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The influence of native macroalgal canopies on the distribution and abundance of the non-native kelp *Undaria pinnatifida* in natural reef habitats

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Abstract: The Asian kelp *Undaria pinnatifida* ('Wakame') is one of the most widespread invasive non-native species in coastal marine habitats and is fast approaching cosmopolitan status, yet its interactions with native species are poorly understood. Within the Plymouth Sound (UK) Special Area of Conservation (SAC) *Undaria* has become a conspicuous and important component of assemblages in shallow rocky reef habitats, where it co-exists with native canopy-forming brown macroalgae. We examined the hypothesis that rocky reef habitats supporting dense macroalgal canopies will have more biotic resistance to the invasion of *Undaria* compared with reef habitats supporting disturbed or sparse native canopies. Field surveys were completed at 2 spatial scales and sampling resolutions and a short-term field-based canopy removal experiment was conducted to examine the influence of native macroalgal assemblages on the abundance, cover, biomass and morphology of *Undaria*. Field surveys indicated that *Undaria* was negatively related to the cover of macroalgal 'competitors', particularly *Laminaria* spp. However, multiple, large *Undaria* sporophytes were observed within dense native canopies, suggesting that disturbance to, or absence of, canopies is not a prerequisite for *Undaria* colonisation. The short-term canopy-removal experiment indicated that *Undaria* functions primarily as a pioneer species in this system. Where native canopies were left intact, *Undaria* sporophytes were far less abundant and were generally smaller with lower biomass compared with those in disturbed patches. The spread of *Undaria* into natural habitats is inhibited by the presence of native competitors, particularly large perennial species such as *Laminaria* spp., although the persistence of intact dense canopies does not completely prevent assimilation of *Undaria* into native assemblages.

Keywords: Temperate reefs, macroalgae, invasive species, competition, canopy disturbance

Introduction

The spread of non-native species (NNS) represents a major threat to global biodiversity (Bax et al. 2003). Due to the inherent connectivity and openness of the marine environment, non-native species (NNS) are particularly prevalent and widespread in coastal marine ecosystems (Ruiz et al. 1997; Bax et al. 2003). Determining the ecological and socioeconomic impacts of marine NNS is critical for prioritising management actions and conservation measures, yet basic information on the population dynamics of NNS outside of their native range is often lacking (Byers et al. 2002). A robust understanding of the mechanisms underpinning the spread of NNS, combined with an appreciation of the direction and magnitude of ecological interactions with native species across a range of habitats, are vital for assessing current and future ecological impacts. Marine NNS are often introduced into, and proliferate within, artificial habitats such as ports, harbours, marinas and modified embayments (Glasby et al. 2007). Once established, they can spread into nearby natural habitats where they may interact with native biota and have the potential to drive ecological change. The rate of spread into natural habitats and the nature of ecological interactions with native species are likely to depend, to some degree, on the competitive ability of functionally-similar native species and the biotic resistance of local communities (Stachowicz et al. 2002; Crooks 2005). This, in turn, will likely vary between invaded regions due to differences in environmental conditions and the identify of native species, so that making predictions of ecological impacts across non-native ranges is problematic.

Macroalgal NNS are of particular importance as they can cause shifts in the structure and functioning of entire communities, alter patterns and rates of primary production and have significant socioeconomic and ecological impacts (Schaffelke and Hewitt 2007; Williams and Smith 2007). Worldwide there are thought to be >227 different macroalgal species which have been introduced outside of their native ranges (Schaffelke and Hewitt 2007), however clear quantitative evidence of their ecological interactions within native communities and their wider impacts is generally lacking. Native to cold temperate areas of the Northwest Pacific (i.e. the coastlines of Japan, Korea, Russia and China) the kelp *Undaria pinnatifida* (Harvey) Suringar, 1873 (Phaecophycae, Laminariales), or 'Wakame' has a worldwide introduced range. First identified as a NNS on the Mediterranean coast of France in 1971 (Perez et al. 1981), *Undaria pinnatifida* (hereafter '*Undaria*') is now established on the coastlines of New Zealand, Australia, Northern France, Spain, Italy, United Kingdom , Portugal, Belgium, Holland , Argentina, Mexico and the USA (James et al. 2015 and references therein).

The primary vectors of introduction are thought to be through fouling on the hulls of commercial vessels (Hay 1990; Fletcher and Farrell 1999), and accidental import with shellfish (Perez et al. 1981; Floc'h et al. 1991), although it was also intentionally introduced for cultivation into Brittany, France, in 1981 (Perez et al. 1981). Following the initial introduction, further regional spread is thought to occur via fouling of leisure crafts and transport to nearby harbours and marinas (Russell et al. 2008; Minchin and Nunn 2014). *Undaria* is prevalent in many ports, marinas and aquaculture sites worldwide (e.g. Floc'h et al. 1991; Fletcher and Manfredi 1995; Veiga et al. 2014; James and Shears 2016). Once established in artificial habitats or modified environments, *Undaria* can spread into natural habitats including rocky reefs, seagrass beds and mixed sediments (Floc'h et al. 1996; Stuart 2003; Farrell and Fletcher 2006; Russell et al. 2008; James and Shears 2016). *Undaria* is considered by the IUCN Invasive Species Specialist Group as one of the 100 worst invasive species in the world, and the second worst invasive seaweed (Lowe et al. 2000), and is considered to be of significant risk to the natural environment.

Undaria was first discovered in UK waters in 1994, in the Hamble Estuary in the Solent (Fletcher and Manfredi 1995). Since *Undaria*'s introduction to the Hamble, it has continued to spread along the UK coastline with the most northerly population in Europe currently being the Firth of Forth, Scotland (NBN 2017). It was first recorded within Plymouth Sound in a marina in 2003 (NBN 2017) and has since successfully colonised natural substrata in intertidal and subtidal rocky habitats dominated by native kelp species including *Laminaria digitata, Laminaria hyperborea, Laminaria ochroleuca, Saccharina latissima,* and *Saccorhiza polyschides* (Heiser et al. 2014; Arnold et al. 2016). The kelp-dominated communities found within Plymouth Sound are a targeted conservation feature within the Special Area of Conservation (SAC) due to their high levels of biodiversity and rates of primary production (Langston et al. 2003). As *Undaria* has become a major component of macroalgae assemblages at many sites within the SAC (Heiser et al. 2014), it is important to better understand its abundance-distribution patterns within native macroalgal stands and the nature of ecological interactions with native kelps. Examining the role of *Undaria* within kelp forest habitats is particularly valuable, given that these habitats support high levels of biodiversity, provide fuel for inshore foodwebs through high levels of primary productivity and support magnified secondary productivity (Steneck et al. 2002; Smale et al. 2013; Teagle et al. in press). Non-trophic ecological interactions, both facilitative and competitive, can be important drivers of community structure and functioning in kelp forests (Flukes et al. 2014; Bennett et al. 2015). Introduction of NNS into native kelp assemblages can influence ecological interactions and, in turn, alter the structure of macroalgal canopies and their

associated assemblages and overall ecological functioning (e.g. Williams and Smith 2007; Krumhansl and Scheibling 2012).

