Linking environmental variables with regional-scale variability in ecological structure and standing stock of carbon within UK kelp forests

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ABSTRACT: Kelp forests represent some of the most productive and diverse habitats on Earth. Understanding drivers of ecological patterns at large spatial scales is critical for effective management and conservation of marine habitats. We surveyed kelp forests dominated by *Laminaria hyperborea* (Gunnerus) Foslie 1884 across 9° latitude and >1000 km of coastline and measured a number of physical parameters at multiple scales to link ecological structure and standing stock of carbon with environmental variables. Kelp density, biomass, morphology and age were generally greater in exposed sites within regions, highlighting the importance of wave exposure in structuring *L. hyperborea* populations. At the regional scale, wave-exposed kelp canopies in the cooler regions (the north and west of Scotland) were greater in biomass, height and age than in warmer regions (southwest Wales and England). The range and maximal values of estimated standing stock of carbon contained within kelp forests was greater than in historical studies, suggesting that this ecosystem property may have been previously undervalued. Kelp canopy density was positively correlated with large-scale wave fetch and fine-scale water motion, whereas kelp canopy biomass and the standing stock of carbon were positively correlated with large-scale wave fetch and light levels and negatively correlated with temperature. As light availability and summer temperature were important drivers of kelp forest biomass, effective management of human activities that may affect coastal water quality is necessary to maintain ecosystem functioning, while increased temperatures related to anthropogenic climate change may impact the structure of kelp forests and the ecosystem services they provide.

KEY WORDS: Blue carbon · Coastal management · *Laminaria hyperborea* · Macroalgae · Marine ecosystems · Primary productivity · Subtidal rocky habitats · Temperate reefs

INTRODUCTION

Kelp forests dominate shallow rocky reefs in temperate and subpolar regions the world over, where they support magnified primary and secondary productivity and high levels of biodiversity (Mann 2000, Steneck et al. 2002). Kelps provide food and habitat for a myriad of associated organisms (Christie et al. 2003, Norderhaug et al. 2005), and underpin a number of inshore commercial fisheries (Bertocci et al.

2015), such as abalone and lobsters (Steneck et al. 2002). They are also among the fastest-growing autotrophs in the biosphere, resulting in very high net primary production rates that rival even the most productive terrestrial habitats (Mann 1972a, Jupp & Drew 1974, Reed et al. 2008). While some kelp-derived material is directly consumed by grazers and transferred to higher trophic levels *in situ* (Sjøtun et al. 2006, Norderhaug & Christie 2009), most is exported as kelp detritus (ranging in size from small fragments to whole plants) which may be processed through the microbial loop or consumed by a wide range of detritivores before entering the food web (Krumhansl & Scheibling 2012).

Kelp forest ecosystems are currently threatened by a range of anthropogenic stressors that operate across multiple spatial scales (Smale et al. 2013, Mineur et al. 2015), including overfishing (Tegner & Dayton 2000, Ling et al. 2009), increased temperature (Wernberg et al. 2011, 2013) and storminess (Byrnes et al. 2011, Smale & Vance 2015), the spread of invasive species (Saunders & Metaxas 2008, Heiser et al. 2014) and elevated nutrient and sediment inputs (Gorgula & Connell 2004, Moy & Christie 2012). Moreover, changes in light availability, through altered turbidity of the overlying water column for example, can dramatically alter the structure and extent of kelp-dominated communities (Pehlke & Bartsch 2008, Desmond et al. 2015). Acute or chronic anthropogenic stressors can cause shifts from structurally diverse kelp forests to unstructured depauperate habitats characterised by mats of turf-forming algae or urchin barrens (Ling et al. 2009, Moy & Christie 2012, Wernberg et al. 2013). Better understanding of the ecological structure of kelp forests in relation to environmental factors is crucial for quantifying, valuing and protecting the ecosystem services they provide.

