best available evidence. This study highlights that where site-specific data are not available, uncertainty should be noted within any confidence assessment. Even where substantial data are available, management can be highly labour intensive, ineffective and costly (Hulme, 2006; Larson *et al.*, 2011; Simberloff *et al.*, 2013; Early *et al.*, 2016). The highly plastic life-history characteristics of *Undaria*, both spatially and temporally, coupled with its year-round reproduction and recruitment, makes it a model species to highlight the difficulties in INNS management.

Chapter 4

Removal treatments and recruitment dynamics

This chapter was published as:

- **Epstein, G.**, Hawkins, S.J. & Smale D. A. (2018) Removal treatments alter the recruitment dynamics of a global marine invader - Implications for management feasibility. *Marine Environmental Research*, 140, 322—331

4.1 Introduction

Invasive non-native species (INNS) can cause significant environmental impacts to the native communities to which they are introduced (Simberloff *et al.*, 2013; Early *et al.*, 2016). There is also major economic cost associated with their management, control and remediation (Pimentel *et al.*, 2005; Williams *et al.*, 2010). Consequently, there is increasing pressure to control the introduction, spread and proliferation of INNS. New legislative tools, such as those adopted in the EU (EU, 2014) and USA (Federal Register, 2016), aim to improve prevention via greater biosecurity, containment and eradication of INNS. Rapid response eradication is generally accepted as the best management option once a new species is detected and biosecurity measures have clearly failed (Beric and MacIsaac, 2015; Early *et al.*, 2016). But when an INNS becomes widespread, available management options are often limited, and can be highly costly, time-consuming and ineffective, especially in highly connected marine environments (Bax *et al.*, 2003; Simberloff *et al.*, 2013; Early *et al.*, 2016; Courtois *et al.*, 2018). As environmental managers have finite resources with which to tackle an ever-increasing number of INNS, management prioritisation procedures are clearly needed (Bonanno, 2016; McGeoch *et al.*, 2016; Seebens *et al.*, 2017; Courtois *et al.*, 2018).

In order to design a prioritisation framework, many factors must be considered, including ecological and economic impacts, the provision of ecosystem services and effects on human health (McGeoch *et al.*, 2016; Epstein, 2017). Many of these factors can be highly subjective and are hard to define and quantify. Therefore more attention has recently been given to the important and less subjective issue of management feasibility (Molnar *et al.*, 2008; Panetta and Novak, 2015; Booy *et al.*, 2017; Corbin *et al.*, 2017). Understanding the likely effectiveness, practicality, risk, cost, impact and timeframe of management options should be fundamental to any prioritisation process.

Evaluating the feasibility of management actions for INNS in terrestrial ecosystems is aided by the historic nature of introductions, the quantity of research and the pre-existence of numerous management programmes (Kettenring and Adams, 2011; Veitch *et al.*, 2011; Panetta and Novak, 2015; Corbin *et al.*, 2017). In contrast, the management of INNS in marine ecosystems is comparatively new and understudied, although some control and eradication programmes have been implemented (Bax *et al.*, 2003; Williams and Grosholz, 2008; Beric and MacIsaac, 2015). The inherent connectivity of marine environments can promote the spread of INNS and re-entry to cleared areas (Ruiz *et al.*, 1997; Bax *et al.*, 2003), while their relative inaccessibility renders monitoring efforts and management actions far more difficult (Ruiz *et al.*, 1997; Bax *et al.*, 2003; Thresher and Kuris, 2004; Booy *et al.*, 2017). Large-scale management of marine INNS is, therefore, highly costly. Thus, small-scale eradication or control experiments, or trials, can be an important step in determining management feasibility and prioritisation (Lovell *et al.*, 2006; Williams and Grosholz, 2008).

The kelp, *Undaria pinnatifida*, is one of the most cosmopolitan marine INNS worldwide (Epstein and Smale, 2017a). Native to the north-west Pacific rocky coastlines of Japan, Korea, Russia and China (Saito, 1975), *Undaria pinnatifida* (hereafter referred to as *Undaria*) can now be found in many parts of the north-east and south-west Atlantic, south-west and east Pacific, and the Tasman Sea (Epstein and Smale, 2017a; South *et al.*, 2017). As an INNS, *Undaria* is generally more widespread and abundant on artificial rather than natural substrates (Floc'h *et al.*, 1996; Fletcher and Farrell, 1999; Cremades *et al.*, 2006; Russell *et al.*, 2008; Veiga *et al.*, 2014; Kaplanis *et al.*, 2016). Both marinas and aquaculture sites are strongly linked to introduction vectors and would therefore be expected to have high propagule pressure. They also contain large expanses of artificial substrates on pontoons or buoys which are held at a constant shallow depth, providing ideal conditions for the establishment and proliferation of *Undaria* populations (Fletcher and Farrell, 1999; Cremades *et al.*, 2006; Grulois *et al.*, 2011; Minchin and Nunn, 2014; James and Shears, 2016a; b). *Undaria* has also invaded natural habitats across its non-native range, predominantly on sheltered to moderately wave-exposed rocky reefs (Hewitt *et al.*, 2005; Russell *et al.*, 2008; Dellatorre *et al.*, 2014; Minchin and Nunn, 2014; Epstein and Smale, 2017b). In many cases the introduction of *Undaria* into natural habitats has been linked to spill-over from source populations in nearby artificial habitats, however in some cases incursions may also occur directly into natural substrates (Floc'h *et al.*, 1996; Fletcher and Farrell, 1999; Russell *et al.*, 2008; Grulois *et al.*, 2011; James and Shears, 2016a; Epstein and Smale, 2017b).

Undaria is one of the most cosmopolitan marine INNS, and is considered of major importance for conservation management; yet there has been little targeted control of this species in most of its non-native range (Epstein and Smale, 2017a). Where management has been implemented, there has been some success in limiting or excluding *Undaria* in isolated environments; however, most management attempts have led to reintroduction and wider-scale spread, with localised reductions in population density being rapidly reversed following cessation of management actions (Wotton *et al.*, 2004; Hewitt *et al.*, 2005; Thompson and Schiel, 2012; Forrest and Hopkins, 2013; Crockett *et al.*, 2017).

Undaria sporophytes recruit from microscopic gametophytes that may grow vegetatively in the understory for up to 2 years (Pang and Wu, 1996; Thornber *et al.*, 2004; Choi *et al.*, 2005). In its native range, *Undaria* has a strictly annual life cycle with recruitment restricted to the winter months (Saito, 1975; Koh and Shin, 1990). In many parts of its non-native range the thermal cues for its strict annual life cycle are lost due to the temperate environmental conditions (James *et al.*, 2015). In these locations recruitment may occur year-round or in multiple pulses per year, however a degree of annularity generally remains (Thornber *et al.*, 2004; Cremades *et al.*, 2006; Casas *et al.*, 2008; Primo *et al.*, 2010; James and Shears, 2016a; b). Although temperature is considered the key factor influencing *Undaria* recruitment patterns (Saito, 1975; Floc'h *et al.*, 1991; Gao *et al.*, 2013; James and Shears, 2016b; Murphy *et al.*, 2017), recruitment may be influenced by a variety of other factors including light, temperature, salinity, depth, exposure, nutrients and competition (Russell *et al.*, 2008; Gao *et al.*, 2013; Watanabe *et al.*, 2014; Epstein and Smale, 2017a; South *et al.*, 2017). More knowledge is needed on the recruitment dynamics of *Undaria* and the effect of removal treatments in order to better design management measures and understand the factors affecting the probability of management success.

Undaria was first recorded in the UK in 1994, attached to floating marina pontoons in Port Hamble (Fletcher and Manfredi, 1995). While the majority of records originate from southern England, it has also been recorded on the east and west coasts of England, north and south west Wales, on the east coast of Northern Ireland and the Republic of Ireland, and in Scotland at Queensferry (Epstein and Smale, 2017b). There is currently no known targeted management of *Undaria* occurring in the UK (Epstein and Smale, 2017a), although it does appear on a list of priority species for monitoring and surveillance of marine INNS as part of obligations to the Marine Strategy Framework Directive (Stebbing *et al.*, 2015). It is highly likely that as *Undaria* continues its spread and proliferation around the UK (Minchin and Nunn, 2014; Epstein and Smale, 2017b), there will be further pressure to contain or restrict the species from proliferating in certain areas. Due to their association with introduction vectors, and their possible association with spread to natural habitats, marina and harbour environments are perhaps the best candidates for implementing management actions to limit proliferation and control the spread of *Undaria* populations in the UK (Epstein and Smale, 2017b).

Four different removal treatments were applied to patches of marina pontoon during an 18-month manipulative experiment, to investigate their effects on *Undaria* recruitment patterns and elucidate the potential for control or removal of *Undaria* from marinas. There are various potential methods to control marine INNS, including biocontrol, genetic modification, biocides, herbicides and environmental remediation, however as with most plant invasions, the most commonly employed and widely accepted methods are selective physical removal or full clearance of invaded substrates (Bax *et al.*, 2001; Thresher and Kuris, 2004; Anderson, 2007; Kettenring and Adams, 2011). The treatments in this experiment were selected to incorporate different aspects of potential physical removal methods – those which target the macroscopic INNS only, those which incorporate a more substrate-wide exclusion method, and those which target both the macroscopic and microscopic sources of INNS (Critchley *et al.*, 1986; Wotton *et al.*, 2004; Glasby *et al.*, 2005; Coutts and Forrest, 2007; Forrest and Hopkins, 2013).Treatments were maintained at two marinas in Plymouth, UK, to: (i) examine how different physical and temporal removal methods affect recruitment patterns; (ii) identify dissimilarities in recruitment patterns and the influence of removal methods between marinas from the same locality; (iii) discern which removal method may be most efficient at reducing or excluding *Undaria*; and (iv) consider the feasibility of managing *Undaria* within marina environments.

4.2 Materials and methods

4.2.1 Site selection

Plymouth Sound is an enclosed embayment fringed by intense coastal development and large port facilities (Knights *et al.*, 2016; Figure 4.1). *Undaria* was first recorded in Plymouth Sound in 2003 within one of the waterfront marinas (NBN, 2017), and can now be found at all marinas and on much of the natural rocky-reef within the Sound at varying density and standing biomass (Epstein and Smale, 2017b). The current study was conducted at two marinas (Figure 4.1), which were selected based on: (i) permission to access the facilities all-year round; (ii) similar pontoon constructions; (iii) large areas of pontoon which would not be disturbed by vessels or maintenance staff; (iv) well established *Undaria* populations (*Undaria* was first recorded at the two chosen marinas in 2004 and 2010) (NBN, 2017). All manipulations were carried out on the vertical side of concrete-based floating pontoons, with the entire experimental area being fully immersed at all times. The depth of the manipulations was therefore 0 - 0.4 m from the surface. Only the sheltered side of pontoons (adjacent to the outer wave-wall) was used in order to minimise disturbance from vessels. As temperature is often considered the key driver of *Undaria* recruitment dynamics (Saito, 1975; James *et al.*, 2015) *in situ* water temperature was recorded adjacent to the pontoons at both study sites (every 30 mins, using a Hobo pendant data logger, Onset). Temperature exhibited typical annual fluctuation across the study period and was similar across the study sites (Figure C.1). Mean daily temperature was 13.87C (± 2.95 SD) at Marina 1 and 13.75C (± 2.88 SD) at Marina 2 and differences in mean daily temperature between sites did not exceed 0.35C (Figure C.1).

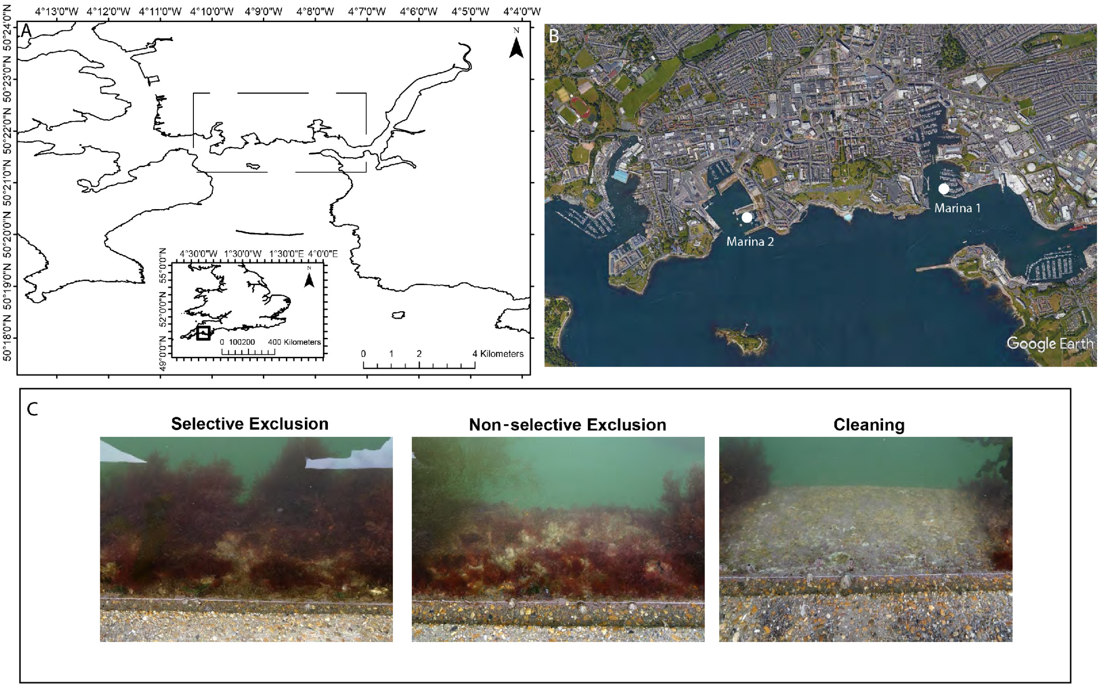

FIGURE 4.1: (A) Plymouth Sound shown in context of southern UK (inset). Dashed line indicates the Plymouth waterfront area, box on inset map indicates position of Plymouth Sound. (B) Plymouth waterfront area with study sites indicated by white points (image from Google Earth^{TM} 11/08/2016). (C) Representative examples of manipulations at the start of the experiment in March 2016.

4.2.2 Removal treatments

At each marina 16 patches of pontoon, 0.2 m^2 in size, were assigned to one of four removal treatments in a pseudo-random manner to ensure relatively even spread of treatments across the study area. Each patch was marked using waterproof epoxy and coloured markers and were separated by 0.2 m^2 of unmanipulated pontoon (40-50 cm apart along the pontoon). The four treatments were: 1) monthly selective removal of *Undaria*; 2) monthly non-selective removal of all macroalgae; 3) cleaning of pontoon surfaces (removal of all biota) in spring followed by monthly non-selective removal of all macroalgae; 4) cleaning in autumn followed by monthly non-selective removal of macroalgae (Figure 4.1). Unmanipulated controls were also established, which is outlined in section 4.2.4.

For all treatments *Undaria* recruits were extracted each month by cutting just above the holdfast (the average length of recruits was 8 cm meaning the remaining holdfast occupied inconsequential substrate space, and is likely to quickly degrade or dislodge as the meristematic zone occurs between the stipe and blade (Saito, 1975; Castric-Fey *et al.*, 1999b; Choi *et al.*, 2007). To avoid any edge effects, only those recruits within the centre 0.16 m^2 of each manipulation were retained for further analysis (see below). For the non-selective removal treatments, all macroalgae were also trimmed back to a height of $1 - 2$ cm from the substrate on each visit, to mimic management of *Undaria* by non-selective removal. The complete removal of all biota was conducted only once for each cleaning treatment (spring = March 2016; autumn = September 2016). In these treatments the pontoon was cleaned by scraping off all fouling with metal scrapers, then vigorously brushing the cleared pontoon surface with a wire brush. Although this may have left some microscopic fouling, the high level of abrasion removed all visible macroalgal and faunal fouling (Figure 4.1). All cleaning treatments were then maintained as the non-selective removal treatments. The number of *Undaria* sporophytes removed from experimental patches during the initial cleaning/removal in March 2016 were counted, and there was no significant difference in abundance between removal treatments (Negative binomial GLM for each marina - Marina 1: $\chi^2 = 12.1$, p = 0.85; Marina 2: $\chi^2 = 11.9$, p = 0.87. Mean number of sporophytes (±SD) per treatment - Marina 1: 28.8±15.5, 26.5±10.3, 27.5±14.8; Marina 2: 7.3±1.7, 6.5±4.5, 6.25±2.8). All removals were maintained until September 2017.

4.2.3 Identification and categorisation

Identifying recruits of large brown macroalgae, or kelps, to species level can be challenging (Figure 4.2). With experience once recruits attain at least ~7 cm in length *Undaria* can be visually identified in the field, as it is the only large brown macroalgal species found in Plymouth Sound that has a midrib and forms pinnate blade divisions (Figure 4.2). For recruits of <7 cm in length, identification to species required microscopic examination to detect the presence of Yendo cells which are absent from all other large brown macroalgal species in the study region (Drew, 1910; Kasahara, 1985; Castric-Fey *et al.*, 1999b; Burrows, 2012) (Figure 4.2). Once identified as *Undaria*, all recruits were categorised as either Type 0 or Type 1 recruits dependent on their developmental stage (Type 0 - absence of pinnate blade divisions and a defined midrib, Type 1 - same features present; adapted from Casas *et al.*, 2008) (Figure C.2); lamina length of all recruits was also measured to the nearest 0.1 cm.

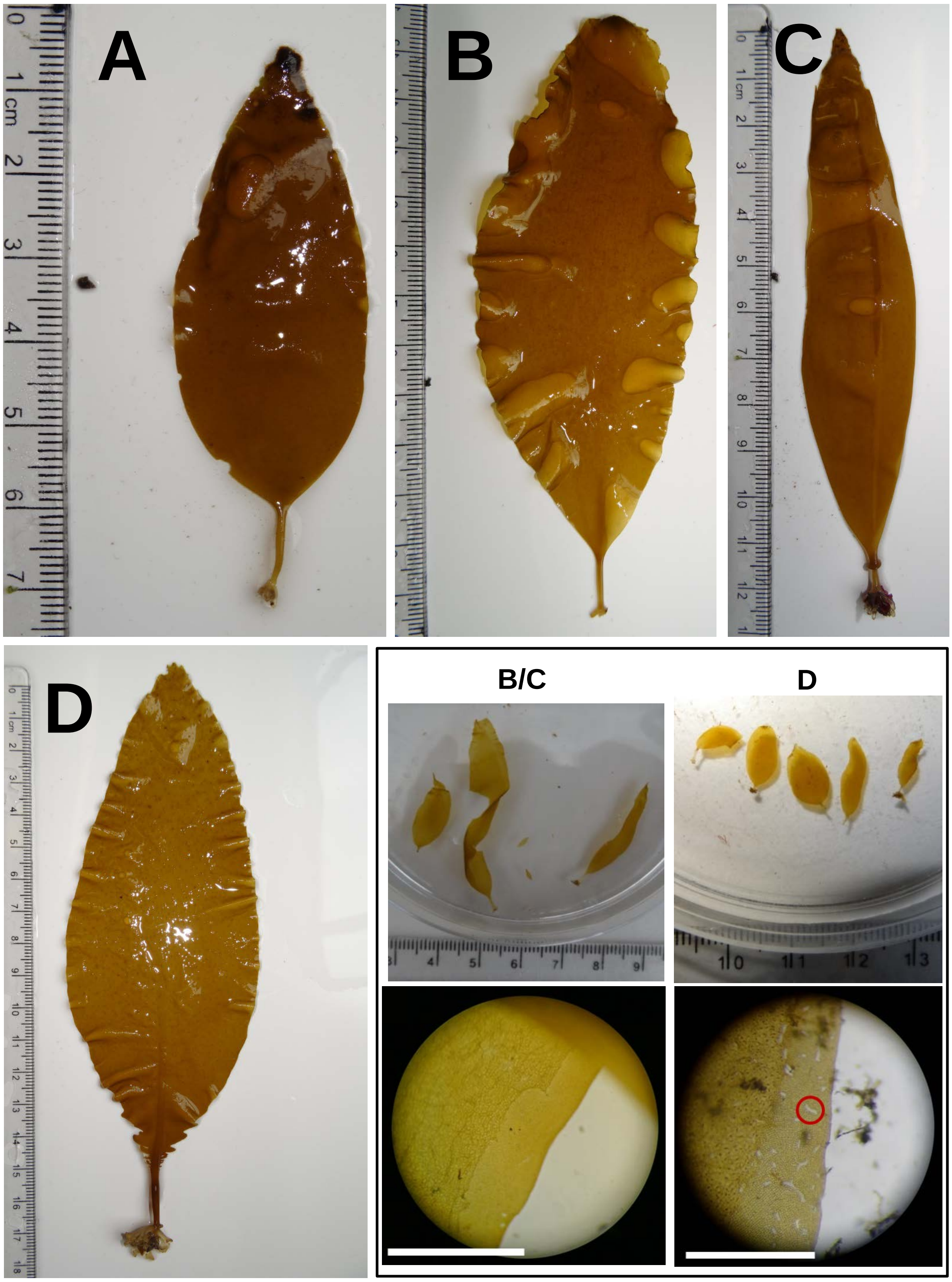

Figure 4.2: Recruits of the four kelp species that can be found within marinas in Plymouth. *Laminaria digitata* (A), *Saccharina latissima* (B), *Saccorhiza polyschides* (C) and *Undaria pinnatifida* (D). Once recruits are ∼≥7 cm in length (as shown in main figure) *Undaria* can be visually identified by the development of a midrib and a pinnate blade (D). Inset images show that confirmation of recruits <7 cm in length as *Undaria* must be carried out using microscopic techniques by noting the presence of Yendo cells (example in red circle) - illustrated by comparison to *S. latissima* / *S. polyschides* (identification uncertain). White bars indicate approximately 1 mm.

4.2.4 Recruitment patterns in unmanipulated areas

To monitor temporal variability in the recruitment of *Undaria* into unmanipulated areas, sampling of an adjacent untreated section of pontoon was carried out every 3 months at both marinas. During each sampling event, 10 haphazard 0.25 m^2 quadrats were placed randomly against the side of pontoons in each marina. Due to the relatively limited area available for sampling, a note of the position of each quadrat was taken to avoid overlapping quadrat samples during the study. All *Undaria* recruits (Type 0 and Type 1) were removed and enumerated (identification was confirmed as above). To allow for comparison with removal patches the density of *Undaria* recruits per 0.16 m^2 was calculated to the nearest whole plant.

4.2.5 Data analysis

Generalized Additive Mixed Models (GAMMs) were used to examine the effect of differing removal treatments on the temporal patterns and magnitude of *Undaria* recruitment at each marina separately. A GAMM is a non-linear regression technique whereby the response variable is modelled with non-parametric smooth functions, or "splines" (Wood, 2004; Wood, 2006). GAMMs were applied using the *gam* command from the *mgcv* package in R 3.2.2 (Wood, 2004; 2011; R Core Team, 2015). The number of recruits was modelled as a function of "Treatment" (categorical; 4 levels: selective, non-selective, autumn clean, spring clean), "month" (continuous; 1-12) and "duration" (continuous; number of months the removal has been running: 1-18). The value of "duration" at each sampling event differed for the autumn cleaning treatment when compared to all other treatments, as the initial removal occurred in September 2016, whereas all other treatments were initiated in March 2016. Individual patch ID (16 levels) was also applied as a random factor to account for the repeated measure nature of this study. As the response variable is count data, all models were fitted using a Negative Binomial error distribution with a log link function, due to overdispersion from the Poisson distribution (Wood, 2011). The smoothing functions for the two continuous predictor variables were estimated by cubic regression splines (Wood, 2004; Wood, 2006). The factor of month was defined with a cyclic cubic spline, taking into account its cyclical nature, allowing no discontinuity between January (1) and December (12). Appropriate smoothness for each applicable model term was estimated using Maximum Likelihood (ML) (Wood, 2011). Interactions between Treatment and the two continuous predictor variables were included within the initial models. Significance of the interaction terms was assessed using a Chi-Square test on the ML scores between models containing and excluding each interaction term; which was carried out using the *compareML* function from the *itsadug* package (van Rij *et al.*, 2017). Where no significant difference was recorded between the two models, Akaike information criterion (AIC) and adjusted R^2 values were used to identify whether an interaction term should be retained in the optimal model. Model validation was carried out using the *gam.check* function from the *mgcv* package (Wood, 2017); diagnostic plots were evaluated and the basis dimensions used for smooth terms were checked to be adequate using k-index tests (Wood, 2017). Overall parametric differences between Treatments were assessed using Wald Tests, with the *wald_gam* function from the *itsadug* package (van Rij *et al.*, 2017). Variation in the influence of duration and month on different treatments was assessed graphically using the *plot.gam* function from the *mgcv* package (Wood, 2017).

To assess differences in recruitment patterns between removal treatments and unmanipulated areas, negative binomial generalized linear models (nbGLMs) were constructed for unmanipulated data and each removal treatment separately. Only those timepoints when both removal and unmanipulated data were collected were used in this analysis. Each nbGLM modelled the number of recruits as a function of "Removal" (categorical; 2 levels: unmanipulated and one of the four removal treatments), "Date" (categorical; 6 levels for all treatments except autumn removal – 4 levels), and their interaction. Testing for significant pairwise differences between removal treatments at each sampling point was carried out by releveling the Date factor within nbGLMs. All nbGLMs were carried out using the *glm.nb* command from the *MASS* package (Venables and Ripley, 2002).

Mapping was carried out within ArcMap 10.3.1 (Figure 4.1). All statistics were carried out in R 3.2.2 (R Core Team, 2015). The *dplyr* package (Wickham and Francois, 2015) was used for data manipulation and all graphs were created using *ggplot2* (Wickham, 2009) or base R (R Core Team, 2015).

4.3 Results

During the experiment, a total of 2,138 and 368 *Undaria* recruits were removed from Marina 1 and Marina 2, respectively. The highest number of recruits from a single removal patch was 151 inds. 0.16 m^{-2}, recorded in April 2016 within a non-selective removal treatment in Marina 1. Most recruits were Type 0 plants, with 75% of sampled individuals being classed as this developmental stage (Figure C.3). The average lamina length of recruits was 8.0 cm (± 7.5 SD) and ranged from 0.4 - 49.7 cm (Figure C.4). Growth and development of recruits was fastest in late spring and summer, with larger recruits and the majority of Type 1 plants being found between April and August (Figure C.3, Figure C.4).

Across all treatments and both marinas there were only 28 out of 132 occasions where no recruits were found in a monthly removal treatment, highlighting the limited success of the experimental removals. In general, most of the recruits were found in late winter and spring, with peak recruitment in Marina 1 from March-May, and a slightly earlier peak in recruitment at Marina 2 from Feb – April (Figure 4.3). Mean monthly recruitment across the study period was highly variable among treatments, however the non-selective removal and autumn cleaning treatment generally had higher recruitment than the selective removal and spring cleaning treatments at both marinas (Figure 4.3). At the start of the experiment (Apr – Jul 16) non-selective removal had the highest recruitment of all four treatments at both sites (Figure 4.3). In contrast, cleaning in the spring led to the lowest recruitment. Towards the latter part of the experiment (Jan – Sept 17) recruitment patterns within non-selective, selective and spring removal treatments became more similar. There were, however, more distinct recruitment patterns in the autumn cleaning treatments. Cleaning treatments resulted in distinct peaks outside of the main recruitment periods, with high recruitment from the spring cleaning treatment in Marina 1 in Aug 2016, and from the autumn cleaning treatment in Marina 2 in Nov 2016 (Figure 4.3).

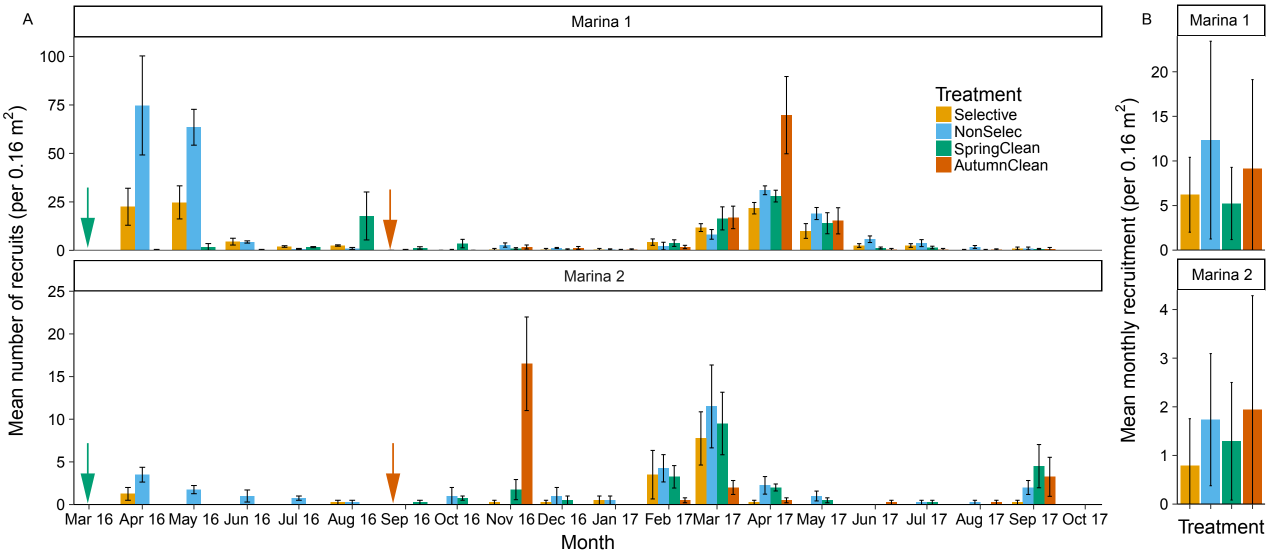

FIGURE 4.3: (A) Mean number of *Undaria pinnatifida* recruits (± standard error) found at each monthly removal for the four treatments at each marina separately. Arrows indicate when each treatment was initiated: green = selective, non-selective and spring cleaning, orange = autumn cleaning. (B) Mean monthly recruitment (± standard error) across the study period within each removal treatment.

