

Climate-driven substitution of habitat-forming species leads to reduced biodiversity within a temperate marine community

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Abstract

Aim: In marine ecosystems, habitat-forming species (HFS) such as reef-building corals and canopy-forming macroalgae alter local environmental conditions and can promote biodiversity by providing biogenic living space for a vast array of associated organisms. We examined community-level impacts of observed climate-driven shifts in the relative abundances of two superficially similar HFS, the warm-water kelp *Laminaria ochroleuca* and the cool-water kelp *Laminaria hyperborea*.

Location: Western English Channel, north-east Atlantic

Methods: We compared algal and invertebrate assemblages associated with kelp stipes and holdfasts, across multiple sites and sampling events. Significant differences were recorded in the structure of assemblages between the host kelp species at each site and event.

Results: Assemblages associated with stipes of the cool-water HFS were, on average, >12 times more diverse and supported >3600 times more biomass compared with the warm-water HFS. Holdfast assemblages also differed significantly between species, although to a lesser extent than those associated with stipes. Overall, assemblages associated with the warm-water HFS were markedly impoverished and comprised far fewer rare or unique taxa.

Main conclusions: While previous research has shown how climate-driven loss of HFS can cause biodiversity loss, our study demonstrates that climate-driven substitutions of HFS can also lead to impoverished assemblages. The indirect effects of climate change remain poorly resolved, but shifts in the distributions and abundances of HFS may invoke widespread ecological change, especially in marine ecosystems where facilitative interactions are particularly strong.

KEYWORDS

benthic communities, climate change, ecosystem engineers, facilitation, foundation species, kelp forests, ocean warming, range shifts

1 | INTRODUCTION

Anthropogenic climate change is a threat to marine ecosystems. The upper layers of the ocean have warmed by 0.11°C per decade since the mid-20th century (IPCC, 2013) and are now on

average more acidic and less oxygenated and have altered salinity and wave regimes (Bijma, Pörtner, Yesson, & Rogers, 2013; IPCC, 2013). Ocean warming, in particular, has resulted in a global redistribution of species with biogeographic ranges generally shifting polewards in line with changing isotherms (Burrows et al., 2011;

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Parmesan, 1996; Pinsky, Worm, Fogarty, Sarmiento, & Levin, 2013; Poloczanska et al., 2013; Sunday, Bates, & Dulvy, 2012; Wernberg et al., 2011). However, the rate of species' redistributions is not uniform (Poloczanska et al., 2013; Sunday et al., 2015), leading to a reshuffling and reorganization of communities and ecosystems, which are increasingly structured by novel ecological interactions (Kordas, Harley, & O'Connor, 2011; Verges et al., 2014b). Indirect effects of oceanic climate change manifest when a range-shifting species influences other species and populations within a novel community, through changes in herbivory (Zarco-Perello, Wernberg, Langlois, & Vanderklift, 2017), predation (Ferrari et al., 2015) or competition (Sorte & White, 2013), for example.

As different species exert different degrees of influence within communities, the indirect effects of some species' redistributions will likely be greater than others. For example, the climate-mediated range expansion of a keystone grazer, the sea urchin *Centrostephanus rodgersii*, resulted in extensive barren formation in kelp forests in Tasmania (Ling, 2008), while a recent rapid range contraction of canopy-forming macroalgae in south-west Australia induced major alterations in community structure due to habitat loss (Smale & Wernberg, 2013). Habitat-forming species (HFS), such as seagrasses, corals and kelps, function as ecological engineers (Jones, Lawton, & Shachak, 1994) by modifying the physical environment and providing biogenic structure for other organisms (Jones, Lawton, & Shachak, 1997). As such, quantifying the indirect effects of climate-driven redistributions of HFS is needed for a holistic understanding of climate change impacts.

Kelps are large brown seaweeds of the order Laminariales. They dominate lower intertidal and shallow subtidal reefs along temperate and subpolar coastlines globally, as well as Arctic coastlines in the Northern Hemisphere (Steneck et al., 2002; Teagle, Hawkins, Moore, & Smale, 2017). They form some of the most productive and diverse habitats on Earth (Mann, 1973; Reed, Rassweiler, & Arkema, 2008; Smale, Burrows, Moore, O'Connor, & Hawkins, 2013) and provide human societies with ecosystem services worth billions of pounds annually (Beaumont, Austen, Mangi, & Townsend, 2008; Bennett et al., 2016; Filbee-Dexter & Wernberg, 2018). Kelp forests are also a major source of primary production in coastal zones (Steneck et al., 2002), and kelp-derived organic matter may either enter food webs in situ or be exported many kilometres into adjacent habitats (Krumhansl & Scheibling, 2012; Vanderklift & Wernberg, 2008). In addition to this primary productivity, kelps also support elevated biodiversity and secondary productivity through the provision of three-dimensional habitat structure (Teagle et al., 2017), which is utilized by a vast array of marine organisms including commercially important species (Bertocci, Araújo, Oliveira, & Sousa-Pinto, 2015). Due to their high biodiversity value and their socioeconomic importance (e.g., fisheries habitat, direct harvesting for food, alginate and other products), kelp forests are managed and protected in many temperate regions (e.g., in France; Birkett, Maggs, Dring, Boaden, & Seed, 1998; and Norway; Christie, Fredriksen, & Rinde, 1998).

Kelps are mostly cool-water HFS and, as such, marginal populations found towards trailing range edges are particularly susceptible

to seawater warming. In recent years, climate-driven losses of several kelp populations have been reported (Fernandez, 2011; Filbee-Dexter, Feehan, & Scheibling, 2016; Verges et al., 2014b; Wernberg et al., 2016), with wider consequences for associated communities and ecosystems (Tuya et al., 2012; Voerman, Llera, & Rico, 2013; Wernberg et al., 2013, 2016). In the north-east Atlantic, sea temperatures have increased significantly in recent decades (Belkin, 2009; Smyth et al., 2010), with many areas predicted to warm by $>2^{\circ}\text{C}$ this century (Philippart et al., 2011). In response to this warming trend, several more northerly distributed kelp species (e.g., *Alaria esculenta*, *Laminaria digitata* and *Laminaria hyperborea*) have contracted, or are expected to contract, their equatorward range edges (Hiscock, Southward, Tittley, & Hawkins, 2004; Müller, Laepple, Bartsch, & Wiencke, 2009; Raybaud et al., 2013). On the other hand, recent evidence suggests that more southerly distributed kelp species have increased in abundance at their poleward range edge (e.g., *Laminaria ochroleuca*; Smale, Wernberg, Yunnice, & Vance, 2015). Any changes in the distributions or relative abundances of these HFS could have significant impacts on the structure and functioning of kelp-associated communities (Blight & Thompson, 2008), but this is likely to be dependent on both the characteristics of the HFS and the environmental context (Smale et al., 2013; Tuya, Larsen, & Platt, 2011).

