



ORIGINAL ARTICLE

The rise of *Laminaria ochroleuca* in the Western English Channel (UK) and comparisons with its competitor and assemblage dominant *Laminaria hyperborea*

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Abstract

The distribution of species is shifting in response to recent climate change. Changes in the abundance and distributions of habitat-forming species can have knock-on effects on community structure, biodiversity patterns and ecological processes. We empirically examined temporal changes in the abundance of the warm-water kelp *Laminaria ochroleuca* at its poleward range edge in the Western English Channel. Resurveys of historical sites indicated that the abundance of *L. ochroleuca* has increased significantly in recent decades. Moreover, examination of historical records suggested that *L. ochroleuca* has extended its distribution from sheltered coasts on to moderately wave-exposed open coasts, where it now co-exists and competes with the assemblage dominant *Laminaria hyperborea*. Proliferation of *L. ochroleuca* at its poleward range edge corresponds with a period of rapid warming in the Western English Channel. Preliminary comparisons between *L. ochroleuca* and *L. hyperborea* highlighted some subtle but ecologically significant differences in structure and function. In summer, the average biomass of epiphytic stipe assemblages on *L. hyperborea* was 86 times greater than on *L. ochroleuca* whereas, on average, *L. ochroleuca* had a greater stipe length and its blade supported 18 times as many gastropod grazers (*Gibbula cineraria*). Differences in summer growth rates were also recorded, with *L. ochroleuca* being more productive than *L. hyperborea* throughout July. Comprehensive seasonally replicated comparisons are needed to examine the wider implications of proliferation of *L. ochroleuca* at its poleward range edge, but our study suggests that local biodiversity patterns and ecological processes (e.g. timing of productivity and trophic pathways) on shallow subtidal reefs may be altered by shifts in the relative abundances of habitat-forming kelp species.

Introduction

Anthropogenic climate change has, and will continue to, impact the Earth's biosphere. The upper layers of the global ocean have warmed at a rate of 0.11 °C per decade in the last 40 years and, on average, have become more acidic, less oxygenated and experienced altered salinity and wave regimes (Bijma *et al.* 2013; IPCC 2013). Unequivocally, these changes in ocean climate have led to the redistribution of marine species (Burrows *et al.* 2011;

Sunday *et al.* 2012; Pinsky *et al.* 2013; Poloczanska *et al.* 2013), with consequences for the structure of communities and the functioning of entire ecosystems (Helmuth *et al.* 2006; Hawkins *et al.* 2009; Doney *et al.* 2012).

The Northeast Atlantic region represents a hotspot of recent warming, as upper ocean temperatures have risen at rates of ~0.3 °C to ~0.5 °C per decade (Belkin 2009; Hughes *et al.* 2010; Lima & Wetthey 2012; IPCC 2013). Temperatures along much of the Northeast Atlantic coastline are predicted to increase by a further >2 °C by

2090 (Philippart *et al.* 2011), with major implications for marine ecosystems. Other human-derived stressors interact with regional-scale climate change in unpredictable and non-linear ways to impact marine ecosystem structure and functioning (Russell *et al.* 2009; Wernberg *et al.* 2011; Russell & Connell 2012). In regions with long histories of human activity, such as the Northeast Atlantic, over-fishing, pollution and habitat alteration have impacted nearshore ecosystems for centuries (Jackson *et al.* 2001; Airoldi & Beck 2007) and continue to interact with climatic variables to induce further ecological change.

Kelps (large seaweeds of the order Laminariales) dominate rocky reefs throughout the world's temperate seas (Steneck *et al.* 2002), where they provide ecosystem services to humans worth billions of pounds (Beaumont *et al.* 2008). Kelp forests support high primary productivity, magnified secondary productivity and a three-dimensional habitat structure for a diverse array of marine organisms, many of which are commercially important (Steneck *et al.* 2002; Smale *et al.* 2013). Canopy-forming kelps influence their environment and other organisms, thereby functioning as 'ecosystem engineers' (*sensu* Jones *et al.* 1994). By altering light levels (Wernberg *et al.* 2005), water flow (Rosman *et al.* 2007), physical disturbance (Connell 2003; Smale *et al.* 2011) and sedimentation rates (Eckman *et al.* 1989), kelps modify the local environment for other organisms. Through direct provision of food and structural habitat, kelp forests support higher levels of biodiversity and biomass than simple, unstructured habitats (Dayton 1985; Steneck *et al.* 2002) and, in general, kelp forests are hugely important as fuels for marine food webs through the capture and export of carbon (Dayton 1985; Krumhansl & Scheibling 2012). Kelps are cool-water species that are stressed by high temperatures (Steneck *et al.* 2002; Wernberg *et al.* 2013); thus, seawater warming will affect the distribution, structure, productivity and resilience of kelp forests (Dayton *et al.* 1992; Wernberg *et al.* 2010; Harley *et al.* 2012). Poleward range contractions of canopy-forming macroalgae in response to oceanic warming have been predicted (Hiscock *et al.* 2004; Muller *et al.* 2009; Raybaud *et al.* 2013) and observed (Diez *et al.* 2012; Smale & Wernberg 2013; Voerman *et al.* 2013) in both hemispheres.

