The distribution and environmental requirements of large brown seaweeds in the British Isles

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Kelps, fucoids and other large brown seaweeds are common and important features of temperate coastal zones. The British Isles is a centre for seaweed diversity in the NE Atlantic, but, despite numerous surveys, an incomplete picture of the distribution remains. Survey data and herbarium specimens were used to examine the environmental preference of 15 species of large brown seaweeds, covering the orders Laminariales (kelps), Fucales (wracks) and one species of Tilopteridales. Habitat suitability models were developed to estimate broad-scale distribution and area of habitat created by these species around the British Isles. Topographic parameters were important factors limiting distributions. Generally, temperature did not appear to be a limiting factor, probably because the British Isles lies in the centre of the NE Atlantic distribution for most species, and not at climatic tolerance limits. However, for the recent migrant Laminaria ochroleuca, *temperature was found to be important for the model, thus range expansion could continue northwards provided dispersal is possible. In contrast, the widespread* Alaria esculenta *showed a negative association with warmer summer temperatures. The total potential habitat around the British and Irish coastline is more than 19,000 km² for kelps and 11,000 km² for wracks, which represents a significant habitat area similar in scale to British broadleaf forest. We conclude that large brown algal species need to be managed and conserved in a manner that reflects their scale and importance.*

INTRODUCTION

Large brown seaweeds (Phaeophyceae) are a diverse and complex group that occur in the littoral and shallow sublittoral of marine environments and which dominate in temperate waters, particularly in the northern hemisphere (Steneck *et al.*, 2002; Critchley *et al.*, 2006; Smale *et al.*, 2013 and references therein). Kelps (Laminariales) dominate rocky reefs in the shallow sublittoral, and fucoids (wracks; Fucales) dominate rocky shores in the littoral. These seaweeds are important primary producers and kelp forests are amongst the most productive on earth (Mann, 1973), supporting high primary productivity and enhanced secondary productivity (Smale *et al.*, 2013). They contribute to many food-chains and constitute a detrital pathway from shallow, highly productive waters into deeper seas. Their structure provides a three-dimensional habitat for a rich variety of marine life, including commercially important species. This structure protects shorelines by acting as a buffer, removing energy from currents and waves, and consequently providing sheltered areas for larger organisms to use when feeding and breeding (Lüning, 1990). Kelps and fucoids have been exploited by humans for food

and chemicals and are increasingly the focus of such products and biofuels (McHugh, 2003; Kraan, 2012).

It is well-documented that kelp and fucoid populations can be temporally and spatially highly dynamic, although reasons for this can be varied and complex (e.g. Hawkins *et al.*, 2008; Smale *et al.*, 2013; Trowbridge *et al.*, 2013). However, in the last decade, there have been an increasing number of reports of the decline or loss of large brown seaweeds. Whilst some of these have been anecdotal, there is increasing evidence to support these observations (Wernberg *et al.*, 2011; Moy & Christie, 2012; Koch *et al.*, 2013; Smale & Wernberg, 2013). Although some changes appear to be linked to climate, there are multiple reasons as to why these seaweeds are under threat (Brodie *et al.*, 2014). Consequently the life histories of these species need to be considered; generally, the large sporophyte alternates with a microscopic gametophyte and each life history phase may respond differently to environmental stressors (see Bartsch *et al.*, 2008). Other possible reasons for changes include the impact of milder winters on the interaction between sporelings and grazers (e.g. top shells and winkles), increase in number and spread of non-native species, changes in current regimes and turbidity, and impact of nutrients.

In order to understand the impact of any threat, we have to start by establishing a baseline of species distribution and abundance. A good knowledge of distribution is necessary to address many important ecological questions. The ideal

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669

approach is a comprehensive survey of all areas to establish the distribution and abundance of the target species. However, this is at best logistically complex, time consuming and expensive, and at worst impossible. A response to this information deficit is to estimate species distributions using knowledge of their environmental requirements (Elith & Leathwick, 2009). Generally, the lower limit of these seaweeds is physiologically constrained by light, and the upper limit by temperature, humidity, emersion, exposure, grazing and competition (Lüning, 1990). Their latitudinal distribution is largely controlled by light and temperature at higher latitudes, and nutrients, temperature and competition at lower latitudes (van den Hoek, 1982; Lüning, 1990). Within their biogeographic range, local populations can be constrained by biotic factors, such as grazing and competition, as well as anthropogenic exploitation (Trowbridge *et al.*, 2013). Other limiting factors include pollutants, ultraviolet (UV) light, global warming, extremes of weather, ocean acidification and turbidity (Steneck *et al.*, 2002; Schils & Wilson, 2006; Koch *et al.*, 2013; Smale & Wernberg, 2013).

Species distribution modelling (SDM) attempts to quantify the environmental preferences of species, using limited distribution data and environmental layers. Once established, these environmental preferences can be used to establish where regions of suitable environment occur and so provide an estimate of distribution (Araújo & Guisan, 2006; Elith & Leathwick, 2009; Robinson *et al.*, 2011). A number of studies have used SDMs to examine seaweed distributions (reviewed in Pauly & De Clerck, 2010). These have ranged from local-scale models incorporating high resolution, directly measured environmental parameters (Méléder *et al.*, 2010; Gorman *et al.*, 2012; Martínez *et al.*, 2012), through to global-scale modelling of widespread species using global-environmental datasets (Verbruggen *et al.*, 2009; Tyberghein *et al.*, 2012). A particular focus has been on modelling distributions of invasive species (Tyberghein *et al.*, 2012; Verbruggen *et al.*, 2013) with the objective of identifying areas at risk of invasion.

One area of investigation has been the impact of the changing climate on macroalgae (Pauly & De Clerck, 2010). The physiological response of many seaweed species to changing temperature is generally well understood due to experimental studies (Eggert, 2012). Van den Hoek (1982) described distribution patterns for North Atlantic seaweeds limited by seasonal sea surface temperature isotherms, which has been followed by observations of temperature limits to macroalgal biogeographic regions (Adey & Steneck, 2001; Schils & Wilson, 2006). This linkage between climate and distribution has led to concerns about the impact of climate change on seaweed populations (Lima *et al.*, 2007; Bartsch *et al.*, 2012; Harley *et al.*, 2012; Smale & Wernberg, 2013).

