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RESEARCH ARTICLE

Climate-driven substitution of foundation species causes breakdown of a facilitation cascade with potential implications for higher trophic levels

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Abstract

1. Climate change can alter ecological communities both directly, by driving shifts in species distributions and abundances, and indirectly by influencing the strength and direction of species interactions. Within benthic marine ecosystems, foundation species such as canopy-forming macro-algae often underpin important cascades of facilitative interactions.
2. We examined the wider impacts of climate-driven shifts in the relative abundances of foundation species within a temperate reef system, with particular focus on a habitat cascade whereby kelp facilitate epiphytic algae that, in turn, facilitate mobile invertebrates. Specifically, we tested whether the warm-water kelp *Laminaria ochroleuca*, which has proliferated in response to recent warming trends, facilitated a secondary habitat-former (epiphytic algae on stipes) and associated mobile invertebrates, to the same degree as the cold-water kelp *Laminaria hyperborea*.
3. The facilitative interaction between kelp and stipe-associated epiphytic algae was dramatically weaker for the warm-water foundation species, leading to breakdown of a habitat cascade and impoverished associated faunal assemblages. On average, the warm-water kelp supported >250 times less epiphytic algae (by biomass) and >50 times fewer mobile invertebrates (by abundance) than the cold-water kelp. Moreover, by comparing regions of pre- and post-range expansion by *L. ochroleuca*, we found that warming-impacted kelp forests supported around half the biomass of epiphytic algae and one-fifth of the abundance of mobile invertebrates, per unit area, compared with unimpacted forests. We suggest that disruption to this facilitation cascade has the potential to

impact upon higher trophic levels, specifically kelp forest fishes, through lower prey availability.

4. *Synthesis*. Climate-driven shifts in species' distributions and the relative abundances of foundation organisms will restructure communities and alter ecological interactions, with consequences for ecosystem functioning. We show that climate-driven substitutions of seemingly similar foundation species can alter local biodiversity and trophic processes in temperate marine ecosystems.

KEYWORDS

climate change, macroalgae, species interactions, temperate reefs, warming

1 | INTRODUCTION

Ecological interactions, such as competition, predation and facilitation, play a key role in structuring communities and ecosystems (Kordas et al., 2011; Stachowicz, 2001; Tylianakis et al., 2008). The disproportionate role of foundation species (sensu Dayton, 1972) that alter local environmental conditions and resource availability, often underpinning positive facilitative interactions with other species, has been increasingly appreciated (Bruno & Bertness, 2001; Thomsen et al., 2010). Moreover, such foundation species can also have indirect positive effects on other organisms via cascading interactions (Thomsen et al., 2010). That is, the presence of a secondary habitat-former may elevate biodiversity, but this is itself dependent on the provision or modification of habitat by the primary foundation species (Altieri et al., 2007; Thomsen et al., 2022). These facilitative habitat cascades are prominent across a range of biogeographical contexts, in both terrestrial (Angelini & Silliman, 2014; Cruz-Angón & Greenberg, 2005; Ellwood & Foster, 2004; Stuntz et al., 2002) and marine ecosystems (Bologna & Heck Jr, 1999; Hall & Bell, 1988; Thomsen et al., 2016), but remain poorly described and understood.

Recent rapid anthropogenic warming has led to a global redistribution of ectothermic species as their thermally favourable habitats shift (Poloczanska et al., 2013; Sunday et al., 2012; Thomas, 2010). Range shifts of foundation species can have disproportionate impacts on communities and ecosystems, given that many associated species are reliant on them directly for habitat and/or food, or indirectly via modification of the local environment (Ellison et al., 2005; Smale & Wernberg, 2013; Thomson et al., 2015). In some cases, however, vacating foundation species may be replaced by functionally similar species that provide comparable primary habitat to support secondary habitat-formers and, as such, wider ecosystem functioning and biodiversity may be maintained (Bulleri et al., 2018). Conversely, where shifting foundation species are not replaced or replaced by dissimilar species that do not facilitate secondary habitat-formers, habitat cascades may be disrupted with consequences for associated communities and local biodiversity. Evidence of climate-driven disruption to habitat cascades is lacking, despite the recognised importance of facilitative interactions in a warming world (Stachowicz, 2001).

Kelps are foundation species that dominate shallow rocky reefs along temperate and polar coastlines (Steneck et al., 2002; Wernberg et al., 2019) and the forests they form represent highly diverse and productive ecosystems (Reed et al., 2008; Smale et al., 2013; Teagle et al., 2017). As kelp species distributions are strongly constrained by temperature (Eggert, 2012), they are sensitive to warming trends and range shifts have been observed all over the world (Fernandez, 2011; Filbee-Dexter et al., 2016; Verges et al., 2014), with wide-ranging implications for associated biodiversity and ecosystem functioning (Tuya et al., 2012; Voerman et al., 2013; Wernberg et al., 2013).

In the North East Atlantic, the cold-adapted boreal species, *Laminaria hyperborea*, is a dominant habitat-former throughout its distribution from northern Norway to northern Portugal (Figure 1a), particularly on wave-exposed shallow subtidal reefs (Kain, 1979; Smale & Moore, 2017). Atypically among kelp species, *L. hyperborea* supports abundant epiphytic algal assemblages on its stipe, which serve as secondary habitat-formers (King et al., 2021; Whittick, 1983). This habitat cascade increases living space and complexity for abundant and diverse assemblages of mobile invertebrate fauna, which represent an important food resource for higher trophic levels (King et al., 2021; Norderhaug et al., 2005).

In the United Kingdom (UK), the morphologically similar warm-adapted species, *Laminaria ochroleuca*, is found towards its leading range edge where it competes with *L. hyperborea* for space and resources. *L. ochroleuca*, which is distributed from Morocco and the Mediterranean northwards to the UK and Ireland, has proliferated in southwest UK in recent decades (Teagle & Smale, 2018), and is predicted to expand polewards with continued warming (Assis et al., 2017). Unlike *L. hyperborea*, however, *L. ochroleuca* lacks the characteristic secondary habitat provided by stipe-associated epiphytic algae (Smale et al., 2015). Intuitively, a climate-driven substitution of the cold-adapted *L. hyperborea* with the warm-adapted *L. ochroleuca* at some locations could disrupt an important habitat cascade, with implications for local biodiversity and higher trophic levels, but evidence is currently lacking. Crucially, relative to facilitation cascades underpinned by other primary foundation species (i.e. seagrass, mangroves, bivalves), little is known about facilitation cascades in kelp forest ecosystems (Gribben et al., 2019).