GAMMs indicated a significant effect of Treatment, Duration and Month on recruitment at both marinas (Table 4.1). There was a significant interaction between Duration and Treatment shown by better model fit with inclusion of the interaction term at both marinas (Marina 1 – $\chi^2{}_{(6)} = 28.58$, $p<0.001$; Marina 2 - $\chi^2{}_{(6)} = 10.40$, $p=0.002$). The interaction term between Month and Treatment was also included in the optimal model for both marinas with significantly better model fit with its inclusion at Marina 2 ($\chi^2{}_{(3)} = 6.25$, $p=0.006$); and although the Chi-sq test showed no significant difference at Marina 1, inclusion of the interaction term led to lower AIC score and higher adjusted R^2 (without interaction AIC = 1181, $R^2 = 0.60$, with interaction AIC = 1178, $R^2 = 0.68$).

Table 4.1: Summary of results from generalized additive mixed models predicting number of *Undaira pinnatifida* recruits within each removal treatment at each marina separately. The results from Wald like tests for each coefficient are shown with relative degrees of freedom (df), effective degrees of freedom (edf), chi-square value (χ^2) and p-values (p).

Model Terms	Marina 1			Marina 2		
Parametric terms	df	χ^2	p	df	χ^2	p
Treatment	3.00	8.03	0.046	3.00	16.53	<0.001
Smooth terms	edf	χ^2	p	edf	χ^2	p
s(Month):TreatmentSelective	4.35	117.58	<0.001	4.41	47.24	<0.001
s(Month):TreatmentNonSelec	5.18	62.01	<0.001	4.03	16.84	<0.001
s(Month):TreatmentSpring	5.88	32.66	<0.001	5.29	48.90	<0.001
s(Month):TreatmentAutumn	5.34	135.78	<0.001	6.66	60.02	<0.001
s(Duration):TreatmentSelective	1.00	1.49	0.222	1.00	0.46	0.496
s(Duration):TreatmentNonSelec	2.21	7.21	0.039	3.13	3.52	0.539
s(Duration):TreatmentSpring	2.99	34.35	<0.001	1.00	14.59	<0.001
s(Duration):TreatmentAutumn	1.00	1.34	0.248	1.00	11.04	<0.001
s(Plot)	<0.01	0.00	0.544	7.41	23.78	<0.001

Overall parametric differences between treatments were found at both marinas. Recruitment in the non-selective removal treatment was significantly higher than both the selective and spring clean removal treatments at both marinas; while at Marina 2 recruitment in the autumn clean treatment was significantly higher than both the selective and spring clean treatments (Table 4.2).

Duration of the monthly removal (i.e. the number of months for which the removal had been maintained) had a significant effect on recruitment within only a few treatments (Table 4.1). The spring cleaning treatment had a significant relationship with duration at both marinas, as recruitment was reduced after the initial cleaning treatment and generally increased over time, although recruitment did decline towards the end of experiment at Marina 1 (Figure 4.4). Similarly, recruitment within the autumn cleaning treatment at Marina 2 was reduced due to the initial cleaning but then increased over time (Figure 4.4). Duration was also significantly related to recruitment in the non-selective removal treatment at Marina 1, with recruitment decreasing slightly towards the middle of the experiment but then increasing towards the end.

At both marinas there were strong temporal patterns with month of the year significantly related to recruitment in all treatments, with each having a distinct monthly pattern (Table 4.1). At Marina 1, the selective removal treatment had a unimodal recruitment pattern, with peak recruitment in April and minimum recruitment in October-November (Figure 4.4). The non-selective treatment had more consistent recruitment throughout the year with comparatively higher recruitment from September-December. The cleaning treatments both had distinct bimodal recruitment patterns, with a secondary peak in

August and November for the spring and autumn treatments respectively (Figure 4.4). Although different monthly patterns were found at Marina 2 (Figure 4.4), there was a similar effect of treatment. The non-selective treatment led to more sustained recruitment than the selective removal, and both of the cleaning treatments induced distinct bimodal recruitment patterns (Figure 4.4).

TABLE 4.2: Post-hoc comparison of pairwise intercept differences between removal factors from GAMMs at each marina separately. Wald like tests compare parametric components only, without considering smooth terms. Parametric coefficient estimates are shown (with the Selective treatment as the intercept level), with pairwise chi-square value (χ^2) and p-values (p). Degrees of freedom are always equal to 1 due to pairwise testing. Significant pairwise differences shown in bold (α <0.05).

		Selective		Non-selec		Spring	
Treatment	Estimate	χ^2	p	χ^2	p	χ^2	p
Marina 1							
Selective	0.830						
Non-selec	0.405	**4.35**	**0.037**				
Spring	-0.088	0.20	0.657	**7.01**	**0.008**		
Autumn	0.173	0.23	0.629	0.44	0.509	0.55	0.460
Marina 2							
Selective	-1.938						
Non-selec	1.770	**9.54**	**0.002**				
Spring	0.295	0.18	0.670	**6.86**	**0.009**		
Autumn	2.195	**8.90**	**0.003**	0.48	0.490	**6.81**	**0.009**

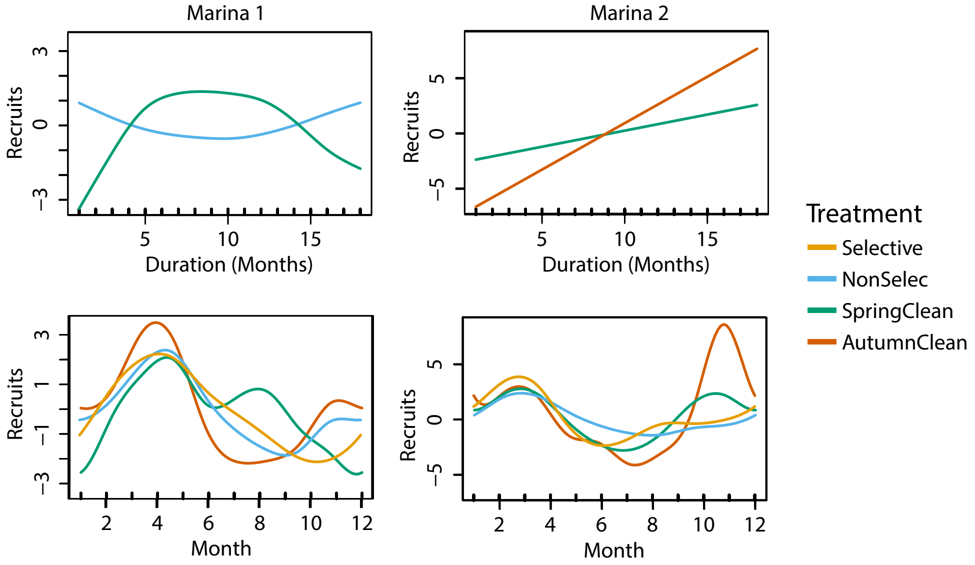

FIGURE 4.4: Regression splines indicating the effect of duration (cubic) and month (cyclic) on recruitment of *Undaria pinnatifida* at each marina. Only those smoothing splines which were statistically significant are plotted.

Variability in recruitment patterns between unmanipulated areas and the removal patches differed between treatments and time points (Figure 4.5) as shown by significant Date-Treatment interactions within all pairwise comparisons (Table 4.3). The selective removal treatment had relatively lower recruitment compared to unmanipulated areas, with less recruits found at each sampling point except September 2017 at Marina 1 (Figure 4.5). The patterns with all other treatments were less clear at both marinas; at some sampling points removal treatments had higher recruitment than in the unmanipulated areas but at other time points recruitment was comparably lower (Figure 4.5). Recruitment into non-selective removals was higher than into unmanipulated areas in 6 out of the 12 contrasts, and lower in 5; spring cleaning was higher in 6 and lower in 6; and autumn was higher in 3 and lower in 5 (Figure 4.5).

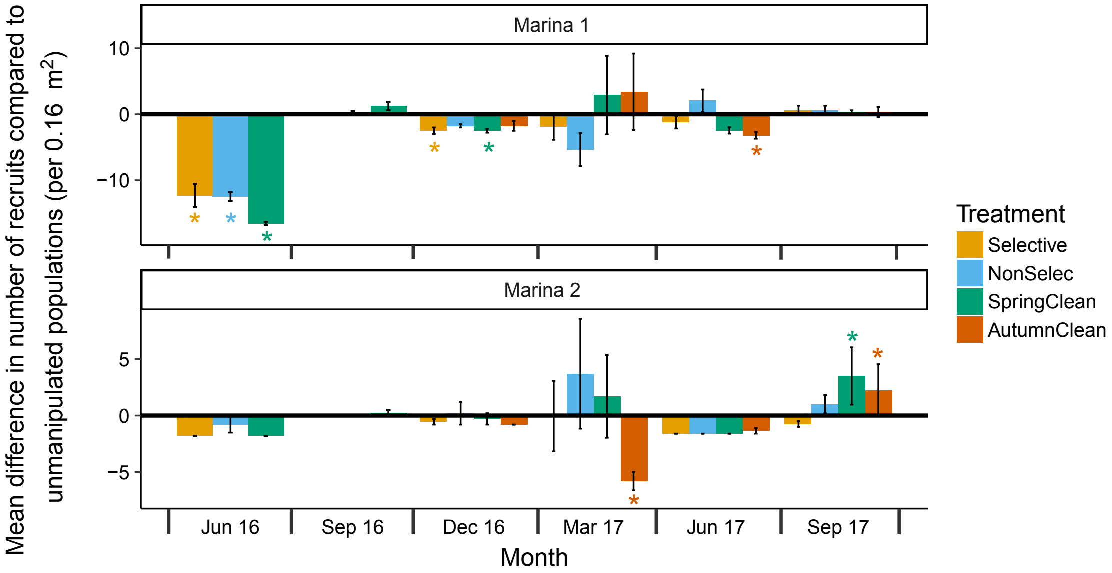

FIGURE 4.5: Comparison of *Undaria pinnatifida* recruitment between unmanipulated areas and removal treatments. Mean difference in number of recruits between unmanipulated areas and removal treatments (± standard error) is shown for 6 time points where both unmanipulated and removal recruitment was measured (data for autumn treatment for 4 time points only Dec 16 onwards). Asterisks indicate significant pairwise differences between a given treatment and unmanipulated areas at each sampling point.

Table 4.3: Sequential likelihood ratio tests for Negative Binomial generalized linear models comparing each removal treatment to unmanipulated recruitment data for each marina separately. Chi-square value (χ^2) and p-values (p) are given for each coefficient - "Removal" (difference between removal treatment and unmanipulated), "Date", and their interaction ("Removal*Date").

	Marina 1			Marina 2		
Coefficient	df	χ^2	p	df	χ^2	p
Selective						
Removal	1	12.86	<0.001	1	4.64	0.031
Date	5	247.08	<0.001	5	173.37	<0.001
Removal*Date	5	12.00	0.035	5	17.06	0.004
Non-selec						
Removal	1	12.41	<0.001	1	0.81	0.367
Date	5	230.5	<0.001	5	155.85	<0.001
Removal*Date	5	16.38	0.006	5	13.17	0.021
Spring						
Removal	1	11.96	<0.001	1	0.42	0.518
Date	5	219.19	<0.001	5	141.62	<0.001
Removal*Date	5	54.44	<0.001	5	33.06	<0.001
Autumn						
Removal	1	0.07	0.793	1	7.51	0.006
Date	3	105.94	<0.001	3	61.34	<0.001
Removal*Date	3	9.53	0.023	3	20.67	<0.001

4.4 Discussion

4.4.1 Efficacy of removal treatments

The current study highlights why the management of *Undaria* populations in invaded regions is logistically challenging and often unsuccessful. *Undaria* recruits may be present throughout the year, can be hard to identify and have temporally plastic recruitment patterns which can be altered by removal treatments. *Undaria* also recruits in extremely high densities onto artificial substrates following significant interventions such as monthly removals. This study should allow better decisions to be made on future management attempts, as our results suggest that the potential to limit *Undaria* recruitment is likely to be very low at sites with established populations and high propagule pressure. However, where there are new incursions, certain removal methods may have some potential to limit *Undaria* populations in artificial habitats.

Of the four removal treatments used in this study the non-selective removal was the least effective. Overall parametric differences indicated higher recruitment within this treatment when compared to spring clean and selective removal treatments at both marinas. Moreover, non-selective removal did not result in consistent reductions in recruitment in comparison to adjacent unmanipulated areas. It also induced more sustained and temporally consistent recruitment of *Undaria* throughout the year, and recruitment intensity did not decline during the duration of the experiment. This pattern was likely driven by the opportunistic life-history traits of *Undaria*, which enable it to take advantage of reduced competition resulting from the non-selective removal of all macroalgae (Valentine and Johnson, 2003; Edgar *et al.*, 2004). This has been shown in previous studies, where a positive recruitment response of *Undaria* was recorded following diminished interspecific competition from co-existing macroalgae. (Valentine and Johnson, 2003; Edgar *et al.*, 2004; South and Thomsen, 2016; De Leij *et al.*, 2017). A non-selective removal method would be easier to implement across wider spatial scales, due to the lack of need for identification skills, time and effort to search for *Undaria*, and the relatively simple logistics involved with mechanically trimming back fouling from pontoons. However, due to the limited success in reducing *Undaria* recruitment intensity in this study, it is unlikely to be a viable control option and may even promote recruitment and ultimately enhance population density.

Although full cleaning of the pontoon surface led to significant short-term reductions in recruitment, recruitment generally increased over the time-course of the experiment. Both autumn and spring cleaning treatments led to short-term reductions in recruitment, with reductions particularly apparent for the spring cleaning treatment which was applied immediately prior to the peak recruitment period of *Undaria.* This short-term reduction was evident at both marinas when compared to recruitment in other removal treatments in April-July 2016, and to unmanipulated areas in June 2016. This reduction is probably due to removal of the microscopic ‘seed-bank’ of *Undaria* gametophytes during rigorous cleaning of the pontoon surface (Schiel and Thompson, 2012; Forrest and Hopkins, 2013; Morelissen *et al.*, 2016). Similar short-term reductions in *Undaria* abundance have been seen in previous studies that used heavy abrasion to clear experimental patches of artificial or natural substrates (Curiel *et al.*, 2001; Thompson and Schiel, 2012; Morelissen *et al.*, 2016). Although cleaning of pontoons using highly abrasive methods before peak recruitment periods of *Undaria* may be viable in reducing abundance in the short term, cleaning treatments also induced a change in *Undaria* recruitment dynamics. As confirmed by this study, *Undaria* has the potential to recruit throughout the year in the UK and northeast Atlantic (Castric-Fey *et al.*, 1999a; James *et al.*, 2015; Murphy *et al.*, 2016), however the majority of recruitment generally occurs in late winter through to early spring (Fletcher and Farrell, 1999; Minchin and Nunn, 2014; Murphy *et al.*, 2017). The cleaning treatments altered this typical recruitment pattern by inducing bimodal rather than unimodal patterns, with notable recruitment pulses in late autumn as well as spring. While low levels of recruitment were observed for 1-2 months following cleaning in some cases, additional peaks in recruitment occurred 2-6 months after the treatments were initiated. If the cleaning methods used in this study effectively removed all gametophytes from the pontoon surface, the observable sporophyte recruits must have originated from recently settled spores. Accelerated development of *Undaria* spores to sporophytes may be viable in as little as 15 – 20 days (Pang and Wu, 1996; Thornber *et al.*, 2004; Choi *et al.*, 2005), and our study suggests that development of sporophytes may occur within this time frame in marina environments. Even so, our results suggest that maturation of spores to sporophytes in high densities is likely to occur over a greater time frame of 2-6 months.

The plastic recruitment dynamics recorded from the cleaning treatments in this study would render long-term control methods more challenging to design, perhaps requiring frequent pontoon cleaning to significantly limit the population in the long term. The complete cleaning of pontoon surfaces will also impact a wide range of other native and non-native fouling species, and would also require considerable expenditure and effort. Such disturbance may have unintended consequences in facilitating other INNS which can establish on marina pontoons (e.g. *Didemnum vexillum*, *Bugula neritina*, *Styela clava*) (Britton-Simmons and Abbott, 2008; Bishop *et al.*, 2015); while disturbance to native species may reduce ecosystem services provided by the fouling assemblages on pontoons including nutrient uptake and biofiltration by sessile invertebrates (Russell *et al.*, 1983; Allen *et al.*, 1992). Whether such a treatment would be logistically achievable, have net benefit, and be successful in limiting *Undaria* populations on a wider scale, requires further investigation.

There was no consistent reduction in recruitment from selective removal of *Undaria,* however there was evidence that this treatment was relatively successful in limiting recruitment. Any significant pairwise parametric differences between other treatments indicated lower recruitment in the selective removal treatment. Recruit density was also generally lower in selective removal treatments when compared to unmanipulated areas and the treatment did not induce deviation from typical annual recruitment patterns. This removal method would require less physical effort than other methods used in this study; although more time would be needed to search pontoon surfaces for *Undaria* recruits and some taxonomic training and expertise would be necessary. Intuitively, this method would reduce overall *Undaria* population density in the long term, by removing individuals before they reach reproductive maturity and thereby reducing localised propagule pressure. However, it is unlikely to lead to local eradication as some individuals will inevitably be missed and the microscopic gametophyte stage is not targeted within the management action. Indeed, this has been demonstrated in Australasia, where long term removals led to declines in *Undaria* population density, but not eradication, with localised reductions in population density being rapidly reversed following cessation of management actions (Hewitt *et al.*, 2005; Forrest and Hopkins, 2013).

4.4.2 Spatial and temporal context

Our study was carried out at two marinas only 1.5 km apart, yet considerable differences in *Undaria* recruitment dynamics were observed between sites. Although the overall effects of removal treatments were similar between both marinas, each had temporally distinct peak recruit periods, highly disparate recruit densities and different temporal recruitment patterns. Temperature is often considered as a key factor influencing *Undaria* recruitment patterns (Saito, 1975; Floc'h *et al.*, 1991; Gao *et al.*, 2013; James and Shears, 2016b; Murphy *et al.*, 2017), but thermal regimes were similar across sites. Disparity in population dynamics between nearby sites has been observed in previous studies, including those conducted within marinas and on natural reef habitats (Schiel and Thompson, 2012; James and Shears, 2016b). The population dynamics of *Undaria* may be influenced by a variety of factors including light, temperature, salinity, depth, exposure, nutrients and competition (Russell *et al.*, 2008; Gao *et al.*, 2013; Watanabe *et al.*, 2014; Epstein and Smale, 2017a; South *et al.*, 2017). More research is needed to examine how population dynamics of INNS vary between sites and habitats, and how spatial variability may influence both ecological impacts and potential management approaches.

Although data was not collected on the composition of co-occurring macroalgae in different treatments or background populations, the community was dominated by a mixture of filamentous and foliose reds, filamentous browns, and seasonal pulses of foliose green algae, interspersed by low numbers of the native kelps *Saccharina latissima* and *Saccorhiza polyschides.* Variation in co-occurring species between plots may have influenced recruitment dynamics both within treatments, and between treatments and background populations. Even so, experimentation was conducted over a relatively small area of pontoon surface which did not vary greatly in its algal community (Epstein pers. obs.). As no significant difference in *Undaria* abundance was detected at either marina at the start of the experiment it would seem evident that any variation in co-occurring community did not exert a strong influence on *Undaria* populations before the manipulations commenced.

It should be noted that the treatments examined here were implemented over relatively small sections of pontoons and over a fixed period of time. Larger scale, or longer-term, management actions may have differing results, such as if *Undaria* was to be removed from an entire site or marina. Multi-factorial experimental manipulations are, however, useful tools for gathering quantitative evidence to support the prioritisation and design of management measures for marine INNS. Implementing a similar experiment at a marina-wide scale would be extremely challenging, requiring replicate marinas and treatments. The data gathered from this small-scale experimental manipulation should aid in the design and prioritisation of future management.

Within marinas *Undaria* is predominantly recorded attached to the sides of floating pontoons, where relatively high light availability and large areas of available substrate may favour recruitment, development and growth. However, fully implemented management measures would need to be carried out over a much wider scale in terms of depth range and habitat type in order to successfully exclude, or significantly limit the density and spatial extent of *Undaria* populations. This may include the entirety of pontoon surfaces, wave-walls, boat hulls, pontoon struts, nearby rocky reefs and even hard substrates on the sea floor below marina structures. Management actions would also need to be sustained over a longer time period than was carried out in this study, as shown by the limited temporal effect and results from previous management attempts in other regions (Hewitt *et al.*, 2005; Forrest and Hopkins, 2013; Crockett *et al.*, 2017). Direct targeted management would also have to be accompanied by stringent biosecurity to avoid further introductions from other invaded ports and marinas. Our experiment was also conducted within one region of the UK, in two marinas of similar design and construction. It is possible that in other regions, or habitat types, the population dynamics and effects of removal treatments may differ. Nonetheless, the results of this study are likely to be applicable to many other situations and will be of importance in informing future management actions.

4.4.3 Future perspectives for management

In the UK, *Undaria* has been present since at least 1994 and although it has been recorded across many regions, it is still largely constrained to artificial habitats, specifically ports and marinas (Epstein and Smale, 2017b). As a priority species designated under the Marine Strategy Framework Directive in the UK (Stebbing *et al.*, 2015), it is necessary to consider the efficacy and feasibility of actions to control its spread. As marinas are considered hotspots of introductions and strongholds of population growth, there may be opportunities to reduce its spread to nearby natural habitats by managing source populations in artificial habitats (Epstein and Smale, 2017b). Marinas can also act as stepping-stones to the *Undaria* invasion, with fouling on hulls of commercial and recreational vessels leading to its spread to uninvaded ports and marinas (Fletcher and Farrell, 1999; Russell *et al.*, 2008; Dellatorre *et al.*, 2014; Zabin, 2014; Kaplanis *et al.*, 2016). Reducing the size of *Undaria* populations in invaded marinas may therefore, also reduce the probability of its transport to new sites or regions. Where *Undaria* has been established for many years and can be found in high abundance on both artificial and natural substrates, such as within Plymouth Sound, it seems that there will be very low likelihood of successful management. However, this study should inform the design of future management measures for *Undaria,* particularly when it is first recorded in newly-invaded locations and where controlling population expansion in artificial habitats may reduce its spread to natural habitats or artificial habitats in uninvaded regions (Zabin, 2014; Epstein and Smale, 2017b). We must be cautious however, as where previous management has been implemented, there has been some success in limiting or excluding *Undaria* in isolated environments; however, most management attempts have led to reintroduction and wider-scale spread, with localised reductions in population density being quickly reversed (Wotton *et al.*, 2004; Hewitt *et al.*, 2005; Thompson and Schiel, 2012; Forrest and Hopkins, 2013; Crockett *et al.*, 2017). Overall we suggest that cleaning of pontoons prior to main recruitment periods, and selective removal of *Undaria* before maturity, may have some potential to reduce recruit density in newly-invaded locations and therefore overall abundance and propagule pressure influencing adjacent habitats. As previously stated, any direct management measure will have to be accompanied by carefully designed and stringent biosecurity measures to avoid re-introductions and further spread.

It is highly probable that *Undaria* will continue to expand its range across temperate regions of the world, which will present opportunities to test the efficacy of management measures across wider spatial scales and varying ecological contexts. Experimental removal studies, such as this, may be a useful tool for management prioritisation of other INNS, particularly in the marine environment where large-scale species control experiments are generally lacking and difficult to undertake. Further research on the management of marine INNS is needed, including testing small and large-scale experimental removal or exclusion measures, to better quantify management feasibility and aid in designing management prioritisation frameworks. Difficult decisions will have to be made on what management is prioritised and implemented, and in which situations and circumstances the presence of an INNS is accepted (Bonanno, 2016; Epstein, 2017). There may be challenging trade-offs of impacts on biodiversity against ecosystem services that INNS provide (Davis *et al.*, 2011; Epstein, 2017).

Chapter 5

Coexistence or competition in macroalgal canopies

This chapter is under review as:

- **Epstein, G.**, Hawkins, S.J. & Smale D. A. (201X) Coexistence or competition: identifying niche and fitness dissimilarities in invaded marine macroalgal canopies. *Oecologia*

5.1 Introduction

The earliest works on invasion ecology predicted that the most successful invasive non-native species (INNS) would be taxonomically or functionally distinct from the recipient communities to which they are introduced (Darwin, 1859; Elton, 1958). This links to classic niche theory (e.g. Elton, 1958; Hutchinson, 1959; Herbold and Moyle, 1986), whereby a newly arriving species is predicted to be more successful if it occupies a vacant or under-used niche (Levine and D'Antonio, 1999). More recent theories in invasion ecology, based on factors such as resource utilisation and species diversity, are fundamentally linked to this 'niche-space' concept (e.g. Levine and D'Antonio, 1999; Shea and Chesson, 2002; Stachowicz *et al.*, 2002a; Dunstan and Johnson, 2007). Niche theory does not, however, take into account that in order for an INNS to become successfully established within a recipient community, some overlap of potential niches will inevitably be present in terms of habitat, climate and other abiotic factors where native and non-native species co-occur (Lodge, 1993).

The invasiveness of a species (i.e. its potential to rapidly colonize large and/or multiple areas) is not necessarily linked to its ecological impact (Ricciardi and Cohen, 2007). This is supported by niche theory, as competition with native species (and therefore potential for impact) is more likely to occur between functionally similar species or those occupying a similar niche, whereas niche dissimilarity would promote invasiveness (Valéry *et al.*, 2008; Ricciardi *et al.*, 2013). Contemporary coexistence theory provides a framework for explaining both the invasiveness and impact of INNS at a given site by considering both niche and fitness differences between the invader and co-occurring native species (Chesson, 2000; MacDougall *et al.*, 2009; Godoy and Levine, 2014; Barabas *et al.*, 2018). Differences in potential niche promote coexistence, and can be quantified by the degree to which population growth is limited by intraspecific, rather than interspecific, competition. Fitness differences drive competition and are based on disparate traits between species which allow the population of one species to expand to the detriment of, or at a faster rate than, a co-occurring species, potentially leading to displacement (Chesson, 2000). It is the balance between these two continuous variables which determines to what extent an INNS coexists with native species, is excluded by native communities, or becomes dominant (MacDougall *et al.*, 2009).

A coexistence invasion framework can be most easily conceptualised spatially across a stable environment. Following an introduction event, an INNS will spread into a given number of microhabitats and proliferate at varying densities based on its potential niche, the niche diversity across a site and fitness differences between co-occurring species; thus eventually leading to a stable coexisting or dominant climax community (Chesson, 2000). Often called 'the storage effect', coexistence can also be mediated by temporal variation, whereby changes in the abiotic or biotic environment lead to fluctuating fitness differences between species and therefore coexistence (Chesson and Warner, 1981). INNS are often considered 'passengers of environmental change', requiring disturbance or degraded ecosystems to establish and spread (MacDougall and Turkington, 2005). This concept is derivative of the storage effect whereby certain INNS require fluctuations in the abiotic environment in order to coexist or proliferate within native communities (Huston, 2004; Britton-Simmons and Abbott, 2008).

The application of coexistence theory has largely been constrained to terrestrial plant invasions (Barabas *et al.*, 2018), rarely being considered within marine ecosystems (e.g. Berkley *et al.*, 2010; Hart and Marshall, 2013; Hannam and Wyllie-Echeverria, 2014). The widespread invasive kelp *Undaria pinnatifida* (hereafter referred to as *Undaria*), native to the northwest Pacific, is now found in parts of the northeast and southwest Atlantic, southwest and east Pacific, and the Tasman Sea (Epstein and Smale, 2017a). In many parts of its non-native range, *Undaria* coexists with native canopy-forming macroalgae on natural substrates (i.e. shallow rocky reefs). However, it is generally recorded at highest abundance where the cover or density of native canopy-forming macroalgae are reduced or absent, often due to abiotic factors such as depth or tidal height (Castric-Fey *et al.*, 1993; Russell *et al.*, 2008; Raffo *et al.*, 2009), wave exposure (Epstein and Smale, 2017b), reduced salinity (Bollen *et al.*, 2016) or substrate type, aspect, and stability (Cremades *et al.*, 2006; Sliwa *et al.*, 2006; Russell *et al.*, 2008; Heiser *et al.*, 2014; Epstein and Smale, 2017b).

Such niche dissimilarity has been supported by manipulative experiments where the removal of native canopies did not lead to *Undaria* recruitment (Morelissen *et al.*, 2016) or, conversely, when the addition or removal of *Undaria* had no effect on its native counterparts (Forrest and Taylor, 2002; Valentine and Johnson, 2005; South *et al.*, 2015; South and Thomsen, 2016). In the majority of cases, however, removal or disturbance of native canopies promotes the recruitment and growth of *Undaria* (e.g. Valentine and Johnson, 2003; Edgar *et al.*, 2004; Thompson and Schiel, 2012; South and Thomsen, 2016; De Leij *et al.*, 2017). Such promotion suggests that *Undaria* occupies an overlapping niche with native canopy-formers, but has lower fitness. This theory is further supported by post-disturbance recovery patterns, where declines in *Undaria* and increases in native species tend to occur over time (Valentine and Johnson, 2003; Edgar *et al.*, 2004; Thompson and Schiel, 2012).

There are some site specific-cases, however, where these generalisations do not apply. Where native canopy diversity is naturally low, *Undaria* may have impacts upon native macroalgal communities or inhibit their recovery on natural rocky substrates (e.g. low diversity sites in Argentina; Casas *et al.*, 2004; Irigoyen *et al.*, 2011). Furthermore, although not conclusive, *Undaria* may have higher fitness than native canopy-formers on artificial substrates (i.e. man-made structures such as marina pontoons, pilings and port walls), where it can proliferate with or without disturbance to native macroalgae and become the dominant canopy-former (Curiel *et al.*, 2001; Cremades *et al.*, 2006; Farrell and Fletcher, 2006; Heiser *et al.*, 2014; Veiga *et al.*, 2014; James and Shears, 2016a; Epstein and Smale, 2017b). A better understanding of the drivers of *Undaria* invasions is needed to predict the potential for ecological impact on native communities and the need for targeted management (Epstein *et al.*, 2018).