The expectation is that increasing temperatures will result in a poleward shift in distributions (Harley *et al.*, 2012), and this has been predicted for some groups of seaweeds (Bartsch *et al.*, 2012). Lima *et al.* (2007), who investigated the changing distributions of Portuguese seaweeds over the last 50 years, concluded that warm-water species expanded northwards in response to warming temperatures, but that cold-water species did not contract in response to the same warming. Lamela-Silvarrey *et al.* (2012) documented changes in abundance of fucoids in northern Spain, some of which were linked to increases in temperature, but other factors, such as

a shift in the seasonality of upwelling, were also linked to observed changes.

The consequences of global climate change extend beyond the effects of warming, for example the increase in extreme climatic events has been linked to a range contraction of Australian habitat-forming macroalgae (Smale & Wernberg, 2013). Declines in abundance have been observed around the coast of Ireland (Simkanin *et al.*, 2005), but possible environmental triggers for these declines were not analysed. Decadal fluctuations in populations of several large brown seaweed species have been observed in Loch Hyne, Northern Ireland, primarily associated with changing predation (Trowbridge *et al.*, 2013). In the UK, both increased temperature and wave exposure have been linked with abundance reductions for some macroalgae (Hiscock *et al.*, 2004; Hawkins *et al.*, 2009).

The aim of this study is to produce a distribution estimate and examine the habitat preferences for 15 species of large brown macroalgae (Phaeophyceae) (Table 1) around the British Isles coast, using a comprehensive database of species observations along with environmental data including temperature, currents, topography and substrata.

The archipelago of the British Isles, in the temperate zone of the NE Atlantic, is a region profoundly impacted by humans (Brodie *et al.*, 2014), and an important biogeographic transition zone. The littoral and shallow sublittoral regions support over 650 species of red, green and brown seaweed, which represents ∼50% of the north Atlantic's and ∼7% of the world's documented seaweed flora (J. Brodie, personal observation). The northern limits of the majority of large brown seaweed species occur outside the British Isles, with the exception of *Laminaria ochroleuca*, which is at its northern limit in England, and *Alaria esculenta* whose southern limit is just into northern France (Lüning, 1990). This makes the British Isles a stronghold for these species. The seaweed flora of the British Isles is expanding with the appearance of invasive species such as *Undaria pinnatifida* and *Sargassum muticum* which are spreading throughout Europe (Smale *et al.*, 2013).

In the waters around the British Isles, substantial coastal surveys were conducted between 1970 and 2000 (Smale *et al.*, 2013), and the majority of these data have been deposited in the National Biodiversity Network database (http://www.nbn.org.uk/). Additionally, institutions such as the Natural History Museum have an extensive collection of specimens of large brown seaweeds dating back to the 18th century. However, the UK has published relatively few studies of seaweed habitats with respect to comparative countries (Smale *et al.*, 2013), and the relative inaccessibility of rocky coastal, intertidal and subtidal habitats mean that many areas around the British Isles have yet to be surveyed adequately.

METHODS

Distribution data

The distribution of 15 species of kelps and fucoids was studied (Table 1). Distribution data for the target species were collated from a variety of sources, including nationwide and regional surveys, museum catalogues and the literature, dating from the 18th century to the present day (Supplementary

Table 1. Species and classification of the large brown seaweeds (Phaeophyceae) in this review. Source for taxonomy: Guiry *et al.* (2014). Source for common names: Bunker *et al.* (2010). N-filtered/unfiltered refers to the number of occurrence observations for each species in this study. Filtered records are spatially unique to the 3 km grid of the environmental data.

Group	Species	Authority	Order	Family	Common names	N-unfiltered	N-filtered
Kelp	*Alaria esculenta*	(Linnaeus) Greville	Laminariales	Alariaceae	Dabberlocks	2920	274
	Undaria pinnatifida	(Harvey) Suringar	Laminariales	Alariaceae	Wakame	163	19
	Chorda filum	(Linnaeus) Stackhouse	Laminariales	Chordaceae	Mermaid's Tresses, Bootlace Weed	7109	483
	Laminaria digitata	(Hudson) J.V. Lamouroux	Laminariales	Laminariaceae	Oar Weed, Tangle	10,624	579
	Laminaria hyperborea	(Gunnerus) Foslie	Laminariales	Laminariaceae	Forest Kelp, Northern Kelp	15,815	1017
	Laminaria ochroleuca	Bachelot de la Pylaie	Laminariales	Laminariaceae	Golden Kelp	603	44
	Saccharina latissima	(Linnaeus) C.E. Lane, C. Mayes, Druehl & G.W. Saunders	Laminariales	Laminariaceae	Sugar Kelp, Sea Belt	17,796	901
	Saccorhiza polyschides	(Lightfoot) Batters	Tilopteridales	Phyllariaceae	Furbellows	4646	435
Wracks	*Ascophyllum nodosum*	(Linnaeus) Le Jolis	Fucales	Fucaceae	Knotted Wrack, Egg Wrack	10,846	433
	Fucus serratus	Linnaeus	Fucales	Fucaceae	Serrated Wrack	15,701	630
	Fucus spiralis	Linnaeus	Fucales	Fucaceae	Spiraled Wrack	9603	455
	Fucus vesiculosus	Linnaeus	Fucales	Fucaceae	Bladder Wrack	16,355	634
	Pelvetia canaliculata	(Linnaeus) Decaisne & Thuret	Fucales	Fucaceae	Channel Wrack	8727	359
	Himanthalia elongata	(Linnaeus) S.F. Gray	Fucales	Himanthaliaceae	Thongweed	4961	209
	Sargassum muticum	(Yendo) Fensholt	Fucales	Sargassaceae	Wireweed	1701	311

Appendix S1). The majority of the distribution data was accessed via the National Biodiversity Network Gateway (http://www.nbn.org.uk/) and the Marine Recorder project (http://jncc.defra.gov.uk/page-1599).

Distribution data were filtered to include those from 2000 onwards in order to be contemporaneous with the environmental data (see below). We note that the lifespan of most of our target species is under a decade (Birkett *et al.*, 1998; Borum *et al.*, 2002), with the exception of *Ascophyllum nodosum* and *L. hyperborea* (Sundene, 1973; Sjøtun *et al.*, 1993), and established canopies can remain stable for many decades (Steneck *et al.*, 2002).

