Large brown seaweeds of the British Isles: evidence of changes in abundance over four decades

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Abstract

The large brown seaweeds (macroalgae) are keystone species in intertidal and shallow subtidal marine ecosystems and are harvested for food and other products. Recently, there have been sporadic, often anecdotal, reports of local abundance declines around the British Isles, but regional surveys have rarely revisited sites to determine possible changes. An assessment of changes in the abundance of large brown seaweeds around the British Isles using historical survey data, and determination of whether any changes were linked with climate change was undertaken. Data were analysed from multiple surveys for 14 habitat-forming and commercially important species of Phaeophyceae, covering orders Laminariales, Fucales and Tilopteridales. Changes in abundance were assessed for sites over the period 1974-2010. Trends in distribution were compared to summer and winter sea surface temperatures (SST). Results revealed regional patterns of both increase and decrease in abundance for multiple species, with significant declines in the south for kelp species and increases in northern and central areas for some kelp and wracks. Abundance patterns of 10 of the 14 species showed a significant association with SSTs, but there was a mixture of positive and negative responses. This is the first UK-wide observation of declining abundance of large brown seaweeds. Historical surveys provide useful data to examine trends in abundance, but the ad hoc nature of these studies limit the conclusions that can be drawn. Although the British Isles remains a stronghold for large brown algae, it is imperative that systematic surveys are undertaken to monitor changes.

Keywords

Change in abundance of large brown seaweeds

Introduction

Seaweed communities in different parts of the world have been profoundly impacted by humans, and in a time of rapid environmental change the large brown seaweeds have been the subject of an increasing number of reports documenting both their decline or loss coupled with an increase in populations of predominantly invasive species (Brodie et al. 2009; Brodie et al. 2014, Koch et al. 2013; Lima et al. 2007; Simkanin et al. 2005). Large brown seaweeds are integral components of marine communities and are the main habitat formers in temperate reef ecosystems (Tuya et al. 2012), with kelp forests (Laminariales) dominating biomass in the subtidal and fucoids (Fucales) in the intertidal. Kelp forests are a major source of primary production and one of the most productive habitats on Earth (Reed et al. 2008). The highly productive fucoids also play a key role in carbon capture and transfer in coastal ecosystems (Gollety et al. 2008). These habitat-forming seaweeds facilitate a diverse community of understory algae, invertebrates and vertebrates (Jørgensen and Christie, 2003). Brown seaweeds are also an economically valuable resource: they were harvested for soda ash and iodine between the 17th and 19th centuries, and remain an important source of alginates (McHugh, 2003; Smale et al. 2013 and refs. therein). More recently, there has been interest in the biochemical properties of macroalgae for potential use in medicine (Wijesinghe and Jeon, 2012), in addition to the potential use of kelps in biofuel production (Roberts and Upham, 2012).

Causes of population level change in large brown seaweed abundance appear to be varied and complex, compounded by the life histories of these seaweeds, for example thermal tolerance changes over different phases of life history (Koch et al. 2013). The geographic distributions of large kelp species (e.g. *Laminaria digitata, L. hyperborea,* and *Saccharina latissima*) appear to be limited by summer and winter isotherms (Harley et al. 2012; van den Hoek, 1982, Breeman, 1990)

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and some reviews have predicted declines in macroalgal abundance due to environmental change (Harley et al. 2012; Hiscock et al. 2004; Koch et al. 2013; Müller et al. 2009). Some species of macroalgae, such as *Alaria esculenta,* have been proposed as indicators of biotic response to climate change (Mieszkowska et al. 2006). Given that sea-surface temperatures in the northeast Atlantic have increased by *ca*. 0.3-0.8 °C per decade over the last *ca*. 25 years (Lima and Wethey 2012), climate change is an important factor influencing coastal seaweed communities (Poloczanska *et al.* 2013).

In order to determine the extent of change in these seaweed communities, and to relate these changes to environmental influences, long term monitoring and/or reliable quantitative survey evidence from sites which can be resurveyed are required. However, frequently both types of evidence are lacking. Where losses of large brown seaweeds have been reported (Table 1), methods have included revisiting sites with historical surveys, undertaking a literature review, and making inferences from anecdotal evidence. Reported losses of *Alaria esculenta* in Ireland (Simkanin et al. 2005) and Britain (Mieszkowska et al. 2006) were determined by comparisons of sites with historical data. In the northwest Atlantic, retraction of this species at its southern edge was inferred from a literature review (Merzouk and Johnson, 2011). Losses of *Saccharina latissima* off the coast of Norway were determined by surveying 660 sites between 2004 and 2009 and making comparisons with a historical dataset (Moy and Christie 2012). For reported losses of *Saccharina latissima* and *Laminaria ochroleuca* from the north coast of Spain, sites were resurveyed between 2007 and 2010 to match previous surveys conducted between 1977 and 1978 (Fernández 2011). In contrast, Tuya et al. (2012), who compared cold and warm water assemblages along the Portuguese coast, inferred that *Laminaria hyperborea* had retreated from its southern edge based largely on anecdotal and personal observations over recent decades.

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The British Isles is an important biogeographic transition zone in the temperate region of the northeast Atlantic, and the littoral and shallow sublittoral regions support *ca*. 50% of the North Atlantic's documented seaweed flora (Yesson et al. in press). The northern and southern limits of the majority of commercially important large brown seaweed species occur outside the British Isles, except for *Laminaria ochroleuca*, which is at its northern limit in England, and *Alaria esculenta* whose southern limit is just into northern France (although the limits of *A. esculenta* and *L. digitata* in France occur at the same isotherm as southern England). Seaweeds have been recorded for over 250 years and the first broad-scale survey of macroalgal populations to use a modern abundance scale classification was conducted over half a century ago by Crisp and Southward (1958) who pioneered a categorical classification of abundance defined by percentage cover thresholds based on a semi-logarithmic scale. This scale came to be known by the initials of the categories (ACFOR - Abundant, Common, Frequent, Occasional and Rare) (Crisp and Southward, 1958). Variants of this classification of abundance have been used regularly in surveys of the British and Irish coastlines. Although additional categories, such as dominant and superabundant, have been incorporated into the scale, and thresholds defining the categories have varied slightly, this system has remained in common use for coastal surveys (Hiscock, 1996; Mieszkowska et al. 2006; Wijesinghe and Jeon, 2012).