In the northeast Atlantic, subtidal rocky reefs along exposed stretches of coastlines are, in general, dominated by the kelp *Laminaria hyperborea* (Gunnerus) Foslie 1884, which is distributed from its equatorward range edge in northern Portugal to its poleward range edge in northern Norway and northwest Russia (Kain 1979, Schoschina 1997, Müller et al. 2009, Smale et al. 2013). *L. hyperborea* is a large, stipitate kelp that attaches to rocky substratum from the extreme low intertidal to depths in excess of 40 m in clear oceanic waters (Tittley et al. 1985) and is often found at high densities on shallow, wave-exposed rocky reefs (Bekkby et al. 2009, Yesson et al. 2015a). Under favourable conditions, *L. hyperborea* can form dense and extensive canopies (Fig. 1) and generates

habitat both directly, by providing living space for epibionts on the kelp blade, stipe or holdfast (Christie et al. 2003, Tuya et al. 2011), and indirectly, by altering environmental factors such as light and water movement for understory organisms (Sjøtun et al. 2006). The southern distribution limit of *L. hyperborea* is constrained by temperature, as physiological thresholds of both the gametophyte and sporophyte stage are surpassed at temperatures in excess of ~20°C (see Müller et al. 2009 and references therein). As such, the equatorward range edge is predicted to retract in response to seawater warming (Müller et al. 2009, Brodie et al. 2014), and recent observations along the Iberian Peninsula suggest that southern populations are already rapidly declining in abundance and extent (Tuya et al. 2012, Voerman et al. 2013). At high latitudes, grazing pressure, wave exposure, current flow, depth and light availability are important factors driving the abundance, morphology and biomass of *L. hyperborea* (Bekkby et al. 2009, 2014, Pedersen et al. 2012, Rinde et al. 2014). Less is known about the relative importance of environmental drivers of the structure of *L. hyperborea* populations and associated communities at mid-latitudes, for example along the coastlines of the British Isles and northern France (but see Gorman et al. 2013 and references therein).

The complex coastline of the UK supports extensive kelp forests, which represent critical habitat for inshore fisheries and coastal biodiversity (Burrows 2012, Smale et al. 2013). However, since the pioneering work on the biology and ecology of kelps conducted in the 1960s and 1970s (e.g. Kain 1963, 1975, Moore 1973, Jupp & Drew 1974), kelp-dominated habitats in the UK have been vastly understudied, particularly when compared with other UK marine habitats or kelp forests in other research-intensive nations (Smale et al. 2013). This is despite the fact that both localised observational studies (Heiser et al. 2014, Smale et al. 2015) and analysis of historical records (Yesson et al. 2015b) have suggested that kelp populations and communities may be rapidly changing in the UK, with potential implications for ecosystem functioning (Smale & Vance 2015). The persistence of significant knowledge gaps pertaining to the responses of kelps and their associated biota to environmental change factors currently hinders management and conservation efforts (Austen et al. 2008, Birchenough & Bremner 2010). For example, within the Marine Strategy Framework Directive (MSFD), a European Directive implemented to achieve ecosystem-based management, there is a need to establish indicators of 'good environmental
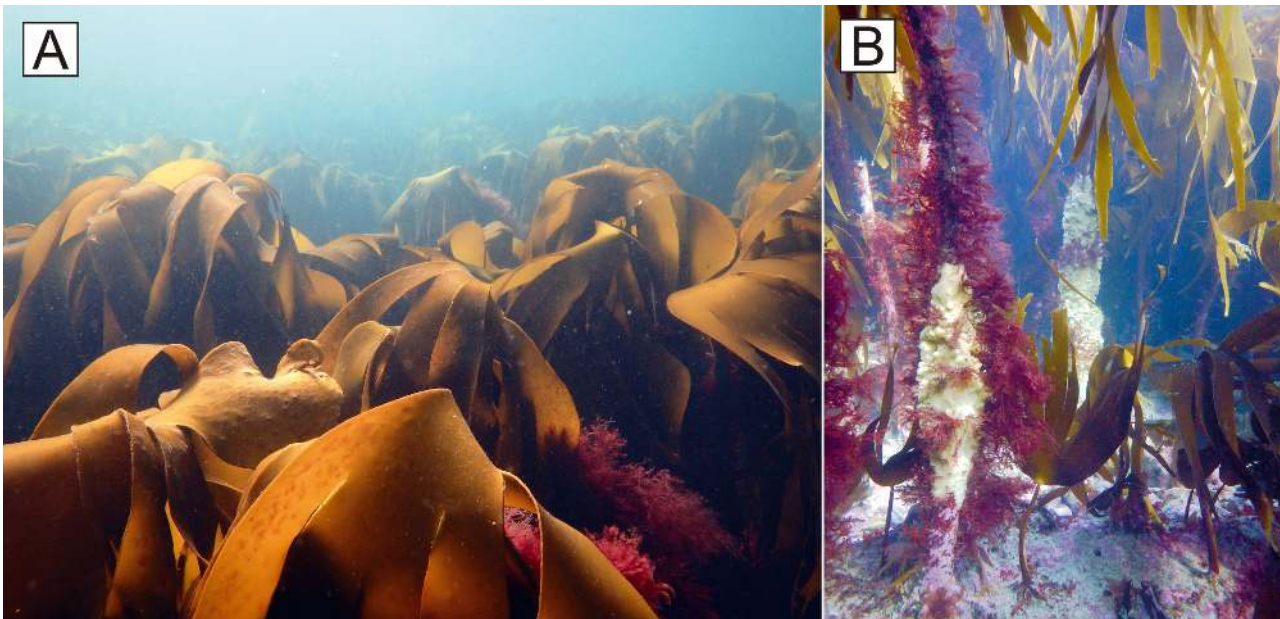
Fig. 1. (A) Extensive kelp canopies formed by *Laminaria hyperborea* in northern Scotland. (B) A wide range of fauna and flora, including sub-canopy kelp plants, is found beneath the canopy