A depth filter was employed to exclude records with unrealistic inferred depths indicative of spatial inaccuracy in the data. For each sample a depth/elevation value was inferred from a bathymetry/digital terrain model. The environmental layers were limited to areas with a maximum depth of 50 m for kelp species and a maximum depth of 25 m for fucoids and a maximum elevation of 20 m which represented approximately the 5th and 76th percentile of kelp data and 9th and 71st percentile of fucoids data. Finally, a spatial filter was employed, where records with a coordinate precision poorer than the dimensions of the environmental grids (3 km) were excluded from the analysis.

Environmental layers

A set of 16 environmental datasets were collated for species distribution modelling, including sea-surface temperature, slope, fetch and percentage of light reaching the sea bed (Table 2). These data represent the environment of the decade 2000–2009 and are based on both direct measurements and oceanographic models, most of which have been used or recommended for use in modelling seaweed distributions (Pauly & De Clerck, 2010). Where the data were available, measurements of both summer and winter conditions (represented as February and August means) were preferred to annual means, as seasonal highs and lows have

been shown to limit seaweed distributions (van den Hoek, 1982).

In addition to the continuously variable environmental parameters, a categorical variable representing substrata was included in the analysis. Seafloor and shoreline geology is an important factor determining the distribution of large brown seaweeds. For example, many species require hard substrata as a surface enabling the physical attachment of the holdfast (Lüning, 1990). The EMODNET-Geology classification (http://www.emodnet-geology.eu/) was used as it is consistent with the chosen bathymetry and oceanographic layers.

Environmental layers were re-projected onto the Ordnance Survey of Great Britain 1936 grid (epsg:27700) of 3 × 3 km. This matches the approximate resolution of the satellite-based layers (2.5 × 2.5 arc minutes). Raster grids representing marine environmental data are often data deficient along the coastline, as pixels covering both land and sea can be excluded from datasets (Tyberghein *et al.*, 2012). To avoid this problem coastal buffering was applied to each marine layer by interpolating coastal pixels from nearby areas (Tyberghein *et al.*, 2012; Holman & Haller, 2013). GIS processing of layers was performed using tools from the Geodata Abstraction Library – 'gdal' v1.9.2 (http://www.gdal.org/). Re-projection of grids used cubic spline interpolation in gdalwarp, terrain analysis used gdaldem and coastal buffering used gdalfillnodata.

Species distribution modelling

Model selection is an important component of the SDM process (Araújo & Guisan, 2006) and can dramatically affect results when modelling coastal plant communities (Downie *et al.*, 2013). The presence-only modelling algorithm Maxent was chosen to analyse our data, as this has been used successfully for seaweeds (Verbruggen *et al.*, 2009; Pauly & De Clerck, 2010; Tyberghein *et al.*, 2012). Our data are treated as a presence-only dataset, as although a small proportion of our data recorded absences (<1.5%), these are strongly biased

Table 2. List of environmental variables used in this study.

Abbreviation	Environmental variable	Native spatial resolution	Temporal resolution	Download site	Source
SST	Sea surface temperature (*C)	2.5 arc minutes ($\sim$ 4 km)	Monthly means (Feb & Aug) 2003–2012	http://oceandata.sci.gsft.nasa.gov/	MODISA sensor
PAR	Photosynthetically available radiation (Einstein m^{-2} Day^{-1})				
Kd	Diffuse attenuation coefficient at 490 nm (m^{-1})				MERIS sensor
CHL	Chlorophyll *a* concentration (mg m^{-3})				
Tidal Energy	Tidal current energy (N m^{-2})	10 arc seconds ($\sim$300 m)	Present day	http://jncc.defra.gov.uk/page-5040	EU SeaMap Energy in the Celtic Sea and North Sea
Wave Energy	Wave energy (N m^{-2})				
Light Per cent	Percentage of light reaching the seabed (%)		Annual mean 2003–2008		EU SeaMap Light for the Celtic Sea, North Sea and Western Mediterranean
DTM[1]	Elevation (m)	3 arc seconds ($\sim$90 m)	Present day	http://srtm.csi.cgiar.org/	SRTM – Shuttle Radar Topography Mission (version 4)
	Depth (m)	10 arc seconds ($\sim$300 m)		http://portal.emodnet-hydrography.eu	EMODnet European Marine Observation and Data Network (Release 4 2012)
Slope	Slope (degrees)	3 km		n/a	
SlopeSlope	Slope of slope (rate of change of slope in degrees)				
Fetch	Fetch (average distance to coastline in metres)				Derived from DTM using bespoke R script
Substrata	Seabed substrata classification	1:1,000,000	Present day	http://jncc.defra.gov.uk/page-5040	EMODnet Geology
Wind Speed	Mean monthly wind speed	15 arc minutes	Monthly means (Feb & Aug) 2007–2012	http://www.myocean.eu	Bentamy A. & Croize Fillon D. (2012). Int J. Remote Sensing 33: 1729–1754
Oxygen	Modelled mole concentration of dissolved molecular oxygen in seawater	$10 \times 6\frac{2}{3}$ arc minutes	Monthly means (Feb & Aug) 2000–2004		NERCPOL ocean biogeochemistry non assimilative hindcast (1967–2004) (http://catalogue.myocean.eu/static/resources/myocean/pum/MYO2-NWS-PUM-004-007-008-V2.1.pdf)
Nitrate	Modelled mole concentration of nitrate in seawater				
Salinity	Modelled monthly mean sea surface salinity				NERCPOL Ocean physics non-assimilative hindcast (1960–2004) (http://catalogue.myocean.eu/static/resources/myocean/pum/ MYO2-NWS-PUM-004-005-006-V2.1.pdf)
Current Speed	Modelled mean surface seawater velocity				

[1]Note that the digital terrain model was constructed by merging terrestrial elevation data.

regionally and there were no absences recorded for the Republic of Ireland, the west coast of England, or the east coast of England north of Essex.