In the Northeast Atlantic, kelps occupy shallow subtidal reefs in all but the most sheltered or turbid locations. Dense kelp forests are found from the lower shore to depths >20 m, from Northern Norway and Iceland through to Portugal and Morocco (Hiscock 1998; Bolton 2010). The structure of entire kelp forests – in terms of the identity and abundance of kelp species and their associated biodiversity – varies considerably in space and time as a function of wave exposure (and storm frequency and

magnitude), light levels (influenced by depth and turbidity), sedimentation, habitat type, water movement and temperature (Burrows 2012; Tuya *et al.* 2012; Smale *et al.* 2013). Even so, the dominant canopy-former along moderately to fully wave-exposed coastlines across much of northern Europe is *Laminaria hyperborea*. Distributed from the Arctic to northern Portugal, *L. hyperborea* (Fig. 1) can outcompete other large macroalgae under most conditions (Hawkins & Harkin 1985). The relative abundance of several kelp species changes with latitude along Northeast Atlantic coastlines, corresponding to a regional-scale temperature gradient, with several habitat-forming kelps found at or near their range edge in the UK and Ireland (Smale *et al.* 2013). Because of these distribution patterns, and because the distributions of some inter-tidal species have shifted (Simkanin *et al.* 2005; Mieszowska *et al.* 2006), it has been predicted (and in some cases observed) that more southerly distributed species (*e.g.* *Laminaria ochroleuca*) will increase in abundance whereas more northerly distributed species (*e.g.* *Alaria esculenta*) will decrease in abundance and/or undergo range contractions in the UK and Ireland (Breeman 1990; Hiscock *et al.* 2004; Vance 2004; Simkanin *et al.* 2005; Brodie *et al.* 2009; Birchenough & Bremner 2010). Empirical evidence for such distributional shifts and appreciation of their wider implications is, however, severely limited.

Laminaria ochroleuca is a warm-temperate Lusitanian species, being distributed from the south of England to Morocco (Fig. 1), and also forming deep-water populations in the Mediterranean and the Azores. It is very similar in morphology to *L. hyperborea* and is thought to serve a similar ecological function, although relatively little is known about its ecology (with the exception of early studies by John 1969; Drew 1974; Sheppard *et al.* 1978). Both species are perennial and relatively long-lived (John 1969) and can form dense canopies in shallow subtidal habitats. *Laminaria ochroleuca* was first recorded in the far southwest of England in 1948 (Parke 1948) and has subsequently progressed eastwards as far as the Isle of Wight and northwards onto Lundy Island in the Bristol Channel (Blight & Thompson 2008; Brodie *et al.* 2009). It is thought that populations on the south coast of England are proliferating and that the species may be expanding its range polewards, but evidence for this trend is largely anecdotal.

As changes in the identity and abundance of habitat-forming species can have wide-ranging consequences for community structure and ecosystem functioning (Jones *et al.* 1994), there is a pressing need to examine distribution shifts and their wider implications. For example, if a cool-water habitat-former is replaced by a warm-water species that is functionally and structurally similar, it is

plausible that the wider community or ecosystem will be relatively unimpacted (e.g. Terazono *et al.* 2012). Conversely, if a structurally or functionally dissimilar species becomes dominant, or habitat formers are lost and not replaced, then widespread changes in biodiversity patterns and ecological processes are likely to ensue (Ling 2008; Thomsen *et al.* 2010). Replacement of *L. hyperborea* with *L. ochroleuca*, which are similar both structurally and functionally, may have relatively few knock-on effects, although subtle differences in kelp species traits have been shown to influence local biodiversity patterns (Blight & Thompson 2008).

This study had two objectives. First, to collate existing data and conduct additional surveys to provide a robust examination of temporal trends in the distribution and abundance of *L. ochroleuca* on the south coast of the UK. Second, to make preliminary comparisons between *L. ochroleuca* and its competitor and assemblage dominant in subtidal habitats, *L. hyperborea*, with regards to their morphology, physiology and ecology.

Methods

Distribution and abundance data

Long-term, continuous quantitative data on the abundance of kelp species in shallow subtidal habitats around much of the UK are lacking (Smale *et al.* 2013). We adopted a three-pronged approach to assess recent trends

in the abundance of *Laminaria ochroleuca* in the Western English Channel. First, we collated presence data from a range of surveys and records from shallow subtidal habitats off Plymouth, UK (Fig. 1). We conducted family-, genus- and species-level searches on all available statutory data, as well as non-statutory data sets held in the Data Archive for Seabed Species and Habitats (DASSH) and additional records from the National Biodiversity Network (NBN). All survey data were collected at appropriate spatial scales and quality checked; these included, for example, records from Seasearch surveys and the Marine Nature Conservation Review (MNCR). Recorded presences of *L. ochroleuca* within the study region were collated, and data collected before the year 2000 (i.e. 1951–1999) were compared with data collected after (i.e. 2000–2013). To examine possible confounding of sampling effort in kelp-dominated habitats between these periods, we simultaneously analysed records for ‘all other kelp species’ (i.e. *Laminaria hyperborea*, *Laminaria digitata*, *Saccharina latissima* formerly *Laminaria saccharina*, *Alaria esculenta*). Trends in the occurrence of *L. ochroleuca* were deemed unlikely to be an artefact of sampling effort, as ‘kelp’ (all other species) were recorded in 716 surveys before the year 2000 and 631 surveys afterwards, with a similar geographical spread of sampling effort in both periods (Fig. 2). With regards to misidentifications and reliability of the data, *L. ochroleuca* is conspicuous in that (unlike other kelps) it has a light ‘golden’ coloured area of tissue at the basal end of the blade and the stipe