Within the wider context of global climate change, the implications of shifts in the relative abundances of HFS for biodiversity are almost entirely unknown in marine systems. We examined community-level responses to climate-driven shifts in the relative abundances of HFS by comparing flora and fauna associated with the stipes and holdfasts of two kelp HFS: *Laminaria hyperborea* and *Laminaria ochroleuca*. These species differ in their geographical distributions and environmental requirements, but are similar in their morphology (Figure 1a–c). *L. hyperborea* is the dominant HFS on wave-exposed shallow reef habitats in the north-east Atlantic, where it supports a diverse array of flora and fauna within its holdfast and on its blade and stipe (Christie, Jorgensen, Norderhaug, & Waage-Nielsen, 2003). *L. hyperborea* is a cool-temperate species distributed from the Arctic southwards to northern Portugal (Tuya et al., 2012), while *L. ochroleuca* is a warm-temperate Lusitanian species, extending from its poleward range edge in south-west UK southwards to Morocco and into the Mediterranean (Franco et al., 2017). *L. ochroleuca* has recently proliferated at its poleward range edge; it was first documented in the UK in 1946, in Plymouth Sound (John, 1969; Parke, 1948), and has since spread throughout the south-west coast of the UK (Hargrave, Foggo, Pessarrodona, & Smale, 2017; Norton, 1985; Smirthwaite, 2006). Species distribution models predict a further poleward range expansion in coming decades (Franco et al., 2017).

The magnitude and spatial extent of proliferation at the range edge by *L. ochroleuca* have not yet been quantified with any certainty, and community-level implications are almost entirely unknown. We examined temporal trends in the relative abundances of these HFS from key monitoring locations and then quantified biodiversity patterns associated with each kelp species. Our overarching aim was to examine how shifts in the relative abundances of HFS,

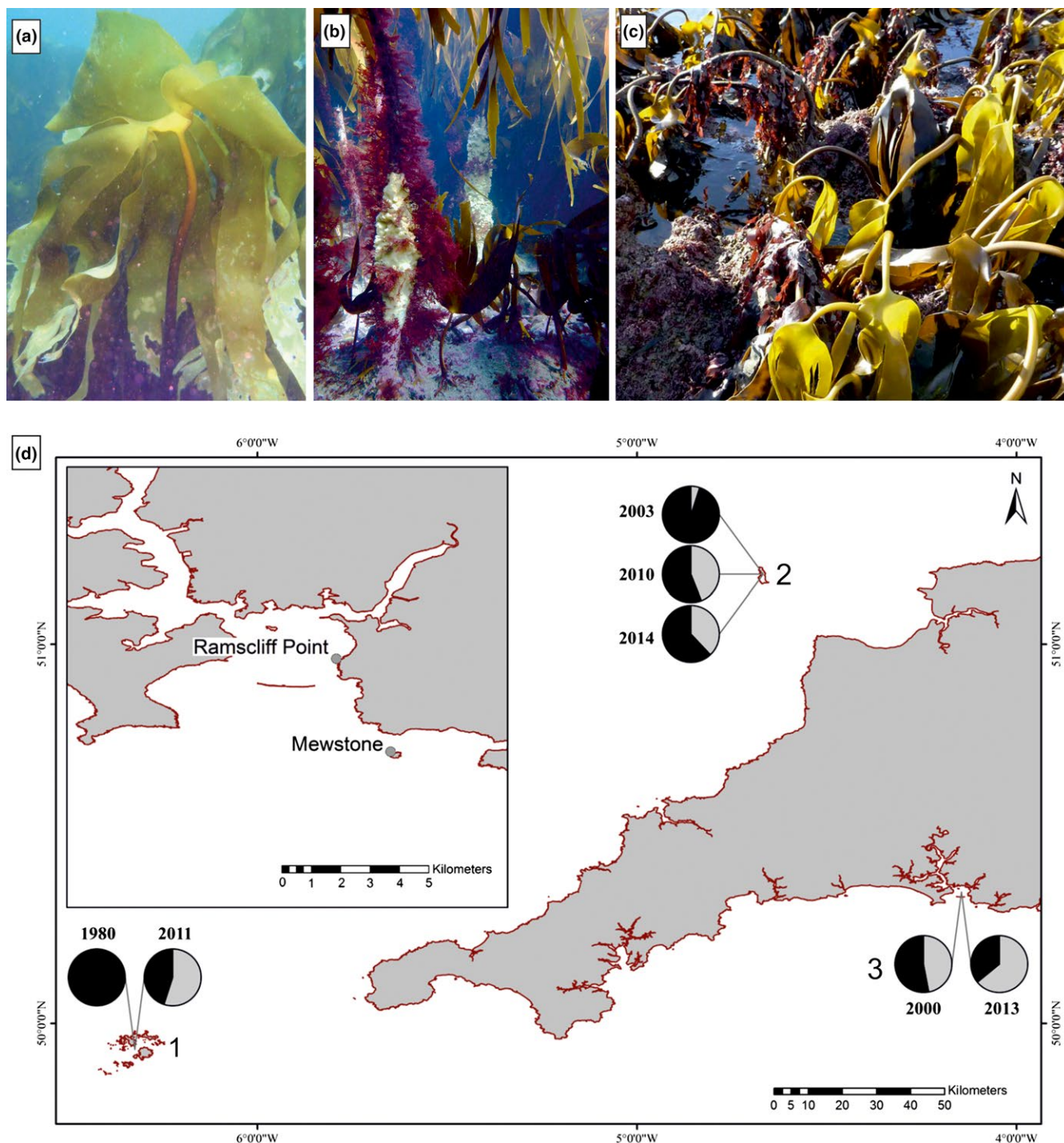


FIGURE 1 Representative examples of (a) the warm-water HFS *L. ochroleuca* and (b) the cool-water HFS *L. hyperborea*, depicting differences in stipe-associated assemblages between the two kelp species. *L. ochroleuca* is typically devoid of all epibionts, whereas *L. hyperborea* tends to support rich and abundant assemblages of red algae and sessile invertebrates. The two HFS coexist at many locations in south-west UK; (c) rocky reef habitat exposed during spring low tides reveals a mixed bed of *L. hyperborea* (top left) and *L. ochroleuca* (bottom right). Also shown are (d) the temporal trends in the relative abundance of *Laminaria ochroleuca* (grey) and *Laminaria hyperborea* (black), at three locations in the south-west UK: (1) the Isles of Scilly, (2) Lundy Island and (3) Plymouth Sound, indicating the recent proliferation of *L. ochroleuca* at the range edge. Inset map indicates the positions of the two principal study sites, Ramscliff Point and the Mewstone, within Plymouth Sound

driven by ocean warming, may influence the structure of associated assemblages and local biodiversity patterns.