The ACFOR surveys of Crisp and Southward (1958) were repeated 45 years later to determine change in abundance of intertidal species around Ireland (Simkanin et al. 2005). Simkanin et al. (2005) found that three kelp species (*A. esculenta*, *L. digitata* and *S. latissima*) had declined significantly in abundance between 1958 and 2003. An equivalent systematic examination of

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changes in macroalgal abundance has not been undertaken in Britain, despite sporadic (often anecdotal) reports of population declines for some species and locations.

Between the 1970s and 2000s, there have been several substantial coastal seaweed surveys around the British Isles (Smale et al. 2013), but often these efforts have been regionally focussed, and there is no ongoing strategy to perform long term monitoring at a national level. Our aim is to combine existing survey data spanning the past four decades in order to examine spatial and temporal trends in the abundance of large brown seaweeds in relation to changing climate.

Methods

Distribution data

A database of 127,569 observations (covering the 18th century to the present day) of large brown macroalgae around the British Isles was collated by Yesson et al. (in press). These data were collected from a variety of sources, including national and regional surveys, museum databases and literature searches. The majority of data was accessed via the National Biodiversity Network Gateway and the Marine Recorder project. These data cover 15 commercially important species of kelp, fucoids and related species: the Laminariales *Alaria esculenta, Chorda filum, Laminaria digitata, L. hyperborea, L. ochroleuca, Saccharina latissima, Undaria pinnatifida*, Tilopteridales *Saccorhiza polyschides* and the Fucales *Ascophyllum nodosum, Fucus serratus, F. spiralis, F. vesiculosus, Himanthalia elongata, Pelvetia canaliculata* and the non-native *Sargassum muticum*. (Although documented in the original database, the alien species *U. pinnatifida* was not included in this study due to insufficient data, reducing the species list to 14). These data were filtered to include only those records with species' abundance data and a spatial accuracy of 1 km or better.

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These data record abundance using variants of the ACFOR scale (Crisp and Southward, 1958). A summary of the categories used by various surveys is presented in Table 2 along with our method to integrate these into a single 5-level system (Abundant, Common, Occasional, Rare and Not recorded – ACORN). Given the discrepancies around the Occasional and Frequent categories in the original classifications, these were combined in order to reduce categorical mismatches. Upon examination of the data, it was found that very few surveys recorded the absence of a species, so the Not recorded category was omitted.

Observations of species presence were grouped onto a 1 km grid, where multiple observations within the same grid and time period were treated as a single observation, with the abundance recorded as the mean of all observations rounded to the nearest integer, using a numerical coding of the classification scheme (4=Abundant, 3=Common, etc). Data were examined regionally based on the biogeographic boundaries described by the Joint Nature Conservation Committees regional seas project (Connor et al. 2006).

Sea surface temperatures

High resolution data of sea surface temperatures (SSTs) were downloaded from the "Ocean Color Web" portal (http://oceancolor.gsfc.nasa.gov/) on grids of 2.5 arc minute resolution. Level 3 monthly mean SST data were processed into annual mean summer and winter layers for the period 2003-2010. As temperature data for earlier periods are not available at such high resolution, a lower resolution dataset was obtained and scaled up to match the high resolution data (Hijmans et al. 2005). Low resolution SST data were obtained from "HadISST", the Hadley Centre Sea Ice and Sea Surface Temperature data set (Rayner, 2003). The HadISST dataset contains global grids of monthly mean SST values at 1 arc degree resolution covering the period 1871 to the present.

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Annual summer and winter layers were generated by calculating the mean of April to September temperatures for summer and October to the following March for winter (so winter of year N incorporates the last quarter of year N and the first quarter of year N+1). These layers were rescaled onto a higher resolution grids by creating difference layers constructed by subtracting present-day values (mean of years 2003-2010) from the required time period (i.e. 1974). This difference layer was then added to a high resolution layer from the present day, in order to generate a high resolution layers for all years of this study. This follows the methodology employed in the construction of the worldclim future and past climate data (Hijmans et al. 2005) described in (http://www.worldclim.org/downscaling). Finally, the rescaled high resolution layers were re-projected onto the Ordnance Survey of Great Britain 1936 grid (epsg:27700), using grid dimensions approximately matching the MODIS layers (3km x 3km). Processing of GIS layers were achieved using the statistical software R (R Core Team, 2013), with package "raster" v3.0.2 (http://CRAN.R-project.org/package=raster), and tools from the Geodata Abstraction Library - "gdal" v1.10.1 (http://www.gdal.org/).

Analysis

Observations of abundance were grouped within years into summer (April-September) and winter (October-March) observations. Only observations from the same season were compared across years to minimise the impact of seasonal variation on trend lines. Rate of change of abundance was calculated for each site using linear regression. Correlation of change in abundance was tested for each pair of species using the Pearson correlation coefficient with data from sites were both species were present.

A generalised linear mixed model was used to test the influence of sea surface temperature on abundance. The response variable, abundance, was coded as 1-4 (1-Rare, 4-Abundant); fixed effects

were summer and winter sea surface temperatures of the year of observation, which were input as

both linear and quadratic terms; year of observation was regarded as a random effect as the response

to temperature is expected to be consistent over the time of observations; and a spatial correlation

structure based on the linear distance between sites was included to correct for spatial

autocorrelation. A model was fitted for each species using the glmmPQL function from the R

package MASS (Venables and Ripley, 2002).

Results

The database of species observations with abundance data contained 76,527 entries. Spatially

inaccurate records were removed and the remaining data aggregated by decade and paired by

overlapping locations (i.e. records located within the same 1 x 1 km square on the ordnance survey

grid), leaving 5,481 abundance observations for the 14 species. Site observations were 1-36 years

apart between 1974 and 2010. The majority of sites (74%) had only two temporal observations per

species, and only 3% of sites had more than 4 temporal observations for any species. The typical

time period between observations was 1 year (11%), but the majority of sites had observations more

than a decade apart, and the median temporal difference between observations was 11 years. The

most frequently observed abundance class was "Common", which accounted for 42% of

observations.