Prior to modelling, an analysis was performed to remove correlating variables. An iterative process was performed to calculate the variance inflation factor (VIF) for all variables whereby at each stage the variable with the highest VIF was discarded (Heiberger & Holland, 2004). This process was continued until all variables showed a low level of collinearity (VIF < 5). This analysis was conducted using the R library HH (Heiberger, 2011).

Models were built using Maxent v3.3 (Phillips *et al.*, 2006) with default parameters. Ten thousand random 'background' points were selected from the study area, but limited to depths of 50 m and elevations of 20 m to match the filtered observations. A cross-validation analysis was performed by dividing the training data into 10 randomly allocated, equally sized, partitions. Each cross-validation replicate excluded one partition from the training data and used this partition to test the model (Phillips *et al.*, 2006). A jackknife analysis was performed to evaluate layer contributions to the model (Elith *et al.*, 2011). The output suitability index was converted to a prediction of presence and absence by employing a threshold suggested by the maximum sum of sensitivity and specificity (Hernandez *et al.*, 2006). Model evaluation examined the area under the receiver operating curve (AUC), a metric showing model predictive power on a 0–1 scale with a score of 0.5 indicating predictions no better than random (Fielding & Bell, 1997) alongside the model fit parameters entropy and gain (Phillips *et al.*, 2006).

RESULTS

The complete database of specimen observations totalled 127,570 records, which were filtered to 6783 spatially unique, depth-validated records since 2000. A map of all distribution records (Figure 1) demonstrates widespread coverage from almost the entire coastline of Britain and Ireland. The large kelps *L. hyperborea* and *Saccharina latissima* were the species with most location data used in the analysis, whilst the invasive species *U. pinnatifida* and the geographically restricted *L. ochroleuca* had the least data (Table 1).

Although there are distribution data available from the 18th century to the present day, the majority of data came from systematic surveys conducted since the 1970s. Recent observations covered an area of ~10,467 km² (calculated by summing the areas of unique observations on the 3 × 3 km grid), whilst all historical and present observations covered ~20,898 km². For comparison, the complete coastline of the British Isles represented as a 1-pixel-wide line on the 3 km grid covered ~59,049 km². Approximately 98% of species observations were within 3 km of the coastline, a consistent pattern for all species, including the larger, subtidal kelps. This suggests an observation bias in favour of accessible coastal areas.

Filtered species' data were used to spatially query the environmental layers to establish environmental profiles for each species (Figure 2). *Sargassum muticum* and *U. pinnatifida* were found in areas with the highest mean summer temperatures, whilst *Fucus* spp. and *A. nodosum* demonstrated the largest range of both summer and winter tolerance (Figure 2). A summary of all continuous environmental

Fig. 1. Distribution of large brown macroalgae. Recent observations from 2000 onwards (black dots) are those used for analysis. Grey crosses are records pre-dating 2000.

variables is presented in Supplementary material Appendix S2. The low resolution data on seafloor geology revealed a marked preference for hard substrata for all species, with the exception of the invasive *U. pinnatifida* (Figure 3).

The iterative variance inflation factor (VIF) analysis rejected the following layers in sequence due to high collinearity: Salinity February (VIF kelp = 21.1, fucoids = 18.2), Chlorophyll *a* Feb (kelp = 16.7, fucoids = 25.1), Photosynthetically active radiation August (kelp = 14.7, fucoids = 9.8), Kd490 attenuation depth Aug (kelp = 9.0, fucoids = 9.9), Wind speed Feb (kelp = 10.0, fucoids = 5.3), Oxygen Feb (kelp = 5.4, fucoids = 9.2) and Nitrate Feb was excluded only for fucoids (VIF = 6.3). The remaining layers were used for species distribution modelling. These were: Kd490 attenuation depth (Feb); Light at seabed; Slope; Slope of slope (rate of change of slope); SST (Feb, Aug); Tidal energy; Wave energy; Chlorophyll *a* (Aug); Fetch; Wind speed (Aug); Current speed (Feb); Oxygen (Aug); Nitrate (Aug); Salinity; Photosynthetically available radiation.