We monitored and manipulated invaded macroalgal canopies over three years to examine the extent to which *Undaria* coexists or competes with native canopy-forming species. Spatial (across both sites and depths) and temporal patterns in species distributions, density and biomass were recorded at multiple sites representing three distinct habitat types: intertidal rocky reef, shallow subtidal rocky reefs and marina pontoons. Furthermore, primary succession patterns were examined at both a marina and intertidal reef site to better elucidate competitive interactions between species. Our hypothesis was that spatial variation both across and between complex marine habitats will drive niche and fitness differences and determine distribution-abundance patterns of the invasive kelp and co-occurring native canopy forming species.

5.2 Materials and methods

5.2.1 Site selection

Undaria was first recorded in Plymouth Sound (southwest UK) in 2003. Since then it has successfully colonised both artificial and natural substrates in intertidal and shallow subtidal habitats (Heiser *et al.*, 2014; Arnold *et al.*, 2016; De Leij *et al.*, 2017; Epstein and Smale, 2017b). Here it interacts with a range of native canopy forming macroalgae, including both perennial and annual species, although its impacts on native assemblages are poorly understood (Langston *et al.*, 2003; Yesson *et al.*, 2015; Epstein and Smale, 2017a).

Within Plymouth Sound, study sites were chosen based on the presence of: (i) available safe access points; (ii) approval for scientific work; (iii) widespread occurrence of *Undaria* (based on previous information or *in situ* sightings); (iv) similar substrate within habitat types; (v) extensive suitable substrate. Nine monitoring sites were selected randomly from a larger pool between 10th March and 5th April 2016. Searches of the low intertidal zone were made across the Plymouth waterfront on low spring tides, subtidal searches were made at seven sites across the same area, and site visits were made at four marina sites (Figure 5.1). Three marina and reef sites were selected, with subtidal sites deeper and adjacent to intertidal sites (Figure 5.1). All marinas were within sheltered, non-drying harbours, with similarly constructed concrete pontoons. The intertidal and subtidal reef sites were all sheltered to moderately-sheltered from wave action, being characterised by extensive bedrock platforms interspersed with areas of larger boulders and compacted cobbles. Two additional reef sites were selected at the eastern end of the Plymouth waterfront to increase replication for depth profile surveys (Figure 5.1). Manipulative primary succession experiments were established at one marina (Marina 1) and one intertidal site (Devil's Point), adjacent to two of the monitoring sites.

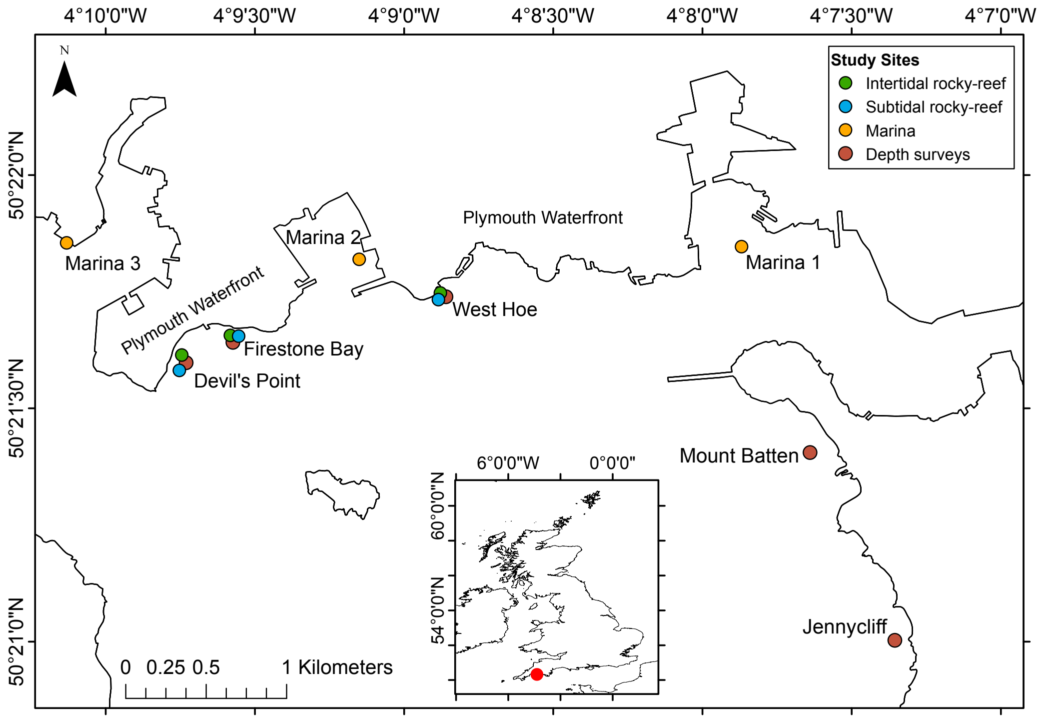

FIGURE 5.1: Study sites in Plymouth Sound (location of Plymouth within the UK shown as red point on inset map). Nine monitoring study sites, three each of intertidal rocky reef (green points) subtidal rocky reef (blue points) and marinas (orange points), were selected in March-April 2016. Depth surveys (red points) were completed in July 2017 at reef monitoring sites and two additional sites (Mount Batten and Jennycliff).

5.2.2 Multi-year monitoring

Macroalgal canopies were surveyed in June 2016, 2017 and 2018. All nine monitoring sites were sampled over a two week period at each sampling event. Although *Undaria* can be found throughout the year in the UK (Epstein and Smale, 2018) it has an annual life-history, predominantly being found in late spring to early summer (Fletcher and Farrell, 1999; Cremades *et al.*, 2006; Minchin and Nunn, 2014; Arnold *et al.*, 2016; Epstein and Smale, 2018) when sampling intensity was concentrated. Sampling in September and December 2016 and March 2017 explored seasonal patterns in density and biomass. This was not used in formal analyses and is used for qualitative comparisons only.

As *Undaria* is predominantly found in low intertidal to shallow subtidal habitats (Heiser *et al.*, 2014; Arnold *et al.*, 2016; Epstein and Smale, 2017b), subtidal sites were restricted to depths of 0.5 - 1.2 m below chart datum (CD) and intertidal sites to 0.3 - 1 m above CD. On each survey, ten replicate 0.5 x 0.5 m quadrats (stratified to rocky substrate) were placed haphazardly (each separated by at least 2 m) within an area of approximately 100 m^2 around a permanent marker at each site. All subtidal sites were sampled using SCUBA, intertidal sites were sampled either with SCUBA or on low-spring tides.

Surveys within marinas were conducted on the immersed vertical sides of floating pontoons at a depth of 0 - 0.5 m below the surface. Ten replicate 0.5 x 0.5 m quadrats were positioned haphazardly against the pontoon surface. Based on substrate suitability, interactions with vessels and human disturbance, sampling was restricted to approximately 40 m^2 of pontoon in the outer section of the marina. Due to the relatively limited area available for sampling, the position of each quadrat was noted to avoid overlapping quadrat samples during the study.

All canopy-forming macroalgae (*U. pinnatifida, Saccharina latissima*, *Laminaria ochroleuca, Laminaria digitata, Laminaria hyperborea, Fucus serratus, Fucus vesiculosus, Ascophyllum nodosum*, *Saccorhiza polyschides*, *Himanthalia elongata, Sargassum muticum*) were destructively sampled from each quadrat by gently prising the holdfast from the substrate, and placed into collection bags for further analysis. The density (inds. 0.25 m^{-2}) and biomass (g 0.25 m^{-2}) of each species was recorded for each quadrat separately. To concentrate further analyses on those species that have the potential to influence distribution-abundance patterns of *Undaria*, species which contributed less than 1% of the total biomass of the native macroalgal canopies in each habitat type were excluded.

5.2.3 Depth profiles

In July 2017 depth-related patterns in the density and cover of canopy-forming macroalgae were examined at five reef sites (Figure 5.1). At each site four replicate transects (each separated by approximately 8 m) were surveyed from +1.5 m to -4 m CD by SCUBA. Based on previous experience and preliminary surveys in Plymouth Sound, depths below -4 m CD are dominated by gravel-sandy substrates lacking canopy-forming macroalgae. Therefore greater depths were not included within this survey; however, in some areas canopy-forming macroalgae may be present at such depths, albeit at low density and cover. For each transect the same two surveyors swam 2-3 m apart along a fixed compass bearing, perpendicular to the depth contour. Each surveyor haphazardly placed a 0.5 x 0.5 m quadrat (stratified to rocky substrate) at eight depths across the survey range (+1.5, +1.0, +0.5, 0, -0.5, -1, -2. -4 CD). These were located using a digital depth meter corrected by estimated tidal height from the POLTIPS-3 software at the median time of the survey. Sampling was non-destructive; within each quadrat both density and cover of canopy-forming macroalgae (species as above) was visually quantified as counts of individual plants and percent canopy-cover per 0.25 m^2. If no suitable rocky substrate could be found at a given depth along a transect, data (counts and cover) was recorded as missing rather than zero and replication at that depth was reduced. Prior to analysis the paired quadrats were averaged.

5.2.4 Primary succession

In March 2016 five new unfouled sections of marina pontoon were replaced at one of the monitoring sites (Figure 5.1). This novel substrate provided an opportunity to monitor colonisation and primary succession of canopy-forming macroalgae over time. From monthly observations, new recruits were noted in August 2016 and could be identified to species by October 2016. The canopy-forming macroalgae were non-destructively sampled monthly from October 2016 – January 2018 (except for November 2016). At each sampling event, three 0.5 x 0.5 m quadrats were placed blindly against the outer side of each of the five pontoon sections. Within each quadrat, the density and cover of each canopy-forming macroalgae species was estimated visually by a single observer. New pontoons were compared to five adjacent pontoon sections which had not been replaced, therefore containing established macroalgal assemblages. These older pontoons (which had been *in situ* for >10 years) were sampled using the same method from March 2016 – January 2018, with sampling intensity initially at three month intervals, but monthly from March 2017.

A similar manipulation was also conducted at one intertidal reef monitoring site to compare primary succession between natural and artificial habitats (Figure 5.1). Eight circular treatment plots, 2 m in diameter (each separated by at least 2 m), were established within *Laminaria digitata* dominated reef habitat at a tidal height of +0.8 to +1.2 m CD. Each plot was randomly assigned as either 'control' or 'clearance' treatments. A permanent marker was placed in the centre of each plot using a stainless steel screw and coloured labels. In March 2017 all biota were removed from clearance plots in three stages: 1) manual removal by hand, 2) heat treatment of substrate using a Sheen x300 weed control flame gun, 3) secondary heat treatment using the same method 12 days later. In all plots, the canopy-forming macroalgae were non-destructively sampled (monthly where possible but at least bimonthly) from March 2017 to July 2018. At each sampling event, three 0.5 x 0.5 m quadrats were haphazardly placed in each plot. Counts were made of each canopy-forming macroalgae (except for *H. elongata* 'buttons' due to time constraints) and the percentage canopy cover of each species was estimated visually by a single observer. For both the marina and intertidal reef, data were averaged within each pontoon/plot at each sampling event before further analysis.

5.2.5 Data analysis

Using the monitoring data, interannual variability in macroalgal canopy composition was examined for each habitat-type separately using multivariate techniques. Raw data were first converted to proportional values and square root transformed (to down weight the importance of dominant species) prior to analysis. Resemblance matrices were constructed based on Bray-Curtis similarity and visualised using threshold metric multidimensional scaling (tmMDS) on bootstrap averages with their 95% confidence regions.

Statistical differences in multivariate canopy structure between years was assessed using PERMANOVA with ‘year’ (three levels, fixed factor), and ‘site’ (three levels, random factor) as factors. Where differences between years were identified, post-hoc tests using pair-wise PERMANOVA, and similarity percentage breakdowns (SIMPER) were used to determine the principal contributors to the observed dissimilarity within significant pairwise contrasts. As a proxy for beta-diversity (β), the PERMDISP routine was used to calculate mean multivariate dispersion between quadrats for each habitat separately. All PERMANOVAs were run with 9999 permutations of residuals under a reduced model with Type 3 (partial) sums of squares. tmMDS plots were visualised using 50 restarts and a minimum stress of 0.01. Bootstrap averages were calculated with 100 bootstraps per group, with automatic selection of dimensions based on $\rho > 0.99$.

Spatial trends between *Undaria* and co-occurring macroalgae were assessed using linear mixed models (LMM) for biomass data (log transformed due to strong right-skewness and heterogeneity of variances) and negative binomial generalized linear mixed models (nbGLMM) for count data (due to overdispersion from the Poisson distribution). Data from the multi-year monitoring survey were analysed for each habitat separately. In all cases *Undaria* was modelled as a function of the biomass/count of each co-occurring species (treated as additive fixed continuous factors). Both ‘site’ (categorical; three levels) and ‘year’ (categorical; three levels) were also included as random factors in order to discern overall spatial trends across sites and years. Validation of all models was graphical, using diagnostic quantile-quantile plots and predicted versus residual plots. Where transformations or random error structures failed to fully reduce residual structuring or heterogeneity of variances, test statistics were interpreted at a conservative level of $\alpha = 0.01$ to decrease the probability of Type 1 errors. LMMs and nbGLMMs were fitted using the *lmer* and *glmer.nb* commands respectively, both from the *lme4* package in R (Bates *et al.*, 2015).

To assess depth-related distribution trends between *Undaria* and co-occurring species, Spearman rank correlation tests were calculated between *Undaria* and each co-occurring species from the depth distribution survey. Data were first averaged across transects within each survey site and only those depths in the range of *Undaria* occurrence were used to calculate correlations. All Spearman correlations and significance tests were calculated with Holm adjust p-values to account for multiple testing using the *corr.test* function from the *psych* package in R (Revelle, 2017).

For the primary succession manipulation, variability in the biomass/count of each species between the cleared (or new) substrate and control areas were examined with two-way analysis of variance (ANOVA). Prior to statistical analysis all count data were log transformed (log[x+1]) and percent cover data were arcsin transformed ($\mathrm{asin}\sqrt{x/100}$). Values of density (inds. 0.25 m^{-2}), and cover for each species were modelled as a function of “date” (categorical; 15 levels for marina, 10 levels for reef) and “substrate” (categorical; two levels: cleared/new, control), with their interaction. The approach to model validation was the same as described above. Significant pairwise differences between substrates at each sampling point were tested using post hoc F-tests with Holm adjusted p-values. ANOVAs were constructed using the *lm* function from base R (R Core Team, 2017) and pairwise tests were implemented using the *testInteractions* function from the *phia* package in R (De Rosario-Martinez, 2015). All univariate statistics were implemented in R 3.4.3 (R Core Team, 2017), multivariate statistics in PRIMER-e version 7 (Clarke *et al.*, 2014), data manipulation used the *dplyr* package (Wickham and Francois, 2015), graphs were created using *ggplot2* (Wickham, 2009) and maps (Figure 5.1) were made within ArcMap 10.3.1.

5.3 Results

5.3.1 Multi-year monitoring

Considering all three sampling years together, intertidal macroalgal canopies were dominated by *Undaria* in June, with it contributing on average the highest density and biomass of any species (Figure 5.2). There was also a relatively high biomass of *H. elongata* and *L. digitata*, and a high density of *S. latissima* (Figure 5.2). The subtidal rocky reef had the most mixed canopy in June, with *L. ochroleuca* being dominant by biomass but with *Undaria, S. latissima* and *S. polyschides* being present in similar densities and only moderately lower in biomass (Figure 5.2). There was also a small amount of the non-native *S. muticum* found at two of the three subtidal sites (Figure 5.2, Figure D.1). Marinas were dominated by *Undaria* in terms of both biomass and density (Figure 5.2), which was interspersed with the native canopy-forming macroalgae *S. latissima* and *S. polyschides*, and small amounts of the non-native *S. muticum* (Figure 5.2). There was very low variation in the density and biomass of species between years across the three June sampling events (Figure 5.2), although within-year seasonal variability was pronounced (Figure D.1). Across all habitats *Undaria* and *S. polyschides* had a clear annual cycle with peak abundance in June and September, respectively. The perennial species *S. latissima* exhibited a similar annual pattern but with higher variation both between sites and habitats (Figure D.1), whereas *Laminaria* species on rocky reefs had low variability both seasonally and between sites (Figure D.1). Mean β-diversity (between quadrats) was highest in subtidal habitats and lowest in marinas (Figure 5.3). The overall composition of macroalgal canopies did not vary markedly across the three years surveyed within any habitat type (Figure 5.3). However, significant between-year variability in assemblage structure (based on count data only) was recorded within intertidal reef habitat, with 2016 being dissimilar to other survey years (Figure 5.3, Table D.1, Table D.2). This was due to lower contributions of *Undaria* and *S. latissima* to total density, and higher contributions of *L. digitata, H. elongata* and *S. polyschides* (Table D.3).

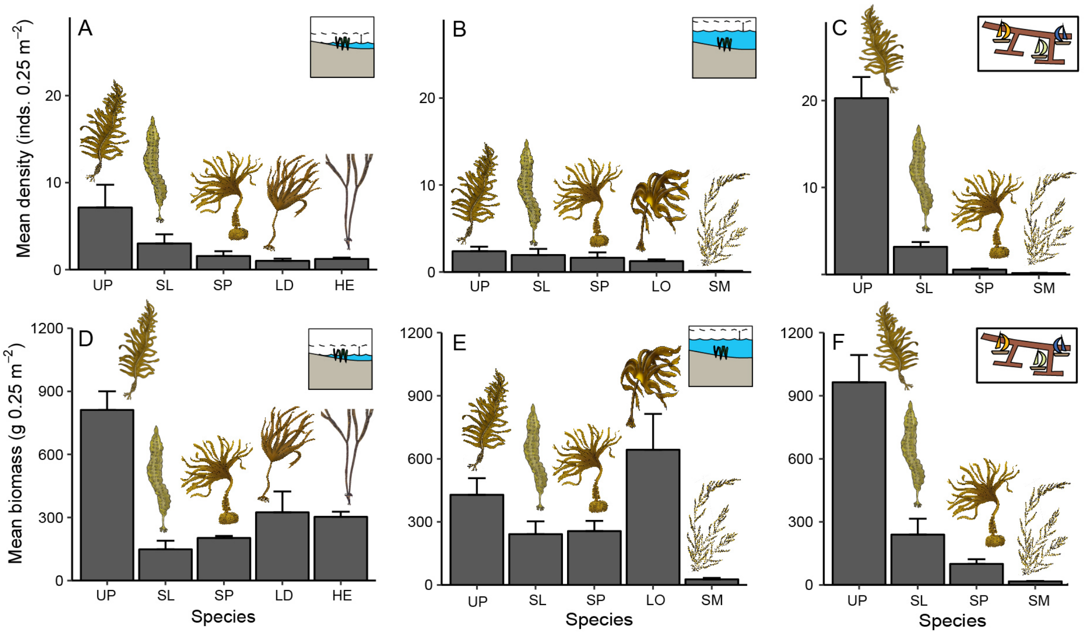

FIGURE 5.2: Mean density (A-C) and biomass (D-F) (± SE between years) of canopy forming macroalgae averaging across the three sites and sampling events in June 2016, 2017 and 2018 for each habitat separately (A, D = intertidal reef; B, E = subtidal reef; C, F = marina pontoons). UP = *U. pinnatifida*, SL = *S. latissima*, SP = *S. polyschides*, LD = *L. digitata*, HE = *H. elongata*, LO = *L. ochroleuca*, SM = *S. muticum*.

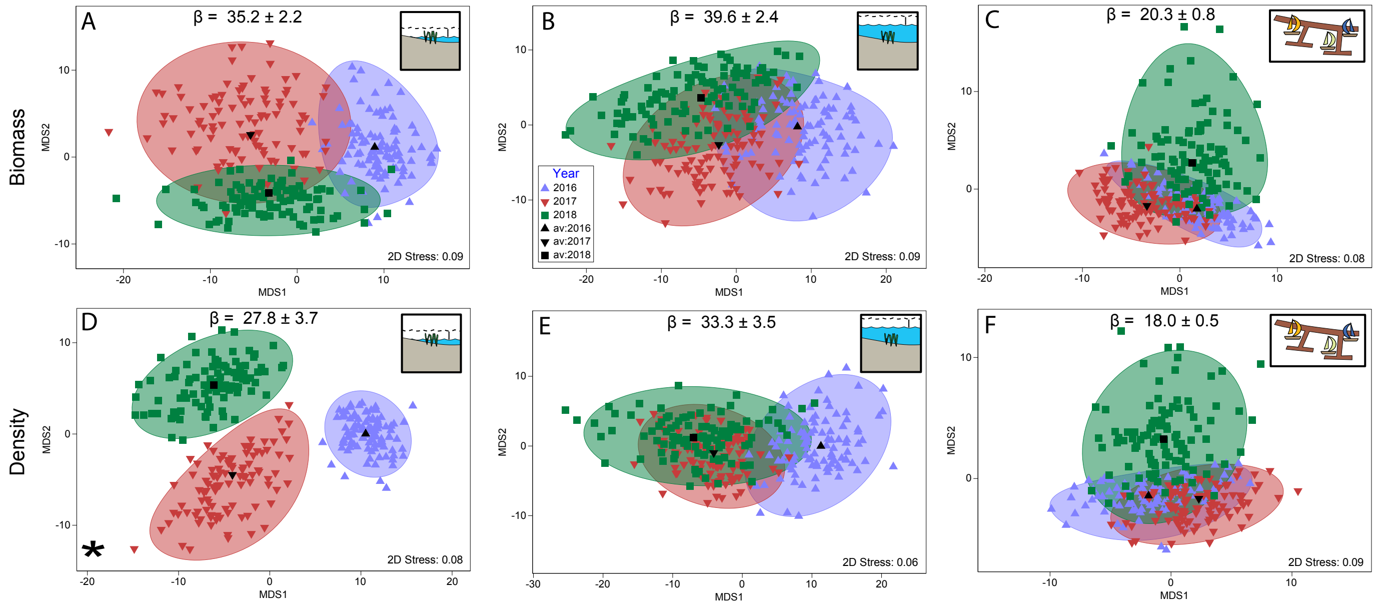

FIGURE 5.3: Threshold metric multi-dimensional scaling (tmMDS) plots of bootstrapped average monitoring data within each year of study (blue triangle = 2016, red triangle = 2017, green square = 2018). Biomass (A-C; g 0.25 m^{-2}) and density (D-F; inds. 0.25 m^{-2}) data for each habitat assessed separately (A, D = intertidal reef; B, E = subtidal reef; C, F = marina pontoons). Circular areas indicate the 95% confidence region around the bootstrap average. Asterisks indicate significant difference between years based on PERMANOVA (Table D.1). β = proxy of mean beta-diversity for each habitat (± SE) measured by multivariate dispersion.

There were significant spatial trends between *Undaria* and co-occurring species in rocky reef habitats. *Undaria* density and biomass had a significant negative correlation with the *Laminaria* species in both intertidal and subtidal habitats (Table 5.1, Figure 5.4). *Undaria* biomass was also negatively related to *S. latissima* in both habitats, although this was only statistically significant for subtidal biomass (Table 5.1, Figure 5.4). For all other species in reef habitats the relationships were less well defined. In the subtidal reef habitat there was a positive relationship between the density of *Undaria* and *S. muticum*, on intertidal reef *H. elongata* was negatively related to both *Undaria* density and biomass, and *S. polyschides* was positively related to *Undaria* density and biomass in both habitats; however, none of these trends were statistically significant (Table 5.1). In marina habitats the density and biomass of *Undaria* was not significantly related to any other species, although the relationship in biomass between *Undaria* and *S. polyschides* was near-significant (Table 5.1).

TABLE 5.1: GLMMS and LMMs identifying the influence of co-occurring canopy-forming macroalgae on the density and biomass of *Undaria* within each habitat. The coefficient estimates (Est) and p-value (p) are shown for each species along with t-values (t) from LMMs for biomass [$\log(\text{g m}^{-2} + 1)$] and z-values (z) from GLMMs for density data (inds. 0.25 m^{-2}). Significant coefficients shown in bold (α=0.01 for biomass, α=0.05 for density).

	Biomass			Density		
Species	Est	t	p	Est	z	p
Intertidal reef						
S. polyschides	4.9x10-4	0.87	0.386	0.009	5.95	0.819
S. latissima	-1.9x10-3	-2.28	0.025	0.035	0.23	0.090
L. digitata	**-2.2x10-3**	**-8.11**	**<0.001**	**-0.186**	**1.70**	**<0.001**
H. elongata	-6.8x10-4	-1.53	0.130	-0.114	-1.95	0.051
Subtidal reef						
S. polyschides	2.3x10-4	0.60	0.550	0.058	1.08	0.281
S. latissima	**-1.8x10-3**	**-3.87**	**<0.001**	-0.031	-0.82	0.410
L. ochroleuca	**-2.2x10-3**	**-10.28**	**<0.001**	**-0.302**	**-2.50**	**0.013**
S. muticum	1.1x10-3	-0.64	0.526	0.468	2.15	0.032
Marina						
S. polyschides	5.2x10-4	2.44	0.017	0.020	0.49	0.623
S. latissima	-1.3x10-4	-0.81	0.421	<0.001	<0.01	0.998
S. muticum	-1.3x10-3	-1.46	0.147	-0.145	-1.57	0.117

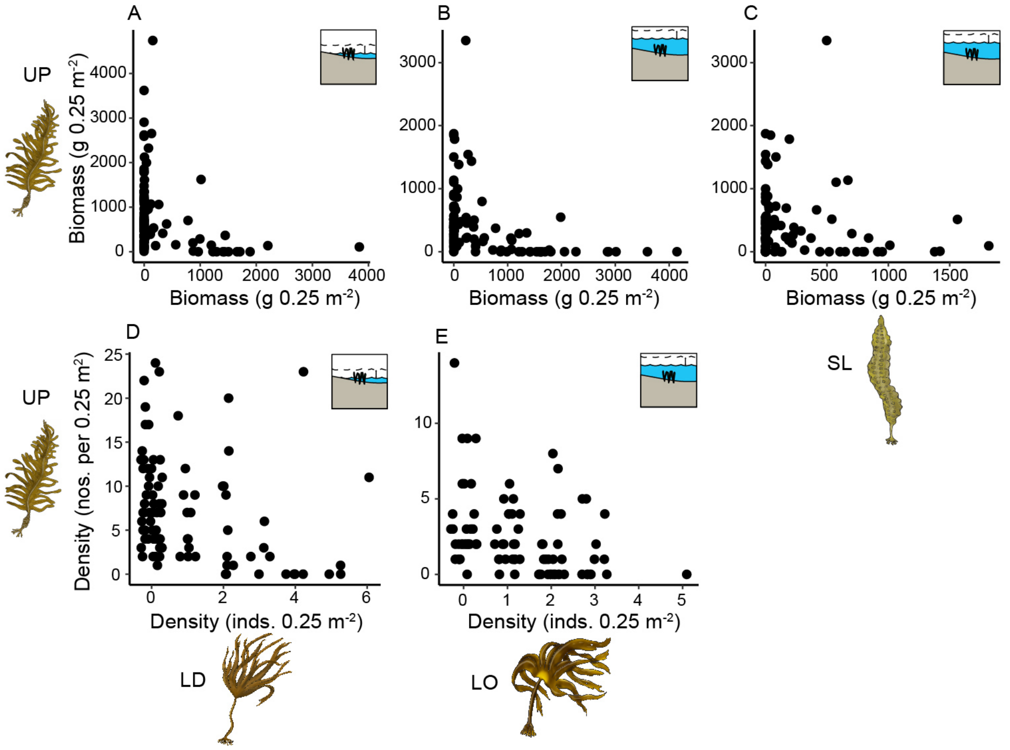

FIGURE 5.4: Spatial relationship between *Undaria* and co-occurring canopy formers. Raw quadrat data from three year monitoring survey plotted for those contrasts shown to be significant from LMMs and GLMMS (Table 5.1). Biomass (A-C) and density (D-E) data for each habitat assessed separately (A, D = intertidal reef; B, C, E = subtidal reef). Density data shown with small random jitter around each integer value on x-axis in order to display overlapping data points. UP = *U. pinnatifida*, LD = *L. digitata*, LO = *L. ochroleuca*, SL = *S. latissima*.

5.3.2 Depth-related trends

On rocky reef *Undaria* was found at depths ranging from +1 to -4 m CD, with highest density and percent cover in the low intertidal to shallow subtidal zone, and a peak at +0.5 m CD (Figure 5.5). Above +1 m CD canopy-forming macroalgal assemblages were composed of *F. serratus* and *L. digitata* only, with *Undaria* completely absent (Figure 5.5). Across the depth range of *Undaria*, it co-occurred with seven species of canopy-forming brown macroalgae: *L. digitata*, *H. elongata*, *S. muticum*, *S. polyschides*, *S. latissima*, *L. ochroleuca*, *L. hyperborea*. The peak in *Undaria* density/cover at +0.5 m CD coincided with the lowest density and percentage cover of *Laminaria* species at any depth (Figure 5.5). A weak positive correlation was recorded between *S. latissima* and *Undaria* across depth; however, this was only significant for count data (Figure 5.5). *Undaria* had a strong and significant positive correlation with *S. polyschides* with similar distribution patterns across depth, but a strong negative correlation with *L. ochroleuca* (Figure 5.5). There was also a negative correlation between *Undaria* and *L. digitata,* although this was not statistically significant (Figure 5.5). When considering all *Laminaria* species together, *Undaria* again exhibited a significant negative correlation across depths (Figure 5.5).