Here, we adopted mixed kelp forests in the UK as a model system to test the following hypotheses: (1) climate-driven substitution

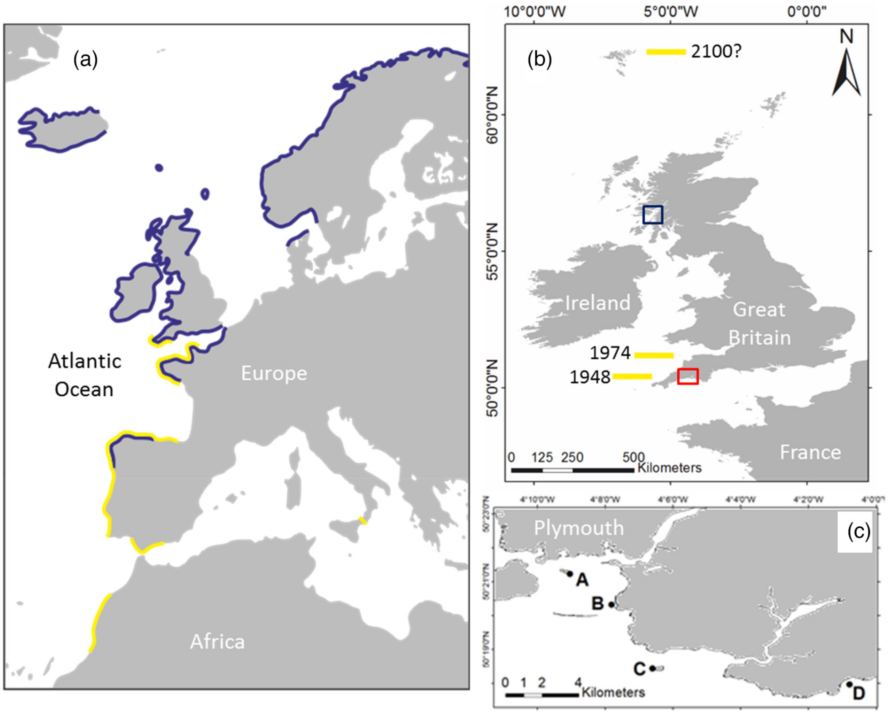

FIGURE 1 Maps indicating (a) the current distributions of *Laminaria hyperborea* (purple) and *Laminaria ochroleuca* (yellow), (b) the spread of *L. ochroleuca* after its first record in the UK in 1948 and the predicted poleward range edge of *L. ochroleuca* in 2100, and (c) the locations of the four study regions within Plymouth sound, Southwest UK: (a) Drakes Island, (b) Ramscliff point, (c) the northwest Mewstone and (d) stoke point. Map (b) also shows the wider location of the study area in the southwest of England (red box), and the comparison region in West Scotland (black box). The predicted future distribution of *L. ochroleuca* is taken from Assis et al. (2017).

of foundation species leads to a weakening of a facilitative interaction; (2) disruption to an important habitat cascade results in impoverished, distinct mobile invertebrate assemblages; and (3) lower abundances of mobile invertebrates potentially reduce prey availability for higher trophic levels (e.g. predatory fish). We thereby explored the consequences of intra-generic replacements of morphologically similar species, differing only in some superficially small traits, but with likely major consequences for community structure and ecosystem functioning.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was primarily conducted in SW England (UK), which is characterised by shallow subtidal reefs that support extensive kelp forests (Smale & Moore, 2017). Surveys and collections were conducted at four sites within and just outside of Plymouth Sound (Figure 1c); Drakes Island (site 'A'), Ramscliff Point (B), the northwest Mewstone (C) and Stoke Point (D). The sites spanned a wave exposure gradient, whereby site A was the most sheltered site and site D the most exposed site. All sites were characterised by extensive gently sloping subtidal rocky reef at depths of 0 to >5 m (below chart datum). Additional survey work was conducted in western Scotland (see Section 2.5 below).

2.2 | Kelp canopy structure

The density of the two kelp species was quantified through in situ surveys by scuba diving. At each site, 10 replicate 1 m^2 quadrats were haphazardly placed within dense kelp stands and the densities (inds. m^{-2}) of mature, canopy-forming *Laminaria hyperborea* and *Laminaria ochroleuca* plants were recorded. Sites were surveyed in summer (June–August) 2015 and values obtained (see Section 3) were comparable to previous more-detailed surveys in the region (Smale et al., 2016; Smale & Moore, 2017), being representative of wider habitat structure. Other habitat-forming macroalgae present at low densities included the more opportunistic *Saccharina latissimia* and *Saccorhiza polyschides* (Smale & Moore, 2017; Smale & Vance, 2015).

2.3 | Sample collection and processing

Five replicate stipe samples were collected from each species in early autumn (i.e. September/October) at each of the four sites (20 samples of each species). Mature, individual canopy-forming plants were selected haphazardly from within well-established kelp stands at depths of 2–4 m (below chart datum). Individual kelp plants were collected from at least two metres apart in areas where the two species were intermixed. Divers removed the blade from selected kelp plants, before immediately enclosing the stipe, its epiphytic assemblage and any associated invertebrates within a fine-mesh cotton bag. The stipe was then removed by cutting immediately above the holdfast and the bag sealed with a cable tie. Samples were immediately processed on return to the laboratory. Stipes were carefully removed from the bag and rinsed thoroughly under freshwater to remove all associated mobile fauna; these were collected in a 1-mm sieve and preserved in 70% industrial methylated spirit (IMS) solution prior to identification. All epiphytic algae were then removed from the stipe (any additional animals were removed and added to the sample), and weighed (wet weight) to quantify biomass. Animals were subsequently identified to species level where possible (~74% of taxa) and counted. The age of each kelp plant was estimated by counting the number of annual growth rings in the basal section of the stipe sample (Kain, 1963).