Each model demonstrated good AUC scores (>0.77 – see Table 3) for all cross-validation replicates, except for the invasive *U. pinnatifida* model (AUC range 0.70–1.00). Selecting a score threshold based on the maximum sum of sensitivity and specificity (MSS) gave low omission rates, meaning a low proportion of validation samples were omitted by these thresholds (0.00–0.21). Based on these thresholds, the area of habitat suitable for species ranged from 2421 km²
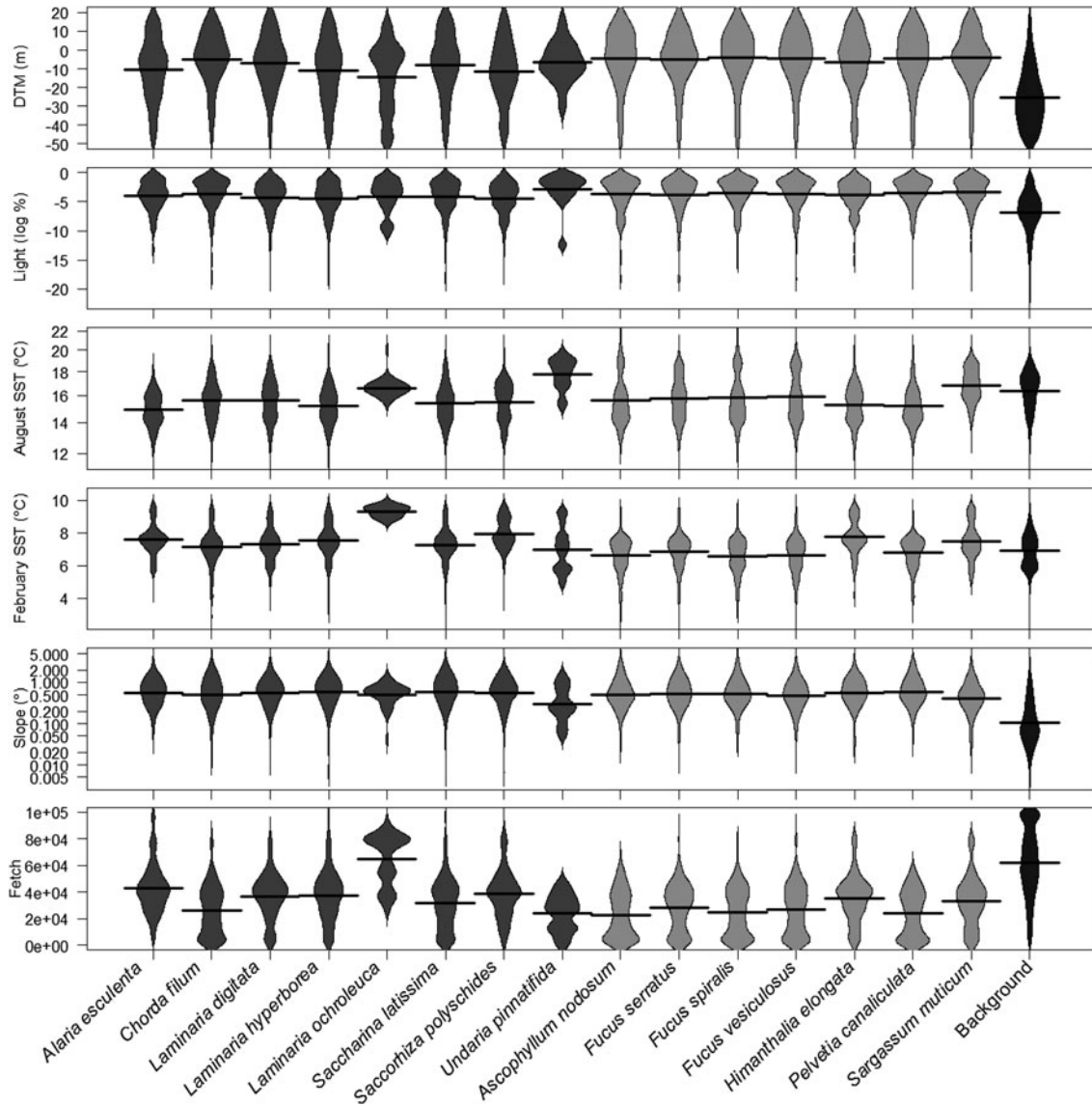
Fig. 2. Profile of selected environmental variables by species. Kelps are dark grey, fucoids are light grey, background profile is dark grey.
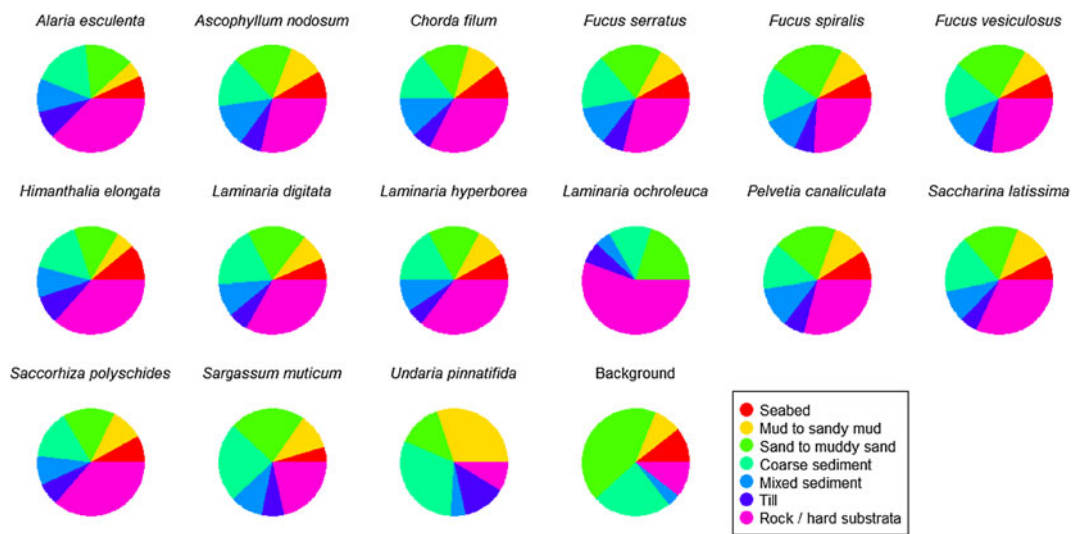

Fig. 3. Profile of substrata for each species based on species observations and the EU seamap substrata classification. Background based on 10,000 randomly selected points in the study area.

(*U. pinnatifida*) up to 48,654 km² (*L. hyperborea*), the latter of which represented >25% of the study area (Table 3). However, if only areas classified as rocky substrata are considered, then the areas range from 180 km² (*U. pinnatifida*) up to 15,984 km² (*L. hyperborea*), the latter being ~9% of the study area. The terrain parameter slope is the most important variable in determining habitat suitability for most species (Table 3). Exposure, as measured by fetch, is most important for *Chorda filum* and *U. pinnatifida*. Slope and fetch are the first and second most important variables by most measures for most species (Appendix S4). Notable exceptions are *L. ochroleuca* and *Himanthalia elongata* for which winter temperatures are important. Images showing patterns of variable response to the models are shown in Supplementary material Appendix S3. Some parameters demonstrate a consistent pattern for the majority of species studied. All species show a positive correlation between habitat suitability and the percentage of light reaching the seafloor. Most kelp species show a smooth positive response to warmer winter temperatures, but this is not repeated for most fucoids, except for *Fucus serratus* and *Pelvetia canaliculata*. Summer temperature does not contribute strongly to the model of most species, but has a strong positive effect for *A. esculenta* and a strong negative effect for *P. canaliculata*. All species show a broadly negative response to fetch (a weak response to greater exposure), although *A. esculenta*, *L. hyperborea* and *S. latissima* show a peak response at the median levels of exposure.

Most species showed a widespread suitability around most of the coastline with the exception of the East of England (Figures 4 & 5). The exceptions are *L. ochroleuca*, which has a strictly south-western distribution, and the invasive *U. pinnatifida*.

The continuous range estimates produced by the models suggested that suitable area is several times greater than that covered by sampling. More than 67,000 km² was predicted as suitable for at least one species of kelp and 39,000 km² for fucoids. However, this approach treats the presence of one seaweed in each grid cell as equivalent to 100% coverage of this cell, which inevitably will lead to a large overestimation of area. For rocky areas, where high abundance is more likely, around 19,000 km² of area is suitable for kelp and around 11,000 km² for fucoids. For reference the coastline covers 59,000 km² on our 3 km grid.