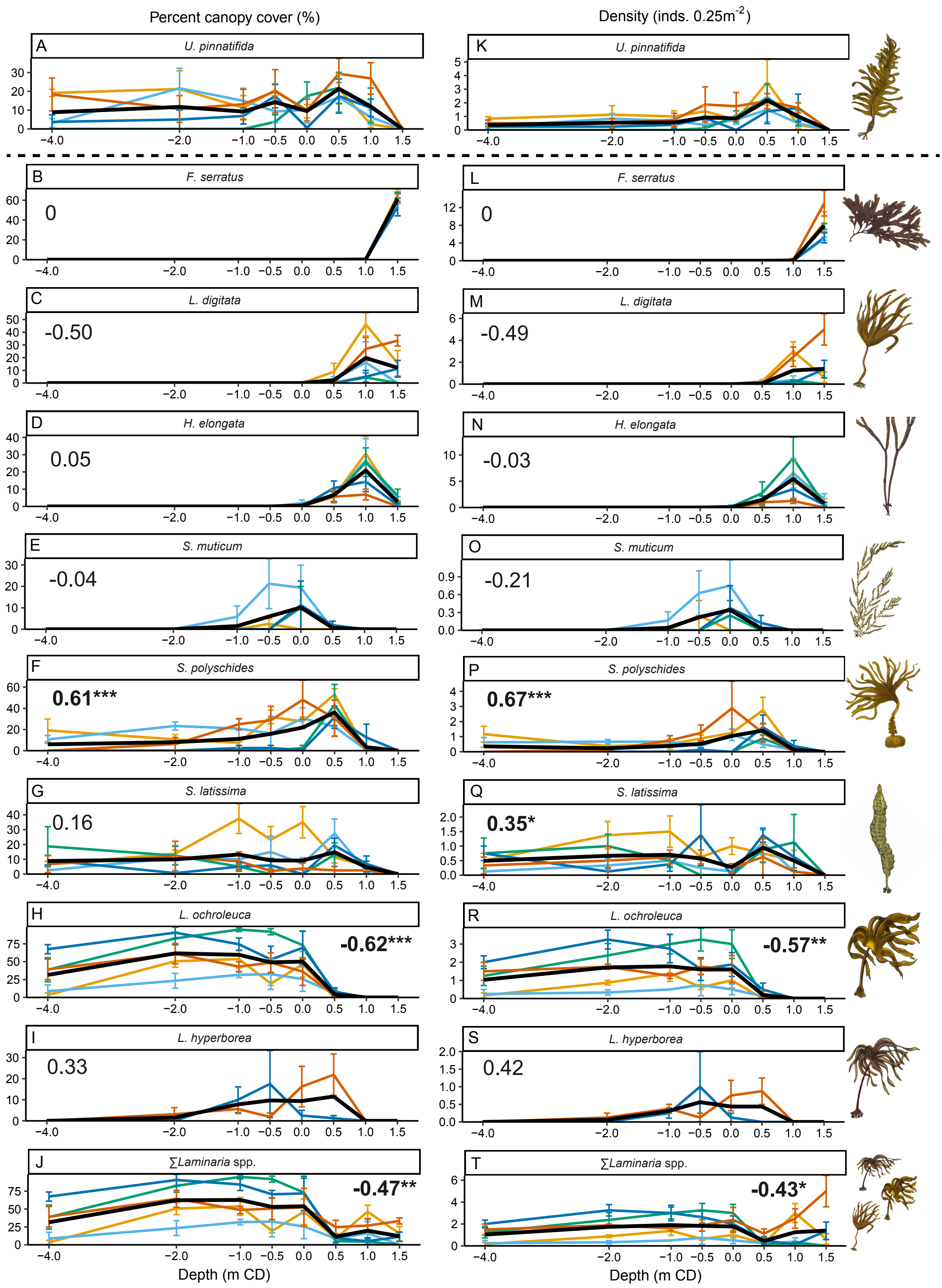

Figure 5.5: Distribution of canopy-forming macroalgae across depth, in reef habitats of Plymouth Sound. Mean percent canopy cover (A-J) and density (K-T) of each species shown ± SE at each of five sites (orange = Devils Point, light blue = Firestone Bay, green = Jennycliff, dark blue = Mount Batten, red = West Hoe). Black lines indicate average across sites. Correlation coefficients with *Undaria* shown for every co-occurring species as well as for the sum of all *Laminaria* spp. Significant correlations shown in bold; asterisks indicate significance level (*=<0.05, **=<0.01, ***=<0.001).

5.3.3 Primary succession

Following the introduction of new unfouled substrate into an *Undaria* dominated marina in March 2016, initial colonisation by canopy-forming macroalgae (Oct 16 to Mar 17) was dominated by *L. digitata* with low levels of *S. latissima* (Figure 5.6). The density and cover of *L. digitata* were significantly higher compared with control areas on older pontoon substrates, whereas values for *S. latissima* were comparable between new and control substrates (Figure 5.6). The first *Undaria* recruits were recorded one year following the installation of the new pontoons. The density of *Undaria* increased rapidly from Mar – Jun 17 and did not differ significantly from the control areas for the remainder of the experiment. The cover of *Undaria* also increased rapidly but remained marginally lower on new pontoons compared with control areas, although this variability was statistically significant at only one sampling event (Figure 5.6). During this period, the density and cover of *L. digitata* on the new pontoons declined, and during the last four months of monitoring were no longer significantly different to values recorded on the older pontoons (Figure 5.6). The density and cover of *S. latissima* increased on new pontoons during the same period, and was significantly higher than that on older substrates (Figure 5.6). However, density and cover subsequently declined and for the last four months of monitoring both metrics were similar between treatments (Figure 5.6).

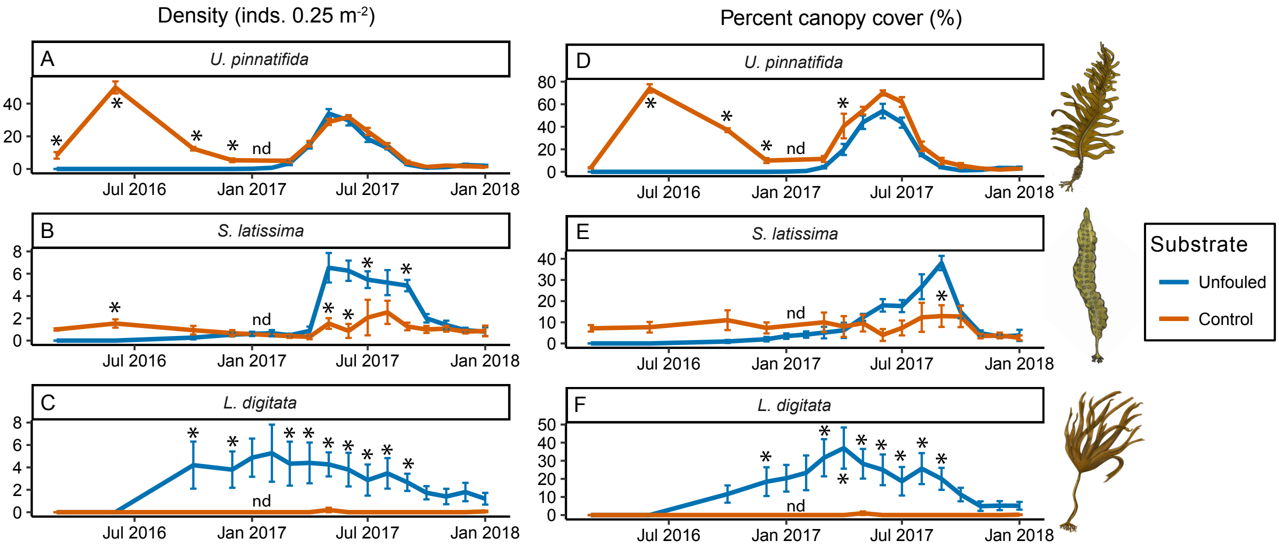

FIGURE 5.6: Marina primary succession manipulation - change in density (A-C) and percent cover (D-F) of canopy-forming macroalgae following introduction of new substrate into a marina habitat. Means shown ± SE. Asterisks indicate pairwise differences between old (red) and new unfouled (blue) substrate at each sampling event (Table D.4). “nd” indicates where data from old substrates was missing so pairwise tests could not be calculated.

Cleared substrates within the *L. digitata* dominated intertidal rocky reef habitat were quickly colonised by canopy-forming macroalgae after only two months. This early colonisation (May to Aug 17) was dominated by *Undaria*, but also *S. polyschides,* both of which were significantly higher in density and cover compared to the control area of undisturbed substrate (Figure 5.7). The density and cover of *L. digitata* and the cover of *H. elongata* on cleared substrates remained low during this period, being significantly lower than values recorded on control plots (Figure 5.7). For the remainder of the experiment (Oct 17 to July 18) *Undaria* and *S. polyschides* remained at low levels within both cleared and control plots, and no significant differences between treatments were recorded at any sampling point (Figure 5.7). During this period there was a sustained increase in both *L. digitata* and *H. elongata* on new substrates. Even so, density and cover remained significantly lower on cleared compared with undisturbed areas for *L. digitata* until the last two months of sampling (Figure 5.7). *S. latissima* density and cover varied greatly on both cleared and undisturbed areas across the study period, and exhibited no significant differences between substrate types (Figure 5.7).

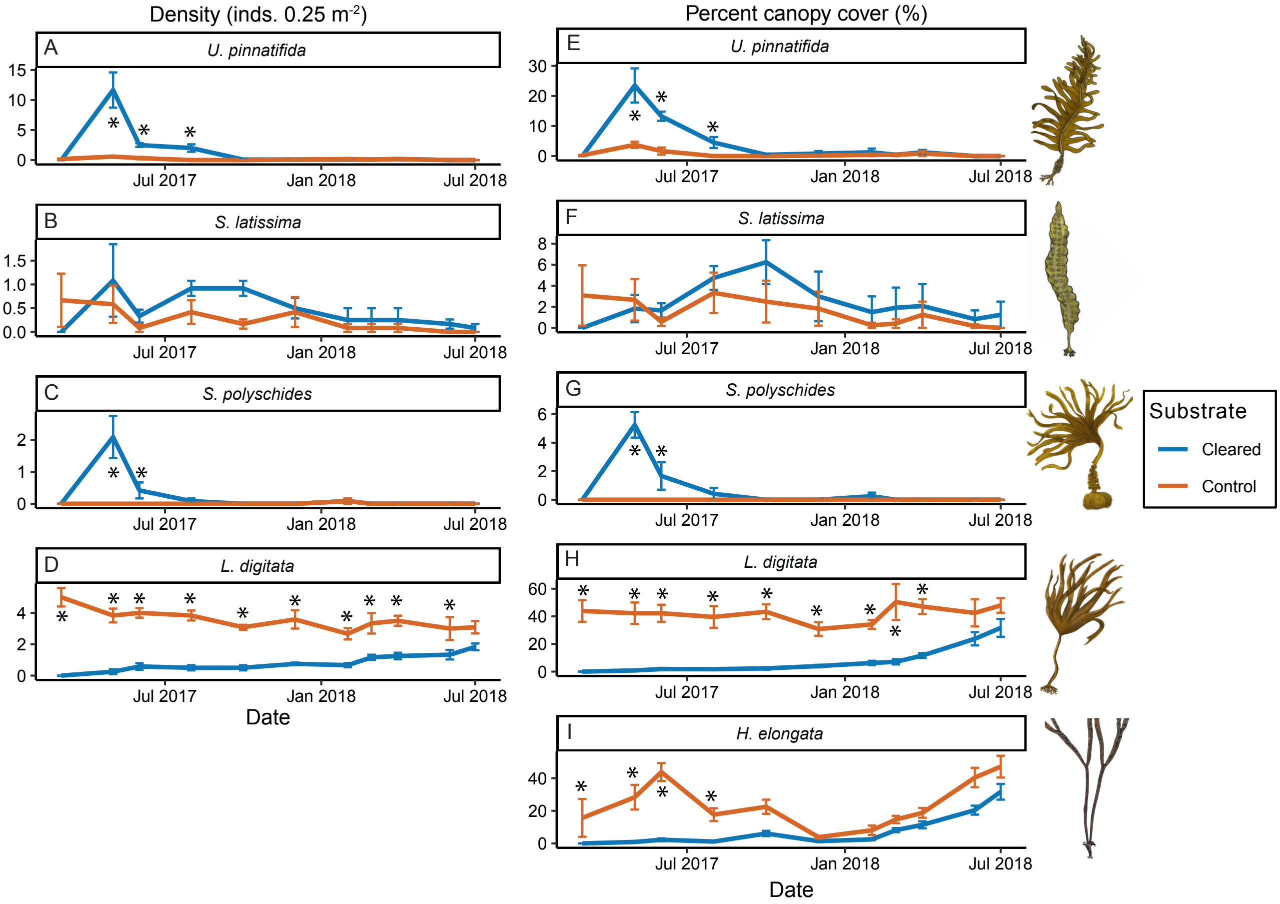

FIGURE 5.7: Intertidal reef primary succession manipulation - change in density (A-D) and percent cover (E-I) of canopy-forming macroalgae following introduction of cleared substrate into intertidal reef habitat. Means shown ± SE. Asterisks indicate pairwise differences between old (red) and new (blue) substrate at each sampling event (Table D.5).

5.4 Discussion

5.4.1 Coexistence or competition?

Interpreting results from manipulative, trait-based or demographic studies within the framework of contemporary coexistence theory allows for examination of the extent to which INNS may be coexisting or competing with native species in recipient communities (HilleRisLambers *et al.*, 2012). Given its rapid rate of spread and inconsistencies in its perceived impacts (Epstein and Smale, 2017a), *Undaria* is a useful model INNS to test coexistence theory within rarely considered marine ecosystems (Barabas *et al.*, 2018). *Undaria* has been present within the current study region for at least 15 years, where it now co-occurs with up to ten different species of canopy-forming macroalgae. Overall, there was very low annual variation and no major changes in macroalgal canopy density, biomass or composition over the three years of monitoring. Although inference is somewhat limited due to the duration of this study, the results suggest that large-scale temporal variability and maintenance of coexistence through the storage effect is not a primary driver of assemblage structure. This also indicates that the invader has reached a relative equilibrium within the recipient community, as none of the species recorded here exhibited significant increases or decreases in abundance over the study period.

We recorded high variation in macroalgal assemblage structure between habitats. In complex rocky reef habitats, *Undaria* was predominantly found in areas that supported low density and cover of perennial species, and reached relatively low abundances in areas where these species were experimentally removed. Conversely, on uniform marina pontoons, *Undaria* was the dominant species, exhibited no significant spatial relationships with native species and became established as the dominant species following post-disturbance succession. Overall, when considering drivers of assemblage structure at the site level, niche diversity primarily promoted coexistence of species on rocky reef, whereas fitness differences governed competition within marinas. It must be noted, however, that at the level of micro-habitats there are complex species-specific patterns which cannot be generalised across a given site. Using coexistence theory to contextualise observational or correlative findings, as shown here, allows for a clearer understanding of INNS distribution patterns and potential community level impacts. These factors should be of primary concern for INNS research, as they will directly contribute to management and conservation priorities.

5.4.2 Interactions between *Undara* and *Laminaria* spp. on rocky reef

On natural rocky reef substrates, *Undaria* exhibited a significant negative spatial relationship with the two dominant perennial species in both intertidal (i.e. *Laminaria digitata*) and subtidal habitats (i.e. *Laminaria ochroleuca*). The depth surveys also indicated that *Undaria* predominantly occupies a depth/elevation zone in which *Laminaria* species are found in low abundance and cover, which may suggest niche differences as the primary driver leading to differing abundance-distribution patterns. There were many instances, however, where the distributions of species overlapped and they occupied similar habitats within sites, suggesting that fitness differences must also be a driver of the significant negative relationship.

One factor which may drive niche differences and spatial separation between *Undaria* and *Laminaria* spp. is the ability of *Undaria* to grow successfully on a wide range of types of substrate, aspects and stabilities (Sliwa *et al.*, 2006; Russell *et al.*, 2008; Epstein and Smale, 2017b). This generalist life strategy may allow it to fill a niche that is not occupied by the perennial Laminarians which generally require stable rocky substrates in order to successfully grow and mature (Kain, 1962). In many cases, however, these species interact on stable rocky substrates, suggesting other drivers influence abundance-distribution patterns.

The primary succession experiment showed that clearance of *L. digitata* dominated areas leads to an opportunistic pulse of *Undaria* recruitment, confirming an overlapping niche. This was followed by recovery of *L. digitata* and a concurrent decline in *Undaria,* indicating higher fitness in *L. digitata.* However, *Undaria* recruited in relatively low density and cover following the removal of *L. digitata*, and it was not able to recruit in the second year after clearances even when there was still significantly lower *Laminaria* density and cover. This would suggest that *Undaria* has an overlapping but distinct niche when compared to *L. digitata*, and where they do overlap *Undaria* has lower fitness.

Due to differences in tolerance to desiccation and temperature stress, the two *Laminaria* species within this study region form two relatively distinct zones on rocky reefs; *L. digitata* on intertidal reef and *L. ochroleuca* on subtidal reef (King *et al.*, 2017). Although there is evidence of relatively high desiccation tolerance in *Undaria* sporophylls and gametophytes, information is lacking on the tolerance of growing blade tissue (Bollen *et al.*, 2017). Due to its inability to successfully proliferate in cleared areas of the *L. digitata* zone, it is likely that *Undaria* has lower resistance to desiccation and temperature stress than *L. digitata.* However, *Undaria* is found at highest density and biomass at elevations above the *L. ochroleuca* zone, potentially indicating an intermediate tolerance between the two *Laminaria* species and allowing it to occupy a depth niche between the two Laminarians.

This does not, however, explain why *L. digitata* is not outcompeting *Undaria* and dominating on stable rocky substrate in the low intertidal to shallow subtidal fringe. In some regions *L. digitata* can be found to depths of up to 15 m, dependent on competition, wave exposure, light, temperature and grazing pressure (Smale *et al.*, 2013;

Yesson *et al.*, 2015). While it is feasible that any of these factors could influence observed abundance-distribution patterns in the current study, *L. digitata* can be present in a wide range of wave exposures (Yesson *et al.*, 2015). 'Top-down' grazing pressure is also not thought to be of major importance to kelp population structure along most of the UK coastline (Smale *et al.*, 2013; Smale *et al.*, 2016; Hereward *et al.*, 2018), except at its deeper extent (Jones and Kain, 1967). *L. digitata* is, however, known to require relatively high light levels to reproduce and grow (Han and Kain, 1996; Delebecq *et al.*, 2013), whereas *Undaria* is able to persist under a wide range of light climates (Campbell *et al.*, 1999; Morelissen *et al.*, 2013; Epstein and Smale, 2017a). In the relatively turbid conditions of Plymouth Sound, it may be that *L. digitata* becomes light limited in the deeper intertidal-subtidal fringe (which is generally immersed in 1-5 m of turbid seawater due to the tidal range in the region), allowing *Undaria* to occupy this vacant space. Further manipulations of assemblages within the intertidal fringe would be needed to fully determine the niche versus fitness differences between these species.

It is also necessary to consider why *Undaria* is not proliferating in the lower subtidal areas which are currently *L. ochroleuca* dominated. One potential driver could be the comparatively low rate of nutrient uptake and nitrate storage in *Undaria* when compared to Laminarians (Dean and Hurd, 2007; Epstein and Smale, 2017a). Increased water motion enhances nutrient uptake in kelps (Gerard, 1982) and can enhance the growth rate of *Undaria* (Nanba *et al.*, 2011; Peteiro *et al.*, 2016). As tidal water flow is likely to be higher in the subtidal fringe when compared to the lower subtidal zone, *Undaria* may have lower fitness than *L. ochroleuca* in lower velocity subtidal waters. Although not possible as part of this study due to logistical challenges in experimental design, providing cleared or clean substrate in lower subtidal areas and assessing the colonisation and succession of these two species would allow identification of potential niche versus fitness differences between *Undaria* and *L. ochroleuca*.

Overall, these results support studies from other regions which suggest that *Undaria* has lower competitive ability when compared to native canopy dominant perennials (Epstein and Smale, 2017a; South *et al.*, 2017; and references therein). The results also highlight that the persistence of *Undaria* in many settings is likely to be due to its relatively broad niche, allowing it to occupy underused resources or vacant space to coexist with native perennials at the site level.

5.4.3 Interactions between *Undara* and *S. polyschides* on rocky reef

On rocky reef, both *Undaria* and the native annual canopy-forming species *S. polyschides* were strongly correlated across depth and showed similar responses in the primary succession experiments. This would suggest that these species occupy a similar niche throughout rocky reefs in the study region. Both species are annual, relatively opportunistic and are found at highest abundance and cover in the subtidal fringe (Norton and

Burrows, 1969; Castric-Fey *et al.*, 1993; Fletcher and Farrell, 1999; Epstein and Smale, 2017b). They also recruit, reach maximum biomass and senesce at similar times of year (Norton and Burrows, 1969; Floc'h *et al.*, 1991; Fletcher and Farrell, 1999). Therefore, it has previously been suggested that these two species occupy a similar niche and may directly compete for space or resources (Castric-Fey *et al.*, 1993; Fletcher and Farrell, 1999; Yesson *et al.*, 2015; Epstein and Smale, 2017b). Species which occupy the same or highly similar niche while having little to no fitness dissimilarities would be expected to have strong positive spatial relationships across a given site. However, in this study, neither the density nor biomass of *S. polyschides* showed a significant spatial relationship with *Undaria* in either intertidal or subtidal reef habitats. This would suggest that there are more complex competitive interactions occurring which does not allow full coexistence between these species.

Observations made during this study and related surveys identified that *Undaria* peak recruitment, biomass and senescence generally occurs 2-3 months prior to *S. polyschides* (Figure D.1). This could allow *Undaria* to exert a competitive advantage over *S. polyschides*, by occupying habitat space and utilising light and nutrient resources, before the recruitment and growth of *S. polyschides*. It may also, however, allow a level of coexistence between species through temporal niche separation. Further manipulative experimentation would be needed in order to discern the strength and direction of fitness dissimilarities between these two species.

If *Undaria* is outcompeting and potentially displacing *S. polyschides,* it would be pertinent to consider how this may alter wider ecosystem functioning. Previous studies have shown that these two species harbour a similar epifaunal and epifloral assemblages and therefore substitution of the species may have minimal community-level impacts (Arnold *et al.*, 2016). Moreover, at the wider regional scale *Undaria* is far less tolerant of wave action than *S. polyschides,* which can dominate under wave-exposed conditions (Burrows, 2012; Epstein and Smale, 2017b), suggesting that competitive exclusion could only occur at wave sheltered sites and that regional displacement of *S. polyschides* is highly unlikely. However, further research is needed to determine wider ecological consequences such as trophic provision to grazers, habitat provision to mobile species, primary production and carbon cycling (Smale *et al.*, 2013).

5.4.4 Species interactions in marinas

In comparison to reef habitats, the environment within marinas is relatively homogenous and as such niche diversity is reduced. The relative homogeneity in community structure was highlighted by the low β-diversity recorded on marina pontoons when compared to reef habitats. The pontoons available for sampling in this study were all of uniform substrate, depth and exposure, and were located adjacent to one another, with similar exposure, light availability, water flow and temperature. It is likely, therefore, that relationships in distribution-abundance patterns between species across a given site will be strongly influenced by fitness differences and competitive interactions. In all three marinas *Undaria* was the dominant species in terms of both density and biomass (Figure D.1); it also exhibited no spatial or temporal correlations with co-occurring species. This would suggest that *Undaria* is able to reach similar population size or density at varying levels of interspecific competition. This fitness difference is supported by results from the primary succession experiment which showed that newly-available substrate introduced into *Undaria* dominated marinas can lead to a significantly higher recruitment of native canopy-forming species (*L. digitata* and *S. latissima*), both of which were eventually replaced by *Undaria*, most likely due higher fitness, although fluctuation in the abiotic factors cannot be discounted. While the high competitive ability of *Undaria* in artificial habitats has been previously suggested in other studies (Curiel *et al.*, 2001; Cremades *et al.*, 2006; Farrell and Fletcher, 2006; Heiser *et al.*, 2014; Veiga *et al.*, 2014; James and Shears, 2016a; Epstein and Smale, 2017b), results from the current study provide strong empirical evidence for such fitness dissimilarities.

Marinas are generally located in areas of intense human activity with modified abiotic conditions. Marina environments are often characterised by low salinity and high turbidity, pollution and nutrient levels, which generally support distinct and often depauperate epifaunal and epifloral communities that lack long-lived native species compared to adjacent natural habitats (Connell, 2001; Glasby *et al.*, 2007). The higher fitness of *Undaria* when compared to native canopy-formers in marinas may in part be due to its ability to tolerate more extremes in environmental variables (e.g. Herbold and Moyle, 1986; Floc'h *et al.*, 1991; Cecere *et al.*, 2000; Curiel *et al.*, 2001; Farrell and Fletcher, 2006). Perhaps the largest abiotic dissimilarity between marina pontoons and rocky reef habitats is the constant shallow depth in which floating pontoons are maintained when compared to tidal rocky habitats. One consequence of this is that macroalgae are subjected to constant high light intensities, which often leads to substantial biofouling and eventual detachment or smothering of blade tissue. Here, *Undaria* plants were observed to support significantly less epiphytic loading compared with native species, potentially due to its fast growth rate and annual senescence, or perhaps the presence of antifouling compounds (Sogn Andersen *et al.*, 2011; Marzinelli, 2012). This may be a further mechanism underpinning the higher fitness of *Undaria* over native perennials within marinas. This study adds further support to the importance of artificial habitats in the invasion pathway of *Undaria* both across regions and locally into adjacent natural habitats (James and Shears, 2016a; Epstein and Smale, 2017b; Guzinski *et al.*, 2018). The optimal habitat for *Undaria* within this study region appears to be floating pontoons in marinas – a habitat that has no natural analogue (Epstein and Smale, 2018).

5.4.5 Ecological impact and management prioritisation

Undaria has been reported to have relatively low ecological impact in many locations to which it has been introduced, particularly where it occurs within dense native canopies (Epstein and Smale, 2017a; South *et al.*, 2017). Although this study largely supports these conclusions, it highlights that there can be many context-specific species interactions which should also be considered before clear conclusions can be drawn. Within this study region, and perhaps across the northeast Atlantic, *Undaria* may exert low community-level impacts within natural habitats, due to its relatively distinct niche and low fitness when compared to dominant native perennial canopy-formers. *Undaria* could, however, influence co-occurring macroalgae within its invaded niche, potentially displacing functionally similar native species with possible community-level impacts. Further targeted research is needed to better quantify both lethal and sub-lethal effects of *Undaria* on species within its niche, as well as consideration of the conservation value of native macroalgal-dominated communities.

The distribution, proliferation and potential impact of INNS is highly dependent on complex niche and fitness differences between individual species, which themselves can vary across habitats. The quantification of INNS impact is therefore wholly dependent on the response metrics recorded and the spatial scale to which conclusions are drawn (Hulme *et al.*, 2013; Chase, 2014; Hannam and Wyllie-Echeverria, 2014). This is particularly evident within complex marine habitats dominated by, for example, macroalgal canopy-formers, which interact across multiple spatial and temporal scales, occupying distinct yet overlapping microhabitats and niches. For management purposes INNS are often ranked in terms of their broad-scale impact on the natural environment, which may occur at a continental or even global scale (Lowe *et al.*, 2000; Nentwig *et al.*, 2017; Carboneras *et al.*, 2018). More consideration must be given to the context-specific nature of INNS impacts prior to wider scale management decisions.

Chapter 6

Ecological and biochemical impact on intertidal macroalgae

6.1 Introduction

Human-mediated introductions of species into areas outside of their native range have caused, and continue to cause, irreversible changes to the natural environment (McKinney and Lockwood, 1999; Early *et al.*, 2016; Gallardo *et al.*, 2016). The magnitude of impact that these non-native species (NNS) have on recipient ecosystems can vary greatly (Ricciardi *et al.*, 2013; Simberloff *et al.*, 2013; Jeschke *et al.*, 2014). There is considerable evidence that NNS can outcompete native flora and fauna (Bullard *et al.*, 2007; Simberloff *et al.*, 2013; Jormalainen *et al.*, 2016), alter nutrient pathways (Cloern, 1996; Simberloff, 2011; Gallardo *et al.*, 2016), change habitat structure (Crooks, 2002; Simberloff, 2011; Dijkstra *et al.*, 2017) and disturb trophic interactions (Green *et al.*, 2012; Dijkstra *et al.*, 2013; Salvaterra *et al.*, 2013), even leading to regional and global species extinctions (Gurevitch and Padilla, 2004; Simberloff *et al.*, 2013). In contrast, in other cases NNS do not drive ecosystem change and can co-exist with native species with little detectable impact (Williamson and Fitter, 1996a; Parker *et al.*, 1999; Ricciardi and Cohen, 2007; Simberloff, 2011). It can, however, be argued that all species introductions must have some impact on recipient communities simply by their presence - reducing the availability of space, food, water or other resources for co-occurring species (Simberloff *et al.*, 2013; Russell and Blackburn, 2017).

Impact is often directly correlated with the range, extent and abundance of the NNS (Parker *et al.*, 1999; Thomsen *et al.*, 2011a; Ricciardi *et al.*, 2013; Blackburn *et al.*, 2014); but even a few individuals can have significant impacts in certain ecological settings (Ricciardi and Cohen, 2007; Jeschke *et al.*, 2014). NNS which spread and proliferate to reach high abundances and achieve widespread distribution (termed invasive non-native species: INNS) also exert varying degrees of impact upon native communities, depending on a wide range of biotic and abiotic processes (Ricciardi and Cohen, 2007; Thiele *et al.*, 2010; Simberloff *et al.*, 2013).

Various unifying frameworks have been developed to better measure, and compare INNS impact; such approaches generally consider measures of abundance, range and per capita effect (Parker *et al.*, 1999; Thomsen *et al.*, 2011a; Ricciardi *et al.*, 2013; Blackburn *et al.*, 2014). Quantifying the per capita effect of an INNS across a given ecosystem is highly challenging because: (i) perceived impacts vary across both space (between sites and habitat-types) and time (between seasons and years); and (ii) perceived impacts vary between studies conducted within the same area due to different methodological approaches or chosen response variables (Thiele *et al.*, 2010; Hulme *et al.*, 2013; Thomsen *et al.*, 2014). The potential for the effects of INNS to manifest themselves across multiple levels of biological organisation adds further complexities to measuring overall impact (Hulme *et al.*, 2013; Simberloff *et al.*, 2013). Where INNS cause widespread mortality or facilitation of native species, impact can be relatively easily identified and (to a certain extent) quantified, by measuring changes in population sizes following manipulative or before-after control-impact (BACI) studies (Ewel *et al.*, 1999; Byers *et al.*, 2002; Forrest and Taylor, 2002; Thomsen *et al.*, 2014). Conversely, more subtle sub-lethal effects of INNS on native species, such as changes in physiology, fecundity, growth and behaviour, are more difficult to measure and are therefore rarely quantified (Hulme *et al.*, 2013; Thomsen *et al.*, 2014). Even so, persistent and prolonged sub-lethal effects could induce population and community-level changes; thus considering a range of INNS impacts across biological scales is important for developing evidence-based approaches to conservation and management.

