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The structure of biogenic habitat and epibiotic assemblages associated with the global invasive kelp *Undaria pinnatifida* in comparison to native macroalgae

Matthew Arnold[1], Harry Teagle[1], Matthew P. Brown[2], Dan A. Smale[1*]

[1]Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

[2]School of Marine Science and Engineering, Plymouth University, Drake Circus, Plymouth, PL4 8AA, UK

*Corresponding author: Email: dansma@mba.ac.uk Tel:+44 1752 633354

Abstract: Kelp forests dominate temperate and polar rocky coastlines and represent critical marine habitats because they support elevated rates of primary and secondary production and high biodiversity. A major threat to the stability of these ecosystems is the proliferation of non-native species, such as the Japanese kelp *Undaria pinnatifida* ('Wakame'), which has recently colonised natural habitats in the UK. We quantified the abundance and biomass of *U. pinnatifida* on a natural rocky reef habitat over 10 months to make comparisons with three native canopy-forming brown algae (*Laminaria ochroleuca, Saccharina latissima,* and *Saccorhiza polyschides*). We also examined the biogenic habitat structure provided by, and epibiotic assemblages associated with, *U. pinnatifida* in comparison to native macroalgae. Surveys conducted within the Plymouth Sound Special Area of Conservation indicated that *U. pinnatifida* is now a dominant and conspicuous member of kelp-dominated communities on natural substrata. Crucially, *U. pinnatifida* supported a structurally dissimilar and less diverse epibiotic assemblage than the native perennial kelp species. However, *U. pinnatifida*-associated assemblages were similar to those associated with *Saccorhiza polyschides*, which has a similar life history and growth strategy. Our results suggest that a shift towards *U. pinnatifida* dominated reefs could result in impoverished epibiotic assemblages and lower local biodiversity, although this could be offset, to some extent, by the climate-driven proliferation of *L. ochroleuca* at the poleward range edge, which provides complex biogenic habitat and harbours relatively high biodiversity. Clearly, greater understanding of the long-term dynamics and competitive interactions between these habitat-forming species is needed to accurately predict future biodiversity patterns.

Keywords: non-native species, epifauna, biodiversity, benthic ecology, temperate reefs, macroalgae

Introduction

Habitat-forming species (HFS) can be considered ‘ecological engineers’ (sensu Jones et al., 1994), as they directly and indirectly alter environmental conditions for other organisms (Thomsen et al., 2010; Angelini et al., 2011). Within benthic marine ecosystems, HFS play a key role in determining the structure of proximal communities by influencing biological and physiological factors and providing key resources (e.g. Wernberg et al., 2005; Messmer et al., 2011; Smale et al., 2011). These HFS, which include large macroalgae, seagrasses and reef-building corals, can harbour diverse assemblages in an otherwise homogenous wider environment, and can also initiate ‘habitat cascades’ by providing biogenic structure for additional secondary habitat providers (e.g. epiphytes, see Thomsen et al., 2010). The identities, distributions and local abundances of marine HFS are, however, changing in response to rapid environmental change and human activities (e.g. Smale and Wernberg, 2013; Vergés et al., 2014). As HFS alter the immediate physical environment and mediate biological interactions, shifts in their identity, abundance or distribution are likely to affect entire communities and therefore warrant detailed investigation.

Kelps and other large brown macroalgae dominate shallow rocky reefs along much of the world’s temperate and polar coastline (Steneck et al., 2002; Smale et al., 2013). Kelp forests exhibit high levels of primary productivity (Mann, 1973; Krumhansl and Scheibling, 2012), form an important component of inshore food webs (Leclerc et al., 2013), and provide habitat for a wide range of associated flora and fauna (Anderson et al., 2005; Smale et al., 2013). The ecological structure and functioning of kelp forest ecosystems is, however, being impacted by a range of environmental change stressors, including oceanic warming (Wernberg et al., 2011; Vergés et al., 2014), extreme climatic events (Byrnes et al., 2011; Wernberg et al., 2013), reduced water quality (Gorgula and Connell, 2004; Moy and Christie, 2012), altered trophic interactions (Tegner and Dayton, 2000; Ling et al., 2009) and the spread of non-native species (Saunders and Metaxas, 2008). Such stressors can cause shifts in the distributions and/or relative abundances of HFS within kelp forests (Smale and Wernberg, 2013; Smale et al., 2015), which can have knock-on effects for the wider community (Ling, 2008; Wernberg et al., 2013). As such, documenting changes in the distribution and abundance of HFS and examining their role in structuring communities is a crucial step towards understanding and predicting the effects of rapid environmental change.

Undaria pinnatifida (Harvey) Suringar 1873 (also known as Wakame or Japanese Kelp), which originates in the temperate northwest Pacific, is widely regarded as one of the most invasive marine species on Earth (listed in the '100 of the World's Worst Invasive Alien Species', Invasive Species Specialist Group, IUCN 2013), having established populations in the northeast Atlantic (Castric-Fey et al., 1993; Fletcher and Manfredi, 1995), northern Mediterranean (Cecere et al., 2000), southwest Atlantic (Casas and Piriz, 1996), southern Pacific (Hay and Luckens, 1987) and the eastern Pacific (Silva et al., 2002). *U. pinnatifida* was first recorded in UK waters in the Hamble estuary in 1994 (Fletcher and Manfredi, 1995) and has since spread along the south coast of England (Heiser et al., 2014). More recently *U. pinnatifida* has been recorded in Wales (Wood et al., 2015) and Northern Ireland (Minchin and Nunn, 2014), indicative of a northward extension through Europe. *U. pinnatifida* was first recorded within the Plymouth Sound Special Area of Conservation (SAC) in 2003 and has since been recorded at multiple sites and on natural and artificial substrata, from the low intertidal zone to depths of ~5m (below chart datum) (Heiser et al. 2014, Smale pers obs).

The mechanism of the initial arrival of *U. pinnatifida* into Europe is thought to be aquaculture, as it was associated with Pacific oysters (*Crassostrea gigas*), but has since been spread through intentional cultivation and, more recently, shipping traffic (Minchin and Nunn, 2014). *U. pinnatifida* populations have predominantly established within artificial habitats, such as marinas, but in some cases *U. pinnatifida* has subsequently colonised nearby natural rocky reef habitat (Heiser et al., 2014) where it may then function as a HFS and interact with native HFS. Native and non-native kelps may support a high diversity of epibiota, including epiphytic algae and a myriad of invertebrate taxa. It may be however, that *U. pinnatifida* supports an impoverished or distinct epibiont assemblage, due to differences in, for example, life-history between it and the native kelps (i.e. *U. pinnatifida* is an annual species whilst the native kelps are longer-lived perennial species), as well as differences in biogenic habitat structure (i.e. morphology of the stipe and lamina) and growth strategies (Smale et al., 2013).

There are very few marine regions around the world that have not been affected by non-native invasions (Molnar et al., 2008), but whether non-native species are 'drivers' or 'passengers' of environmental change, and to what degree they cause biodiversity loss, has been hotly debated (Gurevitch and Padilla, 2004; MacDougall and Turkington, 2005). Nevertheless, certain species have clear ecological or socioeconomic impacts when established outside of their native range (Simberloff, 2011). For example, the cost of non-native invasive species (both marine and terrestrial) has been estimated at £1.7 billion per year in the UK alone (Williams et al., 2010). Despite this, the ecological role and impact of non-native species in coastal marine ecosystems are relatively understudied (Thomsen et al., 2014), which poses a major challenge for management and conservation efforts. For example, *U. pinnatifida* has been listed in the top ten ‘worst’ invasive species in Europe (Vilà et al., 2009), yet the number of environmental impact studies conducted on this marine species is considerably lower compared with its terrestrial counterparts (McLaughlan et al., 2014). Research into the effects of *U. pinnatifida* invasions on recipient macroalgae-dominated systems has shown varying impacts on local biodiversity. Studies have shown both an increase (Irigoyen et al., 2011) and a decrease (Curiel et al., 1998; Casas et al., 2004) in local diversity as a result of *U. pinnatifida* introductions, as well as subtle and inconsistent effects on native species and associated assemblages (Raffo et al., 2009; South et al., 2015). It is likely that *U. pinnatifida* impacts are context-dependent, but it does have the potential to affect the performance and/or abundance of native kelp species within Plymouth Sound because it is an opportunistic fast-growing species that occupies a substantial area of seabed by early summer (Heiser et al., 2014), and can shade co-existing native species (Smale, pers obs.). Previous studies on *U. pinnatifida* have focused on its impacts at the plot or habitat scale and there have been very few direct comparisons between *U. pinnatifida* and native kelps with regards to how they function as biogenic habitat providers.