There is, however, little evidence to suggest that *Undaria* can displace native canopy-forming macroalgal species in invaded habitats from other regions outside its native range. Instead, it has been suggested that *Undaria* is characteristic of an opportunistic pioneer species that can quickly colonise disturbed habitats and attain high abundances in the absence of native canopy formers (South et al. 2015). Indeed, the low competitive ability of *Undaria* on rocky shores has been described by several studies (Valentine and Johnson 2003; Edgar et al. 2004; Raffo et al. 2009; Thompson and Schiel 2012; South et al. 2015; South and Thomsen 2016), with the growth and abundance of *Undaria* in native canopies generally considered to be suppressed by reduced light levels beneath the canopy (Valentine and Johnson 2003). However, the low competitive ability of *Undaria* is not as evident in artificial or highly impacted 'natural' habitats, as in comparison to many native macroalgae it can tolerate wider fluctuations in environmental conditions, which may yield a competitive advantage within these habitats (Farrell and Fletcher 2006; Henkel and Hofmann 2008; James et al. 2015; Bollen et al. 2016). The ability of an invasive species to assimilate into natural habitats is in part dependant on the resident native biota, which in turn influences the availability of key resources such as space and light (Levine and D'Antonio 1999; Arenas et al. 2006). The persistence of dense macroalgal canopies on natural habitats may restrict the ability of *Undaria* to spread from artificial habitats and colonise native communities (Farrell and Fletcher 2006; Thompson and Schiel 2012), despite high abundances and associated propagule pressure from nearby 'strongholds' within artificial habitats. This has yet to be tested, however, within macroalgal canopies on the open coast of northeast Atlantic, which are comprised of multiple native kelp species with divergent life-histories, morphological and functional traits.

Here, we tested the hypothesis that natural rocky reef habitats supporting dense native macroalgal canopies will have more biotic resistance to the invasion of *Undaria* than disturbed or sparse canopies. This hypothesis was examined through three distinct activities: (i) broad-scale field surveys conducted across the Plymouth Sound SAC, to examine relationships between the abundance/cover of *Undaria* and the structure of native canopies; (ii) targeted fine-scale field surveys, where the density, biomass and morphology of *Undaria* sporophytes were quantified and related to the structure of native canopies; and (iii) a short-term canopy-removal experiment, whereby patches of native macroalgae were cleared and colonisation of *Undaria* into disturbed areas was compared with undisturbed canopies. The first two components were observational surveys that examined correlative relationships

between native macroalgae and *Undaria* across different sites and environmental conditions, whereas the third component was manipulative to test the influence of native macroalgal canopies and recruitment on early development of *Undaria* sporophytes.

Methods

Study region

The Plymouth Sound Special Area of Conservation (SAC) is internationally recognised as an ecologically important complex of marine and coastal habitats (Knights et al. 2016). The area supports a wide range of marine habitats and species, many of which are of ecological and socioeconomic importance. Intertidal and shallow subtidal rocky reef habitat is widespread throughout the SAC, typically supporting dense stands kelps and fucoids. The SAC is characterised by strong environmental gradients, in that the outer reefs are more exposed to wave action but less influenced by environmental variability (i.e. fluxes in salinity, turbidity nutrients) driven by fluvial inputs from the Tamar and Plym river systems (Fig. 1). Macroalgal beds within Plymouth Sound and its approaches are dominated by various brown canopy-forming macroalgae, including the native kelps *Laminaria hyperborea*, *L. ochroleuca*, *L. digitata* and *Saccharina latissima*, the fucoid *Himanthalia elongata*, the Tilopteridale *Saccorhiza polyschides* and the non-native kelp *Undaria* (Langston et al. 2003; Heiser et al. 2014).

Field Surveys

To quantify the abundance and distribution of *Undaria* across Plymouth Sound, and to examine how *Undaria* population structure may be influenced by the composition of native macroalgae canopies, two field surveys were undertaken. The population dynamics of *Undaria* are highly seasonal, with the dominant cohort of sporophytes recruiting in spring, growing through summer and senescing in late summer/autumn (Arnold et al. 2016). To capture maximum abundance and biomass values, our field surveys were conducted during the summer months. The first survey was conducted at a 'broad' spatial scale but with lower sampling resolution (i.e. video transects) whereas the second survey was conducted at only two sites but with higher sampling resolution (i.e. quadrat harvesting). For both surveys, the aim was to quantify the abundance and/or cover of large canopy-forming macroalgal species, which were presumed to be competing (to some extent) with *Undaria* for resources (e.g. space, light, nutrients). Hereafter, such species are referred to as the native 'competitors' although competition was inferred and not formally tested here. For the broad-scale video transect survey, eight sites were selected across Plymouth Sound in a

haphazard manner (Fig. 1), based on the presence of shore access and suitable rocky substrate (identified using Google aerial imagery © 2016 and by carrying out site visits). Surveys were completed by snorkel at low slack-tide between 2nd July and 8th August 2016. In order to maintain a similar tidal position on the substrate, large spring and neap tides were avoided, leading to tidal heights between 0.8 m and 1.7 m above chart datum at the time of survey (the maximum tidal range recorded in Plymouth Sound during 2016 was 0.2 to 6.0 m CD). 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. 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. Both horizontal and vertical substrates were included in the video, dependent on the topography at a given site. Following the survey, each video was watched twice. On the first view the video was played in slow motion and the number of *Undaria* (both entire and partial sporophytes) was counted. On the second viewing, the percent cover of other canopy-forming macroalgae (*Laminaria* spp., *S. polyschides*, *S. latissima*) was estimated on 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%]). A quantitative measure of cover for each transect was taken as the median value from the SACFOR scale. Total percent cover of all 'competitors' was calculated as the sum of individual species values, and therefore total percent canopy cover could be over 100%. Although video transects only capture the uppermost layer of the algal assemblage, the approach was deemed to satisfactorily sample the brown macroalgae because (i) the canopy-forming species extend to similar heights above the rocky substrate and do not tend to uniformly cover one another, and (ii) a pilot study indicated that *Undaria* and its native competitors can be observed and identified within mixed stands.

For the fine-scale quadrat survey, two study sites (Firestone Bay and Drakes Island, see Fig. 1) were selected based on the following criteria: (1) a known presence of extensive shallow subtidal (0-2 m depth below chart datum) rocky reef habitat; (2) a lack of point-source anthropogenic impact (e.g. sewage outfall, marina entrance); and (3) confirmed establishment of *Undaria* populations. Both sites were semi-sheltered with respect to wave exposure, with protection from the predominant south-westerly swells offered by both Drakes Island and the Plymouth Sound breakwater (Fig. 1). Firestone Bay was generally characterised by extensive areas of semi-stable boulders and bedrock, interspersed with patches of soft sediment. The rocky substrata at Firestone Bay, although patchy, extends

from the intertidal to depths >20 m (below chart datum), with dense macroalgal assemblages extending to depths of ~3 m. Drakes Island was characterised by sandy substrate with extensive rocky outcrops and platforms, extending from the intertidal to ~5 m depth. In July 2015, both Firestone Bay and Drakes Island were surveyed within a one-week period by SCUBA divers. At both sites, 10 replicate 1 m^2 quadrats were haphazardly placed, at least 2 m apart, within mixed macroalgal canopies at ~0.5-2 m depth (below chart datum). Within each quadrat the abundance of canopy-forming macroalgae (*U. pinnatifida, L. ochroleuca, S. polyschides, S. latissima*) was quantified and the percent canopy cover of each species was estimated visually by a single observer. All *Undaria* sporophytes within each quadrat were harvested by removing beneath the holdfast, placed into separate labelled mesh bags and then returned to the laboratory for processing. On return to the laboratory, the following morphological attributes were measured for each sporophyte: lamina length (cm), lamina width (cm), stipe width (mm), stipe length (cm), sporophyll width (cm), sporophyll fresh weight (g), total sporophyte fresh weight (g) and total sporophyte dry weight (g).