status' for UK marine habitats (see Borja et al. 2010 for a discussion of the MSFD). However, the current lack of spatially and temporally extensive data on the structure and functioning of kelp forests has posed challenges for developing such indicators (Burrows et al. 2014). Here, we present data on kelp forest structure from a systematic large-scale field survey conducted across 9° of latitude and >1000 km of coastline. We explicitly link environmental factors with ecological variables at multiple spatial scales to better understand drivers of kelp forest structure in the UK.

MATERIALS AND METHODS

Study area

Surveys and collections were conducted within 4 regions in the UK, spanning ~50° to ~59° N (Fig. 2). Regions encompassed a temperature gradient of ~2.5°C (mean annual sea surface temperature [SST] in northern Scotland is ~10.9°C compared with ~13.4°C in southwest England) and were situated on the exposed western coastline of mainland UK where kelp forest habitat is abundant (Smale et al. 2013, Yesson et al.

2015a). Adjacent regions were between ~180 and 500 km apart (Fig. 2). Within each region, a set of candidate study sites was selected based on the following criteria: (1) sites should include sufficient areas of subtidal rocky reef at ~5 m depth (below chart datum); (2) sites should be representative of the wider region (in terms of coastal geomorphology) and not obviously influenced by localised anthropogenic activities (e.g. sewage outfalls, fish farms);
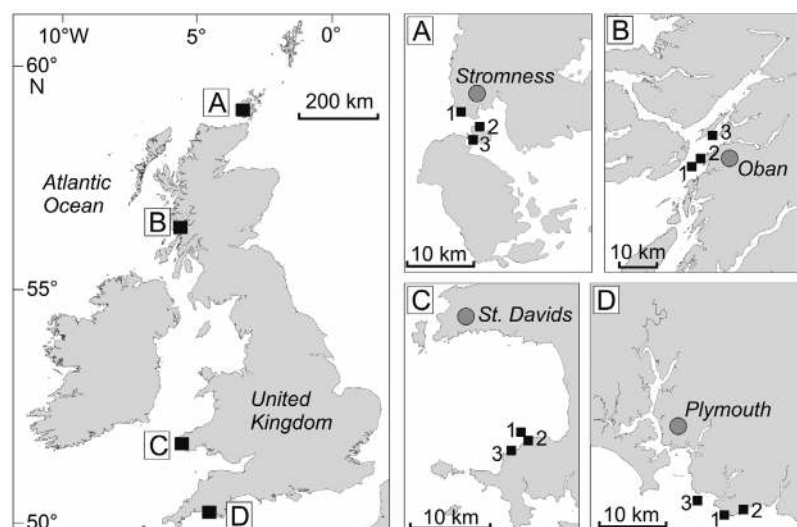