DISCUSSION

The large brown seaweeds of the British Isles are amongst the best-studied macroalgae in the world. However, we are a long way from complete distribution maps for these species (Smale *et al.*, 2013). The distribution maps presented here are a step towards this goal. The models demonstrate that climatic factors do not appear to be limiting habitat suitability for most species around the British Isles. Terrain and exposure are the most critical factors for the majority of large brown macroalgae.

The habitat formed by large brown seaweeds around the British Isles covers a significant area, which is comparable with other major habitats in the geographic region. For example, the area of woodland in Great Britain and Northern Ireland is estimated at 30,000 km² of which 10,000 km² is native woodland (Atkinson & Townsend, 2011). This study is based on 15 habitat-forming and commercially important species, and whilst it does not represent every species of large brown seaweed, it does cover the most widespread and common species and should be representative of habitat coverage. The prediction of extensive suitable habitat outside areas with rocky substrata indicates the potential for the growth of commercially exploited seaweeds on artificial substrata in these areas.

Species distribution

Observations of the invasive *U. pinnatifida* are limited and most are reported from marinas or other artificial environments that are not well represented by our environmental data, although *U. pinnatifida* has established on natural terrain around Plymouth Hoe. Recent invasive species reporting indicates that this species is expanding its range northwards into the Irish Sea, although new reports may be limited to sheltered artificial structures with high human impact (https://data.nbn.org.uk/Taxa/NBNSYS0000188802). This theory is supported by the suitability model, which demonstrates patchy suitability over a relatively small area. These appear to be highly sheltered locations, exposure (fetch) is the most important contributor to the model, and there is a strong negative response to wave energy. *Undaria pinnatifida* is still expanding its range, which means it is moving into areas within its environmental suitability, thus environmental limits are less important in limiting distributions than dispersal potential.

Currently, *L. ochroleuca* is confined to the south-west of England (Brodie *et al.*, 2009), with the most northerly record on Lundy in the Bristol Channel (Brodie, personal observation). It is a relatively recent addition to the UK, first recorded in 1948, with a gradual range expansion (John, 1969; Norton, 1978). John (1969) suggested that the range was not limited by temperature, but rather exposure and light availability. This contradicts our model, which suggests that distribution is strongly influenced by winter temperature. However, there is evidence that temperature is a limiting factor for growth and reproduction (tom Dieck, 1992; Izquierdo *et al.*, 2002). The model for *L. ochroleuca* predicts suitable habitat in several small patches in the SW of Wales and SW of Ireland, although to date, there are no reports of *L. ochroleuca* within these areas or in Ireland as a whole. This may be a dispersal limitation, including the effect of reduced salinity in the Bristol Channel acting as a barrier (J. Brodie, personal observation).

The widespread larger kelps, *L. hyperborea*, *L. digitata* and *S. latissima* are expected to retreat northwards in response to climate change (Hiscock *et al.*, 2004), but our models were influenced more by terrain parameters than temperature, which has no impact on the models. All these species occur at least as far south as northern France and some to Portugal, so they are not yet at the (warm) climatic limit of their distribution. Van den Hoek (1982) suggested that these species are limited to the south by maximum summer isotherms. These isotherms (19–20°C) have not yet reached the British Isles, although rising summer sea surface temperatures may lead to a change in the future. *Alaria esculenta* was predicted to be one of the most widespread species, both overall and in rocky areas. In contrast to most other species, temperature was an important contributor to this species model; summer temperature was the second most

Table 3. Evaluation of models. Evaluation statistics show minimum and maximum values of the cross-validation replicates. Threshold statistics use maximum sum of sensitivity plus specificity to define the threshold. Areas are calculated sum summing the area of pixels with suitability scores exceeding the threshold. Rocky areas are defined by the seabed class 'rocky or other hard substrata'. Max. Contrib. and Max. Import. refer to the variables showing maximum contribution and permutation importance. Max 1-layer AUC and Max AUC Contrib. refer to the jackknife analysis of variable importance, the former is the variable with the highest AUC for models constructed with single environmental layers, the latter is the variable whose omission from the model causes the greatest reduction in AUC, with AUC deficit being the value of the full model AUC less the AUC of the model without the named variable. Variable abbreviations as Appendix S1.