Canopy removal experiment

In March 2015, nine 3 m diameter circular plots were marked at Firestone Bay using rock-bolts secured in the centre of each plot. The plots were established in the low intertidal zone (~0.7 m above chart datum; set up by hand during a spring low tide), ran parallel to the shore, and were separated by a distance of >10 m. Plots were stratified for hard substrata (i.e. bedrock and large boulders) and were established on horizontally-orientated surfaces (rather than on vertical ledges and crevices). Four of the plots were randomly assigned to an experimental treatment, whereby all canopy-forming macroalgae were removed (entire thalli including holdfasts) from the 7 m^2 plot area. The remaining five plots where assigned as controls, where macroalgae assemblages were left unmanipulated. No *Undaria* sporophytes were observed in either the control or removal plots when they were established (which was before the peak recruitment period). After a three-month period, a 1 m^2 quadrat was randomly placed within each plot (excluding the outer 0.5 m edge). The abundance and percent cover of all canopy-forming macroalgae (*Undaria, L. digitata, S. polyschides, S. latissima*) was quantified by a single observer, and five mature *Undaria* sporophytes were randomly selected and harvested for morphological analysis (as outlined above). Total abundance and percent cover of *Undaria* competitors within each quadrat was calculated as the sum of individual species values, and therefore total percent canopy cover could be over 100%.

Data analysis

For the broad-scale field surveys, the relationship between *Undaria* abundance and competitor species cover was tested using generalised linear mixed models (GLMM) with a Poisson distribution to best represent the response data. Site was treated as a random factor, while the cover of competitor species was the fixed effect. Observations were modelled as random effects due to overdispersion in the Poisson distribution (Harrison 2014). A model of *Undaria* abundance and total cover of competitor species was constructed first, and when a significant relationship was identified, individual species effects were assessed as separate terms.

For the fine-scale surveys, the relationship between *Undaria* and competitor species abundance was also assessed using Poisson GLMMs. For *Undaria* cover and biomass linear mixed models (LMM) were fitted to better represent the response data. In all cases site was treated as a random factor, competitor abundance was the fixed factor for the GLMMs, and competitor cover for LMMs. LMMs were assed visually for normality and homogeneity of variance using quantile-quantile plots and predicted versus residual plots. For all models the relationship between *Undaria* and total abundance or cover of competitor species was tested first. When a significant relationship was identified, individual species effects were assessed as separate terms.

The effect of the canopy removal treatment on the abundance (log transformed) and percent cover (arcsin transformed) of kelps was examined with Welch's two sample t-tests. Pairwise comparisons between disturbed and control treatments were carried out for each kelp species separately.

Variability patterns in the morphology of *Undaria* sporophytes for both the fine-scale field surveys and the canopy removal experiment were examined with multivariate permutational analyses of variance (PERMANOVA) and metric multidimensional scaling (mMDS). Morphological attributes of individual plants were treated as a multivariate response and a similarity matrices were constructed from Euclidean distances between square-root transformed data. For visualisation of the data, mMDS was conducted over two dimensions under Kruskal fit scheme 1 using 100 restarts. For the field survey data, variability between site, quadrat (nested within site), and either the total percent cover or abundance of competitors (covariate) was tested by PERMANOVA with 999 permutations under a reduced model with sequential sums of squares. For the canopy removal experiment, the effects of treatment (fixed factor) and plot (random factor nested within treatment) on multivariate morphology was tested with PERMANOVA, using 999 permutations under a reduced model with partial sums of squares. As significant differences in morphology were observed between treatments, SIMPER analysis was used to identify the primary morphological

response variables contributing to the dissimilarity. All univariate statistics were run in R 3.2.2 using base and *lme4* packages (Bates et al. 2015; R Core Team 2015). The *dplyr* package (Wickham and Francois 2015) was used for data manipulation and all univariate graphs were created using *ggplot2* (Wickham 2009) or Sigma Plot v.12. Multivariate procedures were conducted on the PRIMER v.7 software package with the PERMANOVA add-on (Clarke et al. 2014).

Results

Field surveys

From the broad-scale field surveys, the total percent cover of competitors showed a significant negative relationship with *Undaria* abundance (Table 1, Fig. 2A). When separating by competitor species this relationship was shown to be due to a mixture of all species (Table 1). Scatterplots of *Undaria* abundance and each competitor species alone identified some relationship between *Undaria* abundance and *Laminaria* spp., as *Undaria* abundance generally decreased with increasing coverage of *Laminaria* spp. (Fig. 2B). However, no clear relationships between the spatial coverage of the other main competitors, *Saccorhiza polyschides* and *Saccharina latissima*, and the abundance of *Undaria* were observed (Fig. 2C and 2D).

For the fine-scale surveys at Drakes Island and Firestone Bay, the abundance and percent cover of kelp species varied between sites (Fig. 3). *Undaria* was higher in abundance and percent cover at Firestone Bay, and the main competitor at both sites in terms of abundance and percent cover was *L. ochroleuca* (Fig. 3). The total abundance of competitors showed a significant negative relationship with *Undaria* abundance (Table 2, Figure 4A). When separating by competitor species this relationship was shown to be primarily due to *L. ochroleuca* abundance, with no significant effect from *S. latissima* or *S. polyschides* (Table 2). The total percent cover of competitors also exhibited a significant negative relationship with *Undaria* percent cover (Table 2, Figure 4B). This was due to a combination of *L. ochroleuca* and *S. latissima* percent cover, with no significant effect from the percent cover of *S. polyschides* (Table 2). Similarly, the total biomass of *Undaria* was negatively related to the percent cover of native competitors (Table 2, Figure 4C) which, when broken down by species, was primarily related to the percent cover of *L. ochroleuca.* The morphology of *Undaria* significantly differed between sites ($F_{(1,46)}$ = 6.05, p = 0.022), however neither the total abundance ($F_{(1,46)}$ = 0.35, p = 0.912) nor percent cover ($F_{(1,46)}$ = 1.08, p = 0.385) of competitors had any effect on *Undaria* morphology (Figure 5).

Canopy removal experiment

Three months following the canopy removal treatment, *Undaria* was present in both treatment and control plots (Fig. 6). However, the average number of sporophytes was 5.6 times greater in the removal plots compared with controls and the percent cover was 3.3 times greater in removal plots (Fig. 6); these differences between plots were statistically significant. With regards to other canopy-forming macroalgae, *L. digitata* was not recorded in the removal plots but was the dominant species (by cover) in the control plots (Fig. 6); both abundance and cover of *L. digitata* were significantly greater in control plots. *S. latissima* was more abundant but covered less area in the removal plots, but these differences were non-significant (Fig. 6). *S. polyschides* has slightly higher abundance and cover values in the removal plots but again variability between treatments was non-significant (Fig. 6). An MDS plot based on the multivariate morphological characteristics of *Undaria* suggested that sporophytes in removal plots were distinct from those in control plots (Fig. 7); a PERMANOVA test indicated that differences between treatments were significant ($F_{(1,8)} = 2.50$, $p = 0.012$). Further examination of morphological variables showed that the dissimilarity between treatments was primarily due to total fresh weight, sporophyll weight and lamina length of sporophytes , which were, on average, all greater in removal plots than those in control plots (Table 3). Additionally, sporophytes from removal plots had greater average values for total sporophyte length, stipe width, sporophyll width and total dry weight compared with those in control plots, but these differences were not important contributors to the observed dissimilarity.