Examining abundance observations by site between 1974 and 2010 (Table 3) revealed that for all

species, except *Laminaria ochroleuca*, there were more sites showing an increase in abundance than

a decline. Five species, *Chorda filum*, *Laminaria ochroleuca*, *Saccharina latissima*, *Fucus serratus*

and *F. spiralis* showed a negative trend in abundance. Comparing abundance trends between

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species, there were 25 pairs of species that showed significant correlations (Table 4). Nineteen of these significant correlations were positive, indicating that it is common for multiple species to either increase or decrease in tandem at a particular site. The greatest negative correlation was between *F. serratus* and *A. nodosum.*

Examining patterns by biogeographical region (Fig. 1a, b, Table 5), shows disparate changes for kelps (Fig. 1a) and wracks (Fig. 1 b). The general trend for kelps was a decrease in abundance in the southern geographic regions, and relatively stability or an increase in abundance in the northern regions. Species with a marked contrast between regions (red to green, Table 5) included *Chorda filum* and *L. hyperborea* (decrease in the English Channel versus increase in the Irish Sea), and *Saccorhiza polyschides* (decrease in the Western Channel and Celtic Sea versus increase in the Irish Sea). In contrast, the wracks showed an insignificant decline in Western Scotland, but *F. vesiculosus* and *A. nodosum* had strong increases in Northeast England (North Sea). Only one species, *Sargassum muticum*, revealed a significant decrease in the south (Western Channel & Celtic Sea) and a significant increase in the west (Irish Sea).

Regional Sea Surface Temperatures (SSTs) showed annual fluctuations between 1974-2010 (Fig. 2). The general trend has been a 1-2 °C increase during this time period, with the East coast (North Sea) experiencing the greatest increases. Regions with the least change were West Ireland and Western Scotland (Table 5). For several species, *L. digitata*, *L. hyperborea*, *F. vesiculosus*, *Pelvetia canaliculata* and *S. muticum*, abundance was positively correlated with summer temperature, and of those, *F. vesiculosus* and *S. muticum* abundances were also positively correlated with winter temperature (Table 5 & Table S1; Supplementary material). In contrast, abundance of *L. digitata*

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and *L. hyperborea* were negatively correlated with winter temperature. Only abundance of

Saccharina latissima responded negatively to both summer and winter temperatures. Species'

abundances which were only negatively correlated with winter temperature were *F. spiralis* and

Himanthalia elongata.

Discussion

Here, for the first time, we have demonstrated change in abundance in the large brown seaweeds of

the British Isles using a comprehensive and novel meta-analysis approach. There is an expectation

that climate change will lead to changing distributions for many coastal species (Harley et al. 2006;

Koch et al. 2013). However, this study did not establish a clear, replicated pattern of association

between areas of decline and greater changes of SST. There is a striking difference in biogeographic

signal: in the south, several species have declined significantly compared to central and northern

regions where they have remained relatively stable or shown a significant increase (*C. filum, L.*

hyperborea, S. polyschides). The kelps, which are predominantly subtidal, appear to have declined

more than the intertidal wracks. These observations support the prediction in Brodie et al. (2014)

that there will be significant changes in the distribution and composition large brown seaweeds, but

the role of temperature as the main driver of change is not clear. For some species (i.e. *F.*

vesiculosus, A. nodosum, C. filum), , warmer summer and winter temperatures appear favourable,

but for 5/14 species abundance is negatively correlated with winter temperature (Table 5), which

may be cause for concern in a time of rapid warming.

There are two species, *L. digitata* and *L. hyperborea,* that show a conflicting pattern of temperature

and abundance: both show a positive correlation to summer temperature, but a negative response to

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warmer winter temperatures. However, the abundance of *L. digitata* has increased significantly in

the northern North Sea, the region in the British Isles that has seen the largest temperature rises over

the last 30 years. In contrast, *L. hyperborea* shows a significant decrease in abundance in the

English Channel and a significant increase in abundance in the Irish Sea. Conflicting seasonal

patterns may be driven by the conditions required for the initiation and development of different life

history stages. *L. digitata* is a summer fertile species and Bartsch et al. (2013) have shown that for

Helgoland populations, sporogenesis is a cold adapted process with the narrowest temperature

window of all the reproductive stages, with an optimum at 5-10 °C. In contrast to *L. digitata*, *L.

hyperborea* is fertile in winter and early spring (Müller et al. 2008). For optimum development,

gametophytes require temperatures up to 14-15 °C (Lüning 1990). Therefore, whilst warmer

temperatures may favour some aspects of the life history, they may negatively affect sporogenesis

in *L. digitata* and gametogenesis in *L. hyperborea*. Short term fluctuations in temperature may also

cause changes in abundance. For example, short term declines in abundance were observed in SW

Scotland after a period of extreme cold, coinciding with spring tides (Todd and Lewis 1984) but

such events will not necessarily influence long term trends. Declines have also been reported on the

Atlantic coast of France (Cosson, 1999), coincident with increases in abundance of *S. muticum.*

Laminaria ochroleuca, in contrast to *L. digitata*, and *L. hyperborea*, is a warm water species, first

recorded in UK waters in the middle of the 20th century (Parke, 1948), reaching its northern limit in

the UK (John 1969) and is an example of a range-expansion species. Although abundance was not

significantly related to temperature in the summer or winter, this species showed a significant

decline in abundance in the W. English Channel & Celtic Sea. However, data are limited for the

first decade of this study and spatially clustered around Plymouth and the Scilly Isles. It has been

reported that elevated UV radiation may negatively impact on both zoospores (Wiencke et al. 2000)

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and sporophytes of *L. ochroleuca* (Roleda et al. 2006), but there was no significant pattern

associated with changing SST. Pereira *et al.* (2011) suggested that *L. ochroleuca* may be out-

competed by *Saccorhiza polyschides* in northern populations but we found no significant correlation

between changing abundance of these species. The observed decline is contrary to expectation of

increased abundance and northward spread for this warmer-water, range-expanding species in light

of increasing temperatures (Hiscock et al. 2004).

There is evidence for a north-south divide for some species, with southern populations showing

declines but increases evident further north. Two such examples are *Chorda filum* and *S.

polyschides*. *Chorda filum* is an amphi-oceanic cold-water species, tolerant of high sedimentation

and reduced salinity and shows a significant decline in the English Channel. *S. polyschides* is a kelp

of temperate waters with a relatively restricted distribution (Lüning 1990) that appears to be

declining in the W. Channel & Celtic Sea. Both species show an increase in the Irish Sea and

relative stability further north. The decrease of abundance in *C. filum* may be influenced by

temperatures in the south being too high for gametogenesis, which occurs in autumn at temperatures

between 5 and 10 °C, with 15 °C halting reproduction completely (Lüning 1990). Although the

relationship with temperature differs, *L. hyperborea* has the same pattern of abundance as *C. filum*,

reflecting their optimum environmental requirements ('comfort zone'). Although *S. polyschides* is a

warmer water species than *C. filum*, temperature is a critical determinant of zoospores viability,

gametophyte fertility and juvenile sporophyte survival. Sporophytes appear from spring to summer,

but later recruits tend not to survive in warmer southern areas.