Fig. 2. Four study regions in the UK: (A) northern Scotland, (B) western Scotland, (C) southwest Wales, (D) southwest England. Smaller maps indicate the locations of 3 study sites within each region. See Table 1 for additional details of study sites

(3) sites should be 'open coast' and moderately to fully exposed to wave action to ensure a dominance of *Laminaria hyperborea* (rather than *Saccharina latissima*, which dominates sheltered coastlines typical of Scottish sea lochs, for example); and (4) within this exposure range, sites should represent the range of wave action and tidal flow conditions as is typical of the wider region. Three sites were randomly selected from this set of candidate sites; these were between ~1 and ~13 km apart within each region, with an average separation of ~4.5 km (Fig. 2).

Kelp forest surveys

At each study site, scuba divers quantified the density of *L. hyperborea* by haphazardly placing 8 replicate 1 m^2 quadrats (placed >3 m apart) within kelp forest habitat. Within each quadrat, *L. hyperborea* populations were quantified by counting the number of both canopy-forming plants and sub-canopy plants (Fig. 1), which included mature sporophytes as well as juveniles with a developed stipe and digitate blade (small, undivided *Laminaria* sporelings were counted but not included in the analysis because of uncertainties in identification and considerable spatial patchiness). Practically, sub-canopy plants were defined as being older than first-year recruits (i.e. having a developed stipe and digitated blade) but were still relatively small individuals, found beneath taller canopy-forming individuals. The density of sea urchins (exclusively *Echinus esculentus*) and the depth of each quadrat (subsequently converted to values below chart datum) were also recorded. At each site, both mature canopy-forming kelp plants (n = 12–16) and mature sub-canopy/divided juvenile plants (n = 20) were sampled by cutting the base of the stipe immediately above the holdfast; plants were then returned to the laboratory for immediate analysis. Plants were haphazardly sampled, spatially dispersed across the site and collected from within the kelp forest (rather than at the canopy edge). Surveys and collections were completed within a 5 wk period in August and September 2014 following the peak growth period of *L. hyperborea*, which tends to run from January to June (Kain 1979).

For canopy-forming plants, the fresh weight (FW) of the complete thallus, as well as the stipe (including holdfast) and blade separately, were obtained by first draining off excess seawater and then using a spring scale or electronic scales as appropriate. The lengths of the stipe (excluding holdfast), blade and complete thallus were also recorded (see Fig. S1 in the Supple-

ment at www.int-res.com/articles/suppl/m542p079_supp.pdf), and kelp plants were aged by sectioning the stipe and counting seasonal growth rings, as described by Kain (1963). Segments of stipe and blade (both basal and distal tissue) were removed to investigate the relationship between FW and dry weight (DW) for subsequent estimation of standing stock of carbon (see following 'Statistical analysis'). The stipe, basal blade and distal blade were examined separately because the relationship between FW and DW may vary between different parts of the kelp thallus. Stipe segments (at least 10 cm in length) were taken from the middle of the stipe and dissected longitudinally to facilitate drying (Fig. S1). Basal blade segments were taken by first cutting at the stipe/blade junction and then cutting across the blade, perpendicular to the stipe, 5 cm from the base (Fig. S1). Distal segments were taken by aligning the tips of the highly-digitated blade and then cutting across the blade 5 cm back from the distal edge (Fig. S1). Stipe, basal and distal blade segments were weighed to record FW, labelled and then dried at ~60°C for at least 48 h before being reweighed to obtain DW values. The FW of the complete thallus of each sub-canopy plant was also recorded.

Environmental variables

At each study site, an array of environmental sensors was deployed to capture temperature, light and relative water motion data at fine temporal resolutions. All arrays were deployed within a 4 wk period in July and August 2014 and retrieved ~6 wk later. To quantify water motion induced by waves or tidal flow, an accelerometer (HOBO Pendant G Logger, Onset) was attached to a small buoy and suspended in the water column near the seafloor to allow free movement in response to water motion. The subsurface buoy was tethered to the seabed by a 0.65 m length of rope attached to a clump weight (Fig. S2 in the Supplement), and the accelerometer recorded its position in 3 axes every 5 min (see Evans & Abdo 2010 for similar approach and method validation). A temperature and light level sensor (HOBO Temperature/Light weatherproof Pendant Data Logger 16k, Onset) was also attached to the buoy and captured data every 15 min (Fig. S2). The sensor array was deployed for >45 d at each site (between July and September 2014), and all kelp plants within a ~2 m radius of the array were removed to negate their influence on light and water movement measurements.