The relative inaccessibility of the marine environment creates further challenges to quantifying INNS impact (Bax *et al.*, 2003; Molnar *et al.*, 2008; Williams and Grosholz, 2008; Ojaveer *et al.*, 2014). As distribution-abundance patterns of INNS are often poorly resolved, this fundamental component of impact frameworks is likely to be based on inaccurate estimations or predictions. With specific regards to impact, in most areas "before invasion" status is difficult to define as the necessary baseline information gained from comprehensive long-term monitoring studies is often scarce or non-existent. Similarly, complex manipulative experiments generally require frequent and/or intensive maintenance, which is often logistically challenging, expensive or impractical within marine habitats. As a result, comparatively few empirical studies have examined the impact of marine INNS when compared to terrestrial or freshwater systems (Hulme *et al.*, 2013; Thomsen *et al.*, 2014; Gallardo *et al.*, 2016). The interconnectivity and inaccessibility of the marine environment also leads to higher costs and lower probabilities of management success (Thresher and Kuris, 2004; Booy *et al.*, 2017; Courtois *et al.*, 2018). Prioritising species for targeted management is therefore crucial, as managers have limited resources with which to implement species control or eradications (McGeoch *et al.*, 2016; Epstein, 2017). There is a pressing need for more detailed studies on the impact of marine INNS to support evidence-based decisions on management prioritisation.

The invasive kelp, *Undaria pinnatifida* originating from the northeast Pacific (hereafter referred to as *Undaria*) is a global invader, prevalent in many parts of the northeast and southwest Atlantic, southwest and east Pacific, and the Tasman Sea (Epstein and Smale, 2017b). As *Undaria* has been present in parts of its non-native range for over 40 years, there have been a relatively high number of studies on its ecological impact. Most of these studies, however, have been conducted within a single biogeographical region (i.e. Australasia), with the majority focussing on broad-scale high-magnitude effects (i.e. mortality leading to population or community impacts) on native macroalgae and macrofauna (Epstein and Smale, 2017b; South *et al.*, 2017; and references therein). The impact of *Undaria* in rocky reef habitats of the northeast Atlantic is less well understood (Castric-Fey *et al.*, 1993; Floc'h *et al.*, 1996; Cremades *et al.*, 2006; Heiser *et al.*, 2014; De Leij *et al.*, 2017; Epstein and Smale, 2017a).

The overall aim of the study was to improve current understanding of the potential impacts of *Undaria* on native macroalgal assemblages in the northeast Atlantic through a long-term experimental manipulation. A high intensity manipulation was established at a heavily invaded, *Undaria* dominated study site. Experimentation was targeted within the optimum niche of the invasive species (see Chapters 2 and 5) with the highest potential for impact. Over two years, *Undaria* was manipulated within experimental patches of low intertidal rocky reef in Plymouth Sound (UK) to yield three treatment intensities (0%, 50% and 100% removal) to ascertain overall impact on native macroalgal communities and identify any density dependent effects. Both ecological responses (population and community level) and biochemical responses (measures of both sporophyte condition and stress/defence) in native macroalgae were quantified to determine both lethal and sublethal effects.

6.2 Materials and methods

6.2.1 Study site

Undaria was first recorded within Plymouth Sound in a marina in 2003, and has since spread to natural rocky habitats (Heiser *et al.*, 2014; Epstein and Smale, 2017a). Kelp-dominated communities on rocky substrates within Plymouth Sound are a designated conservation feature of the Special Area of Conservation (SAC) and a number of Sites of Special Scientific Interest (SSSI) (Langston *et al.*, 2003). As *Undaria* is now a major component of macroalgal assemblages in many locations within these protected sites (Epstein and Smale, 2017a), it is important to better understand the potential for impact on designated features.

The *Undaria* dominated study site was to the west of the Plymouth waterfront at Devil's Point (Figure 6.1). Although lying close to the mouth of the river Tamar, it is on the "open coast" side of the estuary and is considered fully marine. Devil's Point is relatively sheltered from intense wave action, and the reef platform has a gently sloping shallow profile running from the intertidal through to the shallow subtidal zone (Figure 6.1). In the UK *Undaria* is found at highest abundance and cover in the low intertidal zone (Epstein and Smale, 2018); this habitat-type was the focus of the current study. The dominant substrate type in the low intertidal zone at Devil's point is bedrock, which is interspersed with large cobbles and small boulders. The macroalgal assemblage at this tidal height comprises a mix of native canopy-formers, including the kelps *Laminaria digitata*, *Saccharina latissima* and, to a lesser extent, *Laminaria ochroleuca*, as well as the fucoid *Himanthalia elongata* and the Tilopteridale *Saccorhiza polyschides* (which, although not a 'true' kelp, is an important canopy-former that performs a similar ecological function and is referred to as a 'kelp' hereafter). The understory assemblage is dominated by *Himanthalia elongata* recruits (or "buttons"), red macroalgae (including *Palmaria palmata*, *Chondrus crispus* and *Callophyllis laciniata*) and generally low coverage of green macroalgae (predominantly *Ulva* spp.). *Undaria* sporophytes are predominantly found from March to September, but can be present at lower abundance year round (Epstein and Smale, 2018).

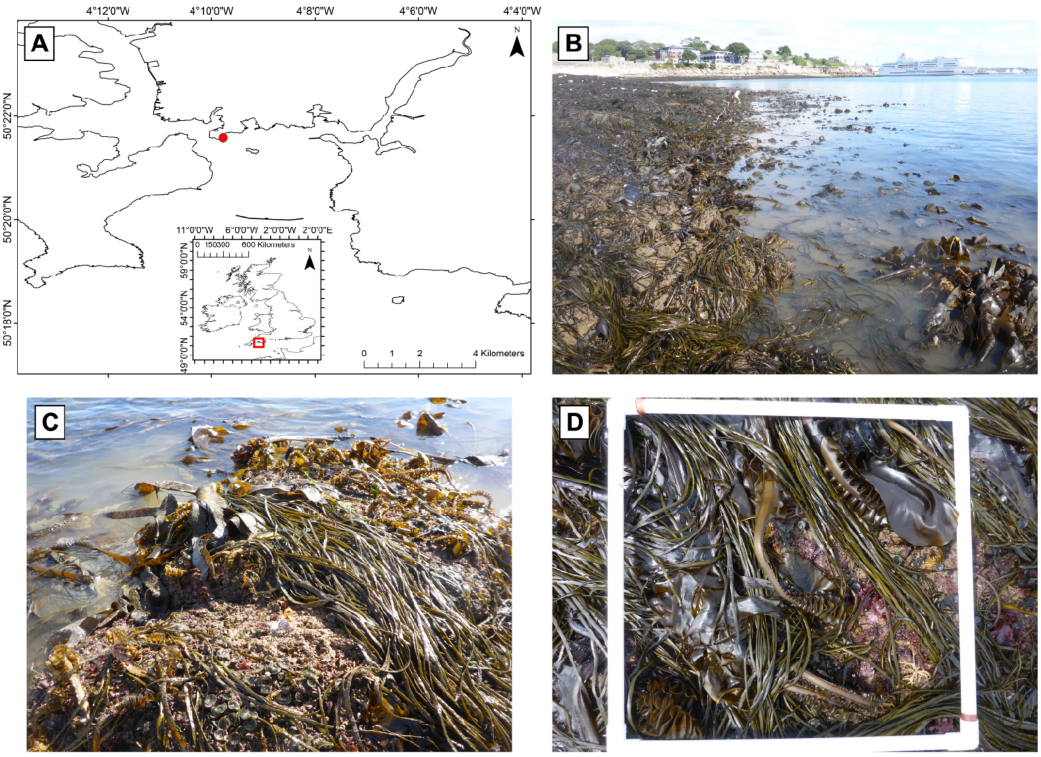

FIGURE 6.1: A) Study site (red circle) shown in the context of Plymouth Sound. Location of Plymouth Sound within the UK shown by red box on inset map. B) The study site, known as Devils Point. C) An example plot with permanent marker in centre. D) An example monitoring quadrat used for recording canopy-forming algae.

6.2.2 Set-up and maintenance

In September 2016, 15 circular treatment plots of ∼3 m diameter were established along approximately 120 m of shoreline on stable bedrock (Figure 6.1). Plots were each separated by at least 4 m, and positioned within the lower tidal zone on the shore (i.e. 0.2 - 0.7 m above chart datum). Due to the low tidal heights of the plots access was only possible during certain periods of spring low tides, which typically occurred monthly but occasionally bimonthly. Each plot was assigned to one of three treatments: 0%, 50% and 100% press-removal of *Undaria.* A randomised block design accounted for spatial variation across the study site, with five blocks each containing three plots randomly assigned to one of each treatment. The *Undaria* press-removal was maintained regularly throughout the 2-year manipulation period (typically monthly but occasionally bi-monthly, 18 times in total). During each visit, *Undaria* was removed from 50% and 100% treatments by gently prising the holdfast from the substrate once sporophytes were of sufficient size for conclusive identification to species *in-situ* (generally >10 cm in total length). The initial 50% treatment was conducted by removing every other *Undaria* sporophyte found within the plot; whereas all subsequent removals aimed to maintain density and canopy-cover in the 50% plots at around half of that found in the 0% plots for each block respectively (*Undaria* was therefore not necessarily removed from the 50% removal plots at each visit). During each maintenance period all plots were visited by a surveyor thus ensuring that all plots, including those assigned to the 0% removal treatment, had similar trampling disturbance. The total number of *Undaria* sporophytes present in, and removed from, each plot was recorded during most (but not all due to time constraints) maintenance visits.

6.2.3 Ecological responses

Macroalgal cover and density was surveyed at the start of the experiment and a further six times during the manipulation (January, April, August and October 2017; February and August 2018). During each survey, data were obtained by haphazardly placing triplicate 0.25 m^2 quadrats within each plot, avoiding the outer 20 cm to reduce any edge effects (Figure 6.1). For canopy-forming brown macroalgae, the abundance counts and percent cover of each species was estimated visually by a single observer. Additionally, in all but one survey period (missed due to tidal time constraints), the understory macroalgal assemblage was quantified. Within each 0.25 m^2 quadrat, canopy-formers were first moved to one side to reveal the understory assemblage before three smaller 0.01 m^2 subsample quadrats were haphazardly placed on the exposed bedrock. Each smaller quadrat was then photographed using a Panasonic Lumix FT5 digital camera. For subsequent analysis, subsample quadrats were ‘gridded’ (into 25 cells of 2 cm x 2 cm) before quantifying (i) the total number of *Himanthalia elongata* ‘buttons’ and (ii) the number of cells containing erect red, brown and green macroalgae (which were then converted to a percentage of total cells within each quadrat and used as a proxy for percent cover). The values were averaged across the three subsample quadrats, and used to estimate the total abundance of *Himanthalia elongata*, and percent understory cover of red, brown and green macroalgae within the larger 0.25 m^2 quadrat.

In September 2018, at the end of the manipulation period, the macroalgae assemblage was destructively sampled by haphazardly placing four 0.25 m^2 quadrats within each plot, avoiding the outer 20 cm to reduce edge effects. Canopy-forming brown macroalgae were removed from all quadrats by gently prizing sporophytes from the substrate and placing them into individual, uniquely-labelled collection bags. In three of the four quadrats, all understory macroalgae were also removed by hand and retained in smaller plastic bags. Samples were returned to the laboratory for identification and counting; all macroalgae were identified to species-level, except for *Ceramium* spp. and *Corallina* spp. which were identified to genus and green macroalgae which were treated as one taxonomic group due to being taxonomically complex and present at very low biomass. All species were immediately weighed (fresh weight biomass) and the density of each canopy-forming brown macroalgae species was also recorded for each quadrat.

6.2.4 Biochemical responses

Investigation of biochemical impacts (i.e. condition of sporophytes and level of stress/defence compounds) was confined to the native co-occurring kelps *Laminaria digitata, Saccharina latissima*, and *Saccorhiza polyschides.* During the destructive sampling in September 2018, three individuals of each species were haphazardly selected within each of the 15 plots (*L. digitata* was not found in 4 plots and *S. polyschides* was absent from 3 plots, leading to reduced replication for these two species). Two sections of tissue ($\sim$20 g fresh weight) were removed from the middle of the blade of each sporophyte, stored in individual collection bags and immediately placed on ice (leading to 228 samples in total). Following collection, each section was cleaned to remove any epiphytes and cut into approximately 2 cm^2 sections, before being frozen at -18°C for subsequent analysis.

Each sample was freeze-dried (Lablyo Freezedrier, Frozenin Time Ltd) for at least 48 hours, ground to a fine powder, passed through a 0.25 μm sieve and stored in individual bags in a dehumidified -18°C freezer. Calculation of semi-quantitative relative concentrations of Laminarin, Mannitol, Phenols, Lipids and total Polysaccharides (hereafter referred to as “Polysaccharides”) was carried out using Fourier Transform Infrared (FTIR) Spectroscopy (Perkin Elmer Spectrum 2000 FT-IR spectrometer) and an Attenuated Total Reflection (ATR) method on dried powder material (Mayers *et al.*, 2013; Meng *et al.*, 2014). The absorbance spectra were collected between 4000 and 600 cm^{-1}, at a spectral resolution of 2 cm^{-1} with 32 scans co-added and averaged. In order to remove machine error, each sample was run twice and the spectra averaged using the

OPUS 7.5 software package (Bruker Optik GmbH, Ettlingen, Germany). Active peaks of Laminarin (1034, 1158,1634 cm^{-1}) and Mannitol (1077, 1044,1017 cm^{-1}) were determined by FTIR of tableted pure Laminarin and Mannitol (Sigma-Aldrich) (Shekhar *et al.*, 2012). Polysaccharides peaks (1024-1030, 1053, 1080 cm^{-1}) were derived from C-O-C bond structure vibrations typical of polysaccharides (Meng *et al.*, 2014). Phenols were assigned wave numbers (889, 931, 1080, 1606, 2931, 3257 cm^{-1}) after FTIR of pure tannic/caffeic acid standards and cross-validation of previous FTIR data with known concentrations of polyphenols. Lipids were validated by comparison with a known kelp standard which was put through a defatting regime and measured dry mass change with peak elimination at 2927 cm^{-1}. Baseline correction was used to account for differences in powder thickness and further procedural error; this was carried out with final absorbance values at each wavelength taken as a ratio of absorbance at 2156 cm^{-1} (wavelength which corresponds to no known bond). Absorbances at each wavelength were then standardised $[(x\text{-})/\sigma]$ to evenly weight different peaks, and then averaged where a compound group was explained by multiple wavelengths. Following calculation of all response measures, the two replicate samples from each sporophyte were averaged prior to further analysis.

An Elemental Microanalysis CHN Analyser (EA1110, CE Instruments Ltd., Wigan) was also used to estimate carbon-nitrogen ratios (C:N). For each sample, 2 ± 0.5 mg of powder was sealed in tin capsules prior to mineralization and separation in a gas chromatographic system for quantification of percentage carbon, nitrogen and hydrogen. Cyclo-hexanone-2,4-dinitrophenylhydrazone was used as the standard and L-cystine as the Certified Reference Material, which were each run in triplicate. Percentage carbon and nitrogen was then converted to C:N ratios for each sample. The two replicate samples from each sporophyte were averaged and data standardised $[(x\text{-})/\sigma]$ to allow comparison with FTIR response metrics.

6.2.5 Data analysis

All ecological data were analysed using multivariate generalised linear models (GLMs) using the *mvabund* package in R (Wang *et al.*, 2018); *mvabund* allows model-based approaches to be used for multivariate data which has many benefits over traditional distance-based analyses (for detail see Warton *et al.*, 2011; Warton *et al.*, 2017). Abundance data were modelled using negative binomial GLMs (due to overdispersion from the Poisson distribution), while percent cover and biomass data used Tweedie GLMs (with a variance power of 1.5 to account for a compound Poisson distribution of non-negative values with mass at zero). *Undaria* was removed from the dataset prior to analyses as it was the manipulated species, while *Laminaria ochroleuca* was removed due to very low abundance/cover values (only 9 occurrences were recorded across the entire study) and consequently insufficient replication between blocks and sampling months. Canopy-forming macroalgae and understory macroalgae datasets were analysed separately. All data were analysed in three steps; firstly the initial pre-treatment survey data were analysed to determine whether any differences between treatment plots were evident prior to the long term manipulation; secondly all non-destructive survey data were analysed to examine the effects of treatments over the timespan of the manipulation; and finally data generated from the destructive end point sampling were analysed to assess treatment effects following two years of manipulation. For both start and end point datasets the multivariate response was modelled as a function of Treatment (categorical; 3 levels), with restricted bootstrap resampling within 'Block' (5 levels) to account for the randomised block design. For the non-destructive temporal sampling, data were modelled as a function of Treatment and 'Month' (categorical; 6 levels – indicating the number of months since the initial manipulation), with their interaction. Restricted bootstrap resampling was again constrained to Block, however individual Plot ID (15 levels) was also applied as an additional grouping factor to account for temporal repeat measures. All multivariate GLMs were calculated using 999 resampling iterations with the restricted bootstrap resampling defined using the *permute* package (Simpson, 2016). Validation of models was carried out graphically using simulated scaled residuals (Warton *et al.*, 2017). For end point sampling data, unconstrained ordination using latent variable models (negative binomial and Tweedie distributions for abundance and biomass data, respectively) was used to visualise multivariate dissimilarities between plots, using the *boral* package (Hui, 2016).

Where multivariate analyses indicated a significant treatment effect, univariate post-hoc test statistics and p-values were calculated for each species separately. For negative binomial GLMs p-values were adjusted for multiple testing using a step-down resampling procedure. For Tweedie GLMs this step-down procedure is not currently available, therefore test statistics were interpreted at a conservative level of α=0.01 to decrease the probability of Type 1 errors. For those species found to have a significant treatment effects, pairwise differences between treatment levels (and months where appropriate) were assessed using univariate generalised linear mixed models (GLMMs). Negative binomial models were fitted to abundance data (using the *lme4* package; Bates *et al.*, 2015); while compound Poisson models were fitted to cover/biomass data (using the cplm package; Zhang, 2013). Block was applied as a random factor for start and end point sampling, with Block and Plot ID fitted as random factors for temporal sampling.

Biochemical data were analysed using multivariate linear techniques, with the 6 different biochemical metrics treated as a multivariate response. For each kelp species separately, multivariate dissimilarity between plots was visualised using Principal Component Analysis (PCA) using the *prcomp* function from base R (R Core Team, 2017). Differences in biochemistry between press-removal treatments was then statistically tested with multivariate linear models (LMs) using the *manylm* command from the *mvabund* package in R (Wang *et al.*, 2018). Model structure, bootstrapping, validation and post-hoc testing followed the same procedure as ecological end point sampling as explained above.

For those univariate responses found to have a significant treatment effects, pairwise differences between treatment levels were assessed using univariate linear mixed models (LMMs) with Block as a random factor, using the *lme4* (Bates *et al.*, 2015) and *multcomp* (Hothorn *et al.*, 2008) packages.

All statistics were implemented in R 3.4.3 (R Core Team, 2017), data manipulation used the *dplyr* and *reshape2* packages (Wickham, 2007; Wickham and Francois, 2015), graphs were created using *ggplot2* (Wickham, 2009) and maps (Figure 6.1) were made within ArcMap 10.3.1. Where relevant all data are shown ± standard error.

6.3 Results

6.3.1 Ecological responses

At the start of the study, prior to the first manipulation, there were no significant differences between treatments; either in the abundance of *Undaria* (negative binomial GLMM, $\chi^2 = 2.21$, $p = 0.331$), abundance and percent cover of native canopy-forming macroalgae or percent cover of understory macroalgae (Table 6.1; Figure 6.2; Figure 6.3). Over the course of the two year manipulation >1,630 and >500 individual *Undaria* sporophytes were removed from 100% and 50% treatments, respectively (Figure 6.2). *Undaria* was recorded at the study site year round, with some individuals removed in each of the 18 maintenance events; however maximum abundance, cover and removal density occurred in Spring (i.e. March to May) (Figure 6.2).

Throughout the experiment the surveys revealed high variation in the abundance and cover of native canopy-forming and understory macroalgae, both between plots and sampling months (Figure 6.3). A significant overall treatment and sampling month effect was detected for both the abundance and cover of native canopy-forming macroalgae, whereas the interaction between treatment and month was non-significant (Table 6.1; Figure 6.3). Univariate tests indicated that the significant treatment effect was primarily due to differences in the abundance and cover of *S. polyschides*, and the abundance of *L. digitata* (Table 6.2). For *S. polyschides* abundance, pairwise tests identified significant differences between all treatments with abundance in 100% removal plots > 50% > 0%; whereas *S. polyschides* canopy-cover was significantly higher in the 100% removal plots compared with both 50% and 0% treatments (Table 6.3). For *L digitata* abundance, however, pairwise tests indicated no significant differences between treatments (Table 6.3). For understory macroalgae, the non-destructive surveys detected no significant treatment effect on the cover of the assemblage, although it did differ significantly between sampling months (Table 6.1; Figure 6.3).

TABLE 6.1: Multivariate GLMs testing for the effect of treatment and sampling month on native canopy-forming and understory macroalgae. Start sampling and temporal monitoring quantified the abundance (inds. 0.25 m^{-2}) and canopy cover (%) of canopy-forming macroalgae, and cover (%) of understory macroalgae. End point sampling quantified the abundance (inds. 0.25 m^{-2}) of canopy-forming macroalgae, and the biomass (g 0.25 m^{-2}) of canopy-forming and understory macroalgae. Significant coefficients shown in bold (α=0.05). df = degrees of freedom, LR = sum of likelihood-ratio test statistic, p = p-value.

Coefficient	df	LR	p	df	LR	p	df	LR	p
Start		*Canopy cover*			*Canopy abundance*			*Understory cover*	
Treatment	2	49.77	0.588	2	2.60	0.952	2	11.96	0.307
Temporal monitoring		*Canopy cover*			*Canopy abundance*			*Understory cover*	
Month	**5**	**1512.50**	**<0.001**	**5**	**107.97**	**<0.001**	**5**	**187.04**	**<0.001**
Treatment	**2**	**361.18**	**<0.001**	**2**	**65.89**	**<0.001**	2	10.02	0.419
Month*Treatment	10	89.71	0.993	10	18.88	0.884	10	42.97	0.336
End point		*Canopy cover*			*Canopy abundance*			*Understory cover*	
Treatment	**2**	**1199.10**	**0.003**	**2**	**27.76**	**0.002**	2	291.98	0.141

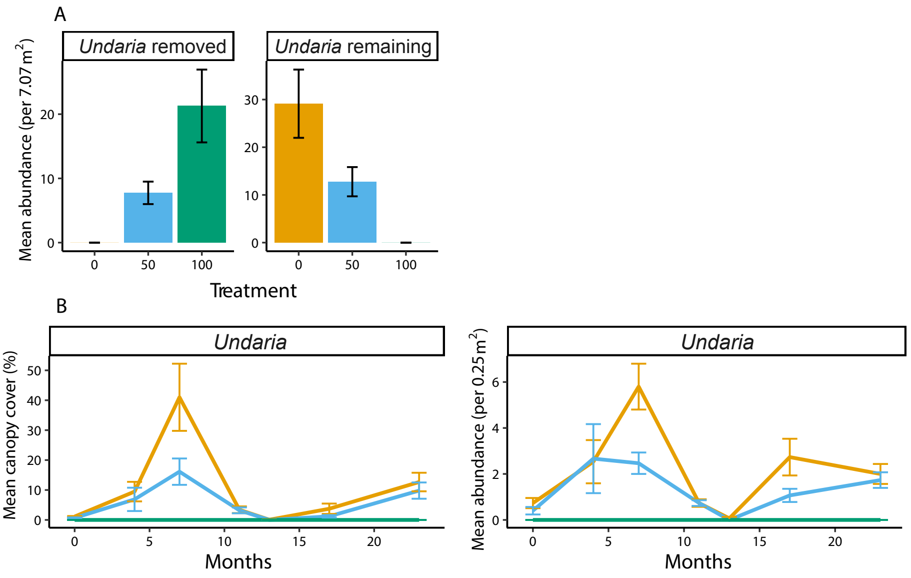

FIGURE 6.2: A) Mean number of *Undaria* removed and remaining in plots across maintenance events. B) Temporal monitoring data of mean abundance (inds. 0.25 m^{-2}) and cover (%) of *Undaria* over the 23 month manipulation. Data shown for each press-removal treatment separately.

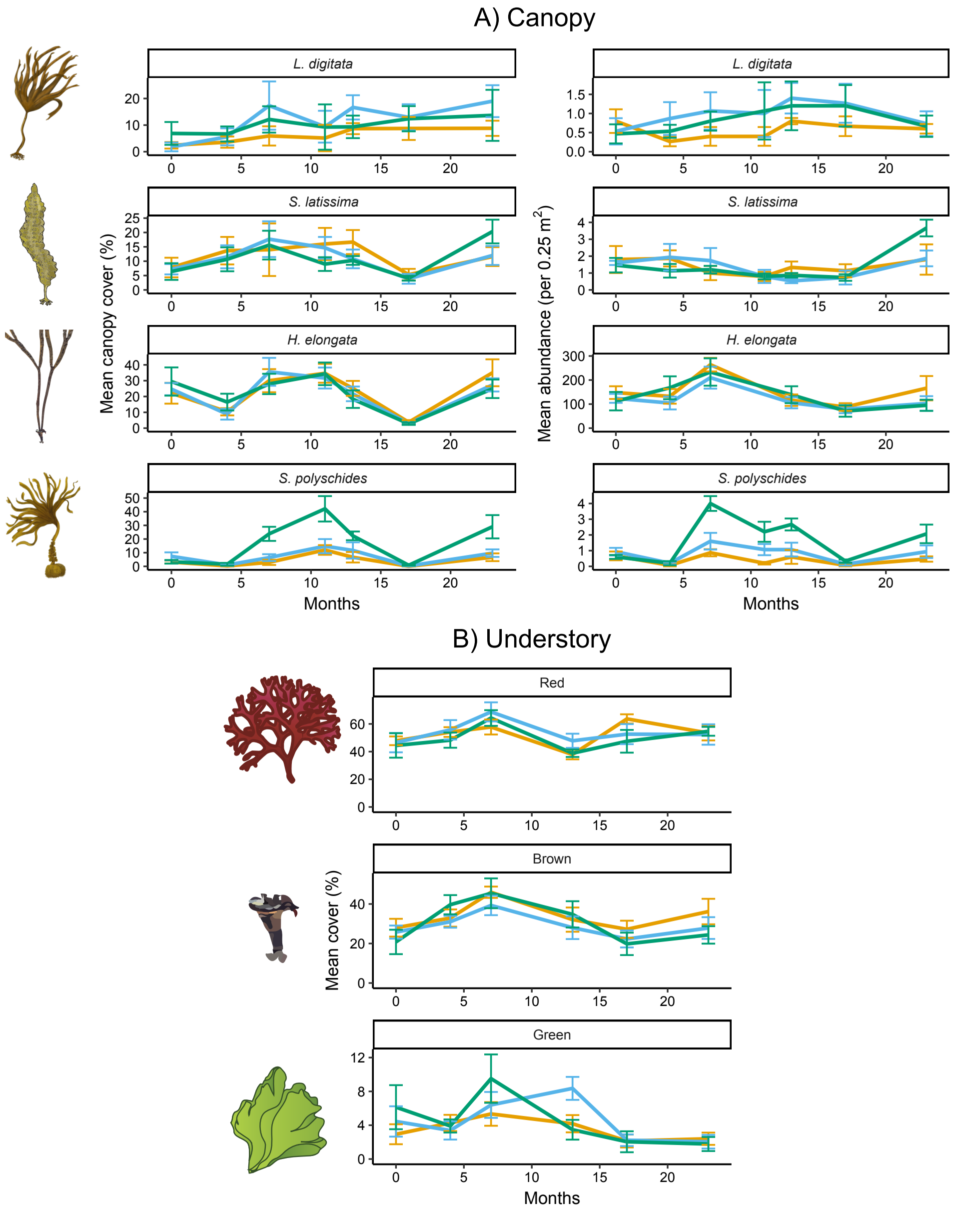

Figure 6.3: Temporal monitoring of native canopy-forming (A) and understory macroalgae community (B) within the three different *Undaria* press-removal treatments (0% = orange, 50% = blue, 100% = green). Mean abundance (inds. 0.25 m^{-2}; canopy only) and cover (%; canopy and understory) was estimated for each species/taxonomic unit *in-situ* for 23 months. Macroalgae drawings courtesy of Jack Sewell and the Integration and Application Network (ian.umces.edu/symbols/).

End point destructive sampling also identified a significant treatment effect on abundance and biomass of native canopy-forming algae, but no effect on understory macroalgae (Table 6.1; Figure 6.4; Figure 6.5). For canopy species biomass and abundance, ordination of multivariate community data showed some partitioning of 100% removal plots when compared to 50% and 0% treatment plots (Figure 6.4); there was, however, no clear separation in understory communities between treatments (Figure 6.5). Univariate test statistics highlighted that the significant treatment effect in canopy-forming community was primarily due to differences in abundance and biomass of *S. polyschides*, and abundance of *S. latissima* (Table 6.2). In all cases, pairwise tests identified that the effect was due to higher abundance/biomass values in 100% removal plots compared with the 50% and 0% removal plots (Table 6.3).