The specific aims of this study were: (1) to document temporal variability in kelp species’ abundance/biomass within a mixed kelp canopy invaded by *U. pinnatifida* within the Plymouth Sound SAC, and, (2) to compare the structure of epibiont assemblages associated with *U. pinnatifida* with those associated with three co-occurring native kelp HFS: *Saccharina latissima* (native, perennial), *Laminaria ochroleuca* (native, perennial) and *Saccorhiza polyschides* (native, pseudo-annual; taxonomically not a ‘true’ kelp as it within the Order Tilopteridales but performs similar ecological function and is an important canopy-former and is referred to as a ‘kelp’ hereafter). Ultimately, we tested the hypothesis that *U. pinnatifida* harbours a distinct and less diverse sessile epifaunal assemblage compared with native kelps and that proliferation of *U. pinnatifida* could result in lower local biodiversity.

Materials and methods

Study site

Firestone Bay (50° 21' 39"N, 4° 9' 36"W), situated within the Plymouth Sound Special Area of Conservation (SAC), was selected for study because (i) the widespread occurrence of *U. pinnatifida* on natural substrata has recently been confirmed (Heiser et al., 2014) and (ii) the site also supports extensive mixed stands of native kelps and is representative of other subtidal reefs within Plymouth Sound (Smale pers obs). Firestone Bay comprises a range of habitat types, including soft sediments supporting seagrass patches and bedrock and cobbles supporting benthic communities dominated by sessile invertebrates (below ~5 m depth) and macroalgae (above ~5 m depth). The site experiences strong tidal flows (in excess of 1 m s^{-1} during spring tides, Fitzpatrick, 1990) and is influenced by fluvial input (e.g. sediment, organic matter) from the adjacent Tamar River system. It is well protected from wind or wave-derived water motion and the embayment has a gently-sloping shallow profile before deepening towards the main channel of the Tamar estuary (>40 m depth). The low intertidal zone is dominated by the fucoid *Himanthalia elongata* and the kelp *L. digitata*, whereas the extreme low water and shallow subtidal zone is characterized by mixed macroalgal stand comprising the kelps *L. ochroleuca*, *S. latissima*, *S. polyschides* and *U. pinnatifida*.

Field surveys, sample collection and processing

Surveys were completed with standard scientific diving techniques at ~2 m depth (below chart datum) within Firestone Bay. Five replicate 10 x 1 m belt transects were haphazardly placed, at least 10 m apart, with each transect orientated parallel to the shore along a constant depth. Sampling was stratified to target bedrock and cobble beds (i.e. patches of soft sediment were not sampled). Each kelp sporophyte within the belt transect was identified to species *in situ*. In 2014, five subtidal transects were conducted at each sampling event in April, May, June, August and December to examine temporal variability from spring through to winter. In addition to the surveys, sporophytes were collected from the subtidal to quantify the biomass and morphology of each kelp species. At the study site, 20 individual mature-stage sporophytes of the species *L. ochroleuca*, *S. latissima*, *S. polyschides* and *U. pinnatifida* were collected in April, June and August (with the exception of *L. ochroleuca* in June, when 16 individuals of this species were collected). Adult sporophytes were randomly selected, removed below the holdfast and carefully placed in mesh bags. The sporophytes were then transported to the laboratory, in cool seawater, whereupon the following morphological measurements were obtained: total length, stipe length, wet weight, internal holdfast volume (after removing any attached stones and epibiota) and the combined surface area of lamina and stipe surfaces. Internal holdfast volume (i.e. 'living space') was estimated by covering the holdfast structure in plastic wrap and then measuring its volume through displacement of freshwater. The volume of the holdfast structure itself was obtained (without plastic wrap) and the difference between the 2 measurements represented the internal holdfast volume. High resolution images were obtained for each sporophyte and subsequently analysed (using ‘Image J 64’ software) to quantify surface area. The wet weight of all epiphytic algae attached to the sporophytes, which increases available living space and represents an important habitat and food source for associated epifauna, was also obtained.

Following initial processing, holdfast structures were removed by cutting the base of the stipe and immediately frozen (-18°C). Holdfasts were subsequently thawed and carefully dissected, and all sessile epibionts were removed, identified to the highest taxonomic resolution possible (mostly species with the notable exception of sponges) and weighed (damp weight). In April, 20 mature holdfasts of *L. ochroleuca*, *S. latissima* and *U. pinnatifida* were examined (*S. polyschides* was not present at this time). In June and August, 20 holdfasts were examined for each kelp species, with the exception of *L. ochroleuca* in June when only 16 holdfasts were sampled. In addition, epifaunal assemblages attached to the stipe and lamina were also quantified in August, when the abundance of sessile fauna is generally high (Smale, pers obs). The spatial coverage of epifauna on the stipe and lamina was quantified by identifying all fauna and estimating their spatial coverage using a semi-quantitative SACFOR scale (using percent cover categories as defined by Connor et al., 2004). Epifaunal species were removed from the stipe and lamina and stored in 70% IMS for subsequent taxonomic confirmation. In total, 20 mature sporophytes of each kelp species were examined.

Statistical analysis

Variability in biogenic habitat structure (i.e. morphology and epiphytic load) between the kelp species were statistically examined with univariate permutational analysis of variance with ‘kelp’ and ‘month’ as fixed factors (permutations were based on Euclidean distances between untransformed data, performed under a reduced model using 4999 permutations). Where a significant interaction term was recorded pairwise tests between kelps were conducted within each level of month. Significance was accepted at $P<0.01$, in order to reduce the likelihood of a Type I error arising from multiple testing of morphological response variables. Variability in epibiont assemblage structure between host kelp species and sampling month was examined using multivariate permutational analysis of variance (PERMANOVA; Anderson, 2001), using the model described above with permutations based on a Bray-Curtis similarity matrix constructed from square-root transformed areal coverage/biomass data. As some sporophytes were devoid of epibionts, a dummy variable was added to every sample before construction of the similarity matrix (Clarke and Warwick, 2001). Where significant differences between host kelp species were detected (at $P<0.05$) SIMPER analysis was conducted to determine which taxa contributed most to the observed differences. Univariate assemblage-level metrics (i.e. total areal cover, total biomass, taxon richness as expressed by the number of distinct taxa) were examined with univariate permutational analysis of variance (as per kelp morphology described above). All statistical procedures were conducted using PRIMER (v.6) software with the PERMANOVA add-on (Clarke and Warwick, 2001; Anderson et al., 2008). Patterns were visualised with standard bar plots (± standard error) and PCO plots (for multivariate assemblage structure data).

Results

Temporal variability in kelp canopy composition

Subtidal kelp canopies at Firestone Bay were dominated by the native perennial *S. latissima,* which was the most abundant species in each sampling month and reached a maximum density of 9.2 inds.m^{-2} ± 0.4 in June (Fig. 1). The other native perennial species, *L. ochroleuca*, was recorded throughout the year but was comparably low in abundance, peaking at 1.6 inds.m^{-2} ± 0.3 in August. As expected, the (pseudo)-annual species, showed strong seasonal variability in their actual and relative abundances, with the native annual *S. polyschides* being absent in April and reaching a peak of 3.7 inds.m^{-2} ± 0.9 in June and the non-native *U. pinnatifida* increasing in abundance from April to June (peaking at 5.0 inds.m^{-2} ± 0.7) and then decreasing rapidly in August and not recorded in December (Fig. 1). From April to June, *U. pinnatifida* was the second most abundant species (in terms of actual and relative abundance) at Firestone Bay (Fig. 1). With regards to standing stock, biomass values for *S. latissima* were markedly greater than the other species in April and June but comparable to *S. polyschides* in August (Fig. 1). *U. pinnatifida* was the second most important contributor to kelp biomass in June (Fig. 1).