2 | METHODS

2.1 | Temporal trends in the relative abundances of kelp HFS

Historical data were collated from three monitoring sites in the south-west UK: Plymouth Sound, the Isles of Scilly and Lundy Island (Figure 1). Data were extracted from a variety of sources including reports commissioned by government agencies (Axelsson, Dewey, & Wilson, 2014; Irving & Northern, 2012; Mercer, Howson, & Bunker, 2004), historical survey data (e.g., the Marine Natural Conservation Review data set compiled by the Joint Nature Conservation Committee) and from the published literature (e.g., Smale et al., 2015). All data were originally collected using comparable traditional ecological methods (i.e., in-situ identification and quantification by scuba divers using transects and quadrats; see cited sources for more information). Within each location, we examined the relative proportion of *L. ochroleuca* to *L. hyperborea* at 2–3 shallow subtidal survey sites, which were moderately exposed to wave action, supported mixed kelp beds and were sampled at least twice between 1980 and 2014.

2.2 | Sample collection

Kelp samples were collected from two sites in south-west UK: north-west Mewstone (50°18.485'N, 04°06.521'W) and Ramscliff Point (50°20.572'N, 04°07.766'W), both within the wider Plymouth Sound region (Figure 1d). The sites fall within the Plymouth Sound Special Area of Conservation (SAC), within which kelp forest communities are recognized as important conservation features. Both sites support mixed stands of *L. hyperborea* and *L. ochroleuca*, extensive subtidal rocky reef habitat, and are moderately exposed to wave action, although the Plymouth Sound breakwater offers some protection to the Ramscliff Point site (Figure 1d). The Mewstone, being situated further offshore, was characterized by slightly higher light availability and water movement than Ramscliff Point, whereas temperature regimes were comparable between sites (Supporting information Figures S1 and S2). Sampling was undertaken on two occasions by scuba divers (in April and June 2014) as kelp-associated assemblages exhibit strong seasonality, and, as such, any differences between HFS may vary between seasons. Twelve mature canopy-forming sporophytes of both *L. hyperborea* and *L. ochroleuca* were collected haphazardly from within mixed stands at each site during each sampling event. Samples were collected from within kelp stands on relatively flat rocky platforms at 2–4 m depth (below chart datum). Following removal of the blade, a fine cotton bag was placed over the stipe of each specimen, which was then cut approximately 5 cm above the holdfast and the bag carefully sealed with a cable tie to retain all attached organisms. The holdfast was then covered with a second cotton bag and was carefully removed from the substrate

before being sealed. Samples were immediately returned to the laboratory.

2.3 | Sample processing

Morphology and biomass (fresh weight) of stipe and holdfast samples were quantified in the laboratory. Sessile fauna and flora on the stipes were identified and weighed to quantify biomass (tissue-dried fresh weight). Holdfast specimens were placed into a 1% propylene phenoxetyl solution for ~30 min, in order to relax any associated fauna to aid identification. The holdfast specimens were then transferred to a 70% industrial methylated spirit (IMS) solution for preservation. Holdfast volume was determined by displacement, wrapping each holdfast in plastic food wrap to establish total holdfast volume (see Blight & Thompson, 2008); holdfast haptera were then removed to expose the inner structure of the holdfast and any associated flora and fauna. Haptera volume was determined by measuring displacement of the removed and cleaned haptera; subsequently being subtracted from total holdfast volume to give the volume of the potential habitable space among the haptera of the holdfast. Identification of all organisms was to species level wherever possible, and all sessile taxa (mobile fauna were not quantified in this study) were carefully removed and weighed to establish biomass (tissue-dried fresh weight). Kelp samples collected in summer were also aged by cross-sectioning the basal section of the stipe and counting annual growth rings (as per Kain, 1963).

2.4 | Statistical analysis

All analysis was conducted with univariate/multivariate permutational analyses using the PERMANOVA add-on (Anderson, Gorley, & Clarke, 2008) for Primer v7 software (Clarke & Gorley, 2015); assemblages associated with stipes and holdfasts from each site were analysed separately. Variability in multivariate structure was initially examined with a three-factor design, with kelp species (two levels), site (two levels) and sampling event (two levels) all as fixed factors. To examine the influence of habitat availability, holdfast volume/stipe surface area was also included in the analysis as a covariate. Permutations (4,999 under a reduced model) were based on a Bray–Curtis similarity matrix constructed from fourth-root transformed biomass data (chosen to downweight the influence of large sponges). Differences in multivariate dispersion between kelp species were examined with the PERMDISP routine, and multivariate patterns were visualized with PCO (principal coordinate analysis) plots, with each site shown separately for clarity. Euclidean distances between untransformed univariate metrics (i.e., taxon richness and total biomass) were examined using the 3-factor model described. Where significant main effects or interaction terms involving the main factor of interest (i.e., “species”) were detected (at $p < 0.05$), pairwise comparisons within each level of the relevant factors were conducted. Where significant differences in assemblage structure between kelp species were detected (at $p < 0.05$), a SIMPER analysis was performed to determine which taxa contributed most to the

observed dissimilarity. The factors “site” and “sampling event” were treated as fixed to test *a-priori* expectations that assemblages would be different between sites (as they differed in wave exposure) and between sampling events (due to seasonal succession of epiphytic assemblages). However, the inference space of this approach is limited, compared with a mixed model involving random factors, as the analysis tested for differences specifically between these two sites and events, rather than for more general patterns (see Section 4). Univariate assemblage metrics were plotted as mean values ($\pm SE$) for each site and sampling event, to visualize any trends in dissimilarity between the host kelp species. At last, we examined the relationship between habitat availability (i.e., stipe surface area and holdfast living space) and associated taxon richness and abundance for each HFS, using scatter plots and linear regression.

3 | RESULTS

3.1 | Temporal trends in the relative abundances of kelp HFS

Data extracted from various sources showed that the relative abundance of *L. ochroleuca* has increased in relation to *L. hyperborea* at all locations (Figure 1d). At moderately wave-exposed monitoring sites in the Scillies and Plymouth Sound, *L. ochroleuca* is now more abundant than *L. hyperborea* (Figure 1d).

3.2 | Biogenic habitat structure

The two HFS provided somewhat similar biogenic habitat for associated communities, although interspecific differences in habitat provision varied between sites (Supporting information Figure S3). For the stipe habitat, the surface area did not differ between the kelp species at the Mewstone (one-way permutational ANOVA; $F_{1,53} = 0.21$, $p = 0.625$), whereas *L. ochroleuca* provided a greater surface area for colonization than *L. hyperborea* at Ramscliff Point ($F_{1,53} = 18.33$, $p = 0.001$). For the holdfast habitat, *L. hyperborea* offered a greater volume of living space than *L. ochroleuca* at Mewstone ($F_{1,46} = 13.68$, $p = 0.001$), whereas no differences were observed at Ramscliff Point ($F_{1,46} = 0.86$, $p = 0.356$). The age of the sporophytes differed between the two kelp species, with the *L. hyperborea* population being slightly, and significantly, older than *L. ochroleuca* (average age: *L. hyperborea* = 6.0 ± 1.1 year, *L. ochroleuca* = 4.6 ± 1.1 year; $F_{1,46} = 19.84$, $p < 0.001$).