2.4 | Manipulative experiment

In July 2019, a field-based manipulative experiment further examined the nature and strength of facilitative interactions between the foundation species (i.e. kelp), the secondary habitat-former (i.e. red epiphytes) and the focal assemblage (i.e. mobile invertebrates). At two sites ('B' and 'C' described above), three treatments were established on bare *L. hyperborea* stipes: no epiphytes, low density of epiphytes and high density of epiphytes. Initially, an abundant stipe-associated epiphyte, *Palmaria palmata*, was collected from the field and returned to the laboratory, where it was thoroughly rinsed to remove any associated fauna. Epiphytes were then weighed and sorted into low-density (mean ± SD wet weight biomass = 15.7 ± 1.4 g) and high-density (59.8 ± 2.4 g) treatments, with five replicates for each site placed in separate bags. *P. palmata* is a common and abundant epiphyte on *L. hyperborea* stipes and densities (i.e. biomass values) were representative of naturally occurring epiphytic assemblages (King et al., 2021; Teagle & Smale, 2018). For each replicate, multiple *P. palmata* thalli were carefully tied together at the base, secured with tape and affixed to an open cable tie for easy attachment onto stipes in the field. At the site, divers randomly selected and tagged 15 *L. hyperborea* plants, which were rigorously cleaned to remove any flora and fauna on stipes. Epiphytic algae were then carefully removed from each bag and cable tied around the bare stipe (towards it base), with five stipes randomly assigned to each of the low- and high-density treatments and five stipes left bare of epiphytes (see Figure S1 for example). The experiment was set up in summer and after 9 days the plants were relocated; a 10 cm section of stipe (which included the epiphytes where present) was then excised and placed in individual labelled bags. On return to the laboratory, the stipe and epiphytes were weighed, and all fauna was passed through a 1-mm sieve, sorted to a coarse taxonomic level and counted.

2.5 | Latitudinal comparison between pre-and post-range expansion

To examine the likely impacts of continued range expansion of the warm-water kelp *L. ochroleuca* into kelp forests dominated by the cold-water *L. hyperborea*, a space-for-time substitution approach was used by comparing across latitudes a region which has not yet experienced an incursion of the range expanding kelp ('pre-expanded') with the current study region ('post-expanded'). The current northern distribution limit of *L. ochroleuca* in the UK is in the southwest of England (n.b. an isolated marginal population has been recorded at a higher latitude in Ireland—see Schoenrock et al., 2019), but it is predicted to expand polewards to the north of Scotland by the end of the century (Assis et al., 2017, Figure 1b). As such, the west of Scotland was selected as a 'pre-expanded' region in which to examine and compare facilitative interactions and assemblage structure within kelp forests. Subtidal kelp forests in west Scotland were characterised by similar conditions, reef topography and wave exposure to those in sampled near Plymouth (Smale et al., 2016; Smale & Moore, 2017). However, these kelp forests are yet to be influenced by range expansion of *L. ochroleuca* and are dominated by *L. hyperborea*; they therefore offer an opportunity to compare current pre-warming (i.e. monospecific stands of cold-adapted kelp species) with likely future conditions (i.e. mixed kelp stands following the expansion of a warm-adapted species). The overall density of kelps (*L. ochroleuca* and *L. hyperborea*, m^{-2}), the total biomass of stipe associated epiphytic algae (m^{-2}) and the total abundance of epiphyte associated mobile fauna (m^{-2}) were compared between regions, using identical approaches. Two survey sites from within each region were selected for the comparison; all sites were broadly comparable in wave exposure, substrate type, nutrients and light availability, and grazing pressure, but the regions differed in mean sea temperature (by ~2.5°C) and the presence of *L. ochroleuca* (Smale & Moore, 2017).

2.6 | Fish stomach contents

During the late summer of 2015, fish were sampled from within dense kelp forests in southwest England (at sites C&D) using a combination of fyke nets (set by divers) and rod and line fishing. In total, 21 fish were caught, these were weighed, measured and identified to species, before immediately removing the stomach and digestive tract and transferring them to 70% IMS solution for preservation. Stomach contents were later analysed; the poor condition of many prey organisms allowed for identification only to a high taxonomic level (i.e. order or class) or to a morphological group. The wet weight and abundance of each group was then quantified (abundances of partly digested prey items were estimated from shell fragments, number of antennae, gnathopods, jaws and other conspicuous remains). The guts of two individuals (both *Pollachius pollachius*, pollack) were entirely empty and were excluded from further analysis. Fish were sampled under a dispensation granted by the Devon and Severn Inshore Fisheries and Conservation Authority (IFCA) and dispatched under a UK Home Office licence granted to MBA; no other permits were required for fieldwork.

2.7 | Statistical analysis

All analysis was conducted using univariate/multivariate permutational analyses using the PERMANOVA add on (Anderson et al., 2008) for Primer v7 software (Clarke & Gorley, 2015). Variability in faunal taxon richness and abundance were examined with univariate PERMANOVA using a two-factor design, with kelp 'Species' (2 levels) and 'Site' (4 levels, representing a gradient in wave exposure) as fixed factors. To examine correlations with habitat size, epiphyte biomass was included as a covariable in the analysis. Univariate habitat metrics (i.e. epiphyte biomass and kelp age) were examined using the same model, but without the covariable.

Kelp density data were converted to the abundance of *Laminaria ochroleuca* relative to the kelp assemblage as a whole (i.e. *L. ochroleuca* + *L. hyperborea*), and was subsequently analysed using a one-factor design with 'Site' (4 levels) as a fixed factor. All permutations (4999 under a reduced model) were based on a similarity matrix of Euclidean distances between untransformed data. Pairwise tests were conducted wherever significant main effects of interactions were observed ($p < 0.05$).

Variability in faunal assemblage structure was examined with multivariate PERMANOVA using a Bray–Curtis similarity matrix constructed from fourth-root transformed abundance data. The model used included the Species and Site fixed factor, with the epiphyte biomass co-variable. Where significant differences in assemblage structure were detected, SIMPER analysis was performed to establish which taxa contributed most to the observed dissimilarity. For all analyses, differences in within-factor dispersion were examined with the PERMDISP routine.

For the manipulative experiment, differences in faunal abundance and richness between treatments were also examined with one-way univariate PERMANOVA (with treatment as fixed factor, each site analysed separately); permutations were based on Euclidian distances between untransformed data.

3 | RESULTS

3.1 | Habitat structure

Relative dominance by *L. ochroleuca* and *L. hyperborea* shifted along the wave exposure gradient, with *L. ochroleuca* becoming more abundant towards sheltered sites, and *L. hyperborea* becoming more abundant with increasing exposure (Figure 2a). The relative abundance of *L. ochroleuca* to *L. hyperborea* thereby exhibited a clear trend with wave exposure (Figure 2b), being significantly different between sites (PERMANOVA; $F_{3,39} = 31.55$, $p = 0.001$; site B = C, all other sites differed significantly from one another). The surface area of stipes was similar between species, but differed across sites ($F_{3,39} = 4.14$, $p = 0.013$; Table S1), with stipes of host kelps being generally larger in more wave exposed conditions (site A was statistically different to all others; Figure 2c). The kelp species were broadly similar in age structure, with study-wide mean age of collected *L. ochroleuca* and *L. hyperborea* plants being 4.6 ± 0.4 (SE) and 5.7 ± 0.3 (SE), respectively. The total biomass (wet weight) of epiphytic algae differed greatly between kelp species (Figure 2d), as the average biomass of epiphytes associated with *L. hyperborea* was >50 g per plant at all study sites. In stark contrast, *L. ochroleuca* was devoid of any epiphytes at all but the most exposed site. The epiphytic biomass associated with *L. hyperborea* was significantly greater, this pattern being consistent across sites ($F_{1,39} = 22.51$, $p = 0.001$; Table S1).