Biogenic habitat structure provided by kelp species

The biogenic habitat structure provided by the longer-lived perennial species, *L. ochroleuca* and *S. latissima,* was largely consistent throughout the sampling period (Fig. 2). In contrast, the physical structure of *S. polyschides* and *U. pinnatifida* varied considerably through time, in accordance with their life histories (Fig. 2). For all the metrics examined, univariate permutational ANOVAs indicated a significant HFS x Month interaction term, suggesting that differences in structure between kelp species was not consistent through time (Table 1). The total length of sporophytes varied between kelp species, as length measurements for *S.*

latissima were significantly greater than the other kelp species in April and June, but not in August when *S. polyschides* had attained a comparable size (Fig. 2, Table 1). *U. pinnatifida* was significantly smaller than the other kelp species in April and August, but was comparable with *L. ochroleuca* and *S. polyschides* in June (Fig. 2, Table 1). The perennial species (*L. ochroleuca* and *S. latissima*) exhibited significantly greater stipe lengths than the (pseudo) annual species (*S. polyschides* and *U. pinnatifida*) in spring, but by late summer the stipes of *U. pinnatifida* were comparable in length to the perennial species and *S. polyschides* stipes were twice as long (Fig. 2, Table 1).

Total weight and surface area showed similar patterns; in April *S. latissima* exhibited a significantly higher biomass and surface area than *L. ochroleuca,* which was significantly greater than *U. pinnatifida* (Fig. 2, Table 1). By June, values for *S. polyschides, S. latissima* and *L. ochroleuca* were comparable and greater than *U. pinnatifida* and by August *S. polyschides* had attained a significantly greater biomass and surface area than the other kelps, with *U. pinnatifida* significantly lower in biomass and area than *L. ochroleuca* and *S. latissima* (Fig. 2, Table 1).

Holdfasts supported the most diverse epibiotic assemblages (see below) and exhibited considerable variability in structure between species and through time. Images of representative samples clearly indicated differences in size and complexity between the 4 species (Fig 3). The volume of the internal living space within holdfasts was highly variable between kelp species and sampling months (Fig. 2, Table 1). In April, *L. ochroleuca* holdfasts had the greatest living space, with *U. pinnatifida* holdfasts being significantly lower in volume. By June, the average volume of *U. pinnatifida* and *S. polyschides* holdfast was equivalent to *L. ochroleuca* and greater than *S. latissima,* and by August the large bulbous holdfasts of *S. polyschides* were far more voluminous than the other kelps (Fig. 2, Table 1). Finally, the biomass of epiphytic algae attached to the kelp sporophytes, which provides tertiary habitat for a wide range of fauna, varied considerably between species and months (Fig. 2, Table 1). The highest biomass values were recorded in August, during which time *S. latissima* and *S. polyschides* supported significantly greater epiphyte biomass than *L. ochroleuca* and *U. pinnatifida* (Fig. 2, Table 1).

Structure and diversity of epibiont assemblages on stipe and lamina surfaces

In total, 7 taxa of sessile fauna representing 4 phyla (Annelida, Bryozoa, Chordata and Cnidaria) were recorded attached to the surfaces of the stipe/lamina habitat in the August sampling event (Table S1). The most common species were the Bryozoans *Tubulipora* spp. and *Celleporella hyalina*. A total absence of fauna was recorded for one *L. ochroleuca* sample, one *S. latissima*, one *U. pinnatifida* and two *S. polyschides* samples. Taxon richness of the stipe/lamina epifaunal assemblages was fairly low (Fig. 4), with a maximum of 5 taxa recorded on a single sporophyte (*S. latissima*). Univariate permuational ANOVA detected a significant difference between kelp species (pseudo-$F_{3,75}$ = 8.14, P = 0.001) with *S. latissima* having greater richness values than the other kelp species (Fig. 4). The total cover of epifaunal assemblages also varied between kelp species, with epifauna on *S. latissima* covering an area ~4 and ~2 times greater than epifauna on *U. pinnatifida* and *L. ochroleuca,* respectively (Fig. 4). Univariate permuational ANOVA detected a significant difference between kelp species (pseudo-$F_{3,75}$ = 8.21, P = 0.001) with *S. latissima* and *S. polyschides* having greater total cover values than *L. ochroleuca,* which in turn supported a more spatially extenisve assemblage than *U. pinnatifida* (Fig. 4).

Differences in multivariate assemblage structure of stipe/lamina epifauna between kelp species were vizualised with a PCO plot, which indicated clear separation in epibiont assemblage structure between *U. pinnatifida* and the 2 perennial species, *L. ochroleuca* and *S. latissima* (Fig. 5). A single-factor PERMANOVA using ‘kelp’ as a fixed factor indicated a significant difference in epifaunal assemblage structure (pseudo-$F_{3,75}$ = 11.78, P = 0.001). Pair-wise comparisons showed that the epifaunal assemblages of all kelp species were significantly different from each other. A SIMPER analysis was conducted on the stipe and lamina assemblages to determine the relative contribution of each epifaunal species to the observed differences (Table S2). The bryozoan *Membranipora membranacea* was consistently a major contributor to the observed differences between assemblages associated with *U. pinnatifida* and the other kelps, being far more abundant on native species (Table S2). The bryozoan *Celleporella hyalina* was also an important discriminatory species between assemblages associated with *U. pinnatifida* and those associated with *L. ochroleuca* and *S. polyschides,* again being more abundant on the native species.

Structure and diversity of epibiont assemblages on and within holdfasts

In total, 35 sessile taxa representing 6 phyla (Annelida, Arthropoda, Bryozoa, Chordata, Mollusca, Porifera, Rhodophyta) were recorded within or attached to holdfast structures throughout the study period (Table S3). The most diverse phylum was the Bryozoa, represented by 16 species, and the most dominant (by weight) phylum was the Porifera (46% of total biomass recorded). In total, 55% of *U. pinnatifida* and 45% of *S. polyschides* holdfasts were entirely devoid of epibionts, compared to just 5% of *L. ochroleuca* and 15% of *S. latissima* holdfasts. With regards to taxon richness, a significant kelp x month interaction term was detected (Table 2), indicating that differences in richness between the kelp species were not consistent through time. In April and June, *L. ochroleuca* holdfast assemblages were significantly richer than those associated with *S. latissima*, which in turn were richer than those associated with *S. polyschides* and *U. pinnatifida* (Fig. 6). This pattern was less pronounced in August, as assemblages within *S. latissima* were comparable in richness to those associated with *L. ochroleuca*, while both species harboured greater richness than *S. polyschides* and *U. pinnatifida* (Fig. 6). The total biomass of epibionts was significantly greater for assemblages associated with *L. ochroleuca* than the other kelps in both April and June (Table 2, Fig. 6). In August, however, the biomass of *S. latissima* holdfast assemblages increased considerably and was statistically comparable to the *L. ochroleuca* assemblages (Table 2, Fig. 6). At this time, the biomass of assemblages associated with *U. pinnatifida* was significantly lower than the other kelp species (Table 2, Fig. 6).