On retrieval, accelerometer data were converted to relative water motion by extracting movement data in the planes of the *x*- and *y*-axes, and first subtracting the modal average of the whole dataset from each value (to account for any static 'acceleration' caused by imprecise attachment of the sensor to the buoy and/or the buoy to the tether, which resulted in the accelerometer not sitting exactly perpendicular to the seabed). Accelerometer data were converted to water motion following Evans & Abdo (2010). The water motion data were then used to generate 2 separate metrics, one for movement induced by tidal flow and another for wave action. For tidal flow, extreme values that were most likely related to wave-driven turbulent water movement were first removed (all values above the 90th percentile). The range of water motion values recorded within each 12 h period, which encapsulated ~1 complete cycle of ebbing and flowing tide, was then calculated and averaged over the 45 d deployment. The representativeness of this metric was assessed by comparing it with regional sea level height over >1 lunar cycle, to test the expectation that periods of high water movement would coincide with phases of greatest tidal range (i.e. spring tides). For wave-induced water movement, the average of the 3 highest-magnitude values recorded (following subtraction of average water motion induced by tides) was calculated for each site.

Temperature data were extracted and converted to average daily temperatures; a period of 24 d during peak summer temperatures where all sensor array deployments overlapped (26 July – 18 August 2014) was then used to generate maximum daily means and average daily temperature for each study site. For light, data for the first 14 d of deployment (before fouling by biofilms and epiphytes has the potential to affect light measurements) were used to generate average summer daytime light levels (between 08:00 and 20:00 h) for each site. Although mounting a light sensor on a non-stationary platform is not ideal because of variation in orientation to sunlight, data from the accelerometers (see 'Results' and Fig. S5 in the Supplement) indicated that light sensors at each site were stationary and horizontally orientated for 51.8 to 88.1% of the light logging events (mean across 12 sites = 72.1% ± 10.4 SD). As such, *in situ* light data were deemed reliable for making relative comparisons between study sites.

At each site, 2 independent seawater samples were collected from immediately above the kelp canopy with duplicate 50 ml syringes. Samples were passed through a 0.2 µm syringe filter and kept on ice without light, before being frozen and analysed (within 2 mo) for nutrients using standard analytical techniques (see Smyth et al. 2010 and references therein).

In addition to these fine-scale 'snapshot' variables, remotely sensed data were obtained for each site to provide broad-scale metrics of temperature, chlorophyll *a* (chl *a*) and wave exposure. Temperature data used were monthly means for February and August (i.e. monthly minima and maxima), averaged from 2000 to 2006, using 9 km resolution data from the Pathfinder AVHRR satellite (obtained from the NASA Giovanni Data Portal, http://giovanni.gsfc.nasa.gov/giovanni/). Land masks were used to remove the influence of coastal pixels, and site values were averaged over all pixels contained within a 30 km radius. Estimates of chl *a* concentrations were generated from optical properties of seawater derived from satellite images. Data were collected by the MODIS Aqua satellite at an estimated 9 km resolution and averaged for the period 2002 to 2012 (see Burrows 2012 for a similar approach). Wave exposure values were extracted from Burrows (2012), who calculated wave fetch for the entire UK coastline based on the distance to the nearest land in all directions around each ~200 m coastal cell (see Burrows et al. 2008 for detailed methodology). For the current study, wave fetch values for each site were extracted from the nearest coastal cell. Finally, average summer day length (mean value for all days in June and July) was used as a proxy for maximum photoperiod for each region.