Discussion

The study supports our principal hypothesis that natural habitats supporting dense native macroalgal canopies have more biotic resistance to invasion by *Undaria* than disturbed or sparse canopies. Across the field surveys, significant negative relationships between *Undaria* abundance, cover and biomass and the density or cover of native macroalgal canopies were observed. Competition for light, nutrients and space may strongly influence the recruitment, germination, survivorship and growth of *Undaria* (Floc'h et al. 1996; Valentine and Johnson 2003; Thompson and Schiel 2012; Morelissen et al. 2013). Decreased light availability beneath macroalgal canopies was likely to have been particularly important in supressing the recruitment and growth of *Undaria*, as dense *Laminaria* canopies can reduce Photosynthetically Active Radiation (PAR) reaching the reef surface by >90% (Pedersen et al. 2014). Due to intense shading, PAR levels reaching the reef surface below *Laminaria* canopies may be as low as ~60 µmol photons m^{-2} s^{-1} during the daytime

(Pedersen et al. 2014) which, although not completely restrictive, is likely to fall below optimal light levels required for sporophyte development and growth (Saito 1975; Campbell et al. 1999; Morelissen et al. 2013; Watanabe et al. 2014). Indeed, Gao et al. (2014) showed that photosynthesis, growth and maturation of *Undaria* sporophytes were enhanced when grown under reduced canopy density, as a result of increased light penetration. As such, we suggest that the negative relationships observed between *Undaria* and native competitors are largely due to competition for light and alterations to the light environment caused by the presence of large native canopy formers. An alternative possible mechanism could be that the abiotic conditions which favour *Undaria* are divergent to those that favour *Laminaria* spp., so that our observed patterns simply reflect differences in ecophysiological tolerances for light, wave exposure, physical disturbance or some other variable. However, given that (i) *Laminaria* spp. persist across a wide range of environmental conditions in Plymouth Sound, from extremely wave exposed to wave sheltered and from highly disturbed (e.g. marinas) to relatively pristine habitats, (ii) previous work has indicated overlapping environmental requirements between *Undaria* and *Laminaria* spp. (Yesson et al. 2015), and (iii) competitive release following canopy removal (see below) increased *Undaria* recruitment and growth, we suggest that ecological interactions were important drivers of observed patterns.

As with previous work in Australia (Valentine and Johnson 2003) we suggest that competition for space was less important than for light, as there was ample reef surface available for attachment of *Undaria* propagules and sporophytes, given that the cover of understorey species was generally low (less than ~40%, authors pers. obs.) and the number of kelp holdfasts attached to the reef was also quite low (i.e. the total abundance of all competitors was generally <10 inds.m^{-2}). Similarly, although *Undaria* is susceptible to low nutrient availability due to limited storage capacity (Dean and Hurd 2007), nutrient concentrations within Plymouth Sound are unlikely to be limiting during the spring-to-early-summer growth season for *Undaria*. To expand, the average surface seawater concentrations for nitrate and phosphate in March-June exceed 2 µM and 0.2 µM, respectively (Smyth et al. 2010, Western Channel Observatory data), which surpass requirements for *Undaria* growth (Wu et al. 2004; Dean and Hurd 2007), and the study area also receives significant nutrient loading from nearby estuaries (Langston et al. 2003). While nutrients may become limiting by late summer, with consequent inter-specific competition for resources perhaps becoming important, the relationships described here were unlikely to have been driven by competition for nutrients

The density and percent cover of *Laminaria* spp. (*L. hyperborea* ,*L. digitata* and *L. ochroleuca*) was consistently an important predictor of *Undaria* abundance, cover and

biomass. *L. hyperborea* and *L. ochroleuca* are long-lived perennial kelps (both can exceed 6 years of age within Plymouth Sound, Smale unpublished data), which form rigid stipes and exhibit upright, stipitate growth forms with large lamina that create dense canopies. As such, the competitive pressure exerted upon understorey macroalgae is likely to be intense, and a high abundance and cover of these species was related to low abundance, cover and biomass of *Undaria*. Although it is shorter-lived and forms a more flexible stipe, *L. digitata* also forms dense monospecifc canopies and its thick, extensive laminae are likely to restrict light penetration to the underlying substrate. In contrast, the relationship between *Undaria* and *Saccharina latissima* was weaker and less consistent. *S. latissima* is a shorter-lived perennial species (generally 2-3 years old in Plymouth Sound, Smale, unpublished data) with a short, flexible stipe that exhibits a prostrate growth form. It is plausible that *S. latissima* exerts less competitive pressure on *Undaria* for three reasons: first, it lies flat on the seabed without forming an elevated canopy and, as such, may allow more light to reach *Undaria* gametophytes and young sporophytes attached the reef. Second, it can function as an early successional species under moderately wave exposed conditions, such as at Drakes Island, where its sporophytes are typically relatively small and short-lived (Leinaas and Christie 1996). Third, it is more patchily distributed and is often found attached to semi-stable substrates in more wave-sheltered environments, where it generally does not form continuous, dense monospecific stands. As such, *S. latissima* may exert less pressure on resources such as space and light and allow for recruitment and growth of *Undaria*.

We did not, however, detect any major influence of the abundance or cover of *S. polyschides* on *Undaria.* This could be due to the fact that like *Undaria*, *S. polyschides* is a pseudo-annual species, which develops young sporophytes in spring that grow rapidly throughout summer before senescing during the autumn/winter period (Norton and Burrows 1969). In contrast to established perennial species (i.e. *L. ochroleuca, L. hyperborea, L. digitata* and *S. latissima*) *S. polyschides* does not produce large canopy-forming sporophytes during the spring period of recruitment and growth of *Undaria* sporophytes and is unlikely to exert strong competitive pressure, at least until late summer when both species have attained maximum size and may compete for resources. Unravelling the strength and direction of competitive interactions requires formal testing, but it is likely that inter-specific differences in life histories and morphological/functional traits between native kelp species will influence the magnitude of competitive superiority over *Undaria* and, as such, variability in the composition of macroalgal stands will influence their biotic resistance to invasion. For example, if *S. polyschides* becomes more abundant in the future in response to increased storminess and temperature, as has been predicted (Hiscock et al. 2004; Smale et al. 2013), the invasibility of the wider macroalgal canopy may increase relative to a canopy dominated

by *Laminaria* spp. Variability in biotic resistance driven by differences in canopy composition and cover has been observed in macroalgal beds in Australasia (Valentine and Johnson 2004; Thompson and Schiel 2012; South and Thomsen 2016), and may be of increasing importance in this region in the near future.

As the presence of canopy-forming macroalgae can reduce light and space availability for understory macroalgal species (Wernberg et al. 2005; Pedersen et al. 2014), physical disturbance to the canopy can reduce competitive pressure for these resources and facilitate the recruitment and growth of understory species (Goodsell and Connell 2005; Flukes et al. 2014). Canopy removal may result from both physical (i.e. storm damage) (Smale and Vance 2016) or biological (i.e. grazing) (Rinde et al. 2014; Ling et al. 2015) agents of disturbance. *Undaria* has been described as an opportunistic species, and evidence of disturbance facilitating its establishment into native communities has been reported (Valentine and Johnson 2003; Edgar et al. 2004; Valentine and Johnson 2004; Thompson and Schiel 2012; South and Thomsen 2016). However, the importance of disturbance on *Undaria*'s colonisation success may be dependent on the recipient biota, the spatial and temporal disturbance regime, and the scale of observation (Thompson and Schiel 2012; Morelissen et al. 2016).