Amongst the wracks, *Sargassum muticum* shows a similar pattern of abundance as the kelp species

Saccorhiza polyschides, although the significant increase in the Irish Sea was much greater than the

significant decrease in the W. English Channel & Celtic Sea. However, the positive association with both summer and winter temperatures is skewed by a smaller dataset for this species, which was first reported for the UK on the south coast of England in 1971 (Farnham et al. 1973) and has spread north since that time. The significant increase in the Irish Sea is a reflection of its northward movement.

Many wracks demonstrated a weakly negative trend in Western Scotland, although (with the exception of *S. muticum*) the only significant trends were increases in abundance for *Fucus serratus*, *F. vesiculosus* and *Ascophyllum nodosum. A. nodosum* and *F. vesiculosus* showed significant increases in the North Sea and both species showed a positive association with temperature, a pattern in keeping with anecdotal reports from the area, but we note that this region has limited temporal sampling and these results are predominantly determined by data from two years. *F. serratus* increased in W. English Channel & Celtic Sea, but there was no pattern between abundance and temperature. The remaining wracks showed no significant regional trends, although the abundance of both *F. spiralis* and *Himanthalia elongata* had a negative correlation with winter temperatures, which may be a concern if the trend for milder winters continues.

Temperature is expected to be a factor in species declines at the edge of ranges, where those species are at the limit of their thermal tolerances (i.e. southern edge for northern hemisphere species) (Harley et al. 2006). Of the 14 species in this study, none are at their southern limits in the British Isles. However, the Arctic and cold temperate species *Alaria esculenta* has its southern limit at approx. the 20 °C August isotherm (Widdowson 1971) and is only found in restricted locations in Northern France (Lüning, 1990). Although studies have shown declines of this species in the northeast Atlantic (Merzouk and Johnson, 2011; Mieszkowska et al. 2006; Simkanin et al. 2005),

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our data show no significant relationship in change in abundance with summer or winter temperature. However, this is the only species to show a significant increase in abundance in Western Scotland, and may be an example of a species flourishing in its optimum environment. tom Dieck (1993) reported that *A. esculenta* zoospores have an upper limit of 18 °C and optimal germination between 2 and 12 °C whereas gametophytes are more temperature tolerant with an upper survival limit of 19-21 °C. *A. esculenta* is proposed as an indicator species for monitoring the effects of climate change in Britain and Ireland (Mieszkowska et al. 2006). Therefore, although we did not find evidence of a significant change in abundance in Britain, the cooler temperatures required for zoospores may ultimately restrict this species in the region if temperatures continue to increase.

Study design

The results reported here are dependent on the assumption that the paired observations of abundance are comparable. These data were collected 1-36 years apart, by a variety of researchers with potentially different objectives and survey methodologies. However, all had the objective of measuring macroalgal abundance, and the abundance scales employed in these surveys were very similar. Although it is possible that there is a systematic bias in the data that we have not appreciated, the authors' experience covering many decades of field surveys, and discussions with other researchers, leads us to believe that these are valid comparisons.

It could be argued that because the majority of site-specific trends (4056) are based on 2 years of observations, that it is difficult to determine a robust site-specific trend. We expect fluctuations in abundance that may not reflect a long term trend, for example, 50% of species absences in north Norfolk were found to be ephemeral (Tittley, 1998). Nevertheless a significant portion of sites

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(1125) have data from more than two time periods. Our objective is not to examine site-specific trends but to combine these to present regional and country-wide patterns. Given the size and extensive regional and temporal sampling, and the broad agreement with results already reported (Table 1), we consider that our findings are noteworthy and are a foundation for further work and discussion.

Although this study examines average climatic conditions, extreme events may be driving some population declines (Smale and Wernberg, 2013). Additionally, there are many factors not considered in this study that have been identified as stressors on macroalgal populations, such as pollution and eutrophication (Coelho et al. 2000), rising atmospheric CO_2 (Brodie et al. 2014) and increasing herbivory from urchins (Steneck et al. 2002).

Historical surveys are useful sources of data for examining long-term trends. However, there are limitations on what can be interpreted from this ad hoc collection of surveys, and it is important to understand these limitations. Sophisticated time series analyses (i.e. Pinsky et al. 2013) rely on multiple repeated sampling of the same sites, which are not available for our data. The observations are temporally biased and the median difference between observations is 11 years, which means we cannot replicate analyses such as those relying on year on-year transitional models (Mieszkowska et al. 2013). Methodological advances are required in order to extract the full potential from these data.

Conclusions

Large brown seaweeds are habitat-forming and fundamental to the functioning of coastal marine ecosystems and the British Isles. Long term trends of change in abundance for large brown seaweeds present serious challenges to the long term future of these ecosystems, particularly as the British Isles is in the centre of the NE Atlantic distributions for most species and not at climatic tolerance limits. Given that temperature alone does not explain all observed increases and decreases in abundance, it is vital to identify both the physical and biological factors that are driving these changes. In addition, a much greater understanding of the different phases of the life history of these species across the population spectrum is required, along with consideration of such factors as increased storminess, turbidity and pollution.

Historical surveys can be useful to examine long term trends in changing abundance, but these data are no substitute for systematic, repeated studies, and the ad hoc nature of sampling can greatly limit our conclusions. At present, population abundances are typically classified as common, but some areas appear to show climate-linked declines. These declines must be monitored to ascertain whether they are ongoing, and if so studied to uncover causes, particularly in reference to potential loss of genetic diversity. This is best achieved by a long term monitoring programme.

Large brown seaweeds were a significant omission from the recent "State of Nature", a report documenting population declines for many species in the UK (Burns et al. 2013). The data presented here suggest that some of these brown seaweeds should be added to the list of declining species for some regions and awareness raised given the important given the habitat they create.