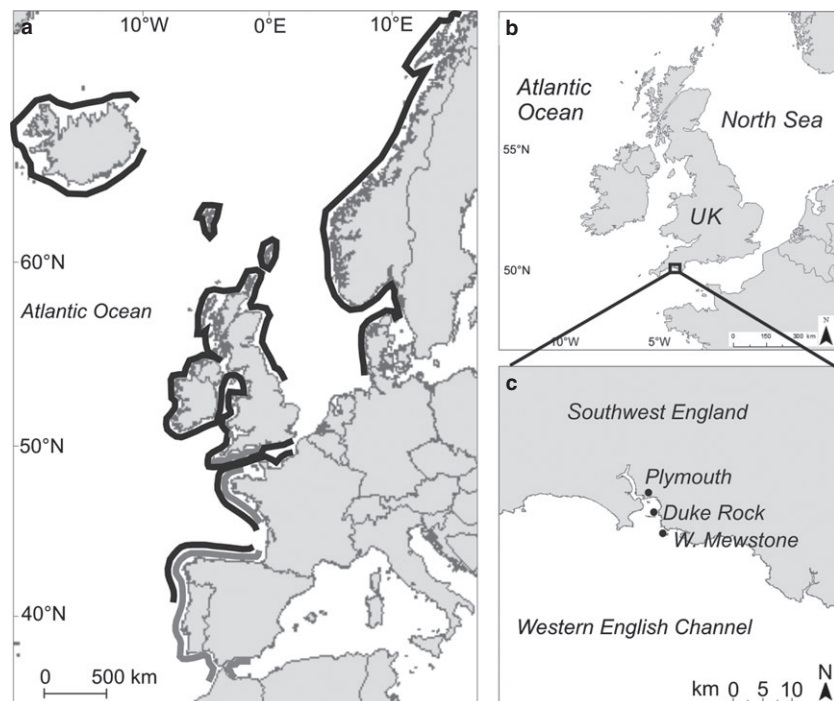


Fig. 1. (a) The approximate distribution of *Laminaria hyperborea* (black line) and *Laminaria ochroleuca* (grey line) along the Northeast Atlantic coastline. The study region (b) and location of the study sites (c) are also shown.

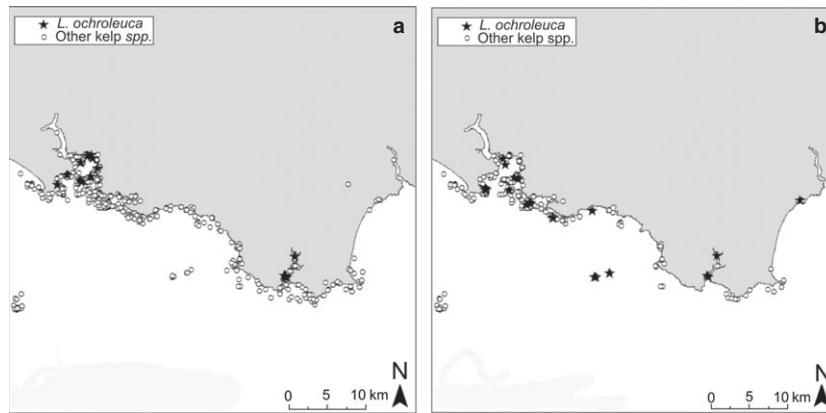


Fig. 2. Records of *Laminaria ochroleuca* (black stars) and all other kelp species (open circles) along the south coast of Devon, UK. Records are shown for all surveys completed before the year 2000 (a) and all those completed during or after the year 2000 (b).

is smooth and generally devoid of epiphytes. Juvenile sporophytes, however, can be difficult to distinguish from *L. digitata* and *L. hyperborea*. As such, any ambiguous records (*i.e.* *Laminaria cf. ochroleuca*, *Laminaria sp.*) or records of juveniles were not included in the analysis.