Here, canopy removal resulted in a >3 and >5-fold increase in the cover and abundance of *Undaria* sporophytes, respectively. Given that the majority of mature *Undaria* sporophytes are present in early-mid summer in the UK (Heiser et al. 2014; Minchin and Nunn 2014; Arnold et al. 2016), it is very likely that the recruiting sporophytes developed from an existing gametophyte 'seedbank' attached to the reef surface. Gametophytes can remain viable for up to 24 months if conditions for sporophyte development are not favourable (Stuart 2003; Choi et al. 2005) and, as such, disturbance to the canopy likely provided inactive gametophytes with the adequate light levels needed to stimulate sporophyte development (Kim and Nam 1997 ; Choi et al. 2005). Morelissen *et al.,* (2013), conducted a study to evaluate how the development of the microscopic life stages of *Undaria* was affected by irradiance and nutrient availability. Their results revealed that under low irradiance, gametophyte growth was stalled and zygotes did not progress to the sporophyte stage. These results suggest that, with the support of field studies from Valentine and Johnson (2003), Thompson and Schiel (2012) and the current study, that the development of the microscopic stages of *Undaria* may be limited by the presence of dense, light-limiting macroalgae canopies. It should be noted that our manipulative experiment was short-term and small-scale, and longer-term multi-site experiments are needed to determine the nature of interactions between *Undaria* and native canopy formers.

In our fine-scale field survey we did not observe any clear relationships between the morphology of *Undaria* sporophytes and the abundance or cover of competitors. We did, however, observe significant differences in morphology between Drakes Island and Firestone Bay, suggesting the importance of local environmental conditions in structuring *Undaria* populations. The influence of water flow dynamics, exposure to waves and tides, and light availability on *Undaria* growth and morphology has been examined elsewhere (Castric-Fey et al. 1999; Shibneva et al. 2013) and considerable morphological plasticity in response to environmental conditions is common in kelp species (Fowler-Walker et al. 2005; Wernberg and Thomsen 2005). The populations at Drakes Island were subjected to greater water motion related to both tidal flows and wave action, which may explain difference in morphology between sites. The lack of any observable relationship between competitors and the morphology of *Undaria* was, to some extent, surprising as previous work on farmed populations has shown that *Undaria* may allocate more resources to stipe growth in response to intense competition, in order to elevate its position in the canopy and attain more light (Gao et al. 2014). In contrast, *Undaria* did exhibit clear morphological responses to the substantial reduction in competitive pressure following canopy removal. In disturbed plots, *Undaria* sporophytes had longer lamina and greater biomass (of both entire sporophytes and sporophylls).Clearly, the ecological performance of recruiting *Undaria* sporophytes is enhanced when interspecific competition from canopy-forming macroalgae is minimal, as more energy is available for growth of the thallus and the development of reproductive structures.

Previous studies have found little evidence that *Undaria* can displace native macroalgae (Forrest and Taylor 2002; Raffo et al. 2009; Thompson and Schiel 2012) although there is some evidence to suggest that it can alter the structure of associated communities (Casas et al. 2004; Farrell and Fletcher 2006; Arnold et al. 2016). Indeed, some studies have suggested that rather than replacing native macroalgae and the species they support, *Undaria* may instead contribute to the complexity, biodiversity, and productivity of invaded temperate reef systems (Irigoyen et al. 2011; South et al. 2015; Tait et al. 2015). The nature and strength of its impacts and influence on native biota appear to be highly context-specific, and depend largely on the local environmental conditions and composition of recipient native communities. It is clear that since its introduction in the early 1990s, *Undaria* has steadily spread along the UK coastline and, can be found as a conspicuous and important component of macroalgal communities within natural habitats. Better understanding of the ecological interactions between native and non-native habitat-forming species is needed to inform management, and future studies should examine the impacts of *Undaria* through long-term field-based experiments using manipulative or BACI (before after control impact)

designs, as has been achieved in Australasia (Forrest and Taylor 2002; Valentine and Johnson 2005; South et al. 2015; South and Thomsen 2016).

Our results suggest that the biotic resistance of macroalgae assemblages to invasion by *Undaria* is likely to vary spatially, depending on the identity and abundance of competing native species and environmental context. Overall, the presence of dense *Laminaria* canopies is likely to limit, but not prevent, assimilation of *Undaria* into native communities, due to the superior competitive ability of the large, stipitate, perennial kelps. Even so, *Undaria* sporophytes were still recorded within dense *Laminaria* canopies, suggesting that disturbance to the canopy is not a prerequisite for successful invasion. Other native macroalgae are likely to exert weaker competitive pressure, perhaps due to their life history or morphology. It should be noted that the majority of our findings were based on observational surveys, which are correlative in nature and cannot determine causation. Clearly, long-term manipulative experiments are required to fully unravel the strength and direction of ecological interactions between *Undaria* and native canopy-forming macroalgae. We suggest that *Undaria* is likely to remain a conspicuous component of macroalgal assemblages on rocky reefs in Plymouth Sound and elsewhere, given its widespread distribution and generally high abundances in nearby artificial habitats (Fletcher and Farrell 1999; Farrell and Fletcher 2006; Heiser et al. 2014; Minchin and Nunn 2014). Perhaps the most effective approach to limiting its spread into native communities is to maintain and promote favourable environmental conditions for the persistence of dense, highly productive *Laminaria*-dominated canopies that provide biotic resistance to invasion.

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Table 1: GLMMs identifying the influence of competitor species on the abundance of *Undaria* from the broad-scale survey. Total = total percent cover of comeptitor species. SL = *Saccharina latissima,* Lam = *Laminaria spp.,* SP = *Sacchorhiza polyschides*. Significance of terms ($p < 0.05$) is shown by an asterisk (*).

Coefficients	Estimate	Std. Error	z	p	
Intercept	5.686	0.257	22.12	< 0.001	*
Total	-1.953	0.332	-5.89	< 0.001	*
Intercept	5.630	0.273	20.66	< 0.001	*
Lam	-1.927	0.409	-4.71	< 0.001	*
SP	-1.939	0.354	-5.48	< 0.001	*
SL	-1.625	0.649	-2.50	0.012	*

Table 2: GLMMs and LMMs identifying the influence of competitor species on the abundance, percent cover and biomass of *Undaria* from the fine-scale survey. Percent cover of competitors was used as a proxy for the biomass analysis. Total = total abundance or percent cover of comeptitor species. SL = *Sacchorina lattismia,* LO = *Laminaria ochroleuca,* SP = *Sacchoriza polyschides*. Significance of terms ($p < 0.05$) is shown by an asterisk (*).

Coefficients	Estimate	Std. Error	z	p	
Abundance (GLMM)					
Intercept	1.703	0.444	3.83	< 0.001	*
Total	-0.091	0.041	-2.21	0.027	*
Intercept	1.747	0.573	3.05	0.002	*
SL	-0.229	0.121	-1.89	0.059	
LO	-0.097	0.042	-2.33	0.020	*
SP	0.066	0.183	0.36	0.720	

Coefficients	Estimate	Std. Error	t	p	
Percent cover (LMM)					
Intercept	1.072	0.201	5.33	0.001	*
Total	-0.661	0.184	-3.59	0.002	*
Intercept	1.082	0.246	4.40	0.029	*
SL	-0.917	0.284	-3.23	0.005	*
LO	-0.702	0.191	-3.68	0.002	*
SP	-0.359	0.276	-1.30	0.213	

Coefficients	Estimate	Std. Error	t	p	
Biomass (LMM)					
Intercept	1.594	0.449	3.55	0.002	*
Total	-1.020	0.470	-2.17	0.044	*
Intercept	1.587	0.485	3.27	0.010	*
SL	-0.938	0.701	-1.34	0.227	
LO	-1.248	0.529	-2.36	0.032	*
SP	-0.390	0.770	-0.51	0.620	

838 **Table 3:** SIMPER analysis to determine the morphological attributes contributing most to the
839 observed dissimilarity in *Undaria* morphology between control and canopy removal plots.
840 The 3 morphological attributes contributing most to the observed dissimilarity between
841 treatments are shown. Average values (square-root transformed) in control and removal
842 plots, average dissimilarity, dissimilarly/standard deviation, and the percentage contribution
843 to total dissimilarity are presented.