3.2 | Assemblage structure

In total, 2430 individuals representing 73 taxa from 6 phyla were recorded from the 40 stipe samples (20 stipes per species; Table S2). Over 70% of taxa identified were recorded exclusively in association with *L. hyperborea*. In contrast, only ~2.5% of taxa were recorded exclusively in association with *L. ochroleuca*. The overall assemblage was dominated by amphipods (26 taxa), which made up >35% of the total fauna recorded. Polychaete worms (14 taxa) and gastropod molluscs (11 taxa) were also well represented. The remainder of the assemblage was made up of pycnogonids (5 taxa), decapods (4 taxa), isopods (4 taxa), chitons (2 taxa), brittlestars (2 taxa), mysids (1 taxa), bivalve molluscs (1 taxa), starfish (1 taxa), platyhelminthes (1 taxa) and nemertea (1 taxa). Nearly 50% of *L. ochroleuca* stipes were devoid of invertebrate fauna.

The total abundance of mobile invertebrates ranged from 19 to 375 per stipe and 0 to 25 per stipe for *L. hyperborea* and *L. ochroleuca*, respectively. Mean abundance values were consistently and markedly higher for *L. hyperborea* assemblages compared with *L. ochroleuca* (Figure 2e). Univariate PERMANOVA detected a significant species × site interaction term ($F_{3,39} = 3.52$, $p = 0.021$; Table S3), as the magnitude of difference between the kelp species was lower at site D (but still significant, $p < 0.01$). The main effect of kelp species was highly significant ($F_{1,39} = 6.89$, $p = 0.013$), as was the epiphyte biomass covariable (Table S3). Taxon richness varied from 8 taxa to 29 taxa per stipe for *L. hyperborea* stipes, and from 0 taxa (9 stipes) to 9 taxa for *L. ochroleuca* stipes. Again, mean taxon richness values were notably higher for *L. hyperborea* assemblages compared with *L. ochroleuca* (Figure 2f). At site D, for example, *L. hyperborea* supported ~5.5 times as many taxa as *L. ochroleuca*. Taxon richness associated with *L. hyperborea* was significantly higher than *L. ochroleuca*, which was consistent across sites ($F_{1,39} = 66.86$, $p = 0.001$; Table S3). Across the survey sites, significant positive relations were recorded between epiphyte biomass and faunal abundance and richness (Figure S2, Table S4).

Principal component ordination (PCO) plots indicated clear partitioning in multivariate assemblage structure between host species, with some small degree of convergence only evident at the most exposed site (site D; Figure 3a). PCO also indicated partitioning between sites, with a gradient evident between the most sheltered and most exposed sites (Figure 5a). PERMANOVA detected a significant site × species interaction ($F_{3,39} = 2.75$, $p = 0.001$; Table S3), suggesting that the magnitude of difference between species was not consistent between sites. Pairwise tests within the interaction term showed that assemblages associated with *L. hyperborea* were statistically distinct from those associated with *L. ochroleuca* at all sites; but the magnitude of dissimilarity was lower at site D. The main effects of species ($F_{1,39} = 26.73$, $p = 0.001$) and site ($F_{3,39} = 3.90$, $p = 0.001$) were highly significant (Table S3). The covariable, epiphyte biomass, was significantly correlated with assemblage structure (Table S3), and bubble plots overlaid onto the PCO plot showed how partitioning in assemblage structure was correlated with epiphytic biomass (Figure 3b). SIMPER analysis was used to identify which taxa were the principal contributors to the observed dissimilarity in assemblage structure between the kelp species. The dissimilarity in mobile invertebrate assemblages between kelp species was consistently related to lower abundances of dominant amphipods and polychaetes on *L. ochroleuca* stipes compared with *L. hyperborea* stipes (Table S5).