| Group	Species	AUC	Evaluation		Threshold dependent statistics				Max. Contrib.		Max. Import.		Max. 1-layer AUC		Max. AUC contrib.	
			Entropy	Gain	Threshold	Omission	Area (km²)	Rocky area (km²)	Name	%	Name	%	Name	AUC	Name	AUC deficit
Kelp	*Alaria esculenta*	0.87–0.95	7.44–7.53	0.94–1.81	0.12	0.07	38,871	13,500	Slope	48.3	Slope	36.9	Slope	0.88	Slope	0.015
	Chorda filum	0.89–0.95	7.46–7.55	1.05–1.95	0.09	0.06	39,132	10,872	Fetch	37.9	Fetch	40.8	Fetch	0.85	Fetch	0.011
	Laminaria digitata	0.88–0.93	7.69–7.74	1.08–1.63	0.14	0.05	44,118	13,536	Slope	52.9	Slope	38.9	Slope	0.86	Slope	0.021
	Laminaria hyperborea	0.89–0.92	7.90–7.94	1.19–1.46	0.14	0.04	48,654	15,984	Slope	64.0	Slope	37.0	Slope	0.86	Slope	0.019
	Laminaria ochroleuca	0.99–1.00	4.78–4.93	3.21–4.97	0.05	0.00	3969	1008	SST-Feb	64.5	SST-Feb	93.1	SST-Feb	0.99	Slope	0.002
	Saccharina latissima	0.89–0.92	7.84–7.88	1.12–1.49	0.14	0.04	44,667	13,356	Slope	55.5	Slope	32.4	Slope	0.85	Slope	0.013
	Saccorhiza polyschides	0.88–0.94	7.47–7.54	1.09–1.83	0.13	0.09	39,429	12,618	Slope	50.0	Slope	26.8	Slope	0.84	Fetch	0.006
	Undaria pinnatifida	0.70–1.00	5.48–6.53	−3.70–5.05	0.27	0.00	2421	180	Fetch	41.4	Fetch	59.8	Fetch	0.84	Fetch	0.133
Wracks	*Ascophyllum nodosum*	0.83–0.93	7.92–8.00	0.68–1.64	0.25	0.12	19,161	5607	Slope	33.4	Slope	21.1	Slope	0.79	Slope	0.014
	Fucus serratus	0.82–0.89	8.09–8.14	0.65–1.20	0.24	0.21	20,511	5985	Slope	44.8	Slope	39.8	Slope	0.76	Slope	0.024
	Fucus spiralis	0.84–0.89	7.96–8.01	0.81–1.25	0.27	0.20	16,902	4410	Slope	39.1	Slope	44.1	Slope	0.77	Slope	0.014
	Fucus vesiculosus	0.77–0.89	8.18–8.26	0.32–1.13	0.23	0.14	26,028	7605	Slope	41.4	Slope	33.8	Slope	0.76	Slope	0.025
	Himanthalia elongata	0.79–0.90	7.82–7.95	0.37–1.29	0.13	0.08	26,442	8325	Slope	41.4	Slope	29.8	SST-Feb	0.82	Slope	0.020
	Pelvetia canaliculata	0.84–0.93	7.81–7.91	0.70–1.83	0.15	0.15	20,466	6129	Slope	31.9	Fetch	22.6	Slope	0.81	Slope	0.026
	Sargassum muticum	0.85–0.95	7.55–7.69	0.68–1.87	0.25	0.14	11,718	2475	PAR-Feb	18.5	Salinity-Aug	15.2	Salinity-Aug	0.75	Slope	0.014
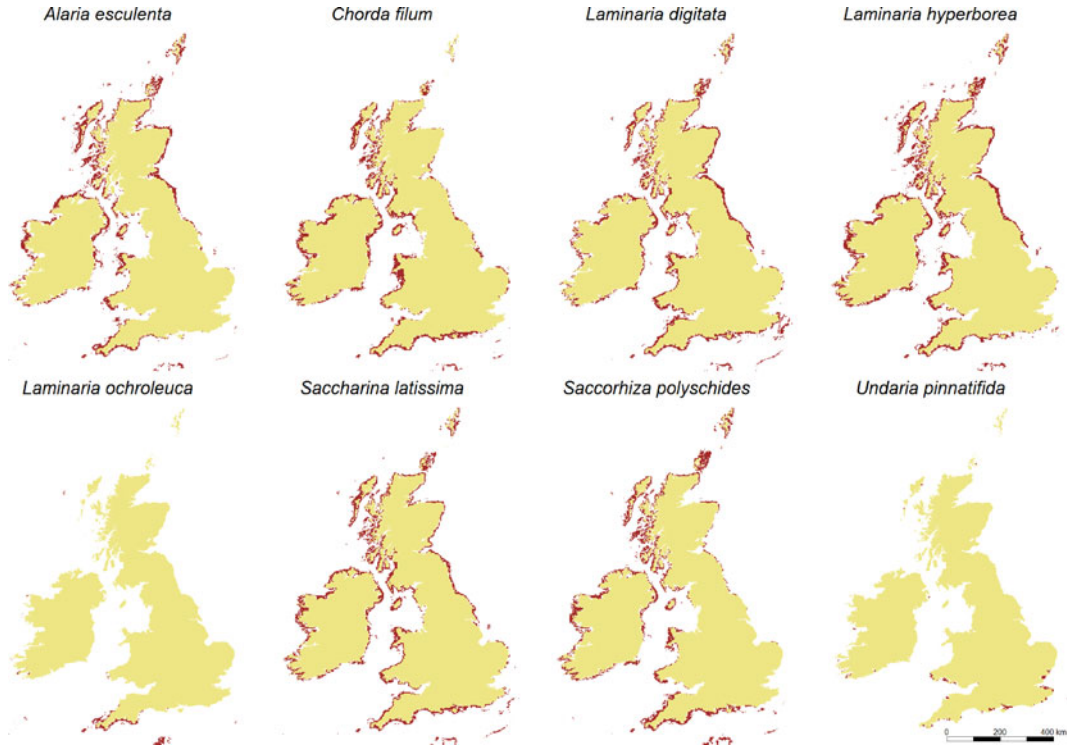
Fig. 4. Habitat suitability for kelp species. Red areas are high suitability.

important variable after slope (Appendix S4), with the response curve showing a particularly a strong negative trend (Appendix S3). This is in agreement with previous observations that the thermal tolerance for *A. esculenta* may be lower than for the *Laminaria* species, and local scale die-backs have recently been observed in response to warm summers (Müller *et al.*, 2009).