844

Attribute	Control	Removal	Av. Diss.	Diss./SD	Contrib. (%)
Fresh weight	7.45	9.93	5.17	1.47	32.46
Sporophyll weight	1.78	3.18	3.34	1.56	21.01
Lamina length	6.73	7.51	1.81	1.32	11.00

845

Figure legends

Figure 1: Map of study area. Sites used for the broad-scale survey are indicated in grey, the 2 sites sampled for fine-scale survey work (i.e. Drakes Island (B) and Firestone Bay (A)) are shown in black. Inset map shows position of the study area within the wider context of the southwest UK**.**

Figure 2: Relationship between *Undaria* abundance and total percent cover of competitors (a), *Laminaria* spp. (b), *Sacchorina lattismia* (c) and *Sacchoriza polyschides* (d) from broad-scale surveys. Points show raw data from each transect. Plotted lines of fitted values from GLMM.

Figure 3: Average abundance (A) and percentage cover (B) of kelp species recorded in quadrats at Drakes Island and Firestone Bay. Bars show mean values from 10 replicate $1m^2$ quadrats (± SE).

Figure 4: The total abundance (A) percent cover (B) and total biomass (C) of *Undaria* in relation to the abundance (A) and percent cover (B&C) of macroalgal competitors from fine-scale surveys. Points show raw data from each quadrat. Plotted lines of fitted values for each site from GLMM (A) and LMMs (B&C).

Figure 5: Metric MDS plot indicating variability in morphology (multivariate response based on 7 individual uncorrelated desciptors) of *Undaria* sporophytes at each site. Bubble sizes represent the total percent cover (pTot shown in A) and total abundance (nTot shown in B) of competitors in the quadrat from which the *Undaria* sporophyte was sampled.

Figure 6: Average abundance (A) and percentage cover (B) of kelp species recorded in canopy removal and control plots at Firestone Bay, 3 months after the experiment was initiated. Bars show mean values from 4 replicate canopy removal plots and 5 unmanipulated control plots (± SE). Significant differences between treatments ($P<0.05$) are indicated with an asterisk.

Figure 7: Metric MDS plot indicating variability in morphology (multivariate response based on 7 individual uncorrelated desciptors) of *Undaria* sporophytes within each of the 4 canopy removal plots and the 5 control plots. Ordination is based on a similarity matrix constructed from Euclidean distance measures between square-root transformed data.

876

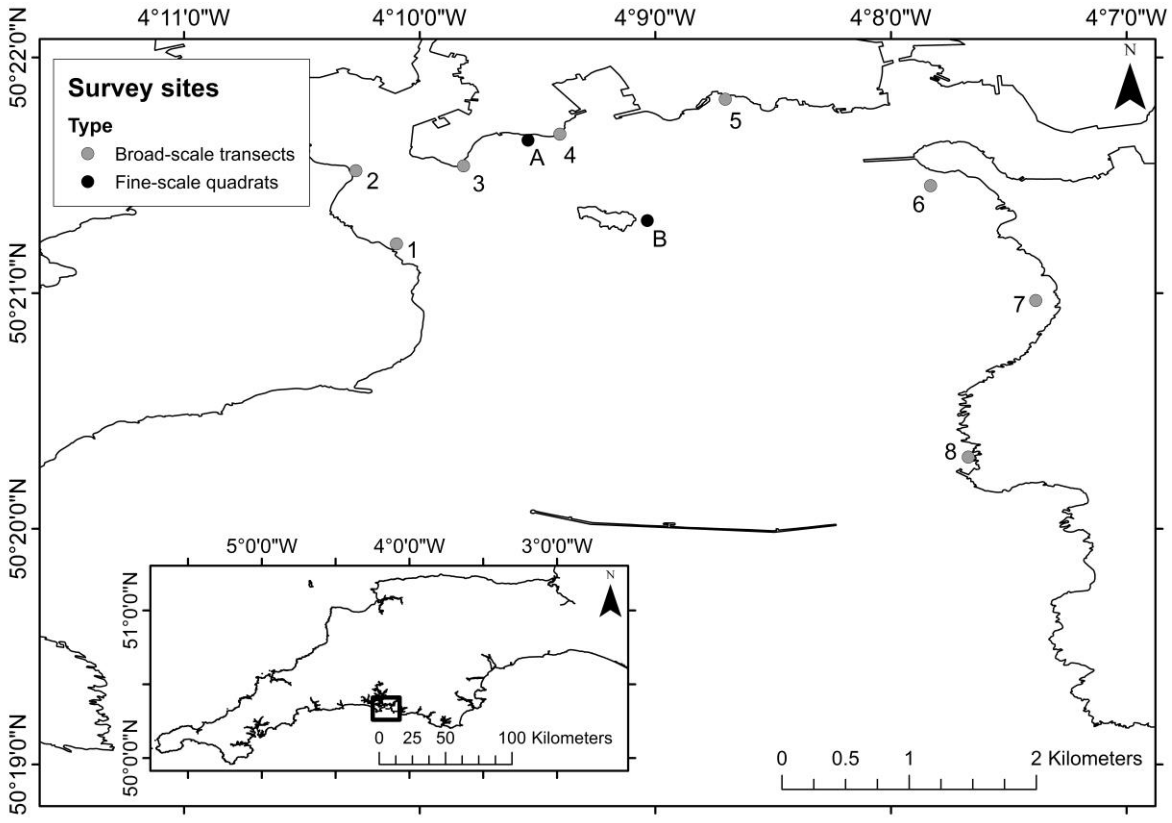
4°11'0"W
4°10'0"W
4°9'0"W
4°8'0"W
4°7'0"W
50°22'0"N
50°21'0"N
50°20'0"N
50°19'0"N
Survey sites
Type
Broad-scale transects
Fine-scale quadrats
1
2
3
4
5
6
7
8
A
B
N
0 0.5 1 2 Kilometers
5°0'0"W
4°0'0"W
3°0'0"W
51°0'0"N
50°0'0"N
0 25 50 100 Kilometers