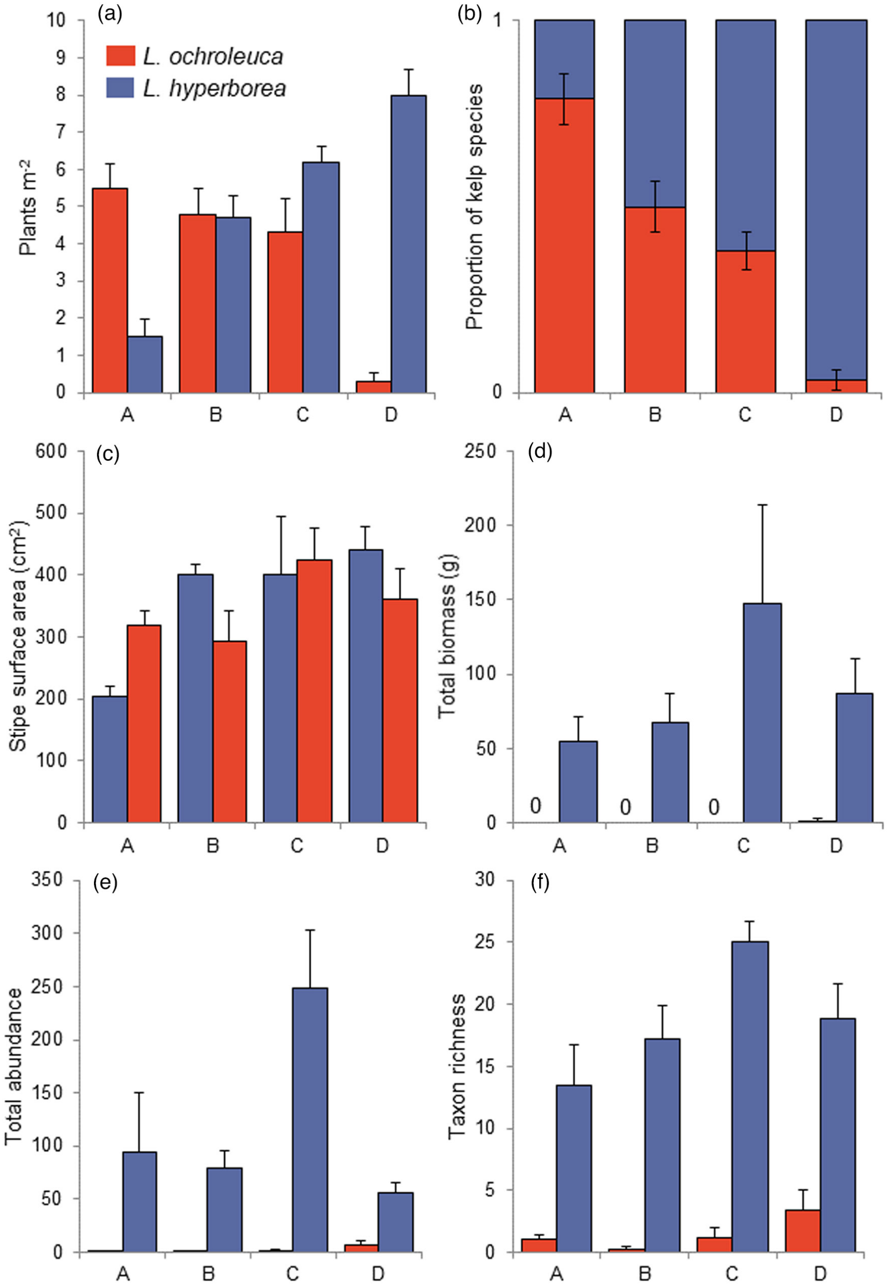

FIGURE 2 Habitat structure of mixed *Laminaria ochroleuca* (red bars) and *Laminaria hyperborea* (blue bars) kelp stands at each site, showing both (a) absolute densities of mature plats and (b) relative densities. Density measurements are means derived from 10 m^2 replicate quadrats at each site. Lower plots show (c) stipe surface area, (d) epiphyte biomass, (e) mobile invertebrate abundance and (f) taxon richness for each kelp species at each site. All values are means derived from five replicate stipes per species, per site (mean ± SE). Sites A–D were situated along a wave exposure gradient, from least to most exposed.

3.3 | Manipulative experiment

The presence and density of epiphytes associated with *L. hyperborea* stipes had a significant influence on the abundance and richness of mobile invertebrates (Figure 4). At both sites, stipes with a low density of epiphytes supported significantly greater numbers of mobile invertebrates than stipes with no epiphytes, and stipes with a high density of epiphytes supported greatest faunal abundances (site B: $F_{2,14} = 12.52$, $p = 0.003$, post hoc tests = all groups different, site C: $F_{2,14} = 24.61$, $p = 0.002$, post hoc tests = all groups different). Similarly, at both sites, the richness of mobile invertebrates increased with increasing density of stipe epiphytes, although low- and high-density treatments did not differ statistically (site B: $F_{2,14} = 14.43$, $p = 0.003$, post hoc tests = N < LD = HD, site C: $F_{2,14} = 18.51$, $p = 0.002$, post hoc tests = N < LD = HD). Across all treatments and sites, significant positive relationships were observed between epiphyte biomass and faunal abundance and richness (Figure S2, Table S4).

3.4 | Latitudinal comparison

The density of kelp plants per square metre was comparable across regions (Plymouth: 10 plants m^{-2}; Scotland: 9 plants m^{-2}; Figure 5a). *L. ochroleuca* comprised ~45% of the plants recorded across both sites in southwest England. The total biomass of stipe-associated epiphytes differed markedly between

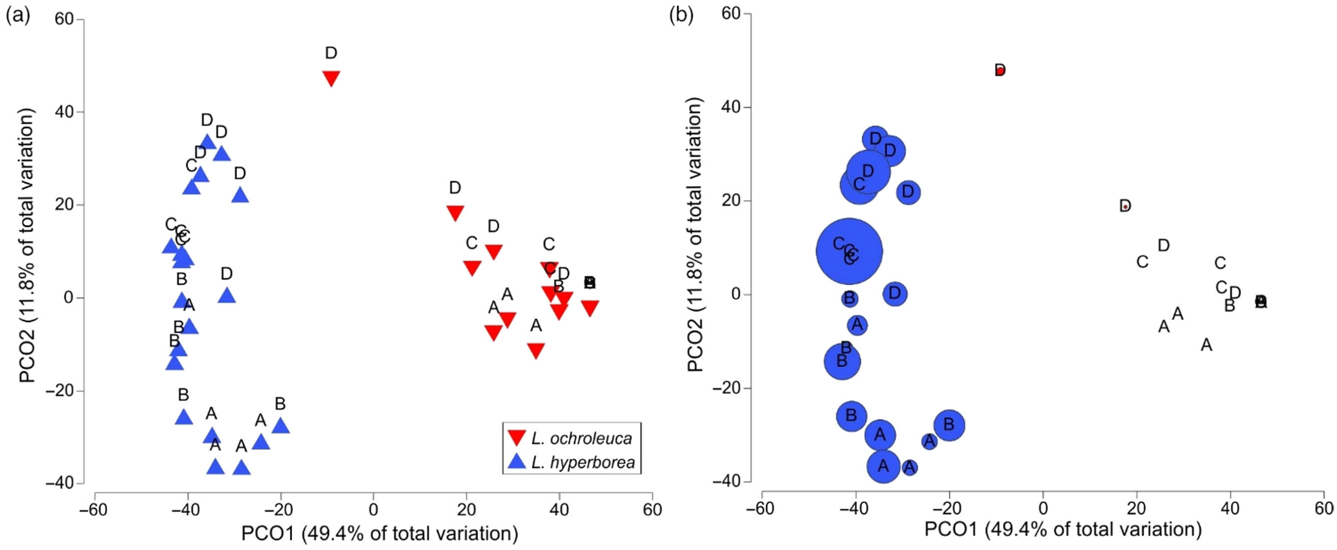

FIGURE 3 Principal component ordinations depicting the structure of stipe assemblages (a) and overlaid with bubbles representing epiphyte biomass (b). Red points indicate *Laminaria ochroleuca* assemblages, and blue points indicate *L. hyperborea* assemblages. Labels indicate site; sites A–D were situated along a wave exposure gradient, from least to most exposed. Circles enclose samples devoid of any faunal assemblage.