3.3 | Stipe assemblages

From 96 kelp stipes, 49 unique taxa (59% of all taxa were identified to species level) were recorded. Rhodophytes dominated the algal assemblage, representing 13 of the 14 species recorded. The sessile faunal assemblage comprised bryozoans (10 species), Porifera (seven taxa), ascidians (five species), molluscs (mainly bivalves, five species), Crustaceans (Cirripedia, four species), Polychaetes (two species) and Hydroids (two species). Across the study, all taxa recorded were

found associated with *L. hyperborea* stipes, whereas only ~50% of both floral and faunal taxa were found on *L. ochroleuca* stipes.

PCO plots depicting multivariate assemblage structure indicated clear partitioning between kelp species, although the degree of partitioning was greater at Ramscliff Point than at the Mewstone (Figure 2). Variability in assemblage structure was greater for *L. ochroleuca* than *L. hyperborea*, which supported relatively homogenous stipe assemblages (Figure 2). PERMANOVA detected a significant three-way interaction between species, site and event, as well as highly significant variability associated with species as both a main effect and within higher order interactions (Table 1). Pairwise tests within the three-way interaction term showed that differences between species were significant for every combination of site and event, although the magnitude of dissimilarity was greatest for Mewstone in summer (Supporting information Table S1). The PERMDISP routine indicated that the multivariate dispersion did not differ significantly between the host kelp species ($F_{1,109} = 1.98$, $p = 0.232$). However, while the mean multivariate distance between samples was comparable between species, the variability in distance was ~3 times greater for assemblages associated with *L. ochroleuca* compared with *L. hyperborea* (LH = 39.1 ± 0.9 , LO = 43.3 ± 2.8).

SIMPER analysis indicated that the differences in multivariate structure between species at the Mewstone were principally driven by the red alga *Phycodrys rubens*, and to a lesser extent the bryozoan *Electra pilosa*, and the red algae *Lomentaria articulata* and *Membranoptera alata*, all of which were more abundant on *L. hyperborea* (Supporting information Table S2). At Ramscliff Point, differences were driven primarily by the red alga *Palmaria palmata*, which was abundant on *L. hyperborea*, but absent from *L. ochroleuca* altogether (Supporting information Table S2). Further differences were caused by *Phycodrys rubens* and *Cryptopleura ramosa*, which again were more abundant on *L. hyperborea* (Supporting information Table S2).

Mean values of taxon richness and total biomass were markedly higher for *L. hyperborea*, across both sites and sampling events, compared to *L. ochroleuca* (Figure 3). Over the entire study, *L. hyperborea* supported on average >12 times as many taxa and >3,600 times as much biomass on its stipes compared with *L. ochroleuca*. Moreover, 55.5% of *L. ochroleuca* stipes were completely devoid of any epiphytic material (compared to 0% for *L. hyperborea*). Univariate PERMANOVA detected a significant interaction between species and event (for total biomass) and between species and site (both metrics), as well as a significant main effect of species and of the covariate (Table 1). Pairwise tests for taxon richness returned highly significant differences between species, with the magnitude of dissimilarity being greater at Ramscliff Point (Supporting information Table S1). Pairwise tests for total biomass again detected highly significant differences between species, with the magnitude of dissimilarity being greater at Ramscliff Point compared to the Mewstone (Supporting information Table S1). We recorded a significant linear relationship between habitat size and taxon richness for *L. hyperborea* at both sites, with the number of epibiont taxa increasing with increasing stipe surface area, but no such relationships were recorded for *L. ochroleuca* (Figure 4).

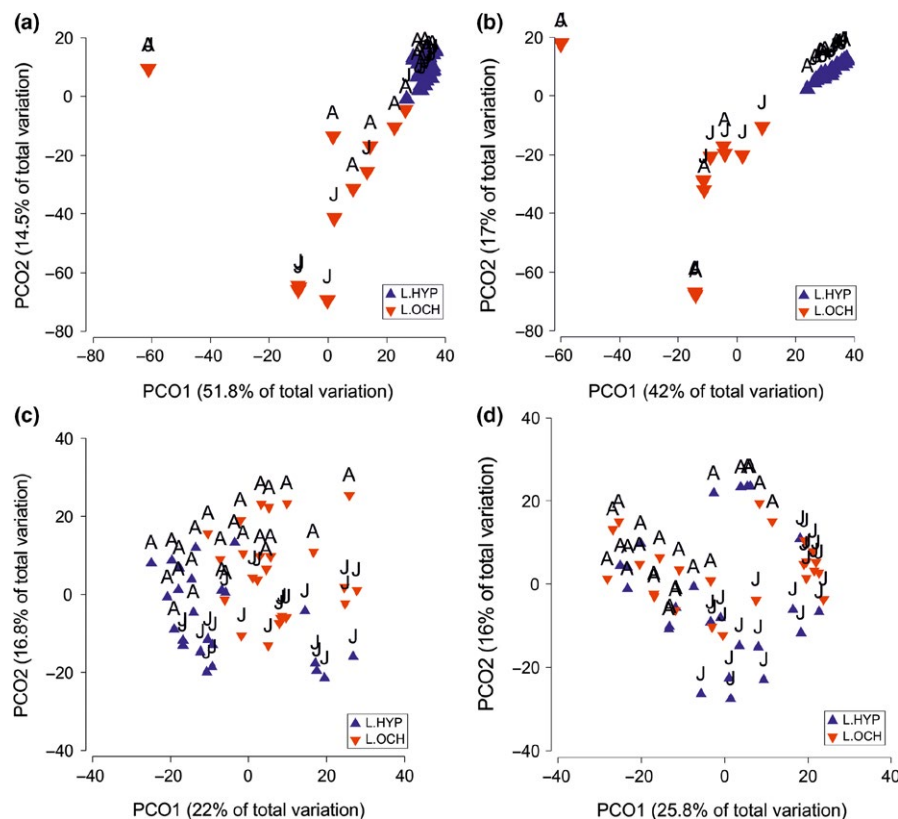


FIGURE 2 Principle component ordinations (PCO plots) depicting the multivariate structure of assemblages associated with kelp stipes and holdfasts. Stipe assemblages are shown separately for (a) Mewstone and (b) Ramscliff Point; holdfast assemblages are also shown separately for (c) Mewstone and (d) Ramscliff Point. Samples labelled with an "A" were collected in April; "J" indicates samples collected in June. Blue triangles represent *L. hyperborea*, and red inverted triangles represent *L. ochroleuca*

3.4 | Holdfast assemblages

From 96 holdfasts, 75 unique taxa of sessile fauna were recorded (64% of all taxa were identified to species level), representing seven phyla. Of these, the Bryozoa were the most species-rich (26 species), followed by Chordata (ascidians, nine species), Mollusca (bivalves, 11 species), Cnidaria (hydroids, eight species) and Arthropoda (Cirripedia, four species). Annelida (polychaetes) were identified to family (Serpulidae only), and Porifera were separated into morphospecies based on physical appearance and analysis of spicules (15 distinct taxa). In total, 91% of all taxa recorded were found on *L. hyperborea* and 79% were found on *L. ochroleuca*.