Fig. 1

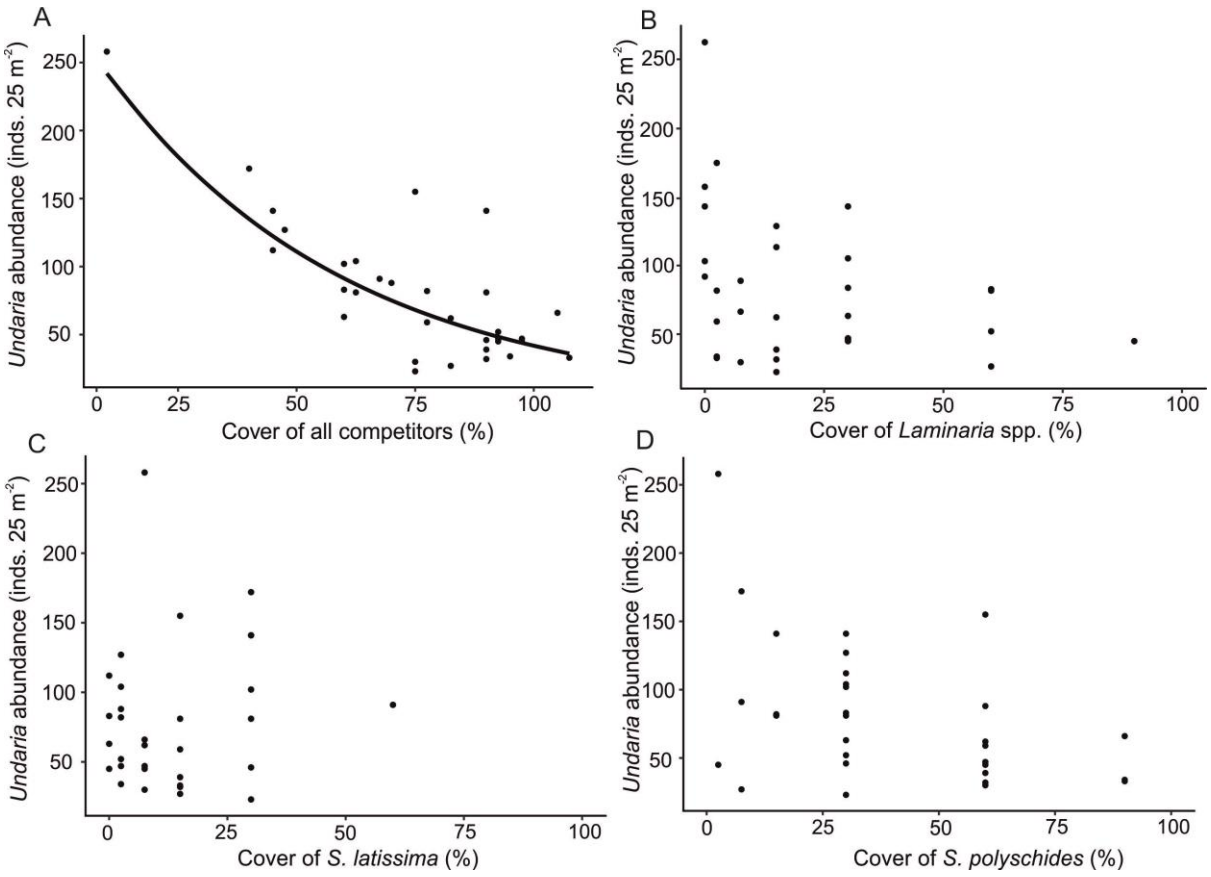
A
B
C
D
Undaria abundance (inds. 25 m-2)
Cover of all competitors (%)
Cover of Laminaria spp. (%)
Cover of S. latissima (%)
Cover of S. polyschides (%)
0
25
50
75
100
50
100
150
200
250

Fig. 2

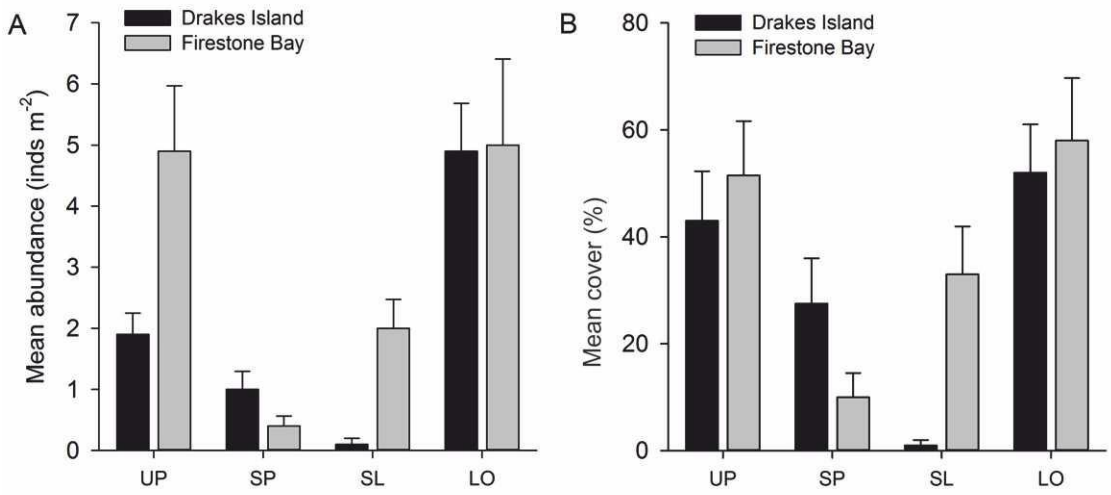
A
Drakes Island
Firestone Bay
Mean abundance (inds m-2)
0
1
2
3
4
5
6
7
UP
SP
SL
LO
B
Drakes Island
Firestone Bay
Mean cover (%)
0
20
40
60
80
UP
SP
SL
LO

Fig. 3

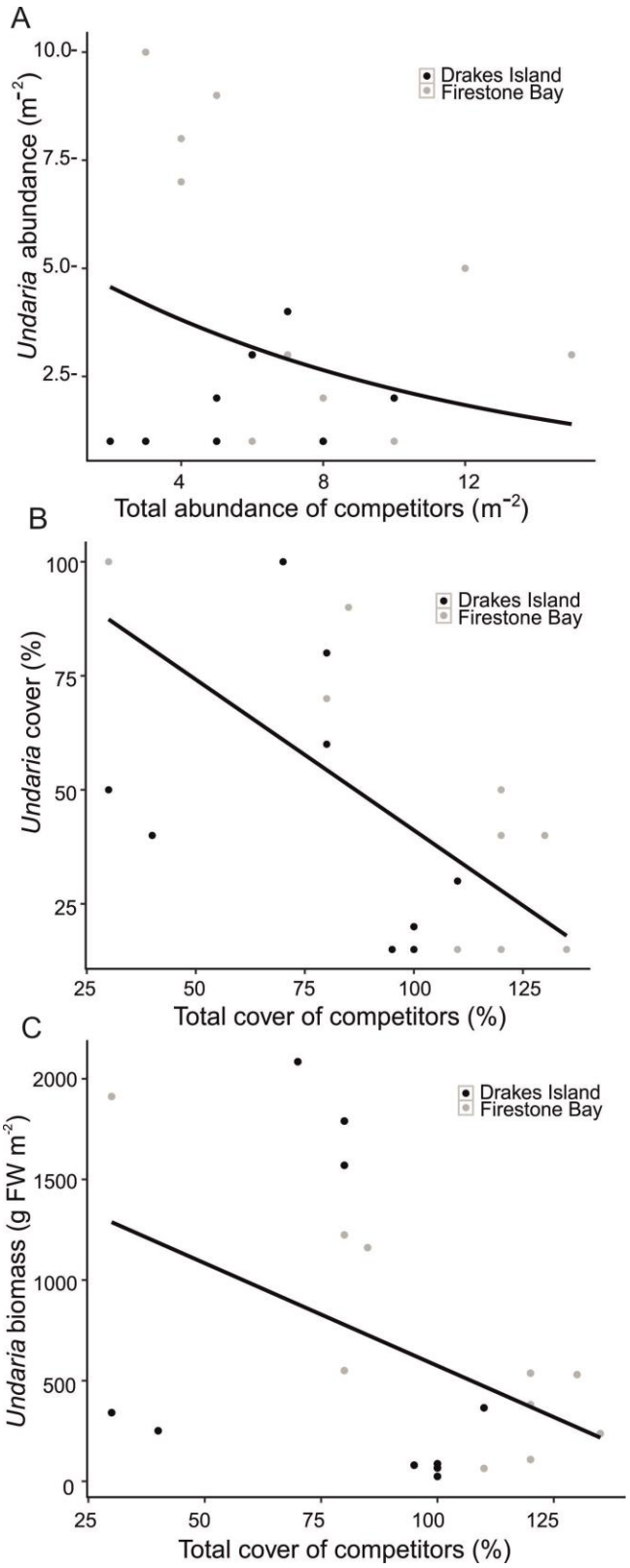
A
10.0
7.5
5.0
2.5
Undaria abundance (m-2)
Drakes Island
Firestone Bay
4
8
12
Total abundance of competitors (m-2)
B
100
75
50
25
Undaria cover (%)
Drakes Island
Firestone Bay
25
50
75
100
125
Total cover of competitors (%)
C
2000
1500
1000
500
0
Undaria biomass (g FW m-2)
Drakes Island
Firestone Bay
25
50
75
100
125
Total cover of competitors (%)