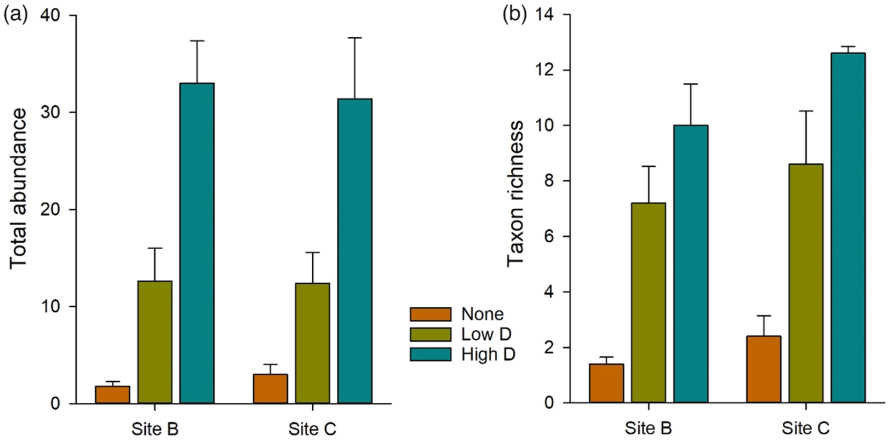

FIGURE 4 Results of manipulative experiment conducted at two sites to examine influence of stipe epiphyte density of mobile invertebrate (a) abundance and (b) taxon richness. All values are means derived from five replicates per treatment, per site (mean ± SE).

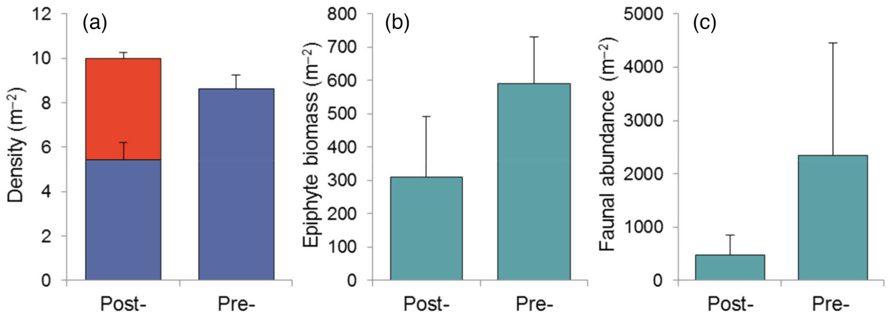

FIGURE 5 Latitudinal comparison across regions that have (Southwest England) and have not (West Scotland) been subjected to a range expansion of *Laminaria ochroleuca*: (a) density of kelp plants, (b) epiphyte biomass, and (c) the abundance of mobile invertebrates per unit area within each region. Red bars indicate *Laminaria ochroleuca*, blue bars indicate *Laminaria hyperborea* and teal bars indicate combined values for the kelp stand (all shown mean ± SE).

regions, with almost twice the amount of algae (per unit area) recorded in Scotland (Figure 5b). Differences in the abundance of mobile faunal assemblages were even more pronounced, with total abundances (per unit area) in the pre-expansion region ~5 times greater than that in the post-expansion region (Figure 5c).

3.5 | Fish stomach contents

From the 19 fish stomachs analysed, 10 higher taxonomic groups (class or order) and 6 morphological groups were identified (Table 1). Prey items were largely comparable across fish species. The exception was *Labrus bergylta* (Ballan wrasse), which fed more heavily on gastropods compared with the other species (Table 1). Generally, the groups observed in the fish stomachs reflected the dominant taxa sampled in the stipe-associated assemblages, with high abundances of decapods, gastropods, isopods and gammarid and caprellid amphipods observed in all instances. Even so, comparisons of the relative abundances of major taxonomic groups between stipe assemblages and fish gut contents showed a higher representation of gastropods and decapods and a lower representation of nemertean and polychaete worms in fish guts, compared with stipe assemblages (Figure S3).

4 | DISCUSSION

Climate-driven shifts in the distribution and abundance of habitat-forming macroalgae can significantly alter the structure and functioning of coastal marine ecosystems (Fernandez, 2011; Smale & Wernberg, 2013; Voerman et al., 2013; Wernberg et al., 2013, 2016). The vast majority of evidence to date, however, has focussed on the loss of these foundation species. Our study suggests that climate-driven substitutions of structurally and taxonomically similar species can have significant impacts on local biodiversity patterns, through weakening of a facilitative interaction leading to complete breakdown of a critical habitat cascade, with consequences for higher trophic levels. A recent increase in the abundance of *Laminaria ochroleuca* relative to *Laminaria hyperborea* at certain locations, driven by recent warming, has disrupted an important habitat cascade associated with the stipe–epiphyte complex, leading to significantly reduced secondary habitat and impoverished faunal assemblages (Figure 6). Reductions in faunal abundances may limit the quantity and composition of available prey items, with potential impacts on kelp forest fishes (Figure 6).

Kelp forests support high biodiversity in coastal marine ecosystems (Steneck et al., 2002; Teagle et al., 2017). The secondary habitat provided by epiphytic algae on kelp stipes has been shown to facilitate the development of highly diverse and abundant faunal assemblages (Christie, 1995; Christie et al., 2003; King et al., 2021). Epiphyte biomass varied dramatically between species, with 90% of *L. ochroleuca* stipes devoid of any epiphytic material. Across our southwest England survey, the total biomass of epiphytes found in association with *L. hyperborea* was 1783 g, over 250 times greater than those observed on *L. ochroleuca*, which supported just 7 g in total and was only present at the most exposed site. Marked variability in the biomass of secondary habitat-formers between host kelp species was consistent across sites, providing strong support for our first hypothesis, that a climate-driven substitution of *L. ochroleuca* over *L. hyperborea* weakens a facilitative interaction.

A number of recent studies have compared habitat provision by different species, and in general have shown that different kelps host distinct assemblages (e.g. Blight & Thompson, 2008; Teagle & Smale, 2018; Tuya et al., 2011). Here, despite offering similar habitat structure (e.g. stipe surface area, plant age), mobile invertebrate assemblages associated with *L. hyperborea* and *L. ochroleuca* stipes differed markedly. Of the 2430 individuals recorded across the study, over 98% were found in association with *L. hyperborea*. On average, each *L. hyperborea* stipe hosted ~120 individuals representing ~17 taxa, whereas *L. ochroleuca* hosted just over two individuals representing ~1.5 taxa per plant. The marked difference in epiphyte biomass observed between these kelp species underpins the observed variation in associated invertebrate assemblage structure, as demonstrated by our manipulative experiment. As such, our second hypothesis, disruption of a habitat cascade leads to impoverished, distinct mobile invertebrate assemblages associated with *L. ochroleuca*, was strongly supported. Given that stipe assemblages associated with *L. hyperborea* in southwest England are comparatively lower in abundance and richness than those further north in Scotland and Norway (e.g. Christie et al., 2003; King et al., 2021), replacement by *L. ochroleuca* in other regions (albeit not predicted until the end of the century, see Assis et al., 2017) could lead to even greater shifts in stipe assemblage structure and diversity.