Second, we selected a historical study site that was quantitatively surveyed as part of a monitoring report for the UK Marine Special Areas of Conservation project in September 1999 (Moore 2000). At ~9 m depth (below chart datum) at Duke Rock (50°20'18" N, 04°08'10" W, Fig. 1), Moore (2000) quantified benthic assemblages within 0.25-m² quadrats (n = 22) positioned along a 16-m transect. In September 2013, 14 years after the original survey, we relocated the same subtidal reef and surveyed 0.25-m² quadrats (n = 20) along the same transect length and bearing. As with the original survey, the abundance of all kelp species was recorded *in situ*. Finally, we conducted detailed surveys of kelp bed structure on a moderately exposed subtidal reef (west of the Mewstone, 50°18'29" N, 04°06'33" W, Fig. 1). The presence of *L. ochroleuca* in moderately exposed conditions in the Plymouth Sound region (*i.e.* outside of the Breakwater, Fig. 1) was first recorded in the early 2000s, yet it is now common along the moderately sheltered faces of the Mewstone (authors' personal observations 2012 onwards). At 5–7 m depth we completed 10-m-long belt transects (n = 6), recording the abundances of all kelp species within 0.5 m of each side of the transect tape (total sampling area per transect = 10 m²). Only mature sporophytes (stipe length >20 cm) were recorded to species, as juvenile *Laminaria* spp. can be difficult to distinguish from one another. Transects were randomly positioned and orientated, and were at least 10 m apart. Surveys were completed in August and September 2013.

Morphology, physiology and ecology

We compared the morphology, associated flora and fauna, growth and photosynthetic performance of mature

sporophytes of *Laminaria ochroleuca* and *Laminaria hyperborea* at our study site off the western face of the Mewstone (Fig. 1). For morphology, 10 adult plants were randomly collected for each species, returned to the laboratory and measured. For associated flora, 18 individuals of each species were harvested (the same individuals used for the growth assay, see below) and returned to the laboratory where all epiphytes were carefully removed from the stipes and weighed (wet weight). Associated gastropod grazers, found on the stipes and blades of the two kelp species, were examined *in situ*. The occurrence of the blue-rayed limpet *Patella pellucida* and the occurrence and abundance of the top shell *Gibbula cineraria* were recorded for 10 individuals of each species. For the growth experiment, the 'hole punch method' described by Mann & Kirkman (1981) was employed, in which a perforation was made 5 cm from the meristem at the junction between the stipe and blade. In early July 2013, 20 individuals of both *L. ochroleuca* and *L. hyperborea* were hole-punched and tagged with fluorescent rubber tubing to assist relocation (loosely cable-tied around the stipe). After 34 days, tagged individuals were collected (n = 19 for *L. ochroleuca* and 18 for *L. hyperborea*) and returned to the laboratory, where the distance between the hole and the stipe-blade junction was re-measured. Starting at the stipe-blade junction, each kelp blade was sliced into 3-cm sections perpendicular to the direction of growth and each section weighed. Productivity was calculated as biomass accumulation [g fresh weight (FW)·day⁻¹] by multiplying blade extension (cm·day⁻¹) with the biomass of the heaviest of the four first thallus sections (g FW·cm⁻¹) (see de Bettignies *et al.* 2013 for further details and application of the method).

Statistical analysis

The Duke Rock data were not comparable to the Mewstone data sets and were analysed separately. For Duke

Rock, comparisons between years (*i.e.* abundances of *Laminaria hyperborea* and *Laminaria ochroleuca* in 1999 compared with 2013) were conducted with one-way permutational ANOVA (Anderson 2001), using the PERMANOVA add-on to PRIMER 6.0 (Clarke & Warwick 2001; Anderson *et al.* 2008). Similarly, response variables at the Mewstone (*i.e.* differences in epiphyte biomass, grazer abundance and productivity between *L. ochroleuca* and *L. hyperborea*) were also examined with one-way permutational ANOVA. In all cases, permutations were based on a similarity matrix constructed from Euclidean distances between untransformed data. Permutations (999) were unrestricted and significance was accepted at $P < 0.05$. Plots show mean values \pm SE.

Results

Survey data indicated that there were more recorded presences of *Laminaria ochroleuca* in shallow subtidal habitats off Plymouth since 2000, compared with preceding years (60 records *versus* 32, Fig. 2). Pre-2000, *L. ochroleuca* was restricted to sheltered sites, such as inside the Plymouth breakwater or within Kingsbridge estuary (Fig. 2). Post-2000, however, *L. ochroleuca* was recorded at moderately exposed sites, near the Mewstone, Hillsea Point and some offshore reefs, for example (Fig. 2). *Laminaria ochroleuca* was recorded within a depth range of 0 to ~ 15 m (below chart datum). The abundance of *L. ochroleuca* significantly increased at Duke Rock between 1999 and 2013 ($F_{1,40} = 4.49$, $P = 0.04$, Fig. 3a), but we recorded no change in the abundance of *Laminaria hyperborea* ($F_{1,40} = 0.25$, $P = 1.00$, Fig. 3a). *Laminaria ochroleuca* was the most abundant kelp species on bedrock [~ 10 individuals (inds) $\cdot m^{-2}$], possibly because Duke Rock is sheltered from wave action by the breakwater, and the reef is subjected to relatively high sediment loading. The reefs off the western face of the Mewstone, which is more exposed to wave action and less prone to

sedimentation, supported a very mixed kelp stand, with four species contributing to the canopy (Fig. 3b). *Laminaria ochroleuca* was the second most abundant kelp species, averaging ~ 2 inds $\cdot m^{-2}$, behind *L. hyperborea*, which was the assemblage dominant at densities of >5 inds $\cdot m^{-2}$ (Fig. 3b). *Laminaria ochroleuca* and *L. hyperborea* were interspersed at the Mewstone and formed mixed canopies (Fig. 4). *Saccharina latissima* and *Saccorhiza polyschides* (order Tilopteridales not Laminariales but an important canopy-former) were also common (Fig. 3b).