With regards to multivariate assemblage structure, a two-way PERMANOVA detected significant variability between host kelp species, months and the kelp x month interaction term (Table 2). Pairwise tests within each month showed that assemblages were dissimilar between each kelp species sampled in April (Table 2). The corresponding PCO plot (Fig. 7) depicted clear separation between assemblages associated with *U. pinnatifida* and the 2 native perennial species. In June, assemblages associated with *L. ochroleuca* were structurally distinct from the other kelps, whereas assemblages associated with *U. Pinnatifida* were statistically similar to those inhabiting both *S. latissima* and *S. polyschides* (Table 2, Fig. 7). In August, pairwise tests showed that assemblages harboured by the perennials *L. ochroleuca* and *S. latissima* were similar to each other but distinct from those associated with *S. polyschides* and *U. pinnatifida*, which in turn were comparable in structure (Table 2, Fig. 7).

A SIMPER analysis was conducted to determine which taxa were the major contributors to the observed dissimilarity in assemblage structure between host kelp species (Table S4). Differences between assemblages hosted by *U. pinnatifida* and those associated with *L. ochroleuca* were principally driven by the bivalves *Anomia ephippium* and *Hiatella arctica* and the polychaete *Spirobranchus* spp., all of which were markedly more abundant on *L. ochroleuca* (Table S4). Similarly, dissimilarity between *U. pinnatifida* and *S. latissima* was driven by greater abundances of the red alga *Corallina officinalis*, the bivalve *Anomia ephippium* and the bryozoan *Celleporella hyalina* within *S. latissima* holdfasts (Table S4). The red alga *Corallina officinalis*, the bryozoans *Celleporella hyalina* and *Tubulipora* spp. and the bivalve *Anomia ephippium* were consistently important discriminatory taxa between the kelp species (Table S4).

A tally of the total number of taxa recorded on each kelp species in the sampling period (i.e. all stipe/lamina and holdfast assemblages combined) showed that *L. ochroleuca* supported both the greatest total richness and number of taxa unique to that host species (Table 3). *S. polyschides* and *U. pinnatifida* supported less than half the number of taxa and did not harbor any unique epibionts (Table 3).

Discussion

U. pinnatifida was first recorded in Plymouth Sound in 2003 and has since become a prominent and widespread component of the marine flora (Heiser et al., 2014). At our study site, which is representative of other sites within the Plymouth Sound SAC, *U. pinnatifida* was the second most abundant canopy-forming macroalga throughout the spring and early summer survey period. During periods of maximum abundance and size (i.e. June), *U. pinnatifida* was also the second most important contributor to total macroalgal biomass. As such, *U. pinnatifida* has become an integral component of the shallow subtidal ecosystem, with regards to ecological functions such as biogenic habitat provision and primary production, at least from early spring until mid-summer. Although some *U. pinnatifida* sporophytes have been observed recruiting in the autumn and persisting through the winter, as is the case in Brittany, France (Castric-Fey et al., 1999) this cohort would appear to be spatially restricted and/or very scarce given that sporophytes were not recorded during the December surveys at either Firestone Bay or additional sites within Plymouth Sound (Smale, unpublished data). Given that *U. pinnatifida* is thought to be competitively inferior to native kelps in the northeast Atlantic (Floc'h et al., 1996; Farrell and Fletcher, 2006), it has seemingly dispersed from artificial habitats and colonized subtidal rocky reefs in Plymouth Sound relatively quickly (i.e. ~12 years). Colonization of natural habitats may have been facilitated by disturbance to native canopies, through storm events or anthropogenic stressors for example, as has been shown elsewhere (Valentine and Johnson, 2003; Schiel and Thompson, 2012)

It is not yet known whether the presence of *U. pinnatifida* in the UK has detrimental effects on native flora and fauna, through increased competition for resources for example, as has been suggested in other temperate regions invaded by *U. pinnatifida* (Curiel et al., 1998; Casas et al., 2004). Alternatively, *U. pinnatifida* may have negligible effects on native macroalgae as it may occupy a different niche than native canopy formers, with minimal spatial or temporal overlap in demand for resources. Indeed, minimal, inconsistent or even positive effects of *U. pinnatifida* have been recorded in other invaded regions (Valentine and Johnson, 2005; Irigoyen et al., 2011; South et al., 2015). What is clear from our study is that, at the scale of sporophyte, *U. pinnatifida* harbours structurally distinct, less abundant and less diverse epibiotic assemblages than the longer-lived native kelps, *L. ochroleuca* and *S. latissima*.

Determining the mechanisms underpinning the observed differences in epibiotic assemblages between *U. pinnatifida* and the native perennial kelps requires manipulative experimentation, but it is likely that (at least) 3 factors are involved. Firstly, time. Mature *U. pinnatifida* sporophytes were recorded in low densities in early spring before rapidly increasing in abundance and size by early summer and subsequently senescing by late summer. As such, the biogenic habitat offered by the thalli was only available for colonization by epibionts for a few months. In contrast, the holdfast and stipe of the perennial kelp *L. ochroleuca* may persist for >10 years in favourable conditions (Smale et al., 2013) and individuals >5 years have been recorded within Plymouth Sound (Smale, unpublished data), while the lifespan of *S. latissima* is typically 2-4 years (Smale et al., 2013). Therefore, the biogenic habitat provided by these species is more stable through time (even though the frond is eroded and replaced through the year) and the period during which it is available for colonization is considerably greater, enhancing the likelihood of recruitment of epibionts. This mechanism is further supported by the fact that assemblages associated with *U. pinnatifida* and *S. polyschides* were similar, and were both lower in richness and structurally distinct from those associated with *L. ochroleuca* and *S. latissima. S. polyschides* is a pseudo-annual species - it was not recorded at the study site in April - and the period of time that the sporophyte was available for colonization by epibionts was therefore restricted. A recent study compared non-native *U. pinnatifida* with annual populations of the native giant kelp *Macrocystis pyrifera*, and showed that holdfast assemblages were similar, most likely because holdfasts were available for colonization for similar periods of time (Raffo et al., 2009).

Secondly, the physical structure of the sporophyte. The surface area of the thallus available for colonization by epibionts offered by *L. ochroleuca* and *S. latissima* was greater and more temporally consistent compared with *U. pinnatifida,* which may have promoted a richer, more spatially extensive epibiotic assemblage. Similarly, the internal living space within *L. ochroleuca* and *S. latissima* holdfasts was greater than that of *U. pinnatifida* (with the single exception of *S. latissima* versus *U. pinnatifida* in June). Habitat volume has been shown to be an important factor in determining the richness and abundance of holdfast assemblages (Anderson et al., 2005; Blight and Thompson, 2008) and it is likely that the greater internal living space within the perennial kelps' holdfasts allowed for development of a more speciose and abundant assemblage. Moreover, the structure of *L. ochroleuca* holdfasts was notably more complex than the other kelp species, with the arrangement of haptera forming an intricate 3-dimensional matrix. Increased holdfast complexity has been shown to correspond with increased assemblage diversity (Hauser et al., 2006), and it is likely that the micro and macro-structure of *L. ochroleuca* influenced epibiont assemblage structure.

Thirdly, variation between kelps in the physicochemical composition of the thallus and production of antifoulants may partly explain variation in epibiotc assemblages. Macroalgae may employ a range of chemical and non-chemical strategies to reduce fouling by epifauna and epiflora (Da Gama et al., 2002; Hellio et al., 2002) and, as such, some species are inherently more prone to fouling than others. For example, a comparison of epibionts attached to farmed *U. pinnatifida* and *S. latissima* sporophytes showed that *S. latissima* generally exhibits higher levels of biofouling (Peteiro and Freire, 2013). *L. ochroleuca* is also known to produce antifoulants, and the surfaces of the stipe and lamina are generally less fouled by epibionts than other kelps including *L. hyperborea* (Smale et al., 2015), *L. digitata* (Blight and Thompson, 2008) and *S. latissima* (this study). Even so, epiphytic loading and the richness and cover of epibionts on the stipe and lamina habitat of *L. ochroleuca* were still comparable to or greater than that of *U. pinnatifida*.