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Acknowledgements

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Species	Decline in distribution	Depleted genetic diversity	No apparent change	Range expansion	References
Alaria esculenta	+				Simkanin et al. (2005), Mieszkowska et al. (2006), Merzouk & Johnson (2011)
Ascophyllum nodosum	+				Simkanin et al. (2005)
Chorda filum	+				Erikkson et al. (2002)
Fucus serratus		+[2]	+[1]		1 Lima et al. (2007), 2 Pearson et al. (2009), 2 Jueterbock et al. (2012)
Fucus spiralis			+		Lima et al. (2007)
Fucus vesiculosus				+	Lima et al. (2007)
Himanthalia elongata	+[1]		+[2]		1 Fernández & Neill (1982), 1,2 Lima et al. (2007), 1 Davies et al. (2007), 2 Simkanin et al. (2005), 2 Merzouk & Johnson (2011)
Laminaria digitata	+				Cosson (1999), Morizur (2001)
Laminaria hyperborea	+[1]		+[2]		1 Simkanin et al. (2005), 1 Müller et al. (2009) 2 Lima et al. (2007)
*Laminaria ochroleuca**				+	Parke (1948)
Pelvetia canaliculata	+				Lima et al. (2007)
Sacchorhiza latissima	+				Simkanin et al. (2005), Pehlke & Bartsch (2008), Brodie et al. (2009), Andersen et al. (2011), Roleda & Dethleff (2011), Moy & Christie (2012)
Saccorhiza polyschides	+				Fernández (2011)
Sargassum muticum				+	Harries et al. (2007)

Table 1: Summary of reported changes to key large brown seaweed species.

Change in abundance of large brown seaweeds

Table 2. Summary of abundance scales and how they are used for this study. Group 1 = JNCC post-1990 / MNCR / SNH / EN (MarCLIM and MBA post2006), Group 2 = Seasearch / Yorkshire Naturalists, Group 3 = MBA pre-2006 / CCW. Superscript signifies categories used for this study, [A] Abundant (Dark Grey), [C] Common (Grey), [O] Occasional (Light Grey), [R] Rare (White). JNCC=Joint Nature Conservation Committee, SNH=Scottish Natural Heritage, MBA=Marine Biological Association, CCW=Countryside Council for Wales, MNCR=Marine Nature Conservation Review.

Class	Group 1	Group 2	MarCLIM	Group 3
Suprabundant	>80%[A]	>80%[A]		100% cover and depth[A]
Abundant	40-79%[A]	40-80%[A]	>30%[A]	>75%[A]
Common	20-39%[C]	20-40%[C]	5–30%[C]	20-75%[A]
Frequent	10-19%[C]	10-20%[C]	<5%[R]	10-19% (probably zone forming but not so much cover)[C]
Occasional	5-9%[O]	5-10%[O]	Scattered individuals [R]	(5-9%?) a few encounters[O]
Rare	1-5%[R]	< 5%[R]	Few plants 30 min search [R]	(<5%) rare [R]

Table 3. Number of observations of species abundance during the period 1974-2010. Sites are 1km^2 regions with 2 or more observations of the same species over this period. The terms decline, stable and increase indicate the number of sites (proportion in parentheses) showing that trend of abundance. Slope indicates the mean value of the slope of abundance change over all sites. Temporal range is the time period for which specific species have data.

Group	Species	Obs.	Sites	Decline	Stable	Increase	Slope	Temporal Range
Kelp	*Alaria esculenta*	130	59	22 (0.37)	3 (0.05)	34 (0.58)	0.122	1974-2010
	Chorda filum	391	171	54 (0.32)	4 (0.02)	113 (0.66)	-0.029	1974-2010
	Laminaria digitata	435	183	63 (0.34)	3 (0.02)	117 (0.64)	0.045	1974-2010
	Laminaria hyperborea	1,283	496	187 (0.38)	8 (0.02)	301 (0.61)	0.007	1974-2010
	Laminaria ochroleuca	78	29	16 (0.55)	0 (0.00)	13 (0.45)	-0.060	1978-2010
	Saccharina latissima	1,050	451	176 (0.39)	13 (0.03)	262 (0.58)	-0.012	1974-2010
	Saccorhiza polyschides	308	121	44 (0.36)	5 (0.04)	72 (0.60)	0.004	1975-2010
Total	Kelp	3,675	1,510	562 (0.37)	36 (0.02)	912 (0.60)	-	-
Wracks	*Ascophyllum nodosum*	281	124	48 (0.39)	2 (0.02)	74 (0.60)	0.033	1974-2010
	Fucus serratus	471	198	73 (0.37)	5 (0.03)	120 (0.61)	-0.007	1974-2010
	Fucus spiralis	196	84	32 (0.38)	2 (0.02)	50 (0.60)	-0.031	1974-2010
	Fucus vesiculosus	394	173	59 (0.34)	2 (0.01)	112 (0.65)	0.061	1974-2010
	Himanthalia elongata	130	53	21 (0.40)	3 (0.06)	29 (0.55)	0.003	1974-2010
	Pelvetia canaliculata	244	103	44 (0.43)	2 (0.02)	57 (0.55)	0.001	1974-2010
	Sargassum muticum	90	37	14 (0.38)	1 (0.03)	22 (0.59)	0.042	1976-2010
Total	Wracks	1,806	772	291 (0.38)	17 (0.02)	464 (0.60)	-	-
Total	Kelp + Wracks	5,481	2,282	853 (0.37)	53 (0.02)	1,376 (0.60)	-	-

Table 4. Correlation of rate of change in abundance between species. Upper right triangle is Pearson correlation coefficient with significance indicated by: *** p<0.001, ** p<0.01, * p<0.05. Lower triangle is number of sites with both species present.

Group	Species	A. esc.	C. fil.	L. dig.	L. hyp.	L. och.	S. lat.	S. pol.	A. nod.	F. ser.	F. spi.	F. ves.	H. elo.	P. can.	S. mut.
Kelp	Alaria esculenta	-	-0.75	0.62**	0.25	-0.12	0.27	0.03	0	0.05	-0.2	-0.24	-0.3	0.97***	0
	Chorda filum	3	-	0.03	-0.1	0	0.40***	0.06	-0.24	-0.02	0.19	-0.13	0.19	-0.03	0.26
	Laminaria digitata	20	32	-	-0.24*	0.36	-0.04	-0.07	0.52**	0.41***	0.02	0.72***	0.50**	-0.3	0.57
	Laminaria hyperborea	49	50	98	-	-0.05	0.35***	-0.12	0.08	0.42***	-0.12	0	0.52**	-0.17	0.01
	Laminaria ochroleuca	3	1	5	27	-	-0.88*	0.18	0	0	0	0	1.00*	0	0
	Saccharina latissima	28	119	98	208	5	-	0.49***	0.16	-0.13	0.34	0.14	-0.26	-0.03	-0.29
	Saccorhiza polyschides	15	18	37	96	15	73	-	0.37	-0.15	-0.27	-0.11	0.22	0.09	-0.1
Wrack	Ascophyllum nodosum	2	29	31	24	0	41	6	-	-0.62***	-0.40**	-0.07	-0.12	0.52***	-0.13
	Fucus serratus	13	43	80	58	0	83	23	85	-	0.55***	0.25**	0.68***	-0.32**	0.14
	Fucus spiralis	8	15	26	21	0	30	6	59	63	-	0.51***	0.26	0.16	-0.22
	Fucus vesiculosus	11	31	50	39	1	53	7	89	117	70	-	0.82***	0.16	0.89**
	Himanthalia elongata	9	8	29	27	3	25	15	12	32	13	16	-	-0.1	-0.05
	Pelvetia canaliculata	8	21	32	23	0	35	6	71	82	65	82	14	-	0.97
	Sargassum muticum	1	18	11	12	1	28	9	8	16	4	7	9	3	-