Laminaria ochroleuca and *L. hyperborea* populations found under the moderately wave-exposed conditions of the West Mewstone site are similar in morphology (Fig. 5). There are, however, two key differences in plant structure; (i) the average stipe length of *L. ochroleuca* was 26% greater than that of *L. hyperborea*, and (ii) the stipes of *L. ochroleuca* are almost entirely devoid of epiphytes, in stark contrast to those of *L. hyperborea* (Figs 4–6). The mean biomass of epiphytes on *L. hyperborea* stipes was 86 times greater than on *L. ochroleuca* stipes ($F_{1,34} = 105.44$, $P = 0.001$, Fig. 6a). The epiphytic assemblage on *L. hyperborea* was well developed, consisting of (amongst others) *Membranoptera alata*, *Phycodrys rubens* and *Delesseria sanguinea*. In addition, a diverse epifauna was observed on *L. hyperborea* stipes (but not *L. ochroleuca*), which included barnacles (*Verruca stroemia*, *Balanus crenatus*), hydroids (*Obelia genticulata*), ascidians (*Distomus variolosus*) and bryozoans (*Celloporella hyalina*, *Electra pilosa*). The abundance of the gastropod grazer *Gibbula cineraria* was significantly higher on *L. ochroleuca* blades compared with *L. hyperborea* ($F_{1,18} = 11.30$, $P = 0.003$, Fig. 6b), with mean abundance being 18 times greater. This was also reflected in the occurrence of *G. cineraria*, which was present on 80% of *L. ochroleuca* plants and only 10% of *L. hyperborea* plants (Fig. 6c). By contrast, the limpet *Patella pellucida* was ubiquitous on both species (Fig. 6d). Overall, the kelp stand at West Mewstone was dominated by *L. hyperborea* but *L. ochroleuca* was

Fig. 3. (a) Mean abundance of *Laminaria ochroleuca* and *Laminaria hyperborea* at Duke Rock (~ 9 m depth) in 1999 and in 2013 (0.25-m^2 quadrats, $n = 22$ and 20 in 1999 and 2013, respectively). An asterisk indicates a significant difference between years (at $P < 0.05$). (b) Mean abundance of kelp species at 5–7 m depth at West Mewstone, Plymouth, 2013 ($n = 6$, 10-m^2 transects). inds, individuals; *S. latissima*, *Saccharina latissima*; *S. polyschides*, *Saccorhiza polyschides*.

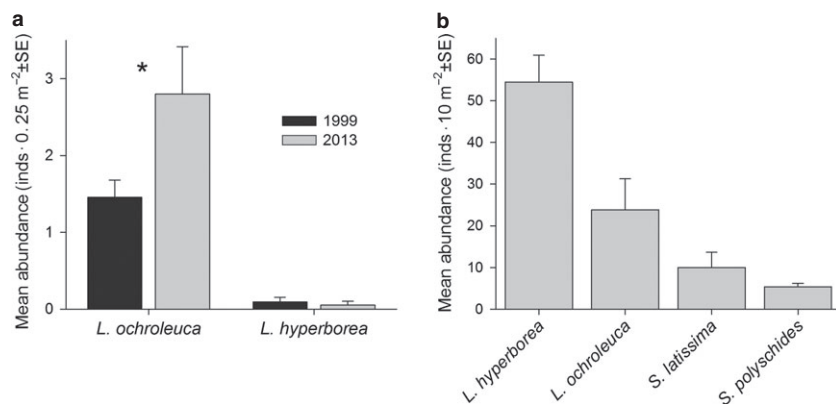




Fig. 4. *Laminaria ochroleuca* at 5–7 m depth at West Mewstone, Plymouth (a), where it forms a mixed stand with *Laminaria hyperborea* (b). Owing to a greater stipe length, *L. ochroleuca* individuals often protrude above the main canopy (c).