There were two important caveats involved with our study that should be noted. Firstly, we did not examine the abundance and richness of mobile invertebrates within holdfast structures. Mobile invertebrate assemblages associated with kelps can be highly diverse and abundant and represent an important component of the kelp forest biota (Anderson et al., 2005; Tuya et al., 2011) that warrant further research. Secondly, our quantification of biodiversity patterns was performed at the scale of individual sporophyte and additional work is needed at larger spatial scales, specifically that of the kelp-dominated habitat. For example, it could be that *U. pinnatifida* alters the physical environment and influences the structure of understorey assemblages in different ways to the other kelps, and that a more diverse macroalgae canopy results in a more diverse associated understorey assemblage, as has been shown in other kelp-dominated systems (Smale, 2010). Again, further work on how *U. pinnatifida* influences associated species' abundance and distribution patterns is required. It is clear from research on other non-native macroalgae that the establishment of populations outside of the native range can enhance local biodiversity, if the non-native species occupies a previously unfilled niche, enhances biogenic habitat complexity and does not adversely impact native HFS (Buschbaum et al., 2006; Thomsen et al., 2009).

This study was the first to examine differences in abundances, provision of biogenic habitat, and structure of epibiotic assemblages between *U. pinnatifida* and co-occurring species of kelp in the UK. Understanding the ecological role of *U. pinnatifida* is of particular importance, given that it is rapidly extending its range along coastlines in the northeast Atlantic (Minchin and Nunn, 2014), southwest Atlantic (Dellatorre et al., 2014), northeast Pacific (Zabin et al., 2009) and southwest Pacific (James et al., 2014). Our study shows that *U. pinnatifida* supports depauperate epibiotic assemblages in Plymouth Sound, when compared with the assemblages associated with native perennial species. *U. pinnatifida* harboured approximately half as many taxa as *L. ochroleuca* and *S. latissima* at markedly lower abundances. However, assemblage structure, richness and abundance of *U. pinnatifida* assemblages were comparable to those associated with the native kelp, *S. polyschides*, which has a similar life history. It has been suggested that both *U. pinnatifida* and *S. polyschides*, which are both fast-growing opportunistic species, will increase in relative abundance in response to increased physical disturbance (i.e. from storms and human activities) and continued ocean warming (Birchenough and Bremmer, 2010; Smale et al., 2013). In contrast, the abundances of cool-water perennial kelp species, including *S. latissima* and *L. digitata* (not examined in this study) will decrease in response to global change stressors, as has been observed elsewhere in the northeast Atlantic (Moy and Christie, 2012; Raybaud et al., 2013; Smale et al., 2013). The shift from long-lived perennial species to short-lived annual species represents a shift in habitat structure from temporally-stable to ‘boom and bust’ and is likely to have major implications for primary production and biogenic habitat provision. However, the situation is complicated by the proliferation of the ‘warm’ water kelp *L. ochroleuca* at its poleward range edge in southwest UK (Smale et al., 2015). On wave-exposed open coastlines *L. ochroleuca* may support less diverse and abundant assemblages than its cool-water competitor *L. hyperborea* (Smale et al., 2015; Teagle unpublished data) but in more sheltered locations *L. ochroleuca* seemingly provides relatively stable and complex biogenic habitat that supports comparatively diverse and abundant epibiont assemblages. As such, elevated abundances of *L. ochroleuca* may positively influence local biodiversity within some habitats. Clearly, improved understanding of the long-term dynamics and competitive interactions between these habitat-forming species is needed to accurately predict future biodiversity patterns.

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TABLES

Table 1. Results of 2-way univariate permutational ANOVAs to examine variability in biogenic habitat between kelp species and sampling month (both fixed factors). Tests used 4999 permuations under a reduced model, and were based on Euclidean distances between untransformed data. The degrees of freedom associated with each factor are shown in parentheses, *F* ratios are 'pseudo-*F*' values generated by permutation and significant P values (accepted at P <0.01) are shown in bold. Where the interaction term was significant, pairwise tests within each level of 'month' were conducted to test for differences between kelps, which were *Laminaria ochroleuca* (LO), *Saccharina latissima* (SL), *Saccorhiza polyschides* (SP, not present in April) and *Undaria pinnatifida* (UP).

	Kelp (3)			**Month (2)**			**Kelp x Month (5)**			**Residual (205)**	***Pairwise tests within interaction term***		
Variable	**MS**	***F***	**P**	**MS**	***F***	**P**	**MS**	***F***	**P**	**MS**	**April**	**June**	**August**
Total length	8.3x10^{6}	90.27	**0.0002**	2.1 x10^{5}	2.23	0.110	4.6 x10^{5}	5.02	**0.0004**	9.2 x10^{4}	SL>LO>UP	SL>LO=SP=UP	SL=SP>LO>UP
Stipe length	440850	45.09	**0.0002**	108690	11.11	**0.0002**	41991	4.29	**0.0002**	9778	LO=SL>UP	SP>LO=SL=UP	SP>LO=SL=UP
Total weight	1.4 x10^{6}	15.45	**0.0002**	5.7 x10^{5}	6.00	**0.0018**	8.7 x10^{5}	9.10	**0.0002**	95791	SL>LO>UP	LO=SL=SP>UP	SP>LO=SL>UP
Surface area	2.8 x10^{8}	24.02	**0.001**	7.5 x10^{7}	6.35	**0.001**	7.4 x10^{7}	6.28	**0.001**	1.17 x10^{7}	SL>LO>UP	LO=SL=SP>UP	SP>LO=SP>UP
Holdfast space	89578	34.25	**0.0002**	11729	4.48	**0.009**	31475	12.03	**0.0002**	2615	LO>SL>UP	LO=SP=UP>SL	SP>LO=SL>UP
Epiphyte weight	373.8	6.28	**0.001**	364.6	6.13	**0.0024**	354.8	5.96	**0.0002**	59.5	LO>SL=UP	LO=SL=SP=UP	SP=SL>LO=UP

Table 2. Results of 2-way univariate permutational ANOVA and PERMANOVA to examine variability in holdfast assemblage structure between kelp species and sampling month (both fixed factors). Tests used 4999 permuations under a reduced model, and were based on either Euclidean distances between untransformed data (for taxon richness and total biomass) or on Bray-Curtis similarities between square-root transformed data (for assemblage structure). The degrees of freedom associated with each factor are shown in parentheses, *F* ratios are 'pseudo-*F*' values generated by permutation and significant P values (accepted at $P < 0.05$) are shown in bold. Where the interaction term was significant, pairwise tests within each level of 'month' were conducted to test for differences between kelps, which were *Laminaria ochroleuca* (LO), *Saccharina latissima* (SL), *Saccorhiza polyschides* (SP, not present in April) and *Undaria pinnatifida* (UP).

	Kelp (3)			**Month (2)**			**Kelp x Month (5)**			**Residual (205)**
Variable	**MS**	***F***	**P**	**MS**	***F***	**P**	**MS**	***F***	**P**	**MS**
Taxon richness	462.06	79.23	**0.001**	16.25	2.78	0.059	29.91	5.13	**0.001**	5.83
Total biomass	5.06	7.06	**0.001**	0.14	0.19	0.841	2.25	3.14	**0.003**	0.72
Assemblage structure	45213	16.72	**0.001**	39740	14.69	**0.001**	12719	4.70	**0.001**	2705

Pairwise tests within interaction term	April	June	August
Taxon richness	LO>SL>UP	LO>SL>SP=UP	LO=SL>SP=UP
Total biomass	LO>SL>UP	LO>SL=SP=UP	SL=LO, SL>SP>UP, LO=SP>UP
Assemblage structure	LO≠SL≠UP	LO≠SL&SP&UP, SL≠SP, UP=SL&SP	LO=SL≠SP=UP

Table 3. Total number of epibiotic taxa recorded on each species of kelp (holdfast, stipe and lamina combined) and the total number of epibiotic taxa unique to that kelp.