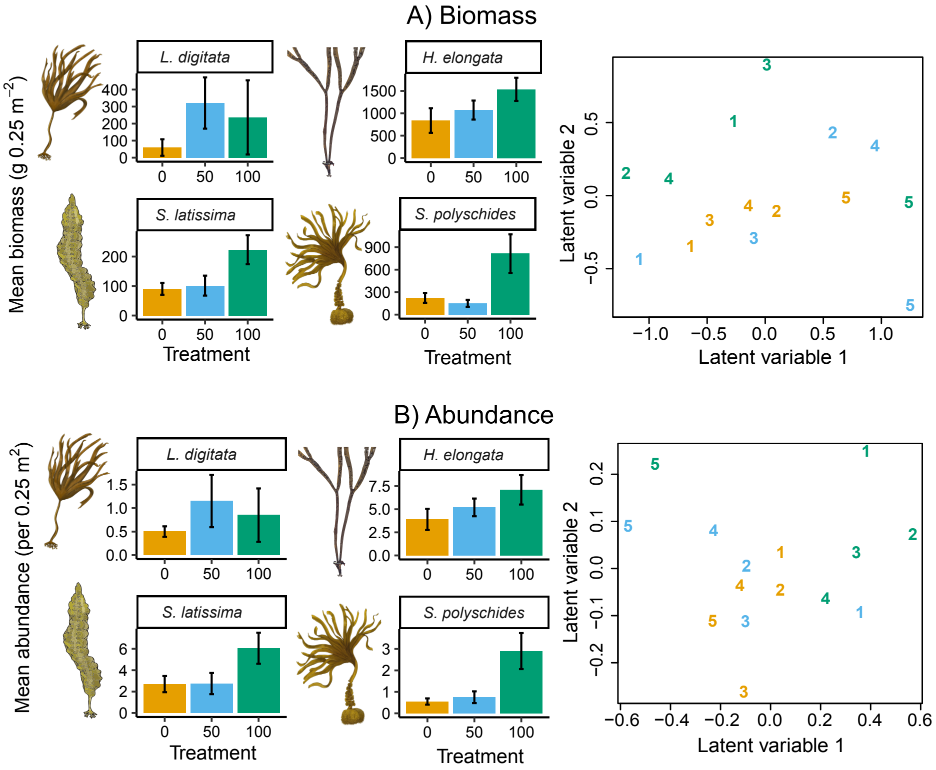

FIGURE 6.4: End point sampling of native canopy-forming macroalgae community within the three different *Undaria* press-removal treatments (0% = orange, 50% = blue, 100% = green). A) Mean biomass (g 0.25 m^{-2}) and B) abundance (inds. 0.25 m^{-2}) was quantified by destructive sampling at the end of the manipulation after 24 months. Data illustrated as univariate species responses (bar plots; ±SE between plots) and multivariate community data (ordination plots of treatment plot averages). Numbers on ordination plots indicate each experimental block. Macroalgae symbols courtesy of Jack Sewell.

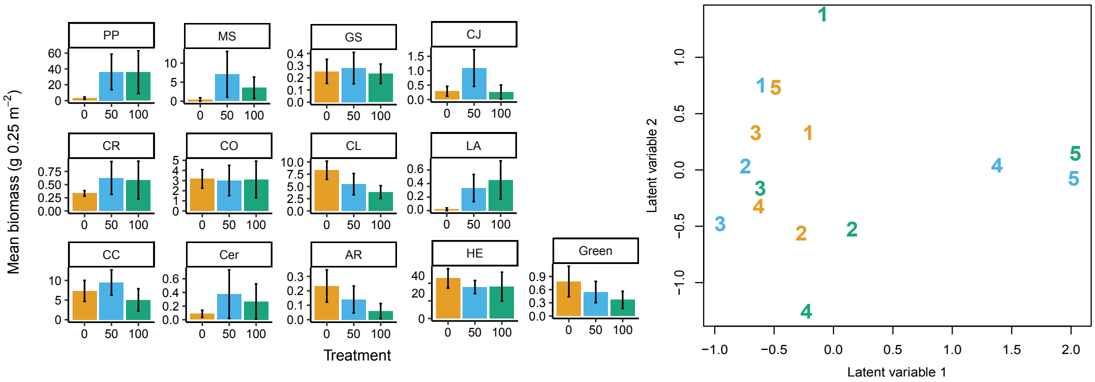

Figure 6.5: End point sampling of native understory macroalgae community within the three different *Undaria* press-removal treatments. Mean biomass (g 0.25^{-2}) was quantified by destructive sampling at the end of the manipulation after 24 months and categorised to the following taxonomic units: PP = *P. palmata*, MS = *Mastocarpus stellatus*, GS = *Gelidium spinosum*, CJ = *Calliblepharis jubata*, CR = *Cryptopleura ramosa*, CO = *Corallina* spp., CL = *C. laciniata*, LA = *Lomentaria articulata*, CC = *C. crispus*, Cer = *Ceramium* spp., AR = *Apoglossum ruscifolium*, HE = *H. elongata*, Green = green algae. Data illustrated as univariate species responses (bar plots; ±SE between treatment plots) and multivariate community data (ordination plots of treatment plot averages). Numbers on ordination plot indicate each treatment block.

Table 6.2: Univariate post-hoc test statistics from multivariate GLMs testing for the effect of treatment (df = 2) on native canopy-forming macroalgae. Temporal monitoring quantified the abundance (inds. 0.25 m^{-2}) and canopy cover (%), while end point sampling quantified the abundance (inds. 0.25 m^{-2}) and biomass (g 0.25 m^{-2}). Significant treatment effects shown in bold (α=0.05 for abundance; α=0.01 for cover/biomass due to unadjusted p-values). LR = likelihood-ratio test statistic, p = p-value.

Species	LR	p	LR	p
Temporal monitoring	*Cover*		*Abundance*	
S. polyschides	**294.10**	**<0.001**	**55.08**	**<0.001**
S. latissima	2.81	0.733	0.19	0.895
L. digitata	2.94	0.012	**10.62**	**0.002**
H. elongata	2.44	0.633	2.97	0.316
End point	*Biomass*		*Abundance*	
S. polyschides	**628.51**	**0.007**	**15.14**	**0.003**
S. latissima	121.74	0.012	**7.50**	**0.036**
L. digitata	322.15	0.050	2.29	0.329
H. elongata	126.67	0.196	2.83	0.329

Table 6.3: Pairwise tests between treatment levels for canopy-forming macroalgae species with significant univariate treatment effects (Table 6.2). Temporal monitoring quantified the abundance (inds. 0.25 m^{-2}) and canopy cover (%), while end point sampling quantified the abundance (inds. 0.25 m^{-2}) and biomass (g 0.25 m^{-2}). Significant treatment effects shown in bold (α=0.05). t = t-value, z = z-value, p = p-value.

Treatment contrast	t	p	z	p
Temporal monitoring	*Cover*		*Abundance*	
S. polyschides				
0-50	1.59	0.111	**3.03**	**0.003**
0-100	**5.94**	**<0.001**	**6.69**	**<0.001**
50-100	**4.54**	**<0.001**	**4.09**	**<0.001**
L. digitata				
0-50			1.80	0.072
0-100			1.35	0.178
50-100			-0.46	0.645
End point	*Biomass*		*Abundance*	
S. polyschides				
0-50	0.63	0.539	0.61	0.540
0-100	**2.52**	**0.012**	**3.93**	**<0.001**
50-100	**3.06**	**0.002**	**3.49**	**<0.001**
S. latissima				
0-50			-0.05	0.962
0-100			**2.99**	**0.003**
50-100			**3.03**	**0.002**

6.3.2 Biochemical responses

Visualisation of multivariate biochemical response data showed some partitioning between press-removal treatments for *L. digitata* and *S. polyschides* (Figure 6.6), but there was no indication of separation between treatments for *S. latissima* (Figure 6.6). Multivariate linear models, identified significant differences between treatments for *S. polyschides* ($F_{(2,33)}$ = 22.61, p = 0.015) and *S. latissima* ($F_{(2,42)}$ = 11.67, p = 0.030), but not for *L. digitata* ($F_{(2,30)}$ = 9.652, p = 0.127). Post-hoc univariate test statistics highlighted that the significant treatment effects were primarily due to differences in Lipids and Laminarin for *S. polyschides*, and Manitol for *S. latissima* (Table 6.4). In general, pairwise tests identified that the significant treatment effects were due to lower concentrations in *Undaria* press-removal treatments when compared with control plots (Table 6.5, Figure 6.7). Univariate visualisation of all biochemical response measures showed marginal differences in most contrasts (Figure 6.7). There was a reasonably consistent negative trend in most compounds with reducing competition from *Undaria* in 50% and 100% removal treatments; however changes in relative concentration were small and in most cases not statistically significant (Figure 6.7). This pattern was not apparent for C:N ratios which marginally increased or was unchanged in press-removal treatments (Figure 6.7). Overall, these trends were particularly apparent for *S. polyschides* but could also be identified in *S. latissima* and *L. digitata* (Figure 6.7).

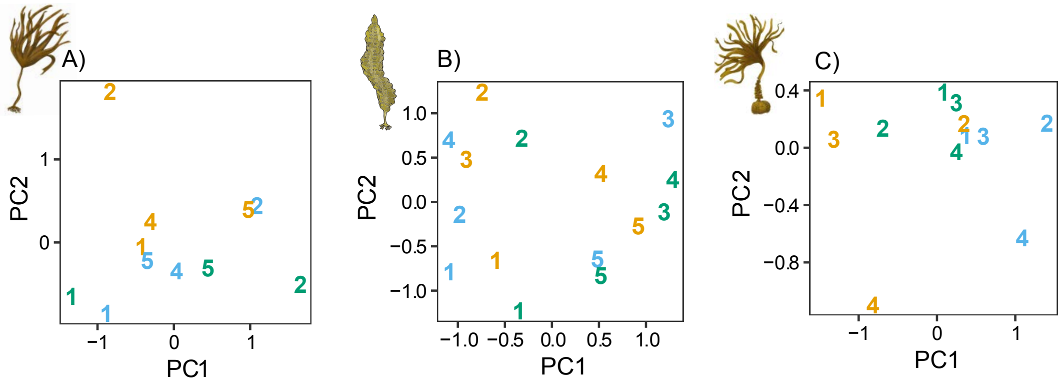

FIGURE 6.6: Principal component analysis of multivariate biochemical response metrics for A) *L. digitata*, B) *S. latissima*, and C) *S. polyschides*. Data was averaged within treatment plots prior to ordination. Numbers within ordination plot indicate each treatment block; colours indicate different *Undaria* press-removal treatments (0% = orange, 50% = blue, 100% = green).

TABLE 6.4: Univariate post-hoc test statistics from multivariate LMs testing for the effect of treatment (df = 2) on biochemistry of native kelps. Significant treatment effects shown in bold (α=0.05). F = F-value, p = p-value.

Biochemical response	F	p	F	p
	S. latissima		*S. polyschides*	
C:N	0.64	0.649	0.17	0.854
Lipids	0.74	0.649	**4.60**	**0.043**
Phenols	1.97	0.314	4.07	0.062
Polysaccharides	2.38	0.212	3.69	0.070
Manitol	**4.08**	**0.043**	3.77	0.068
Laminarin	1.87	0.314	**6.31**	**0.019**

Table 6.5: Pairwise tests between treatment levels for kelps with significant univariate biochemical treatment effects (Table 6.4). Significant treatment effects shown in bold (α=0.05). z = z-value, p = p-value.

Treatment contrast	z	p	z	p	z	p
	Manitol		*Lipids*		*Laminarin*	
S. latissima						
0-50	0.97	0.331				
0-100	**-2.60**	**0.018**				
50-100	**-3.58**	**0.001**				
S. polyschides						
0-50			**-3.06**	**0.007**	**-3.61**	**0.001**
0-100			**-2.40**	**0.033**	-0.98	0.329
50-100			-0.66	0.508	**2.63**	**0.017**

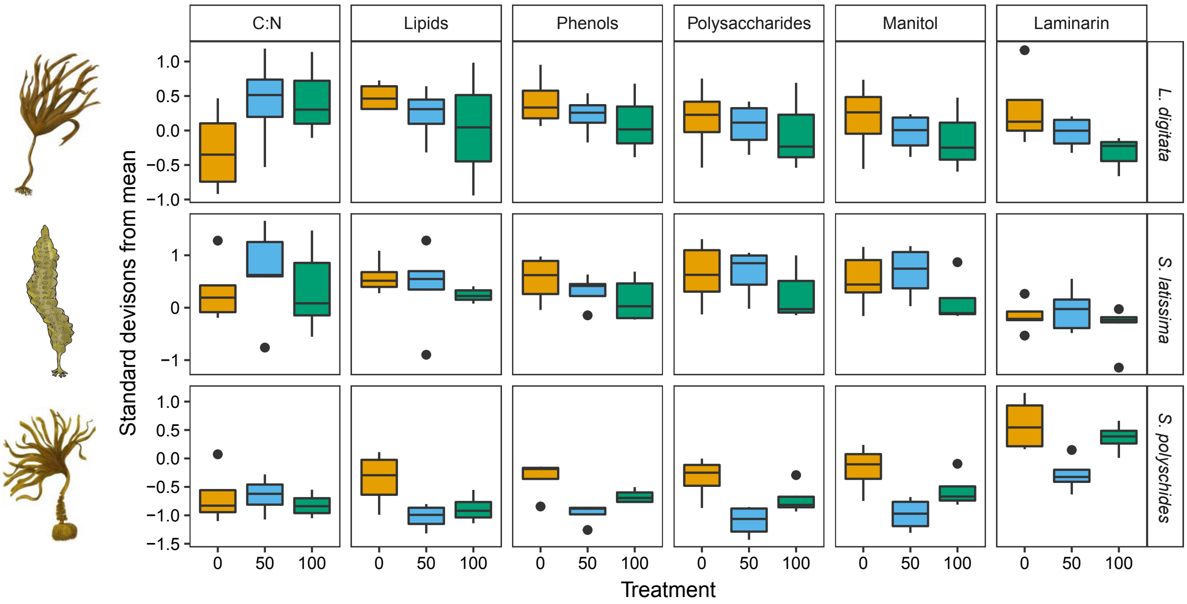

Figure 6.7: Boxplots indicating the relative values of biochemical response metrics for *L. digitata*, *S. latissima* and *S. polyschides* within each *Undaria* press-removal treatment. All measures have been standardised $[(x - \mu)/\sigma]$ and therefore are on the same unitless scale.

6.4 Discussion

6.4.1 Identifying ecological impact

Since its introduction into the northeast Atlantic in 1971, *Undaria* has been considered to have limited impact on rocky reef communities due to: (i) being found more commonly or in higher abundance where the native canopy is limited; (ii) being less competitive than long-lived natives due to its annual and opportunistic life-history characteristics; and (iii) being facilitated by disturbance to canopies (Castric-Fey *et al.*, 1993; Floc'h *et al.*, 1996; Farrell, 2003; Cremades *et al.*, 2006; Heiser *et al.*, 2014; De Leij *et al.*, 2017; Epstein and Smale, 2017b). This study is the first empirical evidence that the proliferation of *Undaria* is having an impact on native macroalgal assemblages on rocky-reefs in the northeast Atlantic, at least under certain environmental conditions. Globally, this is only the second region, along with the coastlines of Argentina, where *Undaria* has been considered to be driving a detectable level of ecological change within natural rocky coastal environments (Casas *et al.*, 2004; Irigoyen *et al.*, 2010; Irigoyen *et al.*, 2011; Epstein and Smale, 2017b). The experimental design used in the current study was specifically constructed to identify the potential for impact rather than quantify broader impacts across different habitats and the wider ecosystem. Manipulation was constrained to a heavily invaded, wave sheltered site within the most favourable habitat for *Undaria* establishment. A high intensity manipulation and sampling regime enabled identification of any cryptic and sublethal impacts. As such, to determine the impact of *Undaria* on native assemblages at wider spatial scales, similar manipulations should be conducted across a range of habitat types (e.g. in subtidal or more wave-exposed sites) and ecological contexts (e.g. different recipient communities or population density of *Undaria*). Even so, this study highlights how highly targeted and long-term manipulative experiments can identify previously undetected impacts of INNS in coastal ecosystems.

6.4.2 Competition and ecosystem functioning

This study recorded statistically significant effects of the presence of *Undaria* on the populations of three co-occurring native kelp species; *L. digitata*, *S. latissima* and *S. polyschides*. The results, however, were only consistent across time, response metrics and statistical analyses for *S. polyschides*. Both *Undaria* and *S. polyschides* are annual species that exhibit marked seasonality in recruitment, maturation, growth and senescence at similar times of year. Typically, sporophytes of both species recruit during early spring, grow throughout summer and senesce in autumn (Norton and Burrows, 1969; Fletcher and Farrell, 1999; Epstein and Smale, 2018). Spatially, they occupy a similar niche in the subtidal fringe and are both considered relatively opportunistic species (Norton and Burrows, 1969; Castric-Fey *et al.*, 1993; Fletcher and Farrell, 1999; Epstein and Smale, 2017a). Previous studies have suggested, therefore, that these species may directly compete for space or other resources, although the strength and direction of such competition has not been quantified (Castric-Fey *et al.*, 1993; Fletcher and Farrell, 1999; Yesson *et al.*, 2015; Epstein and Smale, 2017a). The results of this study indicate that under certain conditions *Undaria* is able to supress and displace, but not exclude *S. polyschides* in invaded communities.

There was some indication of a density dependent effect of *Undaria* within the temporal monitoring data; the effect size on *S. polyschides* density was significantly different between all treatment levels. *S. polyschides* abundance showed a 5.4±1.2 fold increase in 100% treatments and 2.7±0.6 fold increase in 50% treatments when compared to the 0% removal controls. Although this pattern was similar for canopy cover data (5.9±1.4 and 2.7±0.4 fold increases for 100% and 50% treatments respectively), only the 100% treatment was statistically different from the control. At the end of the experiment no density dependent effects of *Undaria* were identified; abundance and biomass of *S. polyschides* were highly similar between 50% treatments and controls. In contrast, 100% treatments had a statistically significant 5.3 and 3.6 fold increase in abundance and biomass of *S. polyschides*, respectively. Overall, that *S. polyschides* did not increase significantly in the 50% removal treatments suggests that *Undaria* exerts a relatively strong suppressive effect on this native species even at relatively low densities and cover.

It is important to consider how this displacement of a native species may alter ecosystem functioning. There is evidence that these two species attract similar epifaunal and epifloral assemblages, so substitution may have minimal community-level impacts (Arnold *et al.*, 2016). Additionally, *Undaria* is far less tolerant of wave action than *S. polyschides*, which can become the dominant canopy-former under wave-exposed conditions (Burrows, 2012; Epstein and Smale, 2017a). This would suggest that competitive exclusion could only occur at wave sheltered sites; thus wider regional displacement of *S. polyschides* is unlikely. Moreover, anecdotal evidence suggests that, regionally, *S. polyschides* may have increased in density and extent over recent decades, perhaps due to increased sea temperatures or changes in canopy disturbance and structure (Birchenough and Bremner 2010; Smale *et al.*, 2013). As such, any localised suppression by *Undaria* may be offset by wider trends on wave-exposed open coastlines. Clearly, the drivers of change are complex, and, further research is needed to determine wider ecological consequences of species substitutions, such as on trophic provision to grazers, habitat provision to mobile species, primary production and carbon cycling (Smale *et al.*, 2013).

Although other species were identified in this study as suffering a potential ecological impact from the proliferation of *Undaria* (*L. digitata* and *S. latissima*), the effect size was inconsistent and relatively small. The impact of these interactions on ecosystem functioning is, therefore, likely to be negligible, particularly as this study was designed to identify the highest likelihood of effect.

6.4.3 Biochemical effects

Subtle yet persistent sub-lethal effects of INNS have the ability to induce population and community-level changes to native species (Hulme et al., 2013; Thomsen et al., 2014). In this study, although changes in native kelp biochemistry were marginal and inconsistent, there were some significant differences between press-removal treatments. Polysaccharides (predominantly in the form of Manitol and Laminarin) and lipids are the primary storage compounds in kelp species (Black, 1950; Guschina and Harwood, 2006; Schiener *et al.*, 2015). During periods of limited growth, these compounds increase in concertation within the kelp blade, acting as long-term energy stores for growth under preferential environmental conditions (Black, 1950; Maschek and Baker, 2008; Schiener *et al.*, 2015). The concentration of these compounds is therefore often negatively correlated to blade elongation rates (Black, 1950; Zimmerman and Kremer, 1986; Schiener *et al.*, 2015). The native kelps investigated in this study (*L. digitata*, *S. latissima* and *S. polyschides*) all had a small, and in some cases significant (*S. latissima* and *S. polyschides*), decrease in these compounds within *Undaria* press-removal treatments. Although further investigation would be needed, this may indicate that the growth rate of native kelps increases in the absence of competition from *Undaria.* The changes in C:N ratios also indicate the potential for competitive inhibition from *Undaria* on native kelps. C:N ratios generally correlate to nutrient availability, with decreased C:N in nutrient replete settings (Harrison and Druehl, 1982). This can be due to changes in external nutrient availability or nutrient uptake - driven by competition, changes in water movement or other abiotic factors (Gerard, 1982; Harrison and Druehl, 1982; Kregting *et al.*, 2016). The small increase in C:N ratios recorded within *Undaria* press-removal treatments for *L. digitata* and *S. latissima* may have been due to increased water motion, and therefore higher nutrient uptake in the native kelps. Finally, phenolic compounds primarily function as defensive or stress response compound in kelps (Arnold and Targett, 2003; Maschek and Baker, 2008). In this study the reduction or exclusion of *Undaria* generally reduced the concentration of Phenols in native kelps, potentially indicating a reduction in stress or defence responses.

Overall, the analyses of biochemical responses to the *Undaria* press-removal treatments indicate that some native kelp species in the region may exhibit sub-lethal responses when persisting within *Undaria* stands. As with the ecological response variables, the largest effect size was identified in the functionally similar annual kelp *S. polyschides*, however some marginal effects were also identified in *S. latissima* and *L. digitata* (although changes in the latter were not statistically significant). Further investigations would be needed to identify how these biochemical changes reflect the physiology, growth or reproduction of native kelps, and therefore the ecosystem function of kelp communities. It should be noted, however, that many of these biochemical responses were marginal and inconsistent and, as such, the overall impacts could be deemed negligible, particularly in relation to the perennial species *S. latissima* and *L. digitata.*

6.4.4 Contrast to previous studies

Previous studies conducted in the northeast Atlantic used observational or correlative data to make predictions on the level of impact from *Undaria* on native macroalgal assemblages (Castric-Fey *et al.*, 1993; Floc'h *et al.*, 1996; Cremades *et al.*, 2006; Heiser *et al.*, 2014; Arnold *et al.*, 2016; De Leij *et al.*, 2017; Epstein and Smale, 2017a). Using these techniques does allow some estimation of the extent of community or ecosystem-level impact, however when compared to this study, the contrasting results highlight that using correlative data alone is unlikely to identify all levels of potential impact. It should be noted that the results of this study do not directly contradict previous results, as significant population declines were only identified in one functionally similar native species. As previously stated, the overall impact on ecosystem functioning may still be limited when considering macroalgal assemblages and rocky reef communities as a whole.

A number of quantitative impact studies using manipulative or BACI techniques have investigated the impact of *Undaria* on recipient macroalgae assemblages on rocky-reefs of Australasia (Forrest and Taylor, 2002; Valentine and Johnson, 2005; South *et al.*, 2015; South and Thomsen, 2016). These studies concluded that *Undaria* has minimal and highly transient effects on native macroalgal assemblages. Suggested reasons for the lack of impact recorded in these regions include the absence of native species with synchronous life-histories (South *et al.*, 2015), the spatial or temporal scale of manipulation (South and Thomsen, 2016), or the density and short annual life-history of *Undaria* (Forrest and Taylor, 2002; South and Thomsen, 2016). However, where transient impacts were identified, they were largely constrained to ephemeral or turf algal species (Valentine and Johnson, 2005; South *et al.*, 2015). In some regions, however, the structure of native populations, communities and ecosystems has been seemingly altered by the invasion of *Undaria.* For example, manipulative studies conducted on *Undaria* invaded rocky-reef habitats in Argentina recorded community wide impacts on macroalgae, macrofauna and fish populations (Casas *et al.*, 2004; Irigoyen *et al.*, 2010; Irigoyen *et al.*, 2011). In contrast to both the northeast Atlantic and Australasia, *Undaria* is the only large canopy forming macroalgae in invaded reefs of Patagonia, and the lack of a functionally similar native species has increased its potential for ecosystem change. The introduction of *Undaria* into the northeast Atlantic seems to have had an intermediate impact between these two regions, with subtle but significant shifts in macroalgal assemblages.

6.4.5 Conclusion

Overall, this study shows that caution must be used when broadly classifying an INNS as having no ecological impacts on recipient communities, especially in the marine environment where INNS impact studies are limited (Hulme *et al.*, 2013; Thomsen *et al.*, 2014; Gallardo *et al.*, 2016). Prioritising species for targeted management, based on impact and management feasibility is crucial, especially in the marine environment where control methods are costly and often ineffective (Thresher and Kuris, 2004; McGeoch *et al.*, 2016; Booy *et al.*, 2017). Complex manipulative studies which consider both ecological and biochemical impacts of INNS on recipient communities should be considered before such prioritisation is made.

The impact of *Undaria* on recipient communities can vary greatly across its non-native range. In the northeast Atlantic, the presence of *Undaria* is likely to displace but not exclude the native kelp *S. polyschides*; more research is needed to consider how this displacement may influence ecosystem function. Overall, the impact of *Undaria* on macroalgal assemblages as a whole may be small, as results showed no consistent significant impacts on other canopy-forming or understory species. Although requiring further investigation, this study did, however, identify the potential for sub-lethal or physiological impacts on native co-occurring kelp species. Whether the potential impact of *Undaria* on rocky reef communities in the northeast Atlantic is sufficient to prioritise the implementation of targeted management measures is unclear, and would require complex cost-benefit analyses (Courtois *et al.*, 2018). Previous attempts to manage or exclude *Undaria* have had some limited success (Wotton *et al.*, 2004; Forrest and Hopkins, 2013), although in most cases such attempts still resulted in reintroduction and wider-scale spread, with localised reductions in population density being quickly reversed following cessation of management actions (Hewitt *et al.*, 2005; Forrest and Hopkins, 2013; Crockett *et al.*, 2017; Epstein *et al.*, 2018). Under certain environmental settings *Undaria* is now an established part of the flora of the northeast Atlantic, which is found at high abundance and cover across a variety of habitats and locations (Epstein and Smale, 2017b). It seems unlikely that *Undaria* can be excluded or controlled in areas where it has already proliferated; however, this study suggests that limiting its further spread may be justified.

Chapter 7

Overview and synthesis

7.1 Overall thesis context

Marine INNS are considered one of the major drivers of global biodiversity decline (Sala *et al.*, 2000; Bax *et al.*, 2003). In the UK alone, there are known to be over 90 established marine NNS, however the ecology and impacts of these species is poorly understood; while the options available for their management has had little consideration (GBNNSS, 2018). If the UK is to meet its obligations to national and intentional environmental legislations, considerably more research is needed to show that "non-indigenous species introduced by human activities are at levels that do not adversely alter the ecosystems" (MSFD; Stebbing *et al.*, 2015)

Undaria is a cosmopolitan INNS, found around much of the UK coastline and, more broadly, across temperate regions globally. It has been recorded in a variety of artificial and natural habitats across numerous locations and environmental settings (NBN, 2018). The aim of this thesis was to improve our current understanding of the ecology, impacts and management feasibility of *Undaria,* to better support the design and prioritisation of management and to advance ecological understanding of marine INNS more generally. In the majority of cases it is likely that *Undaria* will become an accepted component of the natural biota of the UK, due to the minimal ecosystem-level impacts it exerts, the relatively restricted spatial extent into which it is likely to proliferate, and low management feasibility. However, as it cannot be concluded that *Undaria* has no impact on recipient communities, if considered a priority by environmental managers, it may be proportionate and achievable to implement control measures to reduce further spread by conducting targeted exclusions where new incursions occur.

7.2 Key themes

7.2.1 Marinas – impact and importance

Although artificial habitats, such as marinas, are generally considered to have less 'conservation value' than natural habitats (Kueffer and Daehler, 2009), *Undaria* may be strongly impacting marina ecosystems. Chapters 2 and 3 highlighted that *Undaria* is able to reach extremely high densities in marinas, often becoming the dominant canopy forming species. The monitoring and manipulations carried out in Chapter 5 also led to the conclusion that *Undaria* has higher fitness than functionally similar native species in marinas, and is therefore able to outcompete and displace native species from these habitats. Although further research would be needed, this could have ecosystem-wide effects on fouling communities within marinas. Disturbance or impact to these communities may reduce ecosystem services provided by the fouling assemblages, such as nutrient uptake and biofiltration by sessile invertebrates (Russell *et al.*, 1983; Allen *et al.*, 1992). However, due to the cost involved in implementing management measures, remediation of these impacts is unlikely to be considered a management priority unless there were wider benefits to the conservation or ecosystem functioning of nearby natural habitats.

There is considerable evidence that artificial structures in coastal marine environments, such as those within marinas, are subjected to high propagule pressure from INNS, but relatively low competition from native species, thus rendering them favourable habitats for the colonisation and proliferation of invaders (e.g. Glasby *et al.*, 2007; Dafforn *et al.*, 2012; Bishop *et al.*, 2015). What has been rarely shown is that marinas are important beachheads for further spread and proliferation of INNS across UK coastal systems (Zabin, 2014; Airoldi *et al.*, 2015). This thesis consistently highlighted that marinas are paramount to the successful spread, proliferation and reproductive fitness of *Undaria* in the UK. Chapter 2 identified that a key factor influencing the distribution and cover of *Undaria* on natural rocky reefs is the proximity of reef sites to marinas and the density, or total abundance, of *Undaria* within adjacent marinas. The importance of marina habitats to *Undaria* invasion dynamics was also shown in Chapter 3. *Undaria* was found to have extended recruitment periods, higher maturation rates, fecundity, abundance and biomass, when compared to reef habitats, therefore contributing greatly to overall propagule pressure. Overall, it was suggested that limiting the abundance or attempting to exclude *Undaria* from marinas may restrict the likelihood of its spread to new regions and its proliferation to surrounding natural rocky reef communities. These findings have been supported by a newly published genetics study in the northeast Atlantic, which found that marinas drove regional connectivity and establishment of *Undaria* in natural rocky reefs of Brittany, France (Guzinski *et al.*, 2018). If this pattern is found to be consistent across different species and locations, marinas may become important control points for marine INNS management in the future.