PCO plots indicated that holdfast assemblages were far more comparable between host species, although there was some partitioning between species, which was greater at the Mewstone compared with Ramscliff Point (Figure 2). Variability in assemblage structure was also more comparable between host species (Figure 2). PERMANOVA again detected a significant three-way interaction between species, site and event, as well as highly significant variability associated with species as both a main effect and within higher order interactions (Table 2). Pairwise tests within the three-way interaction term showed that differences between species were significant for every combination of site and event, although the magnitude of dissimilarity tended to be greater at the Mewstone than at Ramscliff Point and in summer compared with spring (Supporting information Table S3). PERMDISP found no significant differences in multivariate dispersion between host species, and mean dispersion

distances were comparable ($F_{(1,94)} = 0.06$, $p = 0.805$, LH = 32.9 ± 0.8 , LO = 33.2 ± 0.8).

SIMPER analysis indicated that the differences in assemblage structure at the Mewstone were driven primarily by high abundances of demosponge groups (which contributed to ~25% of the observed dissimilarity) and the barnacle *Verruca stroemia* on *L. hyperborea*, compared to *L. ochroleuca* (Supporting information Table S4). Demosponges were also major contributors to the observed dissimilarity between kelp species at Ramscliff Point, although here the barnacles *Balanus crenatus* and *Verruca stroemia*, and the bryozoan *Escharoides coccinea* were also important as discriminatory taxa identified by SIMPER as contributing most to the observed differences (Supporting information Table S4). All taxa across both sites, with the exception of *Hemedesmiidae* spp. and *E. coccinea*, were more abundant (in terms of biomass) on or within *L. hyperborea* holdfasts compared with *L. ochroleuca* (Supporting information Table S4).

Mean values of taxon richness and total biomass were markedly higher for *L. hyperborea* than *L. ochroleuca* at the Mewstone, whereas values were more comparable at Ramscliff Point, with the expectation of total biomass in summer (Figure 5). Even so, univariate PERMANOVA detected a significant main effect of species on both metrics, with richness and biomass values associated with *L. hyperborea* being greater than *L. ochroleuca* (Table 2). At the Mewstone, we recorded significant positive linear relationships between holdfast habitable space and taxon richness for both species, although the strength of this relationship was weaker for *L. ochroleuca* assemblages compared with *L. hyperborea* assemblages (Figure 4). On

TABLE 1 (a) Results of multivariate PERMANOVA to test for differences in stipe assemblage between kelp species (Sp, fixed), sites (Si, fixed) and sampling event (Ev, fixed)

Source	df	MS	Pseudo-F	p
(a) Multivariate assemblage structure				
CO	1	10,033	6.30	0.0001
Sp	1	145,690	91.70	0.0001
Si	1	13,025	8.18	0.0001
Ev	1	5,255	3.30	0.0019
Sp × Si	1	10,334	6.49	0.0001
Sp × Ev	1	3,929	2.47	0.0132
Si × Ev	1	4,960	3.11	0.0023
Sp × Si × Ev*	1	5,501	3.45	0.0013
Residual	102	1,591		
Total	110			
(b) Taxon richness				
CO	1	22.0	3.17	0.090
Sp	1	3,021	434.63	0.001
Si	1	44.5	6.40	0.014
Ev	1	11.3	1.63	0.237
Sp × Si*	1	27.0	3.88	0.050
Sp × Ev	1	1.34	0.19	0.653
Si × Ev	1	130	18.79	0.001
Sp × Si × Ev	1	22.7	3.27	0.080
Residual	102	6.94		
Total	110			
(c) Total biomass				
CO	1	55.6	0.11	0.754
Sp	1	31,213	64.3	0.001
Si	1	4,787	9.87	0.003
Ev	1	1,384	2.85	0.106
Sp × Si*	1	5,775	11.90	0.002
Sp × Ev	1	2,165	4.46	0.036
Si × Ev	1	2,207	4.55	0.037
Sp × Si × Ev	1	384	0.79	0.387
Residual	102	485		
Total	110			

Note. Stipe surface area was included as a covariate (CO) in the analysis. Permutations were based on a Bray–Curtis similarity matrix generated from fourth-root transformed biomass data. Results of univariate PERMANOVA to test for differences in the assemblage-level univariate metrics (a) taxon richness and (b) total biomass are also shown. Permutations for univariate analysis were based on a Euclidean distance similarity matrix generated from untransformed diversity data. All tests used a maximum of 4,999 permutations under a reduced model; significant effects ($p < 0.05$) are shown in bold. The first significant lower-order effect of interest (i.e., an interaction or main effect involving the species factor) was examined further with pairwise tests (see text and Table S1). Where more than one interaction was detected at the same level, the interaction with greatest significance was selected (marked with an asterisk).

the contrary, no significant relationships were recorded at Ramscliff Point for either species (Figure 4).

4 | DISCUSSION

Climate change is driving a global redistribution of species and consequent reconfigurations of communities and ecosystems (Pech et al., 2017; Scheffers et al., 2016). In the marine realm, where species distributions are strongly influenced by temperature, warming has led to a general poleward shift in species' distributions as they track moving isotherms (Burrows et al., 2011; Parmesan, 1996; Pinsky et al., 2013; Poloczanska et al., 2013; Sunday et al., 2012; Wernberg et al., 2011). While the indirect effects of shifting distributions will vary between species, range shifts involving HFS may have significant consequences for associated communities and ecosystems given that they underpin core ecological processes (Smale & Wernberg, 2013; Sorte, Williams, & Carlton, 2010; Wernberg et al., 2016). Recent climate change has, either directly or indirectly, driven widespread losses of marine HFS, which in turn has invoked biodiversity declines and community reorganization (Ling, 2008; Thomson et al., 2015; Verges et al., 2014a; Wernberg et al., 2016). Previous research has focused primarily on the community-level effects of major structural changes, such as climate-driven loss of foundation species (e.g., Smale & Wernberg, 2013; Sorte et al., 2017; Thomson et al., 2015), and much less is known about the wider consequences of more subtle replacements of seemingly similar HFS. Our study, however, has unequivocally demonstrated that climate-driven substitutions of HFS can also result in depleted levels of biodiversity and significant structural changes in associated communities.