	L. ochroleuca	***S. latissima***	***S. polyschides***	***U. pinnatifida***
Total taxa	37	30	12	16
	8	1	0	0

Figure Legends

Figure 1. The actual (A) and relative (B) abundances and standing stock (wet weight biomass; C) of habitat-forming macroalgae at Firestone Bay, Plymouth Sound. Kelp species were *Laminaria ochroleuca* (LO), *Saccharina latissima* (SL), *Saccorhiza polyschides* (SP) and *Undaria pinnatifida* (UP). Values are means of 5 replicate 10 x 1 m transects (± SE) per sampling event. Note different bar shading scheme and number of sampling events for biomass values compared with abundance data.

Figure 2. Biogenic habitat structure provided by canopy-forming macroalgae at Firestone Bay, Plymouth Sound. During each sampling event, the following metrics were obtained: total length (A), stipe length (B), wet weight (C), surface area (D), internal holdfast volume (E) and wet weight of attached epiphytes (F). Values are means of 20 sporophytes (± SE) collected in each month (with the exception of *L. ochroleuca* in June when n = 16). Kelp species were *Laminaria ochroleuca* (LO), *Saccharina latissima* (SL), *Saccorhiza polyschides* (SP) and *Undaria pinnatifida* (UP).

Figure 3. Representative examples of the holdfast micro-habitat provided by the native species (A) *Laminaria ochroleuca*, (B) *Saccharina latissima* and (C) *Saccorhiza polyschides* and the non-native kelp (D) *Undaria pinnatifida*. Samples collected in late summer/autumn.

Figure 4. Mean taxon richness (A) and total cover (B) of epifauna attached to the surface of the stipe and lamina of habitat forming kelp species at Firestone Bay, Plymouth Sound. Values are means of 20 mature sporophytes (± SE) collected in August. Kelp species were *Laminaria ochroleuca* (LO), *Saccharina latissima* (SL), *Saccorhiza polyschides* (SP) and *Undaria pinnatifida* (UP). Lower case letters indicate significantly different groups, as determined by univariate permutational ANOVA.

Figure 5. Principal coordinates ordination (PCO) plot showing variability in the structure of epibiotic assemblages attached to the stipe/lamina surfaces of kelps at Firestone Bay, Plymouth Sound. The relatedness of samples was examined using a Bray-Curtis similarity matrix generated from square-root transformed biomass data. Centroids circled with a dotted line were devoid of epibionts. Kelp species were *Laminaria ochroleuca* (LO), *Saccharina latissima* (SL), *Saccorhiza polyschides* (SP) and *Undaria pinnatifida* (UP).

Figure 6. Mean taxon richness (A) and total biomass (B) of epibionts associated with kelp holdfasts at Firestone Bay, Plymouth Sound. Values are means of 20 mature sporophytes (± SE) collected in each sampling month (with the exception of *L. ochroleuca* in June when n = 16). Kelp species were *Laminaria ochroleuca* (LO), *Saccharina latissima* (SL), *Saccorhiza polyschides* (SP) and *Undaria pinnatifida* (UP). Lower case letters indicate significant differences between kelp species within each sampling month, as determined by permutational ANOVA.

Figure 7. Principal coordinates analysis (PCO) plots showing variability in the structure of epibiotic assemblages associated with kelp holdfasts at Firestone Bay, Plymouth Sound. The relatedness of samples was examined using a Bray-Curtis similarity matrix generated from square-root transformed biomass data. Centroids circled with a dotted line were devoid of epibionts. Combined data for all sampling events are presented (A), as well as separate plots for assemblages sampled in April (B), June (C) and August (D). Kelp species were

Laminaria ochroleuca (LO), *Saccharina latissima* (SL), *Saccorhiza polyschides* (SP) and *Undaria pinnatifida* (UP).

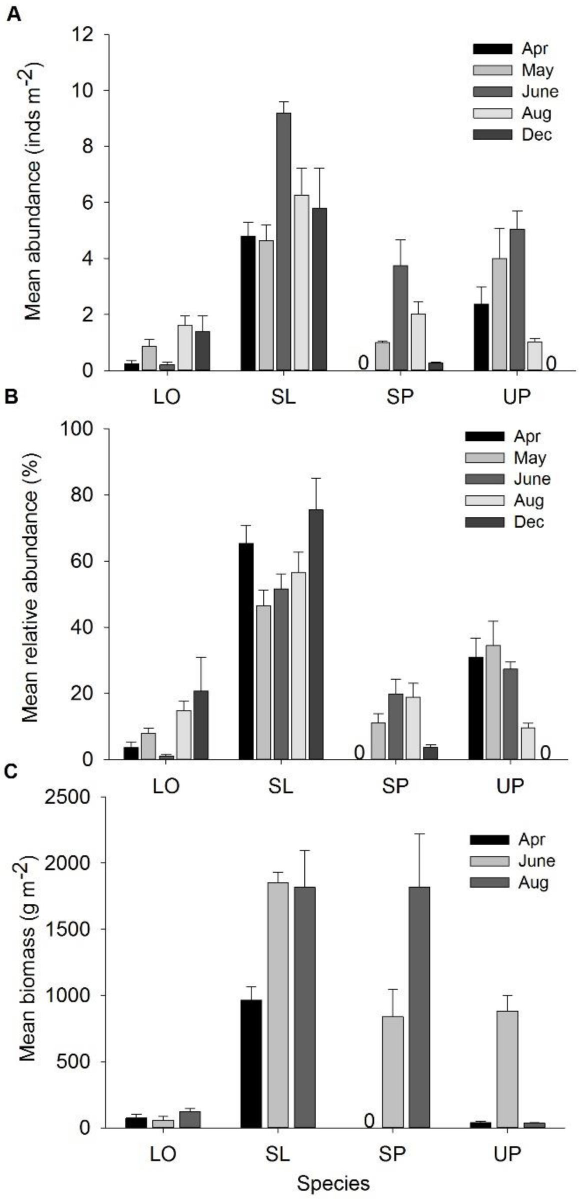
A
Mean abundance (inds m-2)
12
10
8
6
4
2
0
Apr
May
June
Aug
Dec
0
0
LO
SL
SP
UP
B
Mean relative abundance (%)
100
80
60
40
20
0
Apr
May
June
Aug
Dec
0
0
LO
SL
SP
UP
C
Mean biomass (g m-2)
2500
2000
1500
1000
500
0
Apr
June
Aug
0
LO
SL
SP
UP
Species