Statistical analysis

To estimate the standing stock of carbon, our values of FW were first converted to DW, based on results of linear regressions between FW and DW for stipe, basal blade and distal blade tissue separately (Fig. S3 in the Supplement). All relationships were highly significant (p < 0.001), and had R^2 values ≥0.80 (Fig. S3). Study-wide averages showed that DW:FW ratios varied between parts of the plant, with mean values of DW:FW being 0.298, 0.168 and 0.214 for basal blade, distal blade and stipe, respectively (Fig. S3 in the Supplement). FW values were converted to DW, and the mean canopy-forming plant DW for each site (n = 12–16) was then multiplied by the number of canopy-forming plants recorded for each quadrat to give an estimated biomass (DW) per unit area (1 m^2). For sub-canopy plants, which represented a study-wide average of <20% of the total kelp biomass, an average conversion of 22.6% (obtained from the 3 independent values of DW:FW described above) was used to convert FW to DW.

Finally, the conversion of DW to carbon stock was based on previous research on a range of kelp species, which indicated that carbon content is ~30% of DW (Table S1 in the Supplement).

Spatial variability patterns in kelp population structure (i.e. total *L. hyperborea* density, canopy plant density, canopy FW biomass, sub-canopy FW biomass), plant-level metrics (i.e. canopy plant biomass, stipe length, total length and age) and standing stock of carbon were examined with univariate permutational ANOVA (Anderson 2001). A similarity matrix based on Euclidean distances was generated for each response variable separately, and variability between Region (fixed factor, 4 levels: north Scotland 'A', west Scotland 'B', southwest Wales 'C', and southwest England 'D') and Site (random factor, 3 levels nested within Region) was tested with 4999 permutations under a reduced model. Response variables that were highly left-skewed were log-transformed prior to analysis. Where differences between Regions were significant (at p < 0.05), post hoc pairwise tests were conducted to determine differences between individual levels of the factor. Tests were conducted using PRIMER (v6.0) software (Clarke & Warwick 2001) with the PERMANOVA add-on (Anderson et al. 2008). Plots showing ecological response variables at each site are given as mean values ± SE throughout.

Relationships between key ecological response variables (i.e. canopy density, canopy biomass and standing stock of carbon) and multiple environmental predictor variables were examined using the DISTLM (distance-based linear models) routine in PERMANOVA. Before analysis, Draftsman's plots were generated from the environmental variables (see Tables 1 & 2), and Pearson's correlation coefficient was used to test for colinearity between variables. As all temperature variables (i.e. February mean SST, August mean SST, summer mean, summer maximum) and summer day length were highly correlated (r > 0.9), only summer maximum temperature was retained in the analysis. A total of 10 uncorrelated (r < 0.8 in all cases) environmental predictor variables were normalised and included in analyses (i.e. summer maximum temperature, summer mean light, tidal water motion, wave water motion, depth, nitrate + nitrite ($NO_3^- + NO_2^-$), phosphate (PO_4^{3-}), urchin density, mean log chl *a* and log wave fetch). The model was first fitted using a forward selection on the R^2 criterion to examine the importance of each environmental predictor variable. The DISTLM routine was then used to obtain the most parsimonious model by selecting the best out of all possible models using Akaike's information criterion modified for small samples (AIC_c) model selection cri-

terion (McArdle & Anderson 2001, Anderson et al. 2008). AIC_c is a modified version of AIC which adds a 'penalty' for increases in the number of predictor variables and was specifically developed for instances where the number of samples relative to the number of predictor variables is low. Scatterplots and simple linear regressions were used to explore relationships between the response variables and the key environmental predictor variables that best explained the observed variability (as indicated by DISTLM analysis).

RESULTS

Environmental variables

The study regions differed in ocean climate, with a clear distinction between the 2 northernmost regions (A, B) and the 2 southernmost (C, D) based on summer mean, summer maximum and annual mean temperatures (Table 1, Fig. S4 in the Supplement). Peak summer mean and maximum temperatures were, on average, 2.8 and 3.1°C greater in the southernmost regions compared with the northernmost regions, respectively. Temperature regimes were very similar between the 2 northern regions (A, B) and the 2 southern regions (C, D), with minimal variability between sites within regions Table 1, Fig. S4). Ambient light conditions were more variable between sites both within and among regions (Table 1, Fig. S4); maximum light intensity (site A1) was almost 4 times greater than the minimum light intensity (site C2). In general, highest light levels were recorded at sites within the northern Scotland region (Table 1, Fig. S4). Water motion values were also highly variable between sites within each region, indicating that a range of exposure conditions to tidal flow and wave action was encompassed (Table 1). All sites were influenced by tidal flow to some degree, as shown by short-term variability in motion associated with periods of slack and running tide, and also the synchronicity between tidal cycles and the magnitude of daily variability in water motion (Figs. S5 & S6 in the Supplement). Tidally induced water motion was most pronounced in the northern Scotland (A) region (sites A2, A3; Fig. S5). Periods of relatively high water motion were recorded at several sites and were likely associated with wave action during oceanic swell events (Fig. S5). The highest-magnitude peaks in water motion were recorded in northern Scotland (site A1), although periods of high water motion were also recorded at sites in southwest Wales (C1) and southwest England (D1). Broad-scale