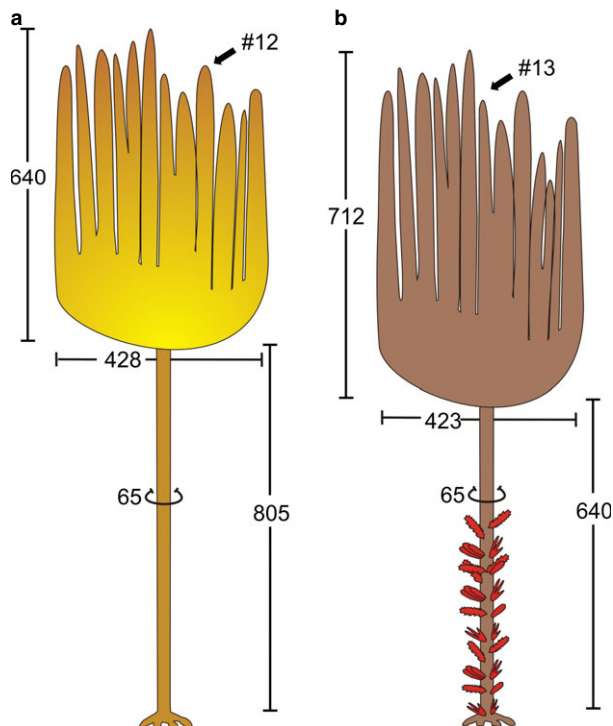


Fig. 5. Typical morphology of mature *Laminaria ochroleuca* (a) and *Laminaria hyperborea* (b) at 5–7 m depth at West Mewstone, Plymouth. Average measurements (mm) were generated from 10 adult plants. Average number of linear segments per plant and indicative epiphyte loads are also shown (see Fig. 6).

both abundant and conspicuous, with larger individuals emerging from the main canopy (Fig. 4).

The growth experiment showed that summer productivity rates differed between *L. ochroleuca* and *L. hyperborea* (Fig. 7). Although the mean lamina weight of *L. ochroleuca* was significantly lower compared with *L. hyperborea* ($F_{1,35} = 29.25$, $P = 0.001$, Fig. 7a), productivity rates during July were significantly greater ($F_{1,35} = 24.68$, $P = 0.001$, Fig. 7b). Both species, however, exhibited low productivity rates during summer (*L. hyperborea* = 0.040 ± 0.006 g FW·day⁻¹; *L. ochroleuca* = 0.097 ± 0.009 g FW·day⁻¹).

Discussion

Our study provides strong, empirical evidence for an increased distribution and abundance of *Laminaria ochroleuca* at its poleward range edge – the southwest coast of the UK – in recent decades. Since the 1980s, sea temperatures around the UK have increased by 0.2–0.6 °C per decade (Hughes *et al.* 2010), with greatest warming in the English Channel and southern North Sea. Within the current study region, sea temperatures are now about 0.8 °C above the long-term average, having undergone rapid warming over the past 20 years (Smyth *et al.* 2010). Sea temperatures are influenced to some degree by the Atlantic Multidecadal Oscillation (AMO), which drives low-frequency temperature variability (phases of 20–40 years) in the North Atlantic Ocean (Knight *et al.*

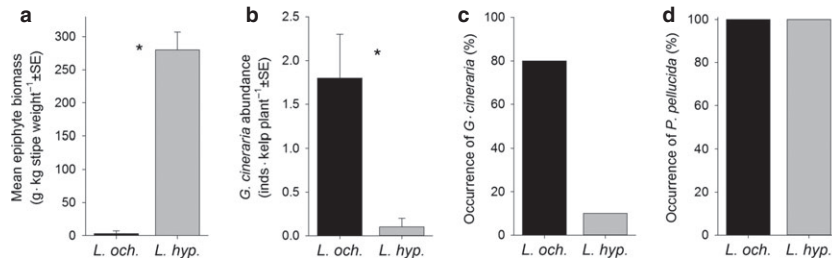


Fig. 6. Flora and fauna associated with *Laminaria ochroleuca* (*L. och.*) and *Laminaria hyperborea* (*L. hyp.*) at 5–7 m depth at West Mewstone, Plymouth. (a) Mean biomass [weight(g) of epiphyte per kg of kelp stipe, $n = 18$ mature plants, \pm SE] of epiphytes attached to kelp stipes; (b) mean abundance of *Gibbula cineraria* on kelp individuals ($n = 10$ mature plants, \pm SE); (c) occurrence of (c) *G. cineraria* and (d) *Patella pellucida* on kelp individuals ($n = 10$ mature plants, occurrence expressed as a percentage). An asterisk indicates a significant difference between species (at $P < 0.05$); occurrence data not testable. inds, individuals.

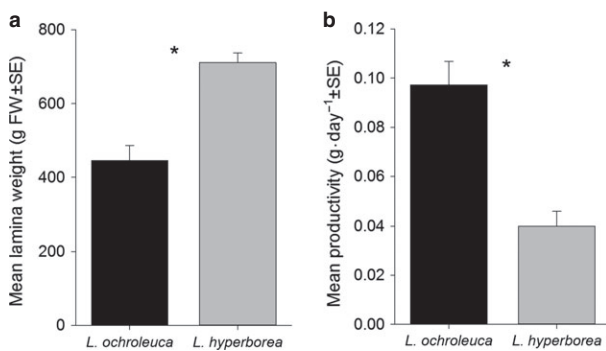


Fig. 7. Mean (a) lamina weight (fresh weight, FW) and (b) productivity rates (FW) of *Laminaria ochroleuca* and *Laminaria hyperborea* at West Mewstone Plymouth, recorded during July 2013 ($n = 19$ and 18 for *L. ochroleuca* and *L. hyperborea*, respectively). An asterisk indicates a significant difference between species (at $P < 0.05$).