Ecological interactions are mediated by the environmental context in which they occur (Harley et al., 2012; Sanford, 1999). In the current study, the strength of the facilitative interaction between kelp plants and stipe-associated epiphytic algae differed between sites along a wave exposure gradient. With regards to *L. hyperborea*, the biomass of epiphytes and the taxon richness (and to a lesser extent, the total abundance) of associated invertebrate assemblages all followed a similar pattern, with higher values generally recorded at the more wave -exposed sites (i.e. C and D) compared with more sheltered sites (i.e. A and B). The importance of wave exposure in structuring epiphytic algal and invertebrate assemblages associated with *L. hyperborea* has been demonstrated previously (Andersen, 2007; Christie et al., 2003; Norderhaug & Christie, 2011). Greater epiphyte biomass at higher wave exposure levels was likely driven by a range of factors, including (i) increased light penetration through the overlying canopy with greater water movement (e.g. in *Macrocystis pyrifera* forests; Wing et al., 1993); (ii) more efficient transfer of nutrients across algal surfaces under greater water motion, leading to increased growth rates (Norderhaug et al., 2014); (iii) greater availability of biogenic habitat for colonisation at higher wave exposures, due to morphological responses of the kelps themselves (Pedersen et al., 2014; Smale et al., 2016); and reduced grazing pressure at higher wave exposures (Rinde et al., 2014; Taylor & Schiel, 2010). Only at the most exposed site did *L. ochroleuca* host any epiphytic algae, at low biomass, being devoid of epiphytes at other sites in contrast to *L. hyperborea*. It is clear, even with site-level variability in epiphyte biomass and assemblage structure for both species, that the facilitative interaction between kelp and epiphytic algae is consistently much stronger for *L. hyperborea* compared to *L. ochroleuca*, regardless of environmental context, which provides further support for our first hypothesis. This is despite both congeneric species being morphologically and functionally very similar,

TABLE 1 Results of fish gut content analysis from fish caught within kelp forests in SW England. Mean values (±SE) for total length (TL) and wet weight (WW) are given below each species. Values for prey items are biomass (g) with abundance values in parentheses

Species	***Pollachius pollachius* (Pollock)** **TL = 316.5 ± 21.4** **WW = 286.2 ± 57.9**						***Labrus bergylta* (Ballan wrasse)** **TL = 296.3 ± 18.5** **WW = 432.7 ± 77.9**		
Fish #	**1**	**2**	**3**	**4**	**5**	**6**	**1**	**2**	**3**
Decapoda	<0.001 (1)	<0.001 (1)	1.818 (1)		0.809 (1)		0.216 (4)	2.175 (22)	0.289 (4)
Gastropoda							1.359 (156)	0.655 (115)	0.062 (22)
Bivalvia								0.011 (3)	<0.001 (1)
Polychaetea				0.002 (1)		0.003 (1)	0.015 (2)	<0.001 (1)	0.011 (1)
Cephalopoda		1.786 (1)							
Gammaridae	0.008 (4)	<0.001 (1)	0.004 (4)		0.047 (14)	0.019 (5)	0.016 (12)	0.017 (21)	0.009 (16)
Caprellidae	<0.001 (1)				0.394 (113)				
Isopoda	0.007 (2)					0.219 (11)	0.008 (7)	0.002 (5)	0.017 (1)
Caridea								0.004 (1)	0.007 (2)
Mysida	0.106 (19)	0.008 (2)	0.066 (6)				0.004 (1)		
Decapod larvae	0.004 (1)		<0.001 (1)						
Fish part				0.005 (1)					
Crustacean part					0.108 (1)	0.272 (1)			
Digested material			0.532				0.202	0.859	0.608
Algae	0.003	0.002					0.066	0.091	0.016
Detritus		1		0.217		0.289			
Unidentified				0.064 (1)					

differing in minor traits such as stipe rugosity. Clearly climate-driven substitutions of foundation species that differ in seemingly minor ways can have consequences for community structure and ecosystem functioning.

It has long been recognised that kelp forests are important for many coastal fish species, which utilise these habitats as nursery and feeding areas and as refugia from predation (Bodkin, 1988; Norderhaug et al., 2005; Reisewitz et al., 2006). Kelp forest extent and structure have been positively linked with local fisheries production (Bertocci et al., 2015). It is clear that some fish species, despite their high mobility, rely heavily on kelp-associated fauna and feed extensively within kelp forests (Fredriksen, 2003; Leclerc et al., 2013). Despite the low taxonomic resolution of our examination of fish gut contents, the main groups recorded aligned closely with those found associated with the stipe–epiphyte complex of *L. hyperborea*, with a number of well represented taxa being known to constitute a high proportion of the diets of kelp forest fish (e.g. *Jassa* spp., *Ampithoe* spp., *Caprellid amphipods*, and *Rissoa* spp. gastropods, see Norderhaug et al., 2005).

Moreover, the accessible nature of the stipe–epiphyte complex to predatory fish, in contrast to holdfast or epilithic algal assemblages for example, and the high abundance of fauna within these assemblages suggests that they enhance prey availability for kelp forest fish. Indeed, previous work has shown that faunal assemblages associated with *L. hyperborea* stipes tend to exhibit far higher abundances than those associated with holdfasts or understorey algae (e.g. Christie et al., 2003; King et al., 2021; Teagle et al., 2017). We cautiously infer, therefore, that fish were feeding within the kelp forests they were sampled from, if not exclusively, and that a breakdown of a facilitation cascade may reduce food availability for higher trophic levels. This provides some evidence to support our third hypothesis that shifts in the structure or abundance of mobile invertebrate assemblages have the potential to impact upon higher trophic levels. However, further work is required to reveal trophic pathways within these systems and to determine the magnitude of impacts caused by shifts in the relative abundances of dominant habitat-formers.