Table 1. Predictor variables recorded at 12 study sites within 4 distinct regions in the UK. 'Peak summer mean (max) temp.' is the average (maximum) daily temperature recorded between 26 July and 18 August 2014, when all sensor array deployments overlapped. 'Summer daylight' is the average daytime (08:00–20:00 h) light intensity during a 14 d deployment of light loggers. 'Tidal water motion' is a proxy for water movement driven by tidal flow, derived from the range in water motion values recorded during a 24 h period, averaged over the 45 d accelerometer deployment. 'Wave water motion' is a proxy for water movement driven by waves, derived from averaging the 3 highest-magnitude water motion values observed during the 45 d accelerometer deployment (following correction for tidal-induced movement). 'Depth' indicates average depth (below chart datum). '$NO_3^-+NO_2^-$' and 'PO_4^{3-}' indicate average concentrations of nitrite + nitrate and phosphate (n = 2 water samples collected from ~1 m above the kelp canopy). 'Urchin density' is the average number of sea urchins (exclusively *Echinus esculentus*) recorded in 8 replicate 1 m^2 quadrats at each site

Region	Site	Locality	Peak summer temp (°C) Mean	Max	Summer daylight (lumens m^{-2})	Tidal water motion (m s^{-1})	Wave water motion (m s^{-1})	Depth (m)	NO_3^- $+NO_2^-$ (µM)	PO_4^{3-} (µM)	Urchin density (ind. m^{-2} ± SE)
N Scotland (A)	A1	Warbeth Bay	13.69	13.99	7124	0.18	1.02	4	0.21	0.22	0 ± 0
N Scotland (A)	A2	N Graemsay	13.49	13.68	4835	0.20	0.30	5	0.21	0.26	0.88 ± 0.13
N Scotland (A)	A3	S Graemsay	13.65	13.87	5144	0.26	0.16	5	0.38	0.25	0.75 ± 0.16
W Scotland (B)	B1	Dubh Sgeir	13.69	13.96	4794	0.15	0.22	6	2.16	0.44	0 ± 0
W Scotland (B)	B2	W Kerrera	13.68	13.93	3094	0.05	0.08	5	2.10	0.32	0 ± 0
W Scotland (B)	B3	Pladda Is.	14.06	14.52	4874	0.19	0.11	4	0.78	0.31	0.25 ± 0.16
SW Wales (C)	C1	Stack Rock	16.54	17.06	1861	0.13	0.73	7	1.48	0.26	0.25 ± 0.16
SW Wales (C)	C2	Mill Haven	16.62	17.15	3657	0.08	0.34	5	1.60	0.26	0.25 ± 0.16
SW Wales (C)	C3	St. Brides	16.63	17.13	2960	0.08	0.23	5	1.36	0.21	0 ± 0
SW England (D)	D1	Hillsea Pt.	16.80	17.62	2746	0.15	0.42	4	0.59	0.13	0.13 ± 0.13
SW England (D)	D2	E Stoke Pt.	17.09	18.31	2840	0.11	0.22	5	0.25	0.11	0 ± 0
SW England (D)	D3	NW Mewstone	17.06	17.71	4432	0.06	0.20	5	0.66	0.71	0.13 ± 0.13

wave fetch values varied between regions, with northern Scotland (A) and southwest England (D) being marginally more exposed (Table 2). Within all regions, a gradient of wave fetch was apparent with site 'X1' the most exposed and site 'X3' the most sheltered (Table 2).