2006). Cool AMO phases occurred in the 1900s–1920s and 1960s–1980s, and warm AMO phases in the 1930s–1950s and from the 1990s to date (Knight *et al.* 2006; Mieszkowska *et al.* 2013). Since the end of the 20th century, anthropogenic climate forcing has been superimposed onto longer-term variability trends, thereby exacerbating the warm phase (Mieszkowska *et al.* 2013). Indeed, when Mary Parke (1948) identified the first *L. ochroleuca* specimen found in British waters, average sea temperatures were ~ 1 °C cooler than at present (Moore *et al.* 2011). Rapid warming of the Northeast Atlantic region since the 1980s has been associated with dramatic shifts in the distribution of plankton (Beaugrand *et al.* 2013), inter-tidal invertebrates (Mieszkowska *et al.* 2006) and fish (Genner *et al.* 2004). In the current study, temporal patterns should be examined with some caution, as historical time-series data were fairly limited. Even so, our ‘weight of evidence’ approach (see Bates *et al.* 2014 for best practices for defining range shifts), which incorporated anecdotal evidence, semi-quantitative

surveys and resurveys of historical sites, would suggest with some confidence that *L. ochroleuca* has increased in abundance and expanded its distribution in the Western English Channel, most likely in response to recent seawater warming. Within the framework recently proposed by Bates *et al.* (2014), it seems likely that *L. ochroleuca* is now in the ‘persistence’ stage of a range expansion in Southwest England, having passed through the ‘arrival’ (Parke 1948) and ‘population increase’ (John 1969) stages. In addition to latitudinal shifts, it is plausible that changes in the depth distribution of *L. ochroleuca* have occurred (in response to temperature, light, competitive release, for example), but these were not considered in the current study. For example, *L. ochroleuca* has recently been recorded at depths of >20 m in the Isles of Scilly (Irving & Northern 2012) and may have proliferated vertically as well as horizontally.

Previous examinations of the distribution of *L. ochroleuca* in Southwest England have concluded that it is generally restricted to areas of low to moderate wave exposure (John 1969; Drew 1974), such as within Plymouth Sound and other protected estuaries, or on the leeward sides of Isles of Scilly. In the last two decades, it appears that *L. ochroleuca* has extended its distribution onto open coastlines, where it now forms a mixed stand with *L. hyperborea*, while also increasing in abundance in more sheltered sites, such as Duke Rock. Since the year 2000, for example, *L. ochroleuca* has been found on both the seaward and leeward faces of the Mewstone, as well as on several wave-exposed submerged reefs. Although *L. hyperborea* still forms monospecific stands on the most exposed reefs in the region, it is almost certainly competing with *L. ochroleuca* for resources (e.g. space and light) along moderately exposed coastlines.

Although the specific ecological mechanisms underpinning the population expansion of *L. ochroleuca* remain largely unknown, it is clear that key processes influencing range-edge dynamics of kelp species, such as growth, survival and reproduction, are strongly influenced by

temperature (for recent studies, see Fredersdorf *et al.* 2009; Pereira *et al.* 2011; Bartsch *et al.* 2013). The northern limit of *L. ochroleuca* corresponds with the 10 °C winter isotherm (Van den Hoek 1982), which lies off the southwest coast of England (Smyth *et al.* 2010). At temperatures around 10 °C, the gametophyte is infertile and sporophyte growth is not competitive (Van den Hoek 1982; Izquierdo *et al.* 2002). In recent decades, the frequency of months where average temperatures were below 10 °C has declined (Fig. 8), which may have promoted higher fecundity and survival rates and, ultimately, facilitated population expansion. Moreover, the optimum temperature for spore germination, gametophyte growth and fertility, and development of young sporophytes is between 15 and 18 °C (Izquierdo *et al.* 2002). As the frequency of months with average sea temperatures exceeding 15 °C in the Western English Channel has increased in recent decades (Fig. 8), it may be that reproductive success and early sporophyte development has improved during the recent warming trend.

At some open-coast sites near Plymouth, such as the Mewstone, *L. ochroleuca* now co-exists with *L. hyperborea*, forming mixed stands, where they are in direct competition for resources (e.g. space and light). As habitat-forming species, differences in the morphology, surface structure and chemical composition of the stipe are likely to be ecologically important for two reasons. First, owing to their greater stipe length many *L. ochroleuca* individuals rise above the main canopy, dominated by *L. hyperborea*, which may be a competitive advantage, especially at greater depths or highly turbid sites where ambient light levels are low. Moreover, a relatively greater stipe length could influence conditions for understory species,

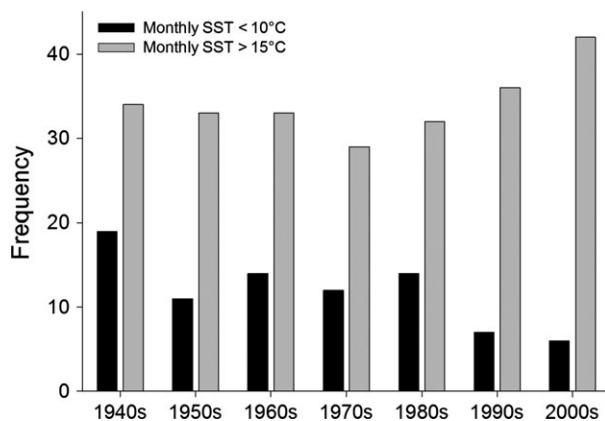


Fig. 8. The frequency of months per decade where average sea surface temperature (SST) in the Western English Channel off Plymouth (50–51° N, 4–5° W) was <10 °C (black bars) and >15 °C (grey bars). Data: Hadley Centre for Climate Prediction and Research (<http://www.badc.rl.ac.uk>).