Fig. 1

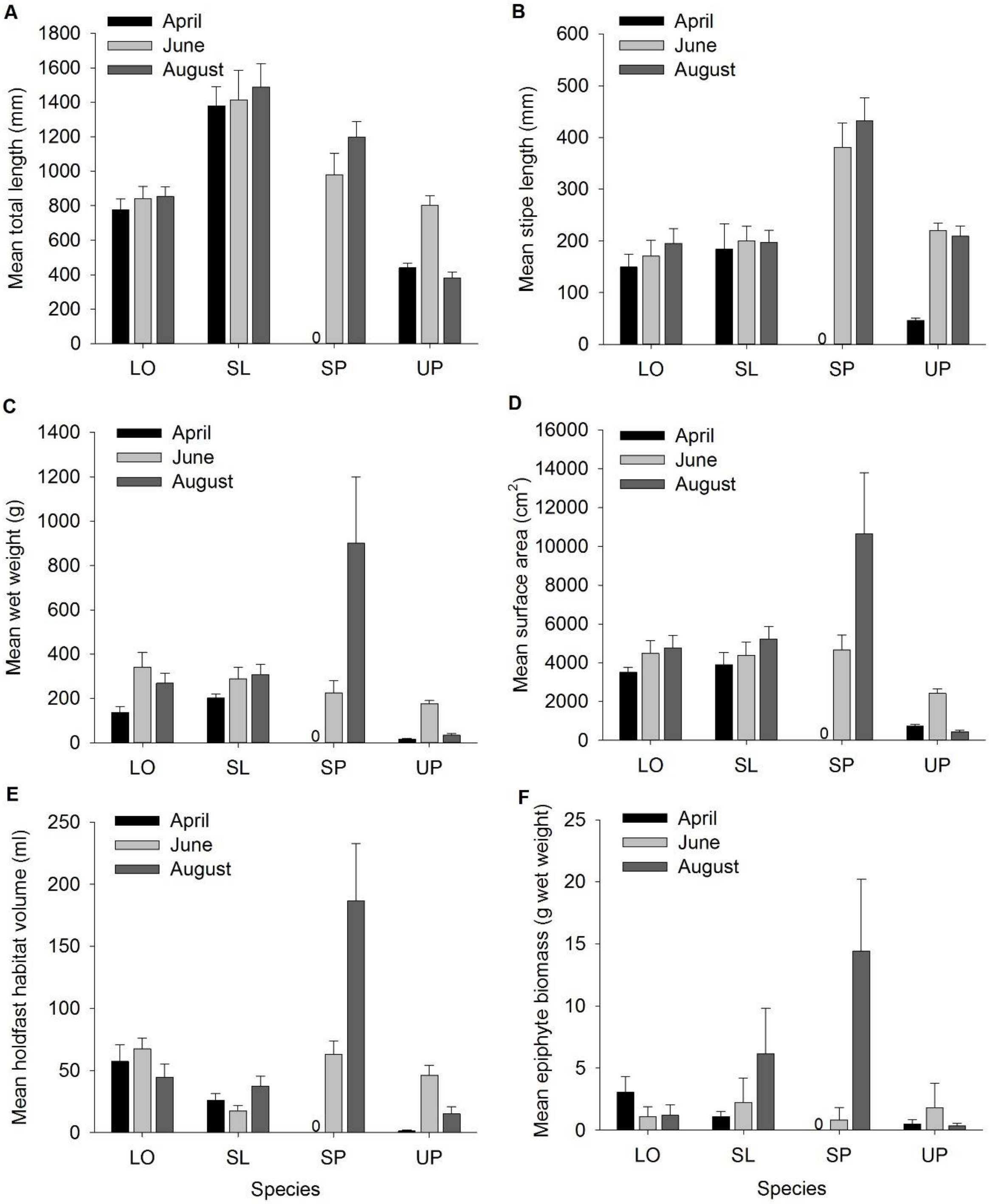
A
April
June
August
Mean total length (mm)
1800
1600
1400
1200
1000
800
600
400
200
0
0
LO
SL
SP
UP
B
April
June
August
Mean stipe length (mm)
600
500
400
300
200
100
0
0
LO
SL
SP
UP
C
April
June
August
Mean wet weight (g)
1400
1200
1000
800
600
400
200
0
0
LO
SL
SP
UP
D
April
June
August
Mean surface area (cm^2)
16000
14000
12000
10000
8000
6000
4000
2000
0
0
LO
SL
SP
UP
E
April
June
August
Mean holdfast habitat volume (ml)
250
200
150
100
50
0
0
LO
SL
SP
UP
Species
F
April
June
August
Mean epiphyte biomass (g wet weight)
25
20
15
10
5
0
0
LO
SL
SP
UP
Species

Fig. 2

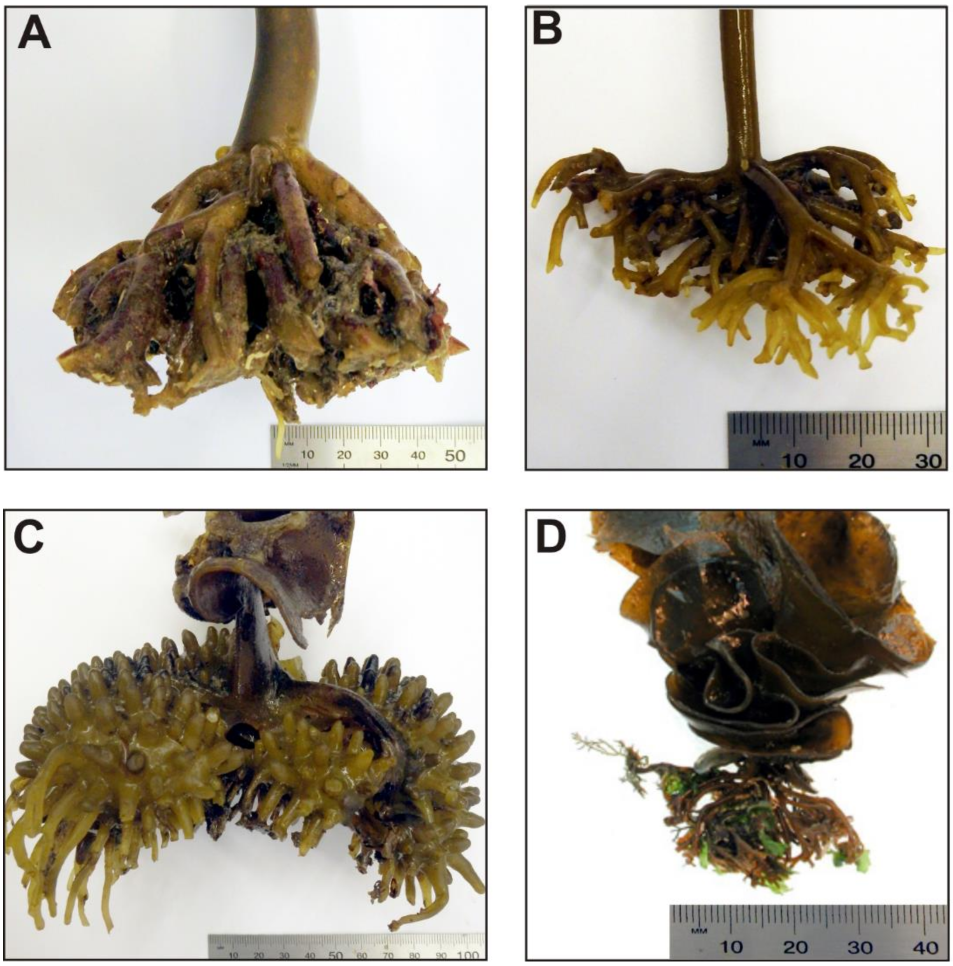
A
10 20 30 40 50
B
MM
10 20 30
C
10 20 30 40 50 60 70 80 90 100
D
MM
10 20 30 40

Fig. 3

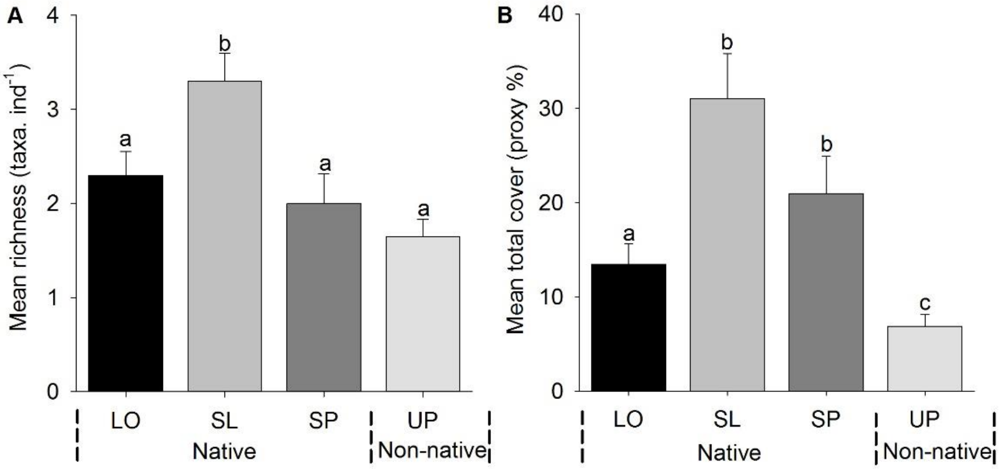
A
Mean richness (taxa. ind^{-1})
0
1
2
3
4
a
b
a
a
LO
SL
SP
UP
Native
Non-native
B
Mean total cover (proxy %)
0
10
20
30
40
a
b
b
c
LO
SL
SP
UP
Native
Non-native