Table 5. Summary of the relationship of change in species abundance and sea surface temperature (SST). The central table shows the slope of abundance over time (black lines of Figure 1). Units relate to number of abundance categories per year, so *P. canaliculata* in Western Scotland has declined approximately one abundance category over the duration of the analysis (-0.0278 ≈ -1/36). Colours indicate trend and significance. Red indicates an overall negative trend with confidence interval (CI) of trend unambiguously negative. Orange is negative trend, but CI incorporates a positive response. Green shows unambiguously positive trend, pale green shows positive trend but CI includes negative response. Yellow indicates no significant trend with slope close to zero. *SST change per year is expressed as the slope of the regression line of seasonal mean SST calculated annually from 1974-2010, deeper blue indicates greater change. [#]Relationship between SST and abundance is based on generalised linear mixed models, + and – indicate the sign of the relationship with the number of symbols indicating the significance (i.e. +++/--- indicates a significant positive/negative relationship of abundance and temperature with $p<0.001$, similarly ++/-- signifies $p<0.01$, and +/- $p<0.05$).

Group	Species	South			Central			North			Relationship with temperature[#]	
		SW Atlantic	W. Channel & Celtic Sea	English Channel	North Sea (S)	Irish Sea	West Ireland	North Sea (N)	Western Scotland	Scottish Shelf	Summer	Winter
Kelp	*Alaria esculenta*		0.0741			-0.0199		-0.0496	0.0500	0.0001		
	Chorda filum		-0.0032	-0.1500		0.0222	-0.2500		0.0000	0.0001		+++
	Laminaria digitata		0.0001	-0.0013		-0.0167		0.0708	0.0000	0.0731	++	---
	Laminaria hyperborea		-0.0084	-0.0352		0.0115	-0.0001	0.0001	0.0001	0.0149	+++	---
	Laminaria ochroleuca		-0.0317									
	Saccharina latissima		0.0094	-0.0318		-0.0001	-0.1250	-0.0309	-0.0079	0.0000	---	---
	Saccorhiza polyschides		-0.0324	0.0035		0.0243			-0.0070	0.1434		
Wracks	*Ascophyllum nodosum*		0.0000			0.0071		0.2500	-0.0298	0.0091		+++
	Fucus serratus		0.0074	-0.0313		-0.0034		-0.0075	0.0000	-0.0379		
	Fucus spiralis		-0.0130			0.0323		-0.0125	-0.0333	0.0000		--
	Fucus vesiculosus		0.0072	0.0395		0.0001		0.1428	-0.0227	0.0113	+++	+++
	Himanthalia elongata		-0.0094			0.0154			-0.0150	0.0776		-
	Pelvetia canaliculata		0.0000			0.0000			-0.0278	-0.0481	+++	
	Sargassum muticum		-0.0439	0.0314		0.3138					+++	+++
SST Change (℃ per year)*	Summer	0.023	0.032			0.031	0.019	0.039	0.018	0.026		
	Winter	0.019	0.022			0.016	0.016	0.031	0.016	0.021		