through reduced thallus scouring of the sea bed during storms and altered light levels beneath the canopy (Toohy *et al.* 2004). Second, the *L. ochroleuca* stipes examined here were almost entirely devoid of epibionts, whereas *L. hyperborea* stipes support rich and abundant epibiont assemblages (Whittick 1983; Christie *et al.* 2003). Epiphytes on *L. hyperborea* stipes represent an important secondary habitat that supports high faunal abundance and diversity. In Norway, for example, epiphytes on a single *L. hyperborea* stipe may harbour up to 80,000 invertebrates (Christie *et al.* 2003). This habitat cascade effect (Thomsen *et al.* 2010) facilitates a wide range of invertebrates, which, in turn, act as a food source for kelp forest-associated fish species (Norderhaug *et al.* 2005). As such, reduction of epiphytic habitat associated with a potential shift from *L. hyperborea* to *L. ochroleuca* may influence trophic interactions within the kelp forest. Differences in the structure and ecology of the holdfast, which represents an important habitat for a diversity of fauna, may also exist between the species, but fall outside the scope of the current study. Blight & Thompson (2008) compared holdfast epibionts of *L. ochroleuca* and *Laminaria digitata* and showed that *L. ochroleuca* supported a distinct, relatively impoverished holdfast assemblage. It is possible that *L. ochroleuca* and *L. hyperborea* harbour distinct holdfast assemblages, and this warrants further investigation.

Our observations also suggest that the timing and fate of kelp-derived primary production may differ between *L. ochroleuca* and *L. hyperborea*. It is well known that peak production of *L. hyperborea* occurs from late winter through to spring, when stored organic material supports rapid growth of the new lamina (Kain 1979; Luning 1979). As such, our July growth measurements did not capture this peak period and productivity rates of *L. hyperborea* were very low, as would be expected. By contrast, very little is known about seasonal productivity of *L. ochroleuca* and there are no published data on *in situ* growth rates from the British Isles. Although seasonal data are needed to adequately assess species differences, our data indicate that growth strategies may differ between *L. ochroleuca* and *L. hyperborea*, as summer productivity rates for the former were significantly higher. Different *Laminaria* species exhibit different growth strategies (Luning 1979), and it could be that *L. ochroleuca* is more akin to *L. digitata* and *Saccharina latissima*, which continue to grow slowly throughout the summer and into autumn (Luning 1979). Furthermore, the route by which this material enters the food web may differ between the species, as *L. ochroleuca* plants supported significantly greater numbers of *Gibbula cineraria*, which were directly consuming macroalgal tissue (as evidenced by grazing marks). Although most kelp production enters the detri-

tal food web (Krumhansl & Scheibling 2011, 2012; de Bettignies *et al.* 2013), some is directly consumed and differences in grazer preference and consumption rates of the different kelp species could alter trophic pathways. Variability in palatability and nutritional value amongst kelp species is important and requires further work. As kelps make a significant contribution to coastal primary production, facilitate export of carbon from high to low productivity systems, and fuel entire food webs, changes in the timing, quality or quantity of kelp production resulting from climate-driven changes in kelp species identity, abundance or productivity could have far-reaching consequences (Krumhansl & Scheibling 2012).

In conclusion, we have empirically demonstrated that a habitat-forming species, *L. ochroleuca*, which has a warm-temperate distribution in the Northeast Atlantic, has increased in abundance at its poleward range edge and has extended its distribution from sheltered to moderately exposed open coastlines. This pattern is in accordance with climate change predictions and it seems likely that the proliferation of *L. ochroleuca* is, at least in part, a response to increasing seawater temperatures in the Western English Channel. However, the distributions of habitat-forming kelp species are influenced by a range of environmental factors, and it is unlikely that increased temperature is the sole driver of the observed pattern. Other interacting factors such as the amount of incident light (John 1969; Burrows 2012), nutrient and sediment input (Connell *et al.* 2008; Moy & Christie 2012), storminess (Byrnes *et al.* 2011) indirect effects of overfishing (Ling 2008) and competitive interactions (Farrell & Fletcher 2006) can influence kelp species distributions and require further study. The wider consequences of shifts in the relative abundances of habitat-forming kelp species are largely unknown, but we have highlighted several key differences in the morphology, ecology and physiology of *L. ochroleuca* compared with the assemblage dominant, *L. hyperborea*. The co-existence of structurally similar canopy-forming kelps with both 'cool' and 'warm' distributions raises some interesting questions concerning climate-mediated competition and other ecological processes occurring at the range edge. Further research is urgently needed to enhance understanding and improve predictions of kelp forest structure and functioning in warmer, stormier seas.

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