Shifts in the structure and functioning of kelp forests in the northeast Atlantic are predicted to occur throughout the coming century in response to ocean warming (Assis et al., 2017; Brodie et al., 2014; Smale, 2020). By comparing the current state of kelp forests across latitudes that include regions where *L. ochroleuca* has proliferated and regions where it does not yet occur, we can gain an understanding of the likely impacts of future range expansions. While the total densities of kelp plants were similar between both study regions, almost half of the assemblage recorded at the lower latitude comprised *L. ochroleuca*. It should be noted that these habitats were targeted as areas of mixed kelp stands and are not representative of wider open wave-exposed coastlines,

				Labrus mixtus (cuckoo wrasse) TL = 273.3 ± 15.3 WW = 294.0 ± 31.8				*Symphodus melops* (corkwing wrasse) TL = 222 WW = 184	*Ctenolabrus rupestris* (Goldsinny wrasse) TL = 129 WW = 17
4	5	6	7	1	2	3	4	1	1
	0.141 (1)		3.921 (1)		1.650 (1)	1.166 (2)	0.293 (1)	<0.001 (1)	0.081 (1)
0.018 (5)		0.334 (1)							
									0.029 (1)
0.049 (9)		0.002 (3)		0.041 (1)					
0.001 (1)									
								<0.001 (1)	
1.280 (3)									
							0.039		
					0.006				
0.637	0.411		1.003						0.0212

which remain dominated by *L. hyperborea* in both regions (Smale & Moore, 2017). At these sites, the lower relative abundance of the cold-adapted *L. hyperborea* led to a per unit area reduction in the biomass of epiphytic algae of ~45%. The reduction in epiphytic algal biomass also had a considerable impact on mobile invertebrate abundances and the structure of faunal assemblages, with those in lower latitude regions supporting five times less mobile invertebrates per unit area than those higher latitude regions that *L. ochroleuca* has not yet expanded into. The magnified effect of a reduction in the quantity of secondary habitat underlines the importance of indirect positive effects to the habitat provision by kelps in temperate marine ecosystems. With further range extensions expected for *L. ochroleuca* populations (Assis et al., 2017), and contrasting range retractions predicted for *L. hyperborea* (Assis et al., 2016, 2017), the weakening of these facilitative interactions and the subsequent impacts to local biodiversity patterns and trophic linkages are likely to be exacerbated in the near future. Outside of the long-lived perennial *Laminaria* species, there is little functional redundancy in this system, with other global change 'winners' (e.g. *Saccorhiza polyschides* and *Undaria pinnatifida*) tending to exhibit shorter, annual life histories and supporting lower diversity (Arnold et al., 2016; Salland & Smale, 2021).

Ocean warming is directly impacting kelp forests in many regions across the world (Fernandez, 2011; Filbee-Dexter et al., 2016; Smale, 2020; Verges et al., 2014). Our study highlights how indirect effects of climate-driven shifts in kelp forest composition may manifest as disruption to an important habitat cascade. Overall, kelp forests formerly dominated by *L. hyperborea*, but now impacted by a range of expansion of *L. ochroleuca*, host a depauperate associated faunal assemblage compared with those still dominated by *L. hyperborea*. More focused research is required to understand the wider implications of this substitution, particularly regarding the feeding behaviour and prey preference of fish within these kelp forests. Even so, we provide compelling evidence that climate-driven substitutions of seemingly similar foundation species can alter local biodiversity and trophic processes in temperate marine ecosystems.

AUTHORS' CONTRIBUTIONS

D.A.S., H.T., S.J.H. and P.J.M. conceived the study; H.T. led collection and processing of samples and data; D.A.S., N.F., C.W., M.J.-B., P.J.M. and N.K. contributed to the field and laboratory work; D.A.S. and H.T. led the development of the manuscript with significant intellectual input from all authors.

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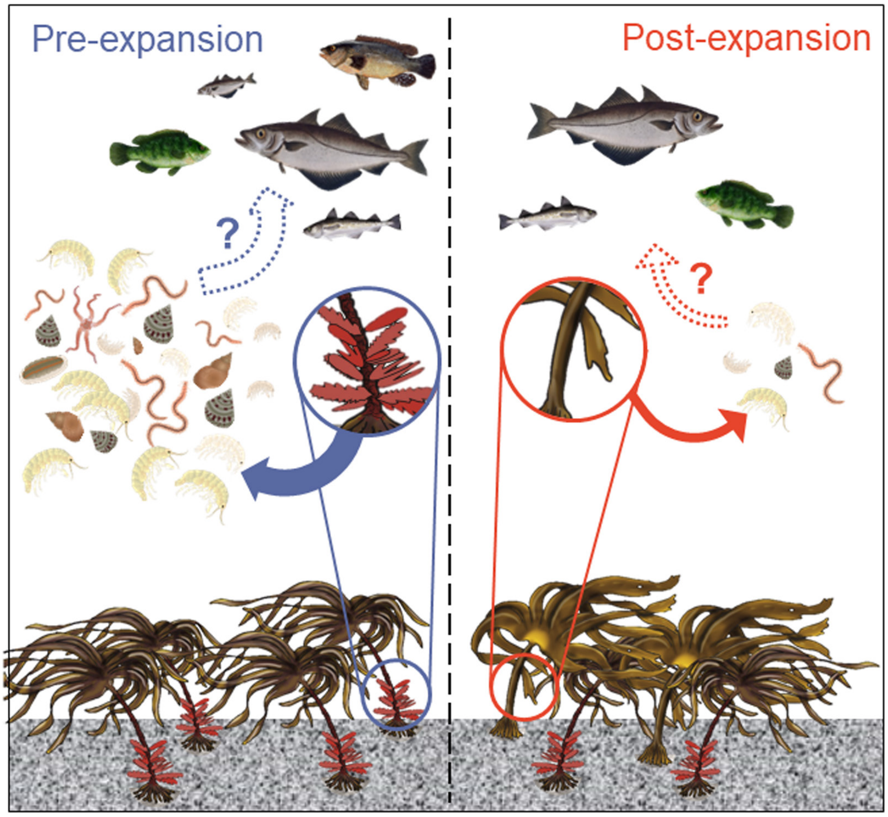

FIGURE 6 Habitat cascades in kelp forests in the Northeast Atlantic, pre- and post-expansion of the warm-water kelp *Laminaria ochroleuca*. An increase in the abundance of *L. ochroleuca* relative to *L. hyperborea* is likely to reduce the extent of secondary epiphytic habitat available for colonisation, and therefore reduce the abundance of faunal assemblages. Higher trophic levels, such as predatory fish, may be subsequently affected.

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CONFLICT OF INTEREST

The authors declare no conflict of interest. D.A.S. is an Associate Editor of Journal of Ecology, but took no part in the peer review and decision-making processes for this paper.

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DATA AVAILABILITY STATEMENT

Data on kelp stipe assemblages can be found at https://doi.org/10.6084/m9.figshare.19902595.v2 (Smale, 2022).

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SUPPORTING INFORMATION

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