Fig. 1a. Change in abundance by geographic region for kelp species. Points indicate records of abundance at a site covering 2 or more different years of observations. Inset line graphs show abundance (y=1-4) over time (x=1974-2010) for individual sites, so each coloured line shows a site-specific trend in abundance. Black lines show median slope of all the site specific trends, dashed grey lines show 95% confidence intervals for the median slope lines. For example, *L. hyperborea* in the English channel has many sites showing declines (red lines), resulting in a strong overall negative trend (black line).
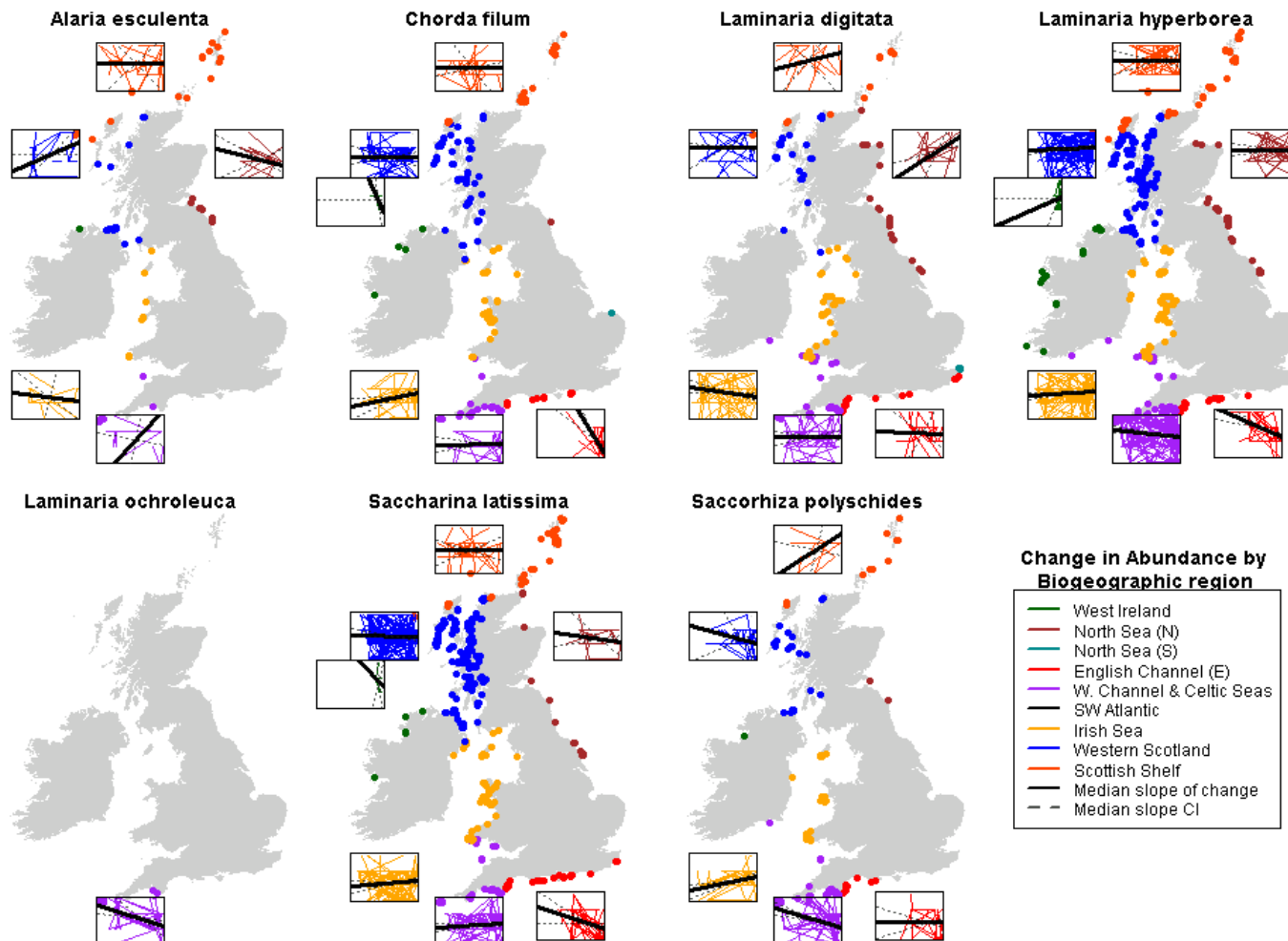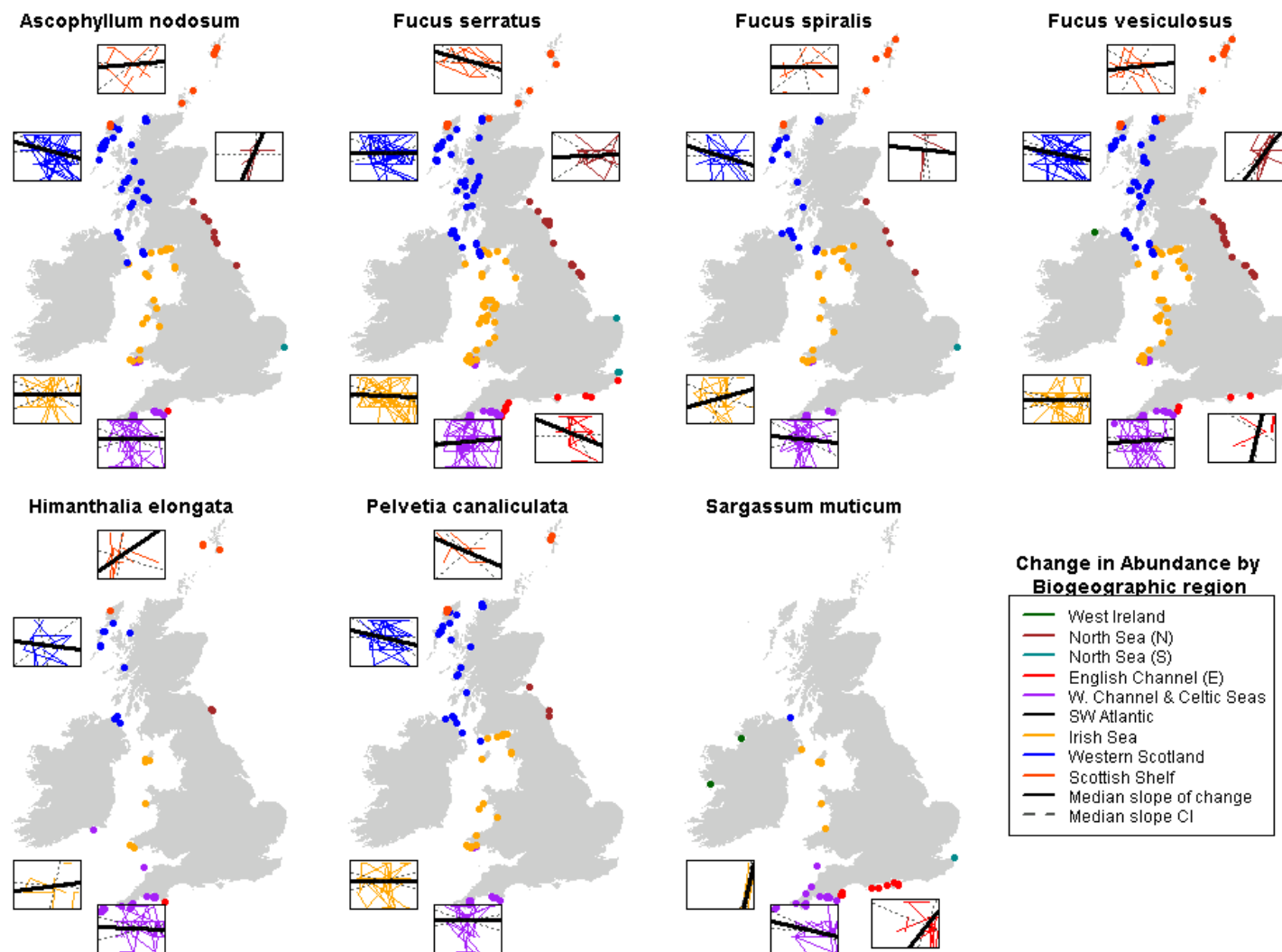
**Fig. 1b.** Change in abundance of Wrack species 1974-2010. Format as Figure 1a.