We observed striking differences in the structure of sessile assemblages associated with the stipes of *L. hyperborea* and *L. ochroleuca*, the direction and significance (but not magnitude) of which were consistent between sites and sampling events. Differences in holdfast assemblages were less pronounced but still evident. The particularly marked dissimilarity in the structure of stipe-associated assemblages was due to significantly greater richness and biomass values associated with *L. hyperborea* stipes compared with *L. ochroleuca*. While all stipe-associated taxa recorded in the study were found on *L. hyperborea*, only ~50% were found on *L. ochroleuca*, and ~55% of all *L. ochroleuca* stipes sampled were altogether devoid of epibionts. In addition, the multivariate structure of stipe-associated assemblages differed markedly between host kelp species. Such pronounced dissimilarity in stipe assemblages was likely driven by subtle differences in the structure of the HFS, including variability in surface roughness, and chemical and mechanical defences.

First, the surface topography and texture of the stipe differ between species as *L. ochroleuca* is characterized by a uniformly smooth stipe, whereas the stipe of *L. hyperborea* is rough and pitted. Surface roughness has been shown to play a role in settlement and recruitment of microbial biofilms (Hutchinson, Nagarkar, Aitchinson, & Williams, 2006), sessile organisms (Köhler, Hansen, & Wahl,

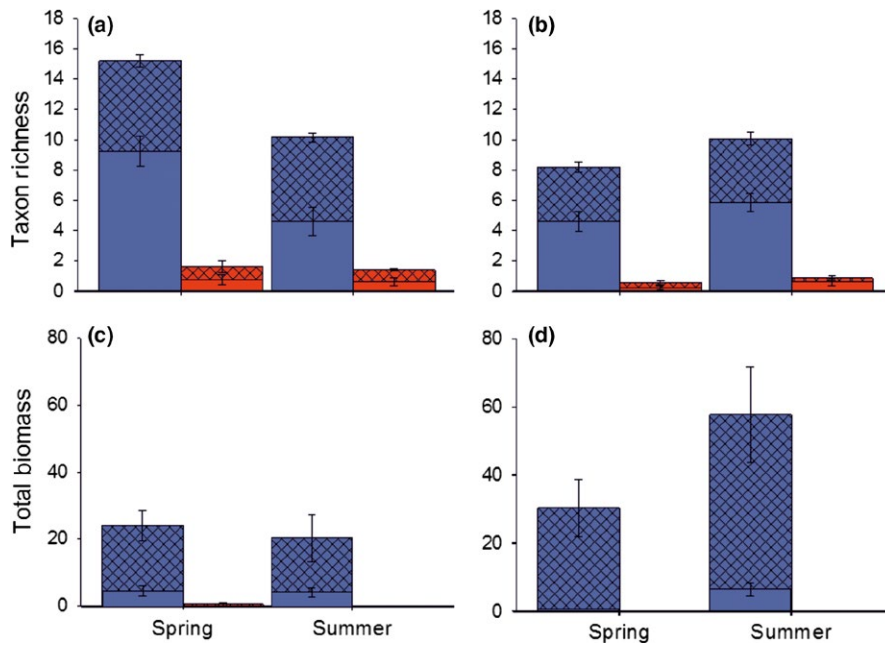


FIGURE 3 Univariate assemblage-level metrics for stipe assemblages: (a) taxon richness at Mewstone, (b) taxon richness at Ramscliff Point, (c) total biomass at Mewstone and (d) total biomass at Ramscliff Point. Blue bars indicate *L. hyperborea*; red bars indicate *L. ochroleuca*. Solid bars indicate sessile faunal assemblage, and hashed bars indicate algal assemblage. Values are means of 15 stipes per site/season/species (\pm SE)

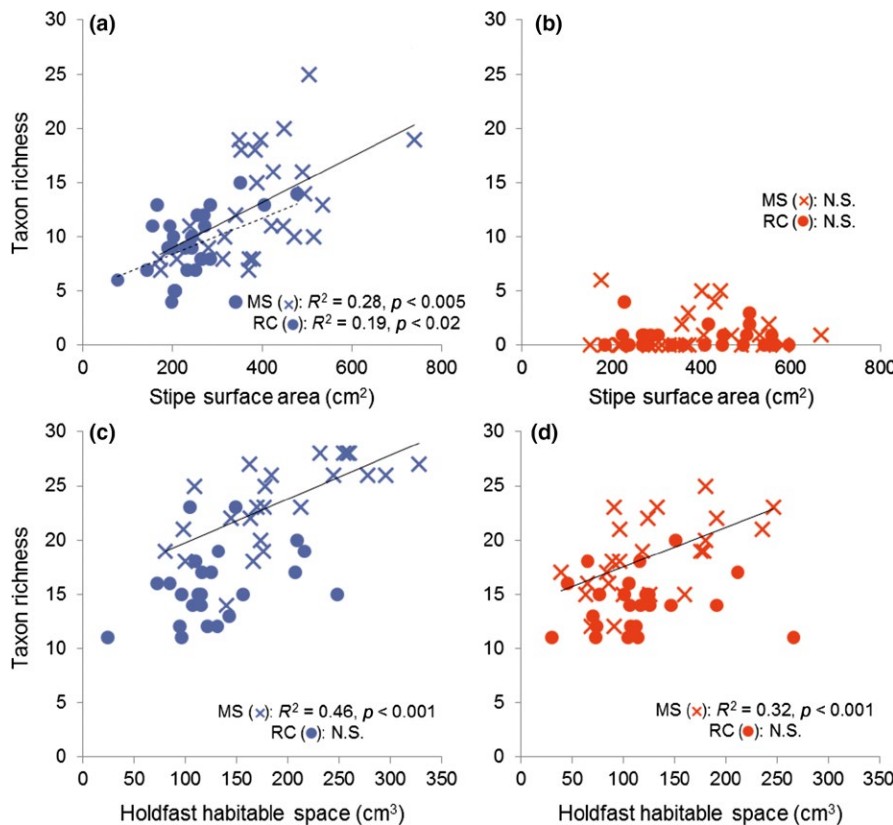


FIGURE 4 Observed relationships between habitat size and taxon richness for both stipe assemblages (a, b) and holdfast assemblages (c, d) for each site and HFS separately. Blue symbols (a, c) indicate *L. hyperborea*; red symbols (b, d) indicate *L. ochroleuca*; crosses represent samples from Mewstone; and circles represent samples from Ramscliff Point

1999) and macroalgae (Harlin & Lindbergh, 1977), to ultimately influence the composition of assemblages. Rough surfaces increase the amount of surface planes available for attachment of macroalgal spores, allow greater penetration by the rhizoids and reduce the likelihood of removal by wave action, leading to more dense growth of macroalgae on these substrates (see Fletcher & Callow, 1992 and references therein). Sessile invertebrates have been demonstrated to settle “preferentially” in concavities and more densely on rough

surfaces than smooth surfaces (e.g., barnacles; Hills & Thomason, 1996, 1998). Postsettlement mortality has also been shown to be lower for sessile invertebrates settling on rough substrates, where the surface features provide refugia (Walters & Wetthey, 1996).