Fig. 4

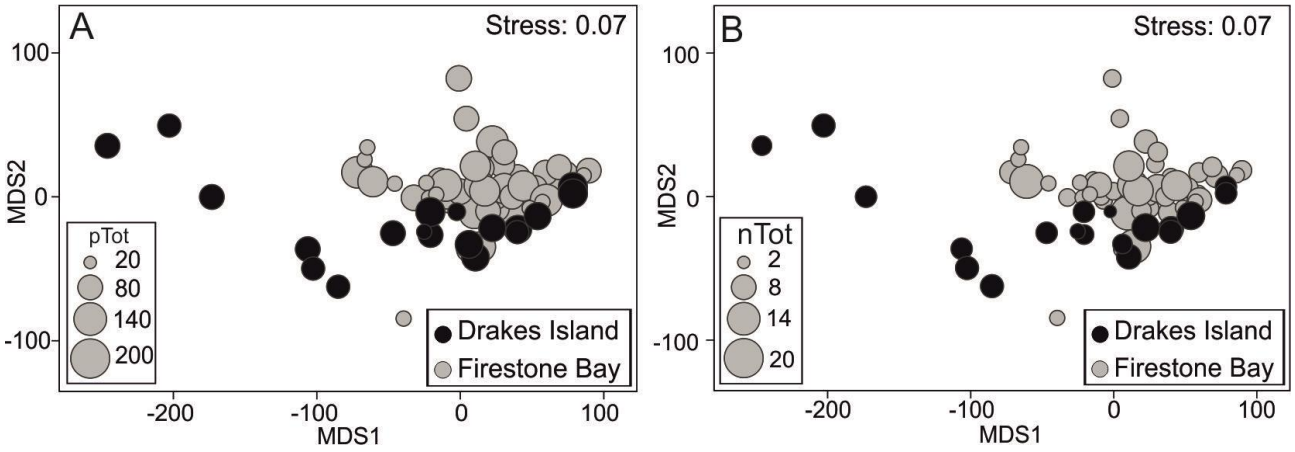
A
Stress: 0.07
100
0
-100
MDS2
pTot
20
80
140
200
Drakes Island
Firestone Bay
-200
-100
0
100
MDS1
B
Stress: 0.07
100
0
-100
MDS2
nTot
2
8
14
20
Drakes Island
Firestone Bay
-200
-100
0
100
MDS1

Fig. 5

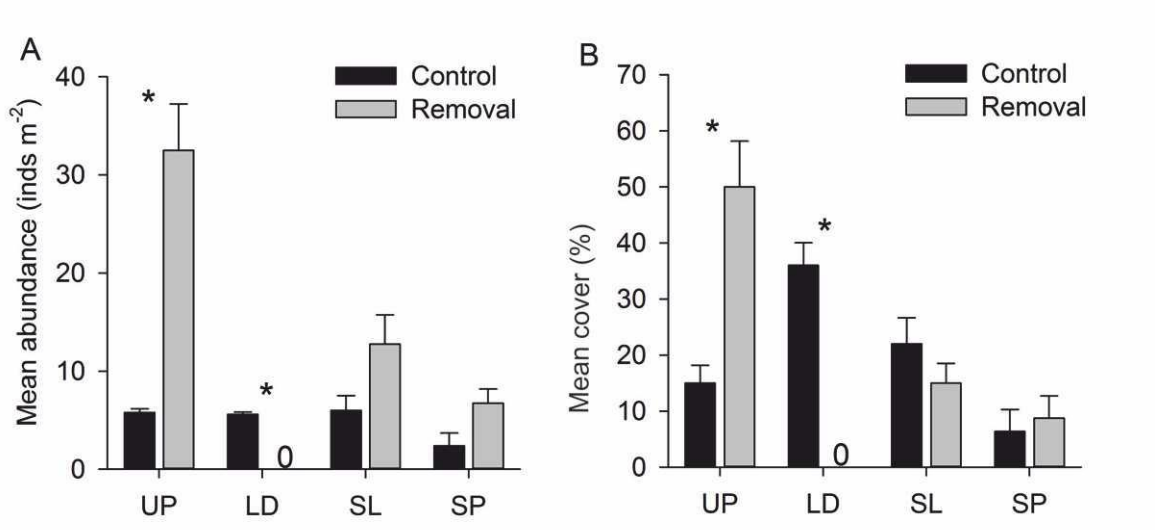
A
Mean abundance (inds m-2)
40
30
20
10
0
Control
Removal
*
*
0
UP
LD
SL
SP
B
Mean cover (%)
70
60
50
40
30
20
10
0
Control
Removal
*
*
0
UP
LD
SL
SP

Fig. 6

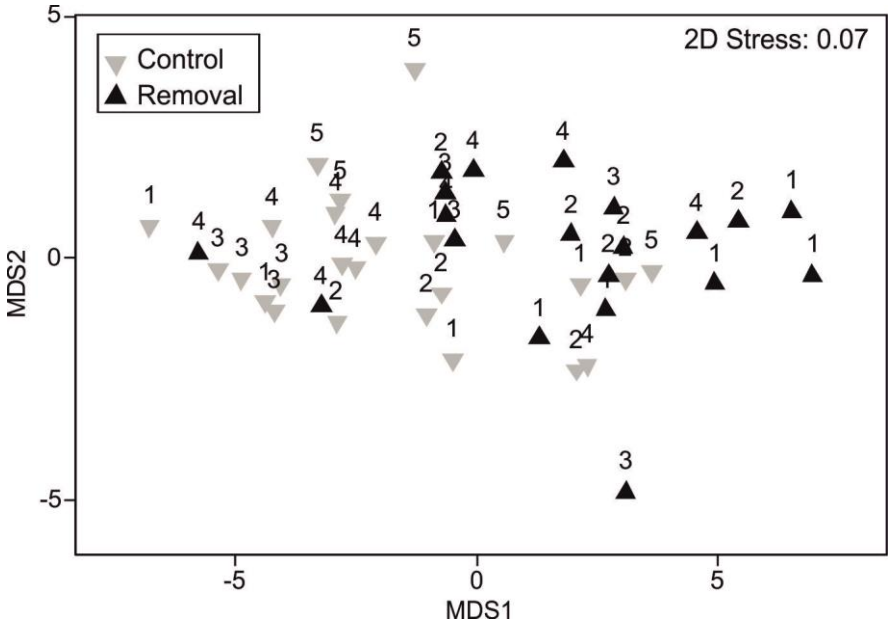

Fig. 7