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Fig. 2. Sea surface temperatures 1974-2010 based on locations with seaweed abundance data. Coloured lines are annual means, black lines show trend. Points show locations with seaweed abundance data. Inset line charts show mean sea surface temperature (SST) for each region.
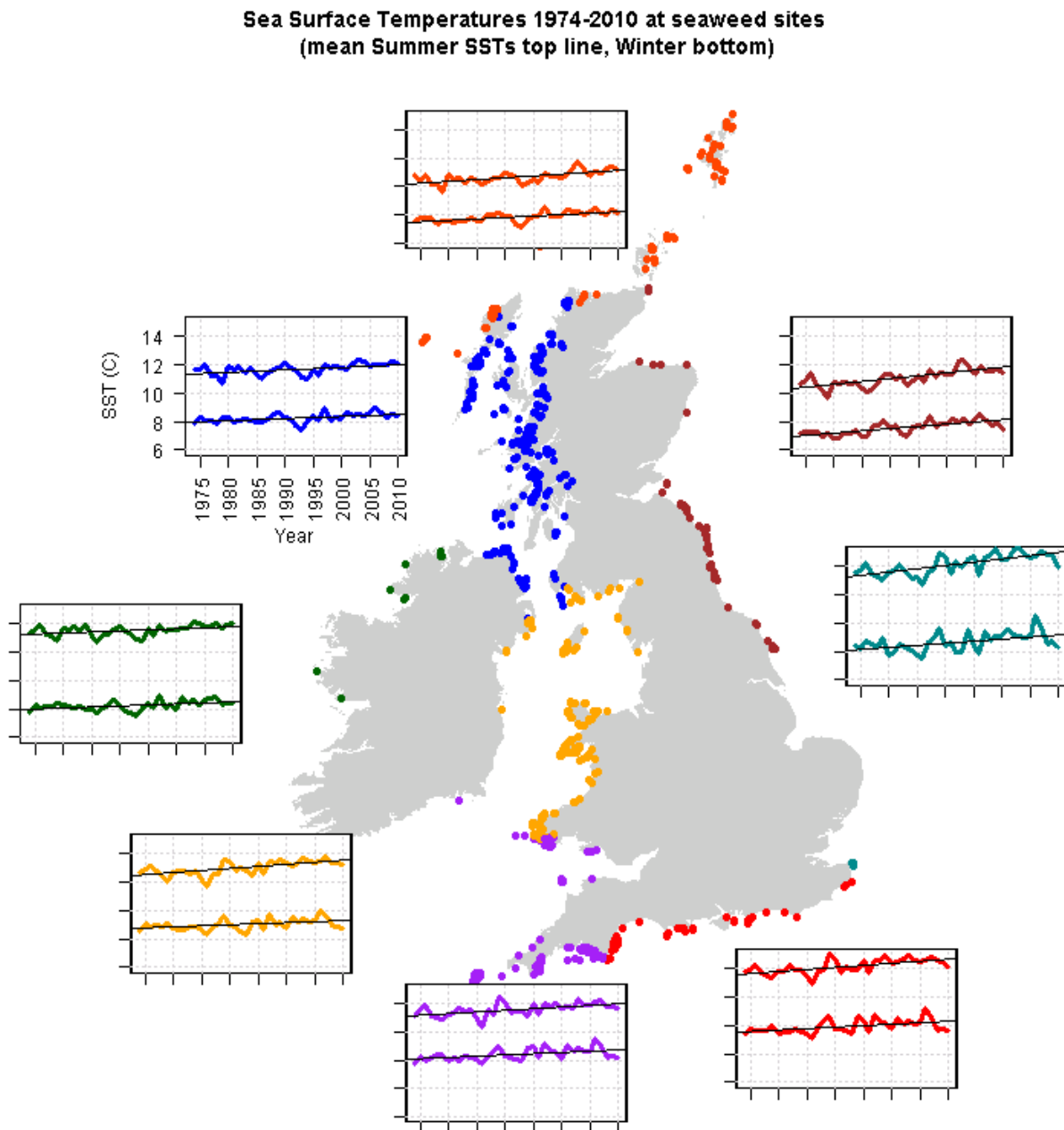
Supplementary Table S1. Details of generalised linear mixed models testing importance of sea surface temperatures in explaining abundance patterns. Highlighted cells show $p<0.05$.

Model details	Species	Alaria esculenta	Ascophyllum nodosum	Chorda filum	Fucus serratus	Fucus spiralis	Fucus vesiculosus	Himanthalia elongata	Laminaria digitata	Laminaria hyperborea	Laminaria ochroleuca	Pelvetia canaliculata	Saccharina latissima	Saccorhiza polyschides	Sargassum muticum
N		747	1,007	1,216	1,603	1,044	1,546	604	1,515	3,239	143	1,019	2,919	1,066	262
Fixed variables															
Time	Std Dev	0.0	1.4212	34.5544	0.2409	0.2206	5.6757	1.3212	4.3213	10.5274	3.0822	3.0918	7.9733	0.0003	3.7741
	Residual	0.6	34.9917	18.8777	0.5109	0.4865	6.7712	13.6231	12.4616	7.0125	8.4701	18.7702	9.5694	3.2227	11.0755
Explanatory variables															
Intercept	Estimate	2.1	-0.9	-6.4	3.1	3.6	0.5	3.4	2.4	6.5	-0.4	2.8	2.7	10.5	1.1
	Variance	0.331	0.788	7.056	0.191	0.261	1.254	1.159	1.160	2.109	4.098	0.974	2.107	0.527	1.940
	z	6.244	-1.155	-0.903	16.058	13.749	0.429	2.937	2.030	3.071	-0.088	2.888	1.266	19.871	0.582
	p	**0.000**	0.248	0.367	**0.000**	**0.000**	0.668	**0.003**	**0.043**	**0.002**	0.930	**0.004**	0.206	**0.000**	0.561
Summer SST (linear)	Estimate	-0.003	-0.017	-0.010	-0.016	-0.027	0.083	-0.041	0.052	0.097	0.282	-0.133	-0.021	-0.192	0.269
	Variance	0.030	0.031	0.022	0.014	0.016	0.010	0.066	0.020	0.021	0.230	0.020	0.015	0.046	0.069
	z	-0.099	-0.559	-0.428	-1.173	-1.632	8.403	-0.629	2.647	4.565	1.228	-6.529	-1.446	-4.163	3.902
	p	0.921	0.576	0.669	0.241	0.103	**0.000**	0.529	**0.008**	**0.000**	0.222	**0.000**	0.148	**0.000**	**0.000**
Winter SST (linear)	Estimate	0.041	0.403	0.500	-0.018	-0.077	0.164	-0.128	-0.223	-0.241	-0.237	-0.027	-0.009	-0.583	0.555
	Variance	0.036	0.058	0.047	0.018	0.024	0.014	0.059	0.030	0.036	0.212	0.028	0.045	0.067	0.096
	z	1.145	6.999	10.712	-1.008	-3.190	11.680	-2.184	-7.482	-6.640	-1.122	-0.960	-0.199	-8.707	5.784
	p	0.253	**0.000**	**0.000**	0.314	**0.002**	**0.000**	**0.029**	**0.000**	**0.000**	0.264	0.337	0.842	**0.000**	**0.000**
Spatial autocorrelation															
Range (m)		1	34,482	78,850	1	1	112,726	84,288	39,196	37,570	2,838	94,811	89,529	4,320	26,247