Fig. 4

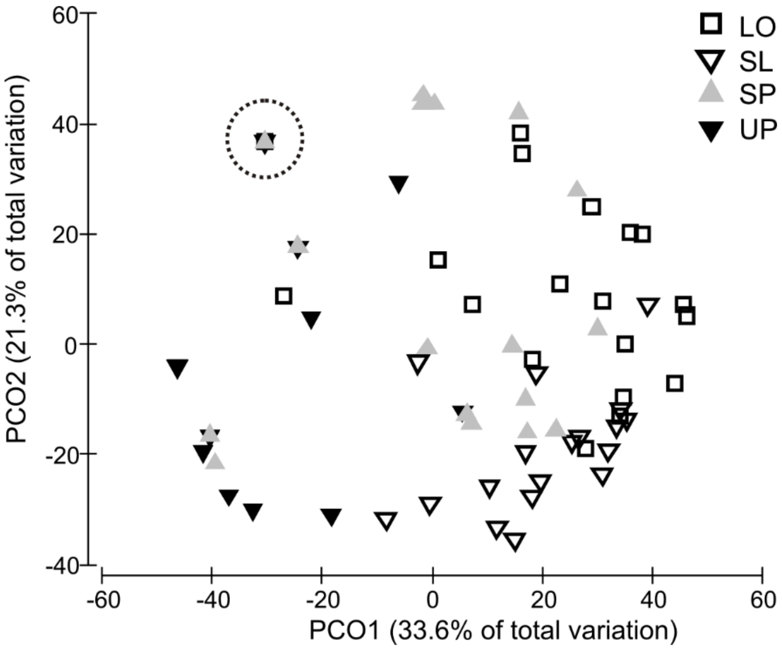
60
40
20
0
-20
-40
-60
-40
-20
0
20
40
60
PCO2 (21.3% of total variation)
PCO1 (33.6% of total variation)
LO
SL
SP
UP

Fig. 5

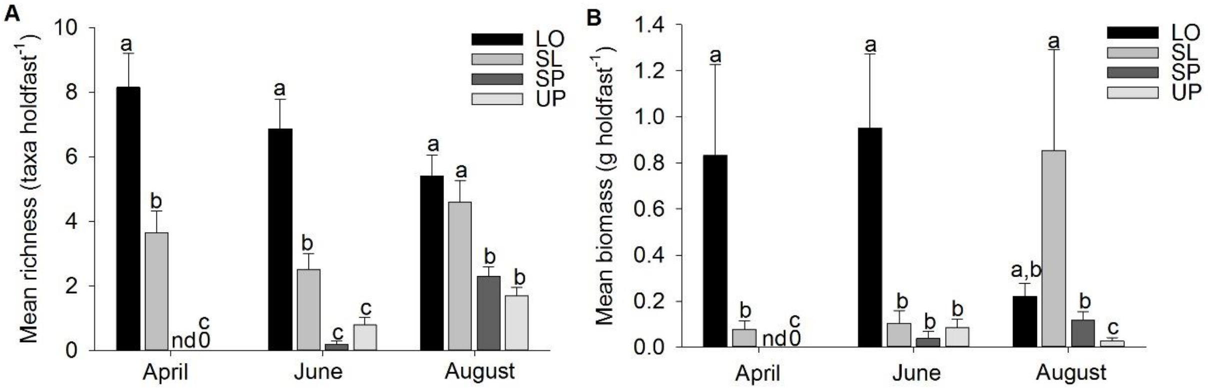
A
B
Mean richness (taxa holdfast^{-1})
Mean biomass (g holdfast^{-1})
0
2
4
6
8
10
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
April
June
August
LO
SL
SP
UP
a
b
nd
0
c
a,b

Fig. 6

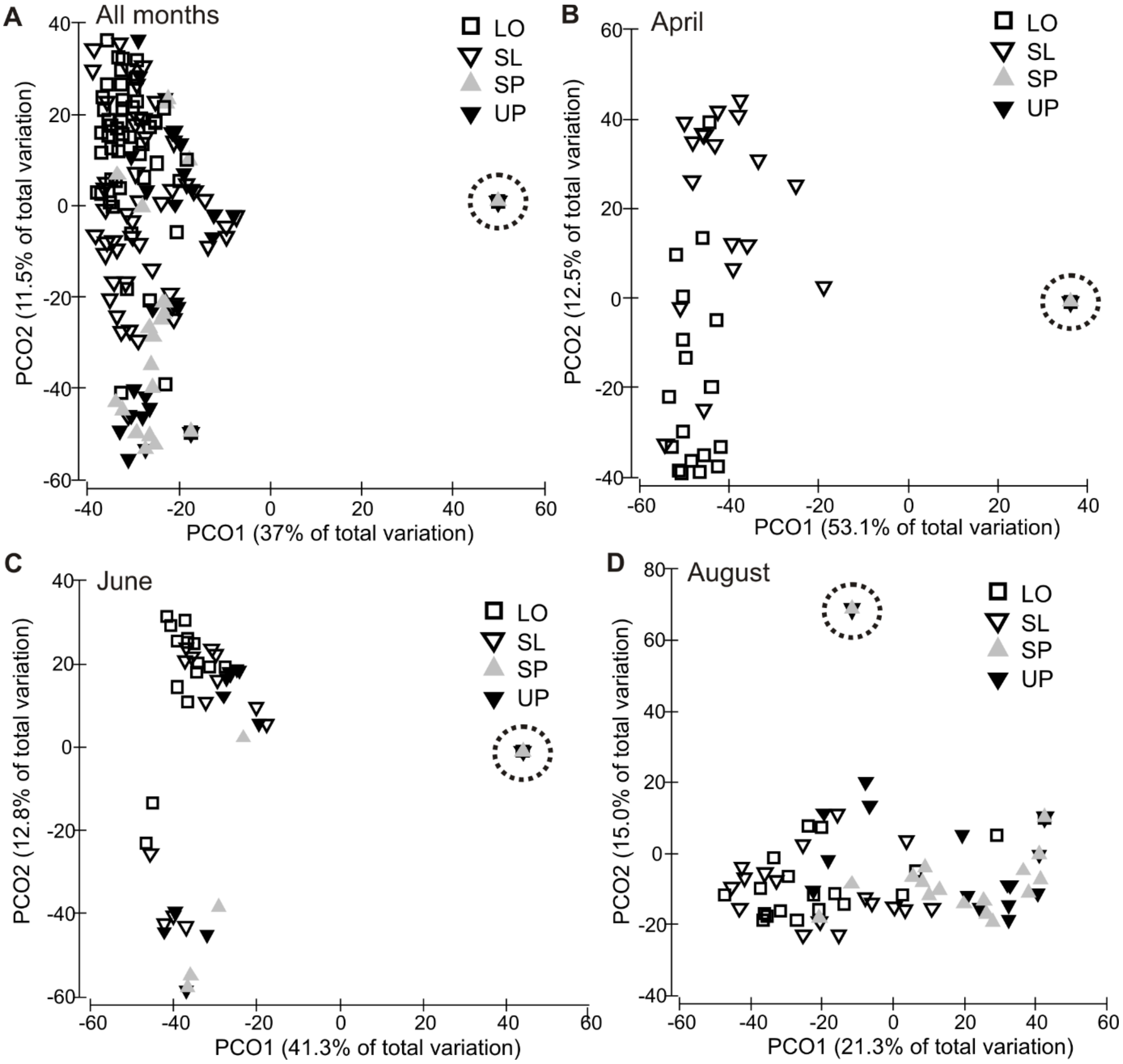
A
All months
B
April
C
June
D
August
LO
SL
SP
UP
PCO1 (37% of total variation)
PCO2 (11.5% of total variation)
PCO1 (53.1% of total variation)
PCO2 (12.5% of total variation)
PCO1 (41.3% of total variation)
PCO2 (12.8% of total variation)
PCO1 (21.3% of total variation)
PCO2 (15.0% of total variation)

Fig. 7