Second, kelps, among other algae, have long been recognized to produce compounds which inhibit the settlement and growth of epibionts (Goecke, Labes, Wiese, & Imhoff, 2010; Hellio, De La Broise, Dufossé, Le Gal, & Bourgougnon, 2001; Hornsey & Hide, 1974). These

TABLE 2 (a) Results of multivariate PERMANOVA to test for differences in holdfast assemblage between kelp species (Sp, fixed), sites (Si, fixed) and sampling event (Ev, fixed)

Source	df	MS	Pseudo-F	p
(a) Multivariate assemblage structure				
CO	1	9,675	13.60	0.0002
Sp	1	3,675	5.16	0.0002
Si	1	17,003	23.91	0.0002
Ev	1	12,258	17.41	0.0002
Sp × Si	1	2,438	3.42	0.0002
Sp × Ev	1	1,543	2.17	0.0106
Si × Ev	1	2,608	3.66	0.0002
Sp × Si × Ev*	1	1868	2.62	0.0020
Residual	87	710		
Total	95			
(b) Taxon richness				
CO	1	834	100.9	0.001
Sp*	1	59.8	7.22	0.008
Si	1	504	61.00	0.001
Ev	1	37.8	4.57	0.042
Sp × Si	1	17.7	2.13	0.154
Sp × Ev	1	12.6	1.52	0.222
Si × Ev	1	31.2	3.77	0.052
Sp × Si × Ev	1	17.7	2.14	0.146
Residual	87	8.30		
Total	95			
(c) Total biomass				
CO	1	396	57.74	0.001
Sp*	1	40.4	5.88	0.017
Si	1	10.4	1.52	0.234
Ev	1	44.4	6.47	0.011
Sp × Si	1	12.4	1.79	0.221
Sp × Ev	1	14.0	2.03	0.170
Si × Ev	1	0.44	0.06	0.813
Sp × Si × Ev	1	0.66	0.97	0.749
Residual	87	6.86		
Total	95			

Note. Holdfast living space was included as a covariate (CO) in the analysis. Permutations were based on a Bray–Curtis similarity matrix generated from fourth-root transformed biomass data. Results of univariate PERMANOVA to test for differences in the assemblage-level univariate metrics (a) taxon richness and (b) total biomass are also shown. Permutations for univariate analysis were based on a Euclidean distance similarity matrix generated from untransformed diversity data. All tests used a maximum of 4,999 permutations under a reduced model; significant effects ($p < 0.05$) are shown in bold. The first significant lower-order effect of interest (i.e., an interaction or main effect involving the species factor) was examined further with pairwise tests (see text and Table S2). Where more than one interaction was detected at the same level, the interaction with greatest significance was selected (marked with an asterisk).

chemicals function as antifoulants and are important in the regulation of biofouling assemblages (Al-Ogily & Knight-Jones, 1977). Exudates from *L. ochroleuca* may inhibit microalgal growth and the attachment and germination of macroalgal spores (Hellio, Bremer, Pons, Le Gal, & Bourgougnon, 2000). In contrast, those produced by *L. hyperborea* exhibit little or none of these effects (Hornsey & Hide, 1974).

Third, and last, loss of epidermatic material has been shown as mechanism for the control of epiphytes in some algae (McArthur & Moss, 1977; Moss, 1982; Sieburth & Tootle, 1981), including some species of kelp (e.g., *Lessonia nigrescens*; Martínez & Correa, 1993). This sloughing of the surface of the epidermis in kelps seems to be most active in young, rapidly growing tissue and has been suggested as a possible driving factor in gradients of epiphyte growth in some *Laminaria* species (see Russell & Veltkamp, 1984 and references therein). While there is currently no evidence of this occurring in relation to *Laminaria ochroleuca*, it may be a possible cause of the stark differences observed between epibiont assemblages found on the stipes of these species and requires further research.

Regardless of the underlying mechanisms driving the observed pattern, the marked differences in the biomass and richness of stipe-associated assemblages between the two HFS are likely to be ecologically significant (as shown in Figure 1). This is because epiphytic algae colonizing kelp stipes represent an important component of temperate reef communities, forming secondary biogenic habitat and increasing overall living space and complexity (Christie, Jorgensen, & Norderhaug, 2007; Thomsen et al., 2010). Indeed, epiphytic algae on kelp stipes can support very high abundances of mobile invertebrates such as gastropods, amphipods and polychaetes (Christie et al., 2003; Teagle et al., 2017), which utilize the habitat for both shelter and food (Christie et al., 2007; Leclerc, Riera, Leroux, Leveque, & Davoult, 2013) and are in turn an important food sources for high trophic levels, such as fish and lobsters (Norderhaug, Christie, Fossa, & Fredriksen, 2005). In addition, stipe-associated algal assemblages can exhibit high levels of primary productivity in their own right and may make a substantial contribution to total primary production within the kelp forest (Leclerc et al., 2013), although the importance of this process can vary considerably between locations (e.g., see Pedersen, Nejrup, Pedersen, & Fredriksen, 2014). As such, a net reduction in the amount of kelp-associated epibionts, caused by a decrease in the strength of an important habitat cascade (sensu Thomsen et al., 2010), is likely to have significant impacts on wider ecological functioning. If the abundance of *L. ochroleuca* relative to *L. hyperborea* continues to increase at its poleward range edge in response to ocean warming, the strength and direction of both trophic and nontrophic species interactions within the kelp forests community will change, with likely shifts in structure and functioning as a result.

In contrast to stipe-associated assemblages, differences in holdfast assemblages between the HFS were less well defined. Both taxon richness and biomass varied between host kelp species and between sites, as greatest values were recorded for *L. hyperborea* populations at the Mewstone. About 78% of the total number of holdfast taxa recorded were found in association with *L. ochroleuca*,