7.2.2 Abiotic drivers and the niche

In many instances this thesis has indicated that *Undaria* has a relatively wide potential niche. Chapters 2, 3 and 5 identified that *Undaria* is able to persist on a wide range of artificial and natural substrates, including different aspects and stabilities, and in a variety of light, salinity, depth, temperature and turbidity and pollution regimes. Due to its wide potential niche, fast growth rate, short annual life-cycle and high investment in reproductive output, *Undaria* is considered a highly opportunistic species. These characteristics are likely to be key drivers promoting its proliferation within both artificial and marginal habitats.

A wide potential niche would also suggest that *Undaria* is able to proliferate over a wide variety of natural habitats and therefore encompass a large invaded range. Within the UK, however, *Undaria* has been present for at least 25 years but records are limited to relatively restricted environmental and geographical settings. This can be partially explained by the findings in this thesis, where certain abiotic drivers of the abundance and distribution patterns of *Undaria* were identified to restrict its overall range. Chapter 2 found a significant negative relationship between wave exposure and *Undaria* occurrence/abundance; while Chapter 5 indicated that desiccation stress and nutrient uptake may limit the potential niche of *Undaria* on natural rocky reefs. The spread and proliferation of *Undaria* may therefore, be restricted to low intertidal and shallow subtidal reefs in relatively wave sheltered sites, with moderate to high tidal water movement. Further to these abiotic drivers, inter-specific competition will occur within the potential niche of *Undaria*, which may further restrict the realised range in which *Undaria* proliferates.

7.2.3 *Laminaria* spp. as buffers to invasion

The dominant canopy forming species along rocky coastlines in the UK are the perennial *Laminaria* spp. – *L. digitata*, *L. hyperborea* and *L. ochroleuca.* This thesis has highlighted that in most environmental settings, the proliferation of *Undaria* on natural rocky reefs is inhibited by these native canopy formers. Chapter 2 demonstrated that the distribution and abundance of *Undaria* is negatively related to *Laminaria* spp. across a relatively wide geographic range. While Chapter 5 showed that where the potential niche of *Undaria* and *Laminaria* spp. overlap on rocky reefs, *Undaria* has significantly lower fitness and is therefore excluded or found in very low abundance. This is a key factor limiting the realised range into which *Undaria* may proliferate.

When setting management priorities for INNS, it is important to consider the potential and effectiveness of indirect or passive management options. Maintaining or restoring good environmental status of natural habitats is likely to increase the biotic resistance of native communities to the proliferation and ecological impact of INNS (Bakker and Wilson, 2004; Balestri *et al.*, 2018). Due to the relatively wide potential abiotic niche of

Undaria, disturbance or degradation of *Laminaria* beds may facilitate significant spread of the INNS. Kelp habitats are subject to a wide variety of anthropogenic stressors across the northeast Atlantic (Smale *et al.*, 2013). Protecting or even restoring these important habitats will have many ecosystem service benefits, while also minimising the further proliferation of *Undaria* and other INNS. Using this approach to management would not be considered acceptable for highly damaging marine INNS; however, for species such as *Undaria,* which may have minimal ecosystem-level impacts, passive management may be justified and in fact necessary, due to the limited resource available for marine INNS management.

7.2.4 Ecological impact on invaded rocky reef communities

The ecological impact of INNS on recipient communities within natural habitats is generally considered the primary factor determining management prioritisation (McGeoch *et al.*, 2016). In Chapters 2, 5 and 6 of this thesis *Undaria* was shown to exert consistent and significant impacts upon the native canopy-forming macroalgae *S. polyschides.* This macroalga is an important annual species in rocky reef habitats of the northeast Atlantic. It provides high spring-summer primary production, biogenic habitat and a trophic resource through direct grazing and detritus production (Norton and Burrows, 1969). The replacement or displacement of a native species by an INNS is often considered a negative ecological impact unto itself (Davis *et al.*, 2011; Schlaepfer *et al.*, 2012). However, as discussed in various parts of this thesis, how the replacement or displacement of *S. polyschides* by *Undaria* would alter wider ecosystem functioning is not clear. Further research is needed to determine wider ecological consequences such as altering trophic provision to grazers, habitat provision to mobile species and carbon cycling (Smale et al. 2013). Overall, however, the impact of *Undaria* on rocky reef communities of the northeast Atlantic as a whole is likely to be small. On the rocky reefs investigated in this thesis, there were no significant ecological impacts on any other macroalgal species, including the canopy dominant *Laminaria* spp.. It was also highlighted that due to their distinct potential niches, the displacement of *S. polyschides* by *Undaria* may be restricted to wave sheltered sites. Chapter 6 did highlight the potential for sub-lethal or physiological impacts of *Undaria* on native kelps, however the effects were marginal and inconsistent. Further experimentation on native kelps measuring response metrics such as growth rate, reproductive output or photosynthetic activity, would be needed in order to fully identify whether *Undaria* is having any significant sub-lethal impacts on these species. Overall, localised or regional management of *Undaria* may well be justified in some settings, but its implementation will depended on management priorities and feasibility.

7.2.5 Management feasibility

A major factor that is often poorly considered in management prioritisation processes, is the less subjective issue of management feasibility - the likely effectiveness, practicality, risk, cost, impact and timeframe of management options (Booy et al. 2017, Kopf et al. 2017). As stated above, Chapters 2 and 3 of this thesis indicated that marinas could act as important control points for the further proliferation of *Undaria* in the UK. This would give potential scope for feasible management options, as it concentrates management actions to within relatively few localities, while implementing control methods in marinas would not be entirely inhibited by issues with practicality or cost. However, Chapter 3 also highlighted that the high inter-habitat and inter-annual variation in population dynamics exhibited by *Undaria,* would add significant complexity to management design and potentially reduce effectiveness. The experimental monthly removal trial carried out in Chapter 4 also revealed significant challenges with conducting management actions within marinas. Over the 18-month experiment there was no consistent reduction in *Undaria* recruitment, and different removal measures altered recruitment patterns and even promoted total recruitment. Overall, it was concluded that even within marinas, the effectiveness of limiting *Undaria* is likely to be very low at sites with established populations and high propagule pressure. However, where there are new incursions in marinas, relatively high intensity removal methods may have some potential in limiting *Undaria* populations, and minimising further spread.

Due to the potential for *Undaria* to alter recipient communities in marinas and natural rocky reefs, targeted management of newly invaded marinas could well be justified by environmental managers. Constricting management measures to artificial habitats, however, will not reduce localised natural spread or abundance of *Undaria* within already invaded natural habitats. As highlighted by previous attempts to manage *Undaria* in other invaded regions, the feasibility of controlling natural spread on invaded rocky reef habitats is likely to be minimal (Wotton *et al.*, 2004; Hewitt *et al.*, 2005; Thompson and Schiel, 2012; Forrest and Hopkins, 2013; Crockett *et al.*, 2017). Overall, due to low practicality, high risk, high cost and limited effectiveness of potential management in natural habitats, *Undaria* may become an accepted component of the biota in many parts of the UK where its presence is no longer constrained or limited to artificial habitats.

7.3 Return to the driver-passenger model

The introduction to this thesis discussed that not all INNS are considered drivers of ecosystem change. INNS classified as “passengers”, establish and proliferate due to the presence of ecosystem stress and are not in themselves the cause of ecosystem change; whereas “drivers” out-compete or overgrow subordinate native species causing them to be limited or excluded in the absence of wider ecological stress (Didham *et al.*, 2005;

MacDougall and Turkington, 2005). A further term "back-seat driver" relates to the situation whereby an INNS is facilitated by ecosystem stress or disturbance but, once established, suppresses or causes further declines in native species (Bauer, 2012). *Undaria* is a pertinent example to show that this model is not categorical but scalar in nature, with high dependence on abiotic factors, the recipient community and the spatial scale under consideration. For example, within marinas of the UK, *Undaria* would be considered a "driver", greatly altering the recipient community and, although not part of this thesis, likely to significantly alter ecosystem function. In areas of *Laminaria* dominated natural reef, *Undaria* is a "passenger" - benefiting from ecosystem disturbance and causing no long term ecological change. In contrast, when considering a wider spatial scale (i.e. an entire sheltered to moderately-sheltered reef site) *Undaria* is not dependent on disturbance for its establishment or spread. *Undaria* cannot therefore, be truly classified as either a "passenger" or "back-seat driver" on natural rocky-reefs. Under certain environmental settings, *Undaria* can also "drive" ecological change on natural rocky reef, causing a reduction or displacement of the native annual species *S. polyschides*. Although this could allow *Undaria* to be classified as a "driver of ecosystem change" on rocky reefs, this would be overstated, as due to its relatively restricted niche and expected magnitude of impact, ecosystem-wide changes are likely to be minimal or non-existent. Clearly, caution must be used when categorising INNS impacts, as a single species can exert varying degrees of impact upon native communities depending on a wide range of biotic and abiotic processes.

7.4 Limitations and future research

The primary limitation of the research conducted within this thesis relates to the spatial scale to which it was constrained. In all but one of the data chapters, research was wholly confined within Plymouth Sound, while Chapter 2 was limited to the south coast of the southwest UK. The need for a limited spatial scale was primarily due to logistical and time constraints of the research methods used. The large majority of this thesis involved labour-intensive field-based survey and manipulation techniques. The work was also predominantly completed by one or two individuals at each sampling/maintenance event and was frequently limited to periods of low spring tides. Plymouth Sound is, however, typical of *Undaria* invaded systems of the UK, as it features a number of invaded marinas and adjacent wave sheltered to moderately-sheltered reef sites. The key themes discussed above are therefore likely to be consistent across the UK and perhaps the northeast Atlantic. In regions outside the southwest UK, however, where recipient communities or abiotic stressors vary, there is the potential for some dissimilarity in invasion dynamics and ecological impact. For example, in northern areas of the UK, where average sea temperatures in shallow subtidal habitats are ~3°C cooler (Smale and Moore, 2017) the recipient communities within both marina and reef habitats are somewhat distinct. As such *Undaria* may interact with, and impact upon, these native communities differently. Further research should be conducted within different invaded regions of the UK to discern the potential for impacts on other co-occurring species and to examine large-scale drivers of invasion dynamics.

The issue of management feasibility was also limited in its scope due to the spatial and temporal scale of the thesis. The experimental removal treatments implemented in Chapter 4 were limited to relatively small sections of pontoons over a period of 18 months. To achieve a more complete understanding of management feasibility, the removal or exclusion of *Undaria* would have to be conducted at a marina-wide or site-wide scale. It is highly probable that *Undaria* will continue to expand its range across the UK, which will present opportunities to test the efficacy of management measures within active management situations. This may occur across wider spatial scales and varying ecological contexts, therefore greatly improving our understanding of management feasibility in the UK.

Further research should also concentrate on the alteration of ecosystem services due to the invasion of *Undaria*. The shifts in the structure of marina and reef communities recorded in this thesis could alter trophic provision to grazers, habitat provision to mobile species, carbon cycling, nutrient uptake and impacts on biofiltration by sessile invertebrates. *Undaria* could also have economic impacts through increased fouling on vessels and infrastructure, costs for management and control, direct harvest of the species for food or other resources, and potential impact on other commercial species. In all cases, these functions and services could be either reduced or facilitated by the presence of *Undaria*. The net impact to these services will greatly affect management prioritisation for *Undaria* in the UK.

7.5 Concluding remarks

Over the last few years there has been a surge in publications regarding the sociology of INNS. One review discussed how INNS management projects often lead to social conflicts (Crowley *et al.*, 2017). Other publications have focused on the perceptions of INNS impacts, some suggesting the rise of INNS denialism (Lidstrom *et al.*, 2015; Russell and Blackburn, 2017), whilst others suggest that species should be judged on their functional role rather than their origin (Davis *et al.*, 2011; Chapman, 2016; Thomsen *et al.*, 2018). These diversity of views all highlight how our perception of INNS can be highly subjective and influence potential management approaches (Sotka and Byers, 2018).

Prioritisation of management and the potential acceptance of INNS should be based on evidence-based, objective frameworks. From a conservationist or environmentalist stand point, all INNS could be considered detrimental due to alteration of the natural environment and intrinsic competition with native species. It is well documented that INNS can have conspicuous and major detrimental impacts on biodiversity, the economy and ecosystem services (Pejchar and Mooney, 2009; Early *et al.*, 2016). A precautionary principle should therefore be applied with any new introductions minimised and the proliferation of established INNS limited where possible. As previously discussed, however, the impact of INNS can vary considerably; while complete prevention of new introductions is an unachievable aim and active management of all established INNS is unrealistic. Therefore management options must be prioritised that are feasible and prevent the largest potential impacts. Where an INNS is shown to have limited feasibility for successful management or minimal detrimental impact on the environment, economy and human health, it may then be appropriate to accept the species and consider how it may provide societal and even environmental benefit (Ewel *et al.*, 1999; Davis *et al.*, 2011; Schlaepfer *et al.*, 2011; Chapman, 2016).

Undaria is a model species to highlight the complexities in marine invasion ecology and management. This thesis showed that for a single INNS the invasion dynamics, species interactions, management options and impacts on recipient communities can vary considerably over a relatively small spatial scale. There are cases where targeted management of *Undaria* may be proportionate and feasible; however, in many locations around the UK, *Undaria* is likely to remain unmanaged and will become an accepted part of the biota. In these cases, it should be noted that *Undaria* is a habitat forming, primary producer with a broad ecological niche and potential commercial value. Although further research is needed to make a fully evidence-based decision, if *Undaria* is accepted, there is potential for it to deliver significant economic, ecosystem service and even environmental benefit in certain settings. 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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Appendix A

Appendix - Chpt. 1

Table A.1: The general areas where *Undaria pinnatifida* can be found as a non-native species. Time of first record is shown to the nearest year where data was available, otherwise it is shown to the nearest decade.

Country	Place	Year of first record	Reference
Argentina	Mar del Plata	2011	Meretta et al 2012
	San Jose Gulf	2007	Meretta et al 2012
	Nuevo Gulf	1992	Meretta et al 2012
	Camarones Bay	2000	Meretta et al 2012
	Ria Deseado	2005	Meretta et al 2012
	San Matias Gulf	2013	Pereya et al 2014
USA	San Fransisco Bay	2009	Kaplains et al 2016
	Pilar Point Harbour	2009	Kaplains et al 2016
	Santa Cruz Harbour	2014	Kaplains et al 2016
	Montery Bay	2001	Kaplains et al 2016
	Morro Bay Docks	2009	Kaplains et al 2016
	Santa Barbara Harbor	2001	Kaplains et al 2016
	Channel Isalnds Harbours	2000	Kaplains et al 2016
	Los Angeles Harbours	2000	Kaplains et al 2016
	Santa Catalina Island	2001	Kaplains et al 2016
	Oceanside Harbour (San Diego)	2013	Kaplains et al 2016
	Mission Bay	2014	Kaplains et al 2016
	San Diego Bay	2004	Kaplains et al 2016
Mexico	Bahia de Todos Santos	2003	Aguilar-Rosas et al 2004
New Zealand	Rangaunu Harbour	2014	James et al 2014
	Fiordland	2010	Environment Southland 2016
	Waitemata Harbour	2004	Russel et al 2008
	Port Taranaki	2005	Russel et al 2008
	Wellington	1987	Russel et al 2008
	Napier	1995	Russel et al 2008

Country	Place	Year of first record	Reference
New Zealand	Gisbourne	1999	Russel et al 2008
	Tauranga Harbour	2005	Russel et al 2008
	Firth of Thames	2002	Russel et al 2008
	Golden Bay	1998	Russel et al 2008
	Nelson	1998	Russel et al 2008
	Marlborough Sounds	1988	Russel et al 2008
	Port Underwood	1997	Russel et al 2008
	Kaikoura	2002	Russel et al 2008
	Lyttleton	1991	Russel et al 2008
	Akaroa	2000	Russel et al 2008
	Timaru	1987	Russel et al 2008
	Oamaru	1988	Russel et al 2008
	Moeraki	1995	Russel et al 2008
	Otago Harbour	1990	Russel et al 2008
	Bluff	1998	Russel et al 2008
	Stewart Island	1997	Russel et al 2008
Austalia	Port Philip Bay	1995	Campbell & Burridge 1998
	Apollo Bay	2009	ALA 2017
	King Island	1992	ALA 2017
	Curtis Group Islands	1992	ALA 2017
	Kent Group Islands	1992	ALA 2017
	Hogan Group Isalnds	1992	ALA 2017
	Rocky Cape	1992	ALA 2017
	Table Cape	1992	ALA 2017
	Cape Barren Island	1992	ALA 2017
	Waterhouse	1992	ALA 2017
	Cape Portland	1992	ALA 2017
	Bathurst Harbour	1993	ALA 2017
	Charlotte Cove	1992	ALA 2017
	Tinderbox	1992	ALA 2017
	Maria Group Islands	1992	ALA 2017
	Ile Des Phoques	1992	ALA 2017
	Schouten Island	1992	ALA 2017
	Freycinet	1994	ALA 2017
	Bicheno	1992	ALA 2017
	Rheban	1988	Sanderson 1990
	Orford	1992	ALA 2017
	Triabunna	1988	Sanderson 1990
Portugal	Pova de Varzim	1999	Arajo et al 2009
	Buarcos	2013	Veiga et al 2014
Spain	Lastres	2007	Petero 2008
	Cudillero	2001	Perez-Ruzafa et al 2002

Country	Place	Year of first record	Reference
Spain	Gijon	1995	Salinas et al 1996
	Ria de Arousa	1988	Santiago Camao et al 1990
	Ferrol	200?	Cremades et al 2006
	A Coruna	1996	Perez-Ruzafa et al 2002
	O Porto de Corme	200?	Cremades et al 2006
	Camarinas	2004	Cremades et al 2006
	Corcubion	1998	Santiago Camao et al 1990
	Noia	1998	Santiago Camao et al 1990
	Sanxenxo	1997	Santiago Camao et al 1990
	Vigo	1997	Santiago Camao et al 1990
	Baiona	200?	Cremades et al 2006
Italy	Venice Lagoon	1992	Curiel et al 1998
	Mar Piccolo of Taranto	1999	Cecere et al 2000
Belgium	Zeebruge	1999	Leliaert et al 2000
Netherlands	Oosterschelde	1999	Stegenga 1999
	Terschelling	2008	Gittenberger 2013
UK	Newlyn	2014	NBN 2017
	Falmouth	2010	NBN 2017
	Plymouth	2003	NBN 2017
	Salcombe	2006	NBN 2017
	Dartmouth	2012	NBN 2017
	Torbay	1996	NBN 2017
	Weymouth-Portland	2011	NBN 2017
	Poole	2006	NBN 2017
	Cowes	1996	NBN 2017
	Southampton Water	1994	Fletcher & Manfredi 1995
	Portsmouth-Chichester	1998	NBN 2017
	Brighton	1997	NBN 2017
	Dover	2008	NBN 2017
	Ramsgate	2002	NBN 2017
	Watchet	2014	NBN 2017
	Milford Haven	2014	NBN 2017
	Belfast Loch	2012	NBN 2017
	Glenarm	2015	NBN 2017
	Holyhead	2014	NBN 2017
	Queensferry	2016	NBN 2017
	Gimsby	2009	NBN 2017
	Liverpool	2012	NBN 2017
	Fleetwood	2007	NBN 2017
	Burnham-on-Crouch	2009	NBN 2017
	Blackwater	2011	NBN 2017
	Stour and Orwell	2009	NBN 2017

Country	Place	Year of first record	Reference
UK	Orford	2014	NBN 2017
	Lowestoft	2009	NBN 2017
	Jersey	1996	NBN 2017
	Guernsey	2006	NBN 2017
ROI	Kilmore Quay	2016	NBN 2017
	Carlingford	2014	Minchin et al 2017
France	lEtang de Thau	1971	Perez 1981
	l'Etang de l'Ayrolle	1981	Floch et al 1991
	Port-Vendres	1988	Floch et al 1991
	Calais	199?	Ghent University 2017
	Saint-Valery-en-Caux	200?	Ghent University 2017
	Le Harve	200?	Ghent University 2017
	Saint-Vaast-la-Hougue	200?	Ghent University 2017
	Cherbourg-Octeville	201?	Ghent University 2017
	Granville	199?	Ghent University 2017
	Isle de Chausey	1992	Castric-Fey et al 1993
	Ushant	1983	Perez 1984
	Groix	1983	Perez 1984
	l'estuaire de la Rance	1983	Perez 1984
	l'estuaire de la Wrac'h	1987	Castric-Fey et al 1993
	l'estuaire de la Trieux	1989	Castric-Fey et al 1993
	Pleubian	1989	Castric-Fey et al 1993
	Guilvinec	1989	Castric-Fey et al 1993
	Pointe de la Varde	1992	Castric-Fey et al 1993
	Brest	199?	Ghent University 2017
	Golfe du Morbihan	199?	Ghent University 2017
	Houat	200?	Ghent University 2017
	Quiberon	200?	Ghent University 2017
	l'estuaire de la Crach	200?	Ghent University 2017
	l'estuaire de la d'tel	200?	Ghent University 2017
	Port de Loctudy	200?	Ghent University 2017
	le de Sein	199?	Ghent University 2017
	Port de Camaret	200?	Ghent University 2017
	Roscoff	200?	Ghent University 2017
	Saint-Pol-de-Lon	200?	Ghent University 2017
	Port de Trebeurden	201?	Ghent University 2017
	Perros-Guirec	199?	Ghent University 2017
	le-de-Brhat	200?	Ghent University 2017
	Saint-Quay-Portrieux	200?	Ghent University 2017
	Plneuf-Val-Andr	199?	Ghent University 2017
	Plvenon	201?	Ghent University 2017
	Saint-Cast-le-Guildo	199?	Ghent University 2017

Country	Place	Year of first record	Reference
France	St Malo	1986	Castric-Fey et al 1993
	Dinard	199?	Ghent University 2017
	les de Czembre	199?	Ghent University 2017
	Saint-Lunaire	199?	Ghent University 2017
	Lancieux	199?	Ghent University 2017
	Pointe du Meinga	199?	Ghent University 2017
	Baie de Bourgeneuf	198?	Ghent University 2017
	La Rochelle	200?	Ghent University 2017
	Oleron	1990	Castric-Fey et al 1993

Appendix B

Appendix - Chpt. 3

Table B.1: Post-hoc pairwise F-tests on the abundance and biomass of *Undaria pinnatifida*, testing for the effect of habitat within each month of the year sampled in the study period. Contrast vale (value), F value (F) and p-value (p) are shown for each pairwise comparison. Degrees of freedom equal 1 for each test due to pairwise contrasts. Significant tests shown in bold ($\alpha \leq 0.05$).

Month	March			June			September			December		
Contrast	Value	F	p	Value	F	p	Value	F	p	Value	F	p
Abundance												
Intertidal – Marina	**-1.32**	**21.68**	**<0.001**	**-0.83**	**8.48**	**0.034**	-0.17	0.37	0.668	-0.55	3.83	0.221
Intertidal – Subtidal	0.53	3.46	0.221	**0.90**	**10.19**	**0.019**	**0.77**	**7.30**	**0.045**	0.28	0.95	0.669
Marina – Subtidal	**1.85**	**42.46**	**<0.001**	**1.73**	**37.26**	**<0.001**	**0.94**	**10.99**	**0.015**	**0.83**	**8.59**	**0.034**
Biomass												
Intertidal – Marina	0.05	0.38	1.000	-0.22	8.46	0.052	0.06	0.70	1.000	-0.02	0.10	1.000
Intertidal – Subtidal	0.09	1.54	1.000	**0.23**	**8.99**	**0.045**	0.07	0.95	1.000	0.04	0.24	1.000
Marina – Subtidal	0.05	0.39	1.000	**0.45**	**34.85**	**0.001**	0.01	0.02	1.000	0.06	0.67	1.000

TABLE B.2: Post-hoc pairwise PERMANOVA on the population structure of *Undaria pinnatifida*, testing for the effect of habitat within each month of the year sampled in the study period. t value (t) and p-value (p) are shown for each pairwise comparison. Significant tests shown in bold ($\alpha \leq 0.05$).

Month	March		June		September		December	
Contrast	t	p	t	p	t	p	t	p
Intertidal – Marina	**2.43**	**0.05**	**1.80**	**0.04**	**2.36**	**0.05**	1.20	0.29
Intertidal – Subtidal	0.05	0.95	1.41	0.18	0.35	0.92	0.03	0.96
Marina – Subtidal	1.46	0.16	**2.26**	**0.01**	1.91	0.07	1.35	0.25

TABLE B.3: SIMPER analysis on *Undaria pinnatifida* population structure, selecting only significant pairwise contrasts indicated from post-hoc pairwise PERMOANOVA (Table S2). Average proportion of each developmental category (recruits, mature and senescing sporophytes) are shown within each contrast, with their percentage contribution to the dissimilarity (Contrib %).

	Average proportion (%)		Contrib (%)	Average proportion (%)		Contrib (%)	Average proportion (%)		Contrib (%)	Average proportion (%)		Contrib (%)
Month	March			June			September			December		
Habitat	Intertidal	Marina		Intertidal	Marina		Subtidal	Marina		Intertidal	Marina	
Recruits	86.2	96.0	49.3	77.0	62.1	40.4	74.4	62.1	36.2	87.9	51.4	47.2
Mature	13.8	3.7	49.3	19.3	21.3	30.4	25.6	21.3	34.4	5.7	38.8	44.0
Senescing	0.0	0.4	1.4	3.7	16.6	29.2	0.0	16.6	29.4	6.4	9.9	8.8

Table B.4: Post-hoc pairwise F-tests on the two reproductive activity metrics of *Undaria pinnatifida*, testing for the effect of habitat over the study period. Contrast vale (value), F value (F) and p-value (p) are shown for each pairwise comparison. Degrees of freedom equal 1 for each test due to pairwise contrasts. Significant tests shown in bold ($\alpha \leq 0.05$).

Contrast	Value	F	p
Spores $cm^{-2}h^{-1}$			
Marina - Intertidal	2.07	2.95	0.182
Marina - Subtidal	**3.41**	**7.97**	**0.019**
Intertidal - Subtidal	1.33	1.23	0.273
Spores $sporophyll^{-1}h^{-1}$			
Marina - Intertidal	2.34	2.00	0.325
Marina - Subtidal	**4.31**	**6.80**	**0.034**
Intertidal - Subtidal	1.97	1.43	0.325

TABLE B.5: Results from PERMANOVA model, testing for difference in morphology of *Undaria pinnatifida* between habitats, for each developmental stage separately. Site (nested within habitat) is included as a random factor in all models. The degrees of freedom (df), mean sum of squares (MS), pseudo F-value (F) and p-value (p) are shown for each coefficient. Significant coefficients shown in bold ($\alpha \leq 0.05$).

Coefficient	df	MS	F	p
Stage 0				
Habitat	3	4.99	0.87	0.443
Site(Habitat)	6	6.02	1.53	0.098
Stage 1				
Habitat	**3**	**24.39**	**5.26**	**0.004**
Site(Habitat)	6	5.69	1.20	0.273
Stage 2				
Habitat	**3**	**102.81**	**13.95**	**0.003**
Site(Habitat)	**6**	**7.52**	**1.76**	**0.035**
Stage 3				
Habitat	**3**	**39.01**	**6.55**	**0.019**
Site(Habitat)	**6**	**7.51**	**2.16**	**0.024**
Stage 4				
Habitat	**3**	**84.75**	**7.22**	**0.009**
Site(Habitat)	**6**	**13.45**	**4.00**	**<0.001**
Stage 5				
Habitat	**3**	**60.75**	**17.75**	**0.002**
Site(Habitat)	6	3.44	1.03	0.416

TABLE B.6: Average morphological attributes of *Undaria pinnatifida* in each habitat, for each developmental stage shown to be significantly different by PERMANOVA (Table B.5). Letters indicate significant pairwise groupings tested by post-hoc pairwise PERMANOVA (Table B.7). Morphological attributes (Morph) measured to the nearest 0.1 cm are: Stipe width (SW), stipe length (SL), lamina width (LW), lamina length (LL), sporophyll width (SPW) and sporophyll length (SL).

Morph	Marina	Intertidal	Subtidal
Stage 1	a	ab	b
LL	19.1	22.4	24.9
LW	7.9	8.6	10.3
SL	4.8	7.1	6.6
SW	0.5	0.5	0.4
Stage 2	a	a	a
LL	48.9	68.2	68.4
LW	25.8	34.7	45.5
SL	13.2	11.5	22.4
SPL	9.3	20.8	15.1
SPW	4.3	4.8	5.1
Stage 3	a	ab	b
LL	64.4	89.3	72.5
LW	37.4	55.0	66.6
SL	15.3	20.6	25.1
SPL	13.3	18.1	25.5
SPW	8.5	10.5	12.0
Stage 4	a	b	b
LL	15.3	11.6	15.1
LW	10.8	14.6	22.2
SL	9.0	22.4	20.3
SPL	6.9	17.3	20.3
SPW	4.4	5.1	5.1
Stage 5	a	b	b
SL	8.9	20.7	16.7
SW	1.1	1.4	1.3
SPL	5.3	14.7	8.4
SPW	3.0	3.6	2.5

Table B.7: Post-hoc pairwise PERMANOVA on the morphology of *Undaria pinnatifida*, testing for the effect of habitat on each developmental stage separately. t value (t) and p-value (p) are shown for each pairwise comparison. Significant tests shown in bold ($\alpha \leq 0.05$).