Himanthalia elongata is the other species for which temperature is an important secondary factor determining habitat suitability. There is a weak positive response to
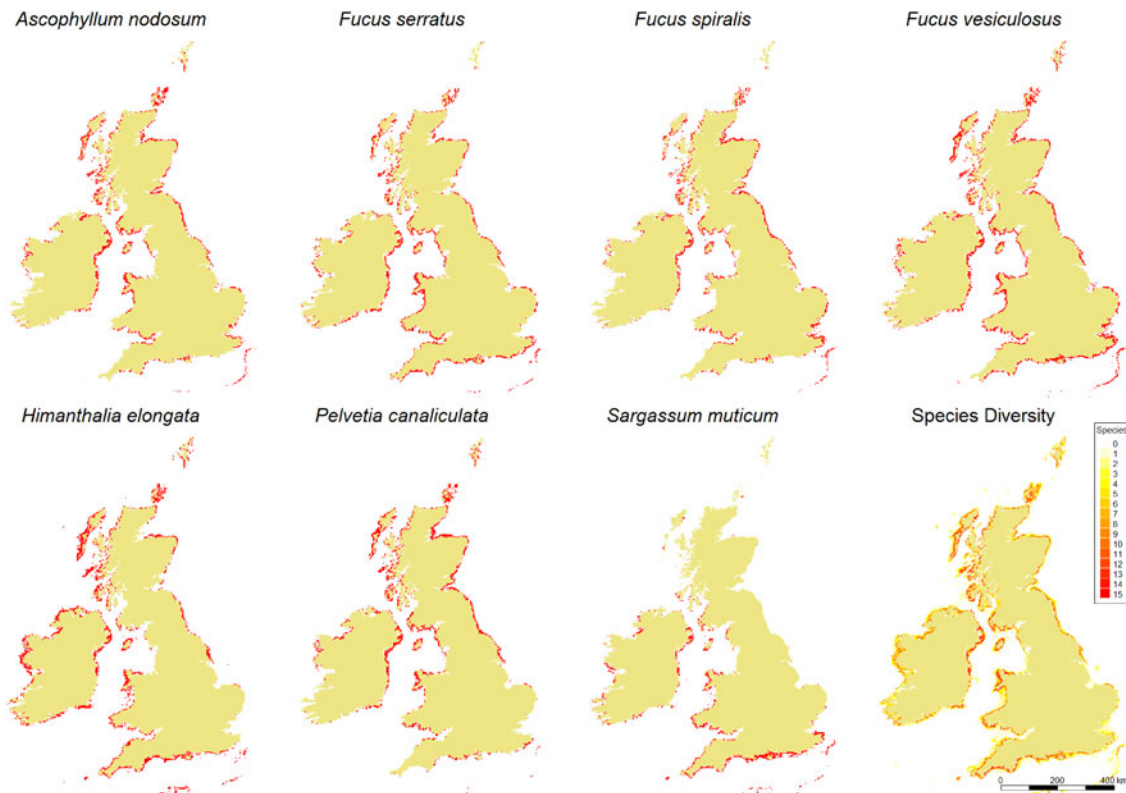

Fig. 5. Habitat suitability for fucoid species. Red areas are high suitability. Bottom right shows diversity for all 15 species.

winter temperatures and a weak negative response to summer temperatures. Studies have demonstrated temperature constraints on receptacle growth and gamete release (i.e. Stengel *et al.*, 1999).

Chorda filum suitability is strongly influenced by exposure (fetch), which is in keeping with its preference for sheltered habitats (Lüning, 1990). Winter nitrate levels and the proportion of light reaching the seabed are shown to be secondary factors determining distribution. These findings warrant further investigation, particularly in light of unexplained declines for *Chorda* observed in Sweden (Eriksson *et al.*, 2002).

Suitability is predominantly influenced by slope and then fetch for many species, including the large fucoids (*Fucus* spp. and *A. nodosum*) and the kelps *S. latissima* and *Saccorhiza polyschides*. These are relatively widespread species that span the length of the British Isles, thus exhibiting a wide climatic tolerance. In these cases the slope variable is probably serving as a proxy for rocky habitats, which is a prerequisite for these species, and is likely the dominant factor at this scale of analysis.

Modelling

The relative coarseness of the grid used for area prediction (3 × 3 km) will result in over-prediction as we must assume presence or absence over the entire cell. In contrast, species distribution models based on partial ranges, such as country-specific data, rather than the full species extent, may suffer from under-prediction (Raes, 2012). All the species in this study also occur outside the British Isles, and for most of them the northern and southern limits (their climatic limits; Lüning, 1990) are not represented in this study. Climatic factors that are linked with latitude (i.e. temperature) will have less influence on a model restricted to the British Isles, which is entirely within their range of climatic tolerance. This may help us understand why, for the majority of species, the enduring terrain parameters appear to explain their distribution better than ephemeral (climatic and oceanographic) variables. This pattern indicates that, in order to assess potential response to climate change, distributions at the limit of the climatic tolerance (outside the British Isles) should be examined.

Specimen-based observations of depth and elevation are typically based on local tide tables. These data represent an up-to-date measurement of depth/elevation relative to the local area. However, in this study, less than a third of the specimen data recorded depth or elevation. To circumvent this restriction, it is possible to infer depth from the specimen locations by referencing a digital terrain model (DTM). However, in contrast to locally and temporally calibrated observations, DTMs are static data that are based on a relative global mean-sea-level of a temporally fixed reference. These data may not reflect accurately the water depth on a local scale. Additionally, the majority of specimen location data were recorded to the nearest 100 m on the Ordnance Survey grid, thus inferred depths can only be derived from a DTM with a similar or coarser grid resolution. Intertidal species are particularly sensitive to small changes in depth or elevation, which may be the difference between permanent or ephemeral submersion (Pfetzing *et al.*, 2000). This kind of depth sensitivity may be undetectable by present datasets. However,

patterns from inferred depths did give deeper profiles for the subtidal kelps as expected (Figure 2).

The environmental profiles for all the species in this study demonstrate a strong preference for hard substrata, with the exception of *U. pinnatifida* (which is commonly found on artificial rocky materials, not well represented in the environmental data). The absence of most species from the East Anglian coast relates primarily to the lack of hard substrata in this area. Although this area has the coldest winter sea-surface temperatures around the British Isles, some of our target species have been observed on artificial hard ground indicating that it is substrata limiting their distribution (J. Brodie, personal observation). The categorical variable of substrata was added to the model, although according to model evaluation statistics there was little added value to its inclusion. This may be due to the inevitable simplification involved in representing the complex variation in substrata with just seven categories. However, terrain parameters are used in modelling the substrata (Bekkby *et al.*, 2008), so it is likely that much of the important substrata variation is also encompassed by other parameters such as slope.

Despite the inherent uncertainties associated with this kind of modelling, these models present the most comprehensive area estimates for these species throughout the British Isles and provide a useful baseline for the extent of these important habitats.

CONCLUSION

Large brown seaweeds create a habitat that extends over a significant area around the British Isles, with fucoid habitats covering 11,000 km² and kelp covering 19,000 km² of rocky areas. The limiting environmental factors are terrain and exposure, rather than climate, which may mean the geographic region has some resilience to climate change. This study presents an estimate of area coverage that greatly exceeds the areas where samples and surveys have been made, providing continuous distribution estimates for the first time for the British Isles. This study also reveals the relative paucity of surveying effort in comparison to terrestrial habitats in the British Isles, a serious imbalance for a group of species that are of such importance to marine ecosystems throughout the British Isles.

Supplementary materials and methods

The supplementary material refered to in this paper can be found online at journals.cambridge.org/mbi.

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