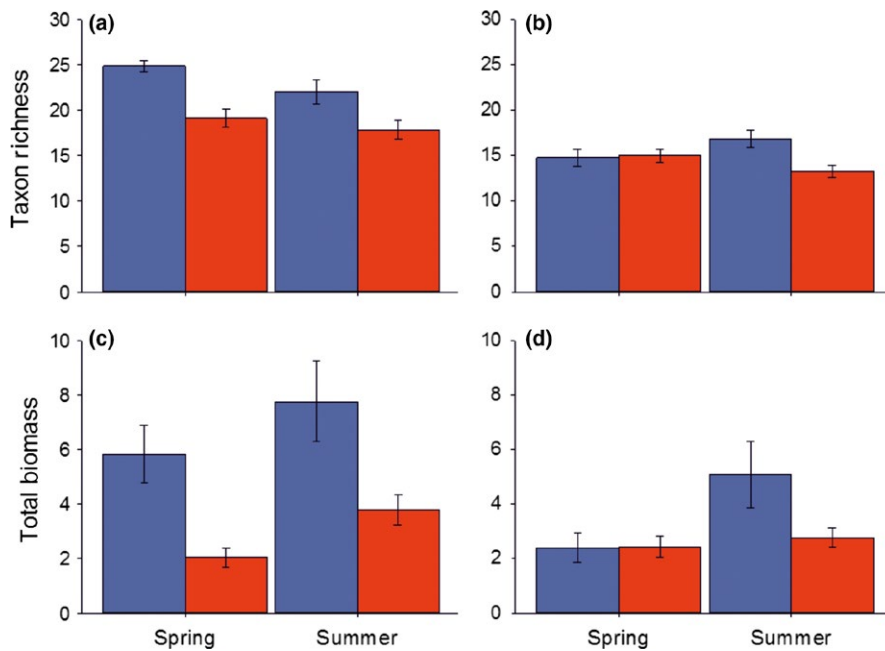


FIGURE 5 Univariate assemblage-level metrics for holdfast assemblages: (a) taxon richness at Mewstone, (b) taxon richness at Ramscliff Point, (c) total biomass at Mewstone and (d) total biomass at Ramscliff Point. Blue bars indicate *L. hyperborea*; red bars indicate *L. ochroleuca*. Values are means of 12 holdfasts per site/season/species (\pm SE)

compared to ~91% in association with *L. hyperborea*. The structure, but not the variability, of holdfast assemblages differed between kelp species. The magnitude of variability between sampling events and sites, however, was greater, indicating the importance of both spatial and temporal environmental variability in structuring kelp holdfast assemblages (e.g., Anderson, Diebel, Blom, & Landers, 2005; Christie et al., 1998). The holdfasts of both species are morphologically and structurally very similar and have similar surface textures, which may account for the similarities between the holdfast assemblages recorded. That said many sessile taxa including red algae and bryozoans were more abundant on the holdfasts of *L. hyperborea*, providing further evidence of a breakdown of an important facilitative interaction with a climate-driven replacement of a cool-water HFS with a warm-water HFS. The majority of previous research into kelps as HFS has focussed solely on the holdfast structure (Teagle et al., 2017). However, the differences between species observed in this study highlight the importance of considering the plant as a whole, as taking into account variability between microhabitats found within species allowed for more representative comparisons to be made across HFS.

The amount, complexity and structure of habitat provided by HFS influence the composition, abundance and richness of associated assemblages. For example, larger more complex holdfast structures have been shown to support more diverse and abundant invertebrate assemblages (Sheppard, Bellamy, & Sheppard, 1980). Likewise, larger stipes that provide a greater surface area for colonization can support a higher biomass of epiphytic algae and, in turn, greater numbers of associated invertebrates (Whittick, 1983). Here, the habitat covariate (i.e., stipe surface area or holdfast living space) was a consistently significant variable in explaining the observed variability in sessile assemblage structure. For the cool-water HFS, *L. hyperborea*, we observed a general pattern of increasing habitat size, for both stipes and holdfasts, corresponding to increased richness in epibiotic assemblages. However,

this pattern was not observed for the warm-water HFS, *L. ochroleuca*, as relationships between habitat size and assemblage metrics were either much weaker (for holdfasts) or not recorded (for stipes). This demonstrates a fundamental breakdown in the facilitative relationship between habitat former and associated organisms and again points to inherent differences in the functioning of these kelp species as HFS.

Due to the substantial level taxonomic work required, our study involved only two sites and events and, as a result, the sampling design and analytical approach did not allow for formal generalizations of the observed patterns across broader spatial or temporal scales. However, anecdotal evidence strongly suggests that the patterns described here are consistent throughout the range of these kelp species and that replacement of the cool-water HFS by the warm-water HFS will alter local biodiversity patterns. In-situ observations made by the authors at >10 sites across these species' overlapping distributions in the south-west UK confirm that *L. hyperborea* consistently supports abundant epiphytic assemblages, whereas *L. ochroleuca* is characteristically devoid of epibionts. Similar patterns have been described for each species independently from other locations across their geographical ranges (Blight & Thompson, 2008; Christie et al., 2003; John, 1969; Norderhaug & Christie, 2011), providing further support and allowing for cautious generalizations to be made.

Within the context of biodiversity conservation, kelp forest communities are protected and managed in some parts of the world, as they provide a range of ecosystem services including habitat provision and high rates of primary productivity, as well as being harvested directly for food, alginate and other products (Blamey & Bolton, 2017; Smale et al., 2013; Vega, Broitman, & Vásquez, 2014). However, ocean warming is driving shifts in the distributions of many HFS of kelp, with knock-on effects for associated communities and habitat structure. When considering the wider impacts of species range shifts, indirect facilitative effects are often overlooked, despite being prevalent in marine ecosystems (Bennett & Wernberg,

2014; Bruno, Stachowicz, & Bertness, 2003). Here, the cool-water HFS facilitated the establishment of abundant and diverse sessile invertebrate and algal assemblages, which in turn will provide habitat for associated mobile invertebrates (e.g., Christie, Norderhaug, & Fredriksen, 2009; Christie et al., 2007), yet the strength of the facilitative interaction was drastically reduced for the warm-water HFS. As such, the positive facilitative interactions that structure this temperate marine community are indirectly broken down by climate, as the relative abundance of *L. ochroleuca* to *L. hyperborea* has increased in response to ocean warming. In actual fact, when considering how communities may change in response to predicted environmental change, it is important to consider not only negative interactions, but also positive facilitative interactions, which are often overlooked but prominent in marine ecosystems (Bulleri, Bruno, Silliman, & Stachowicz, 2016; Thomsen et al., 2010). Recent rapid ocean warming has caused widespread mortality of marine HFS, including seagrasses (Thomson et al., 2015), corals (Moore et al., 2012) and macroalgae (Filbee-Dexter et al., 2016; Smale & Wernberg, 2013), with consequent loss of biodiversity and shifts in community structure (Wernberg et al., 2016). Climate change is, however, also causing species replacements; our study has shown that substitutions of HFS can also lead to a restructuring of communities and depletion of local biodiversity, despite the HFS seeming functionally similar.

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DATA ACCESSIBILITY

Data will be deposited in the GBIF repository.

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BIOSKETCHES

Harry Teagle recently completed his PhD studies, which focussed on the wider indirect effects of climate change on kelp forests in the north-east Atlantic.

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Author contributions: H.T. and D.A.S. jointly conceived the study, analysed data and wrote the manuscript; D.A.S. led sample collection; and H.T. conducted sampling processing and taxonomic analysis.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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