	Stage 1		Stage 2		Stage 3		Stage 4		Stage 5	
Contrast	t	p	t	p	t	p	t	p	t	p
Intertidal - Marina	2.45	0.06	3.06	0.08	2.01	0.09	**3.96**	**0.03**	**5.56**	**0.05**
Intertidal - Subtidal	1.37	0.26	2.34	0.10	1.54	0.13	0.74	0.60	2.55	0.10
Marina - Subtidal	**2.72**	**0.05**	5.32	0.10	**3.48**	**0.05**	**2.76**	**0.60**	**2.58**	**0.05**

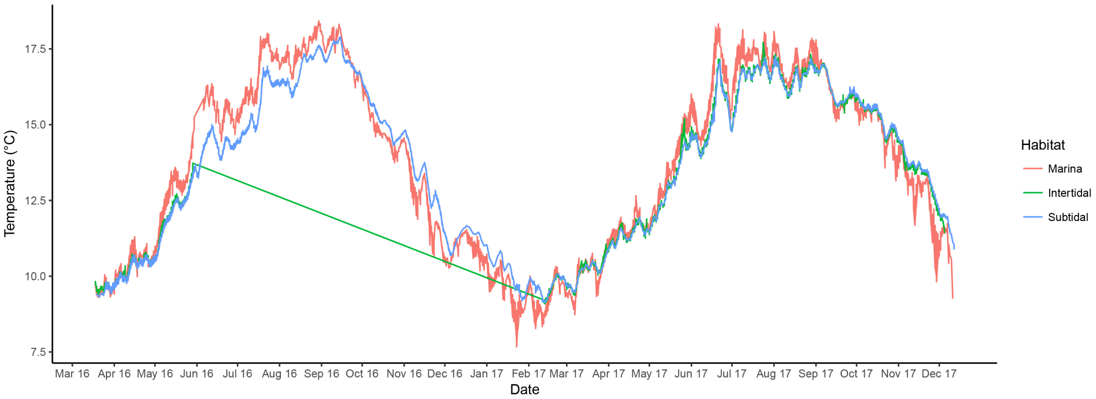

Figure B.1: Mean daily temperature (Celsius) at each habitat for the duration of the study period. The straight green line between June 16 and Mar 17 is due to a missing data from the intertidal as a result of lost or malfunctioning temperature loggers.

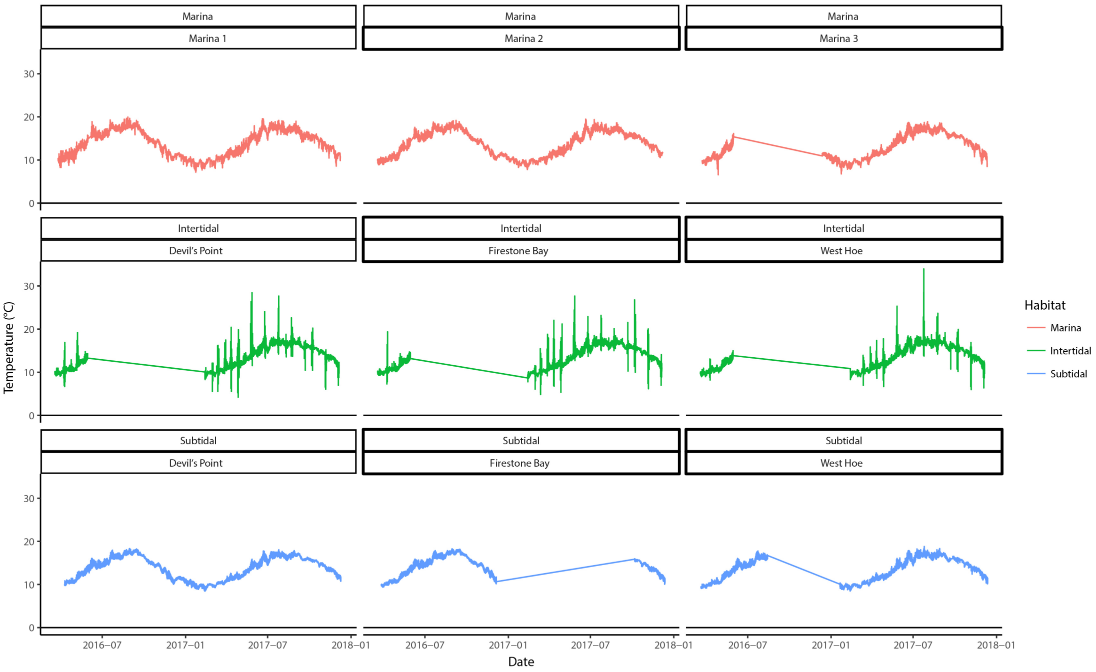

FIGURE B.2: Temperature (Celsius) recorded at 30 minute intervals at each site for the duration of the study period. The straight horizontal lines indicate missing data due to lost or malfunctioning temperature loggers.

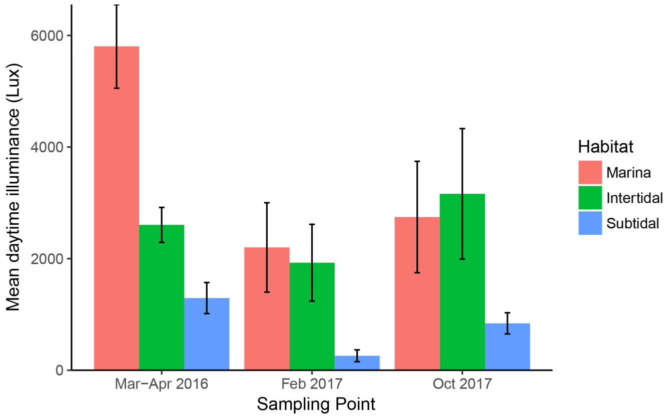

FIGURE B.3: Comparison of mean daytime illuminance between habitat types. As light loggers accumulate biofouling and sediment over the course of their deployment, three 14 day sampling points were selected for comparison. This was based on periods where all light loggers were successfully installed and had just been cleaned or deployed. Mean daytime illuminance (Lux) was calculated for each site first. Overall mean daytime illuminance (± standard error) is shown for each habitat during the three sampling periods.

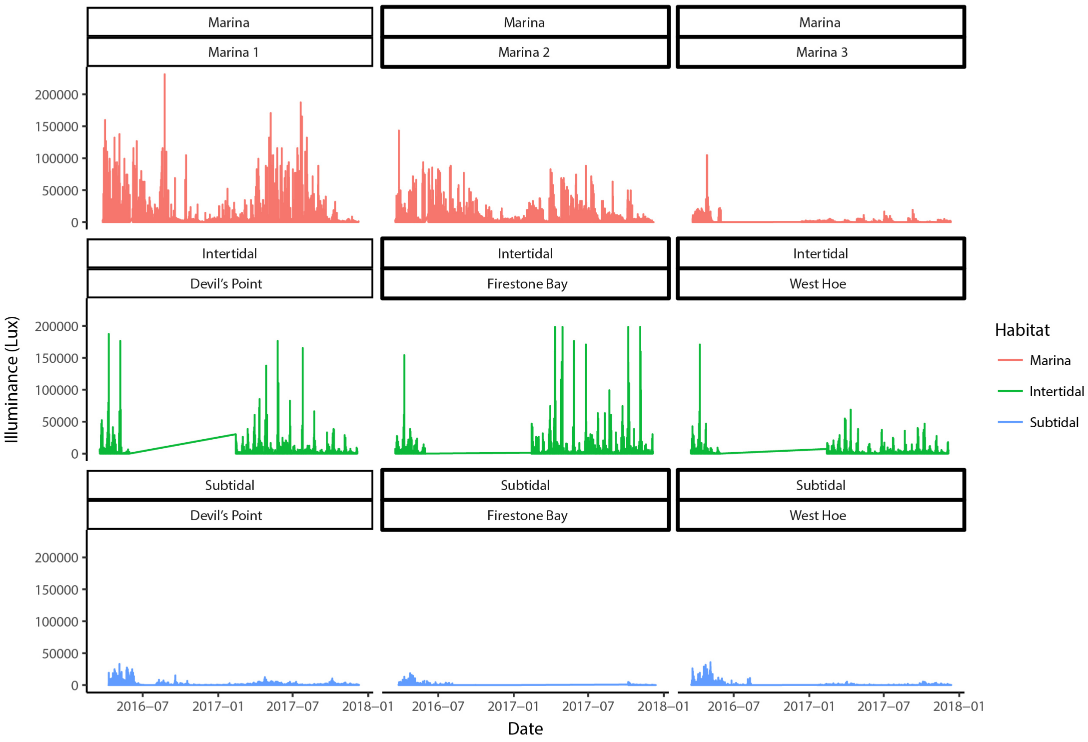

FIGURE B.4: Raw illuminance (Lux) data recorded at 30 minute intervals at each site for the duration of the study period. The straight horizontal lines indicate missing data due to lost or malfunctioning light loggers. Note that this is raw data, loggers are likely to be effected by accumulated biofouling and sediment, dependent on the frequency of cleaning and number of redeployments.

Appendix C

Appendix - Chpt. 4

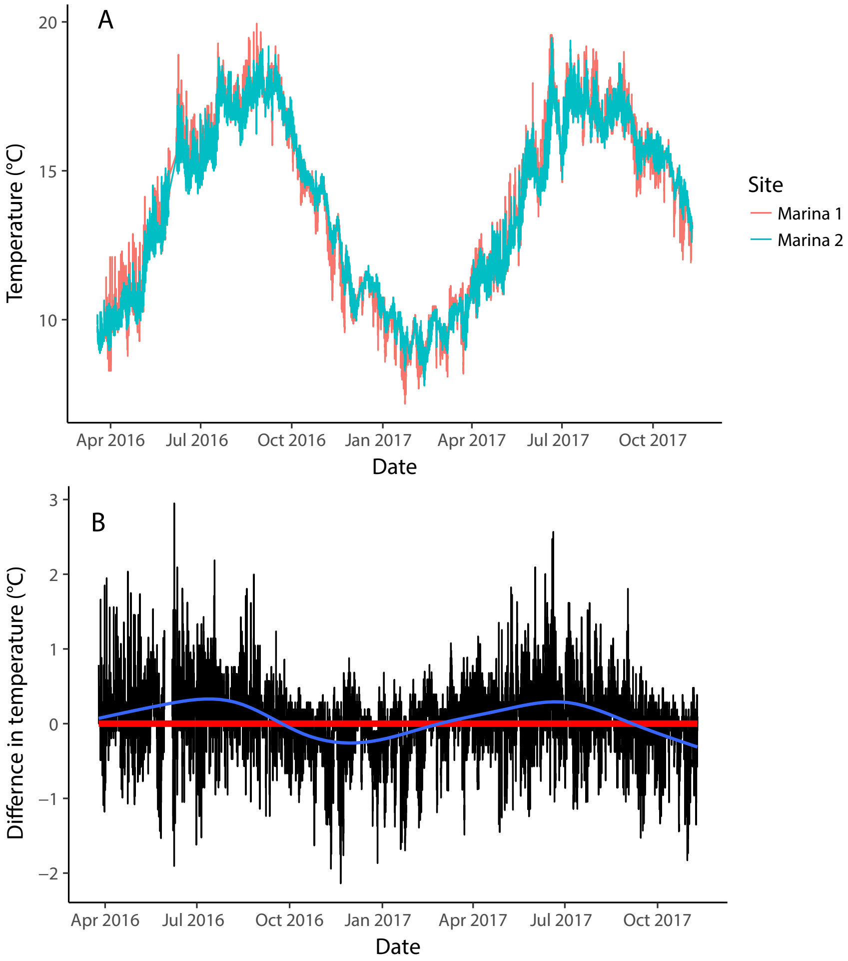

FIGURE C.1: (A) Temperature at the two marinas recorded every 30 mins during the study period. (B) Difference in temperature between Marina 1 and Marina 2 (black line) calculated at each 30 mins where temperature was recorded at both sites. Blue line indicates a daily smoothing line (using a general additive method). Red line highlights the point where there is no difference in temperature between each site.

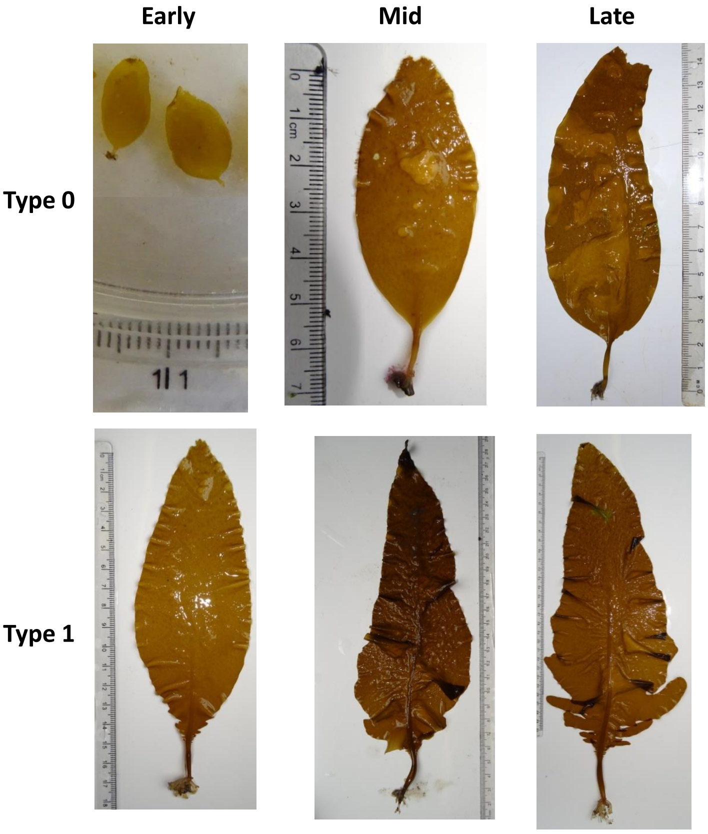

Figure C.2: Developmental stages of *Undaria pinnatifida* recruits. Type 0 is characterised by the absence of pinnate blade divisions and a defined midrib, whereas in Type 1 they are both present. Early-Mid-Late indicates the growth towards the next developmental stage for comparative purposes; however this distinction was not recorded.

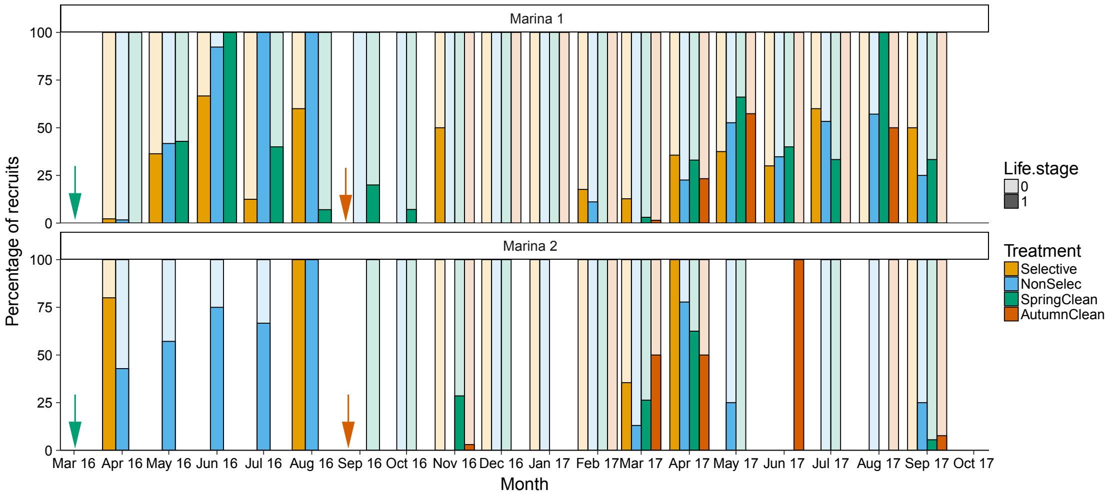

Figure C.3: Percentage of *Undaria pinnatifida* recruits classified to each of two life stages (Type 0 = light, Type 1 = dark; see Figure C.2) for all treatments across the duration of removals. Arrows indicate when each treatment was initiated; green = selective, non-selective and spring cleaning, orange = autumn cleaning.

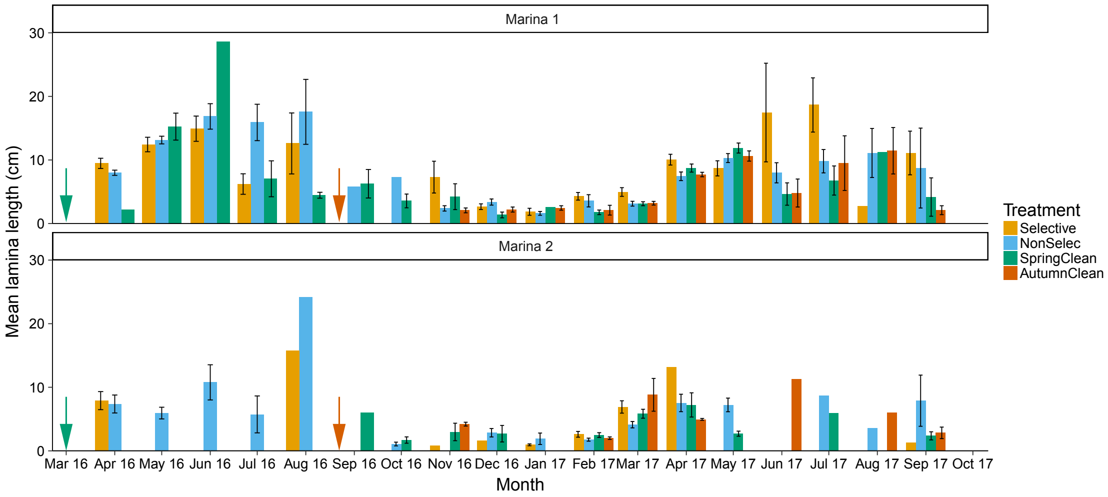

Figure C.4: The lamina length of all *Undaria pinnatifida* recruits was measured at each monthly removal. Mean lamina length (± standard error) is shown for each treatment at all monthly removals for each marina separately. Missing error bars are due to only one individual being found. Arrows indicate when each treatment was initiated; green = selective, non-selective and spring cleaning, orange = autumn cleaning.

Appendix D

Appendix - Chpt. 5

Table D.1: Results from PERMANOVA models testing for difference in composition of canopy-forming macroalgae between years. Each habitat was analysed separately, and models were constructed both on count and biomass data. Site was also included as a random factor in all models. The degrees of freedom (df), pseudo F-value (F) and p-value (p) are shown for each coefficient. Significant coefficients shown in bold ($\alpha = 0.05$).

		Intertidal reef		Subtidal reef		Marina	
Coefficient	df	F	p	F	p	F	p
Biomass							
Year	2	2.27	0.052	0.72	0.574	1.17	0.335
Site	2	**3.75**	**0.003**	1.79	0.134	**20.00**	**<0.001**
Density							
Year	2	**5.13**	**<0.001**	2.02	0.111	1.45	0.205
Site	2	**5.15**	**<0.001**	2.29	0.074	**27.03**	**<0.001**

Table D.2: Post-hoc pairwise PERMANOVA on the composition of canopy-forming macroalgae (by density) in the intertidal habitat, testing for the effect of year. t value (t) and p-value (p) are shown for each pairwise comparison. Significant coefficients shown in bold ($\alpha = 0.05$).

Years	t	p
2016, 2017	**2.26**	**0.006**
2016, 2018	**3.09**	**<0.001**
2017, 2018	1.46	0.136

TABLE D.3: SIMPER analysis on composition of canopy-forming macroalgae, selecting only significant pairwise contrasts indicated from post-hoc pairwise PERMOANOVA (Table D.2). Average proportion of each species (square root transformed) are shown, with their percentage contribution to the dissimilarity when compared to 2016 (Contrib %).

	2016	2017		2018	
Species	Av. Prop	Av. Prop	Contrib (%)	Av. Prop	Contrib (%)
S. latissima	4.21	2.90	22.64	2.97	21.98
L. digitata	0.96	2.95	22.38	2.22	17.47
U. pinnatifida	7.58	5.97	20.50	5.53	20.67
H. elongata	1.95	2.49	17.96	3.07	19.08
S. polyschides	1.90	2.06	16.51	3.84	20.81

TABLE D.4: Pairwise tests for density or percent cover of canopy-forming macroalgae, testing for differences between new and old marina substrates at each sampling event. F-values (F) shown with Holm adjusted p-values (p) for each pairwise contrast. Significant coefficients shown in bold ($\alpha = 0.05$).

	U. pinnatifida		*S. latissima*		*L. digitata*	
Date	F	p	F	p	F	p
Density						
Mar-16	**118.05**	**<0.001**	7.51	0.071	<0.01	1.000
Jun-16	**393.13**	**<0.001**	**12.69**	**0.006**	<0.01	1.000
Oct-16	**170.57**	**<0.001**	2.29	0.931	**17.58**	**0.001**
Dec-16	**79.16**	**<0.001**	0.05	1.000	**17.64**	**0.001**
Mar-17	2.84	0.948	0.07	1.000	**19.57**	**<0.001**
Apr-17	0.13	1.000	1.31	1.000	**20.60**	**<0.001**
May-17	0.61	1.000	**19.05**	**<0.001**	**21.02**	**<0.001**
Jun-17	0.17	1.000	**35.64**	**<0.001**	**18.94**	**<0.001**
Jul-17	1.17	1.000	**20.70**	**<0.001**	**12.42**	**0.004**
Aug-17	0.15	1.000	7.19	0.075	**16.68**	**0.001**
Sep-17	1.91	1.000	**15.73**	**0.001**	**13.82**	**0.002**
Oct-17	1.36	1.000	2.89	0.734	8.22	0.029
Nov-17	3.68	0.631	0.25	1.000	5.52	0.082
Dec-17	2.67	0.948	0.06	1.000	8.22	0.029
Jan-18	1.12	1.000	<0.01	1.000	3.91	0.151
Canopy-cover						
Mar-16	10.08	0.020	8.79	0.048	<0.01	1.000
Jun-16	**313.68**	**<0.001**	8.53	0.050	<0.01	1.000
Oct-16	**123.89**	**<0.001**	6.95	0.105	7.85	0.037
Dec-16	**28.94**	**<0.001**	1.89	1.000	**13.06**	**0.004**
Mar-17	5.60	0.157	0.52	1.000	**25.82**	**<0.001**
Apr-17	**16.23**	**0.001**	<0.01	1.000	**31.16**	**<0.001**
May-17	3.27	0.439	0.97	1.000	**18.77**	**<0.001**
Jun-17	**8.09**	**0.047**	10.67	0.020	**21.06**	**<0.001**
Jul-17	**10.22**	**0.020**	5.03	0.241	**13.47**	**0.003**
Aug-17	2.49	0.468	6.74	0.106	**19.82**	**<0.001**
Sep-17	3.23	0.439	**13.26**	**0.006**	**15.17**	**0.002**
Oct-17	4.46	0.257	0.34	1.000	8.09	0.037
Nov-17	1.00	0.955	0.13	1.000	3.02	0.338
Dec-17	0.88	0.955	0.01	1.000	3.87	0.257
Jan-18	<0.01	0.984	0.06	1.000	2.69	0.338

TABLE D.5: Pairwise tests for density or percent cover of canopy-forming macroalgae, testing for differences between new and old intertidal substrates at each sampling event. F-values (F) shown with Holm adjusted p-values (p) for each pairwise contrast. Significant coefficients shown in bold ($\alpha = 0.05$).

	U. pinnatifida		*S. latissima*		*L. digitata*		*S. polyschides*		*H. elongata*	
Date	F	p	F	p	F	p	F	p	F	p
Density										
Mar-17	0.99	1.000	3.15	0.805	**46.96**	**<0.001**	<0.01	1.000		
May-17	**191.34**	**<0.001**	0.85	1.000	**40.65**	**<0.001**	**147.93**	**<0.001**		
Jun-17	**46.19**	**<0.001**	0.90	1.000	**143.82**	**<0.001**	**11.79**	**0.010**		
Aug-17	**49.07**	**<0.001**	2.61	0.998	**84.53**	**<0.001**	0.67	1.000		
Oct-17	0.25	1.000	5.59	0.231	**62.89**	**<0.001**	<0.01	1.000		
Dec-17	<0.01	1.000	0.18	1.000	**63.37**	**<0.001**	<0.01	1.000		
Feb-18	0.15	1.000	0.23	1.000	**27.89**	**<0.001**	<0.01	1.000		
Mar-18	<0.01	1.000	0.23	1.000	**20.00**	**<0.001**	<0.01	1.000		
Apr-18	0.01	1.000	0.23	1.000	**22.29**	**<0.001**	<0.01	1.000		
Jun-18	<0.01	1.000	0.47	1.000	**11.88**	**0.002**	<0.01	1.000		
Jul-18	<0.01	1.000	0.12	1.000	5.86	0.018	<0.01	1.000		
Canopy-cover										
Mar-17	0.51	1.000	2.00	1.000	**67.03**	**<0.001**	<0.01	1.000	**16.94**	**0.001**
May-17	**39.54**	**<0.001**	0.01	1.000	**52.64**	**<0.001**	**147.93**	**<0.001**	**36.35**	**<0.001**
Jun-17	**33.26**	**<0.001**	0.58	1.000	**44.73**	**<0.001**	**11.79**	**0.010**	**54.85**	**<0.001**
Aug-17	**15.71**	**0.002**	1.23	1.000	**39.05**	**<0.001**	0.67	1.000	**16.86**	**0.001**
Oct-17	0.44	1.000	3.19	0.868	**42.04**	**<0.001**	<0.01	1.000	9.86	0.018
Dec-17	0.27	1.000	0.30	1.000	**19.27**	**<0.001**	<0.01	1.000	0.94	0.576
Feb-18	0.24	1.000	0.23	1.000	**18.45**	**<0.001**	<0.01	1.000	2.19	0.575
Mar-18	<0.01	1.000	0.25	1.000	**35.42**	**<0.001**	<0.01	1.000	1.71	0.576
Apr-18	0.44	1.000	0.05	1.000	**21.49**	**<0.001**	<0.01	1.000	1.74	0.576
Jun-18	<0.01	1.000	0.11	1.000	4.91	0.060	<0.01	1.000	7.94	0.038
Jul-18	<0.01	1.000	0.55	1.000	3.83	0.060	<0.01	1.000	4.3	0.211

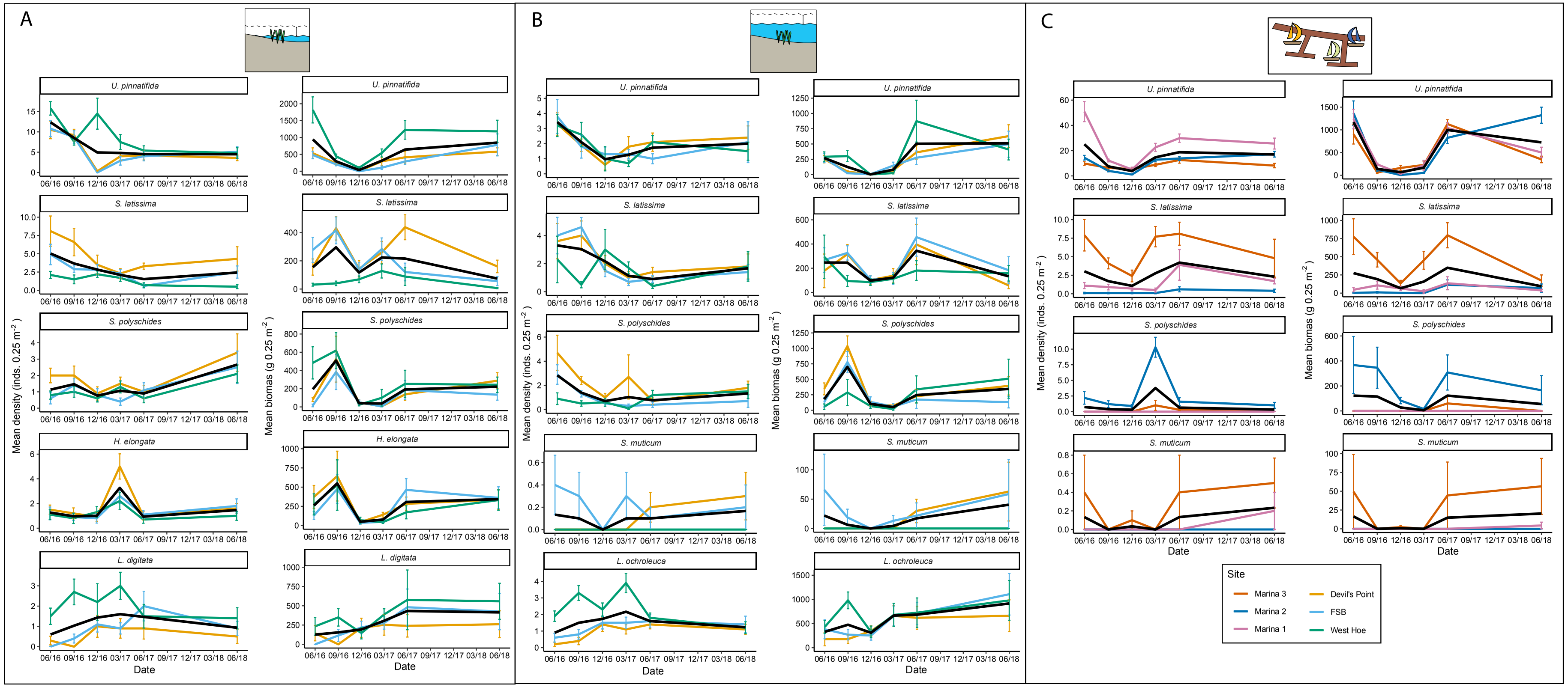

FIGURE D.1: Mean density and biomass of canopy-forming macroalgae per $0.25m^2$ (± standard error) for each site at every sampling event. Data are separated by habitat intertidal reef (A), subtidal reef (B) and marinas (C). Black lines indicate average across sites.