The density of sea urchins and concentrations of phosphate (PO_4^{3-}) were low in magnitude and relatively consistent across the sites (Table 1). Nitrate + Nitrite ($NO_3^-+NO_2^-$) values varied by an order of magnitude between sites, with minimum values of 0.21 µM recorded in northern Scotland (site A1) and maximum values of 2.16 µM recorded in western Scotland (site B1; Table 1). Broad-scale, remotely sensed data indicated that the 4 regions spanned a range of mean temperature of ~1.7°C in February and ~3.6°C in August (Table 2). The magnitude of difference between winter and summer temperatures was greater in the 2 southernmost regions (C, D; ~8°C) compared with the 2 northernmost regions (A, B; ~6°C). Mean chl *a* concentration was compa-

rable between regions, although values were notably higher within the west Scotland (B) region (Table 2).

Table 2. Environmental predictor variables obtained for 12 study sites within 4 distinct regions in the UK (see Fig. 2). Average monthly temperature for February (i.e. monthly minima) and August (i.e. monthly maxima) was calculated from satellite-derived sea surface temperature (SST) data (2000–2006). 'Log chl *a* mean' is the average annual concentration of chlorophyll *a* (log10 mg m^{-3} from MODIS Aqua satellite data, 2002–2012). 'Log wave fetch' is a broad-scale metric of wave exposure, derived by summing fetch values calculated for 32 angular sectors surrounding each site (see Burrows 2012). 'Mean summer day length' is the average day length (all days in June and July)

Region	Site	Locality	Mean SST (°C) Feb	Aug	Log chl *a* mean (mg m^{-3})	Log wave fetch (km)	Mean summer day length (h:min)
N Scotland	A1	Warbeth Bay	7.5	13.5	0.21	3.8	18:07
N Scotland	A2	N Graemsay	7.4	13.4	0.26	3.5	18:07
N Scotland	A3	S Graemsay	7.5	13.4	0.26	3.4	18:07
W Scotland	B1	Dubh Sgeir	7.5	13.8	0.59	3.3	17:19
W Scotland	B2	W Kerrera	7.5	13.8	0.65	3.1	17:19
W Scotland	B3	Pladda Is.	7.5	13.6	0.73	2.8	17:19
SW Wales	C1	Stack Rock	8.4	16.4	0.43	3.7	16:20
SW Wales	C2	Mill Haven	8.4	16.4	0.43	3.5	16:20
SW Wales	C3	St. Brides	8.4	16.5	0.43	3.4	16:20
SW England	D1	Hillsea Pt.	9.2	17.0	0.28	4.1	16:08
SW England	D2	E Stoke Pt.	9.1	17.0	0.28	3.9	16:08
SW England	D3	NW Mewstone	8.4	16.4	0.43	3.5	16:08

Kelp forest structure

All sites were dominated by *Laminaria hyperborea* (>80% relative abundance of all canopy-forming macroalgae), although *Saccharina latissima*, *Saccorhiza polyschides*, *L. ochroleuca*, *L. digitata* and *Alaria esculenta* were also observed at some sites. The density of *L. hyperborea* plants (both canopy-forming plants and total plants) was spatially highly variable (Table 3, Fig. 3), with some sites supporting 3 times as many *L. hyperborea* individuals compared with other sites within the same region (Fig. 3). Overall, the mean density of canopy-formers ranged from 4.5 ± 0.4 (site B3) to 10.6 ± 1.5 ind. m^{-2} (site A1), while mean total plant density ranged from 6.4 ± 0.6 (site B3) to 27.4 ± 2.6 ind. m^{-2} (site C2). Similarly, biomass per unit area was highly variable between sites (Table 3, Fig. 3) and ranged from 3.0 ±

Table 3. Results of univariate permutational ANOVAs to test for differences in kelp individuals and populations between regions and sites (see Fig. 2). Permutations (4999) were conducted under a reduced model and were based on matrices derived from Euclidean distances, with 'Region' as a fixed factor and 'Site' as a random factor nested within 'Region'. Response variables that were log-transformed prior to analysis are shown with (l). Significant values (p < 0.05) are indicated in **bold**, and where significant differences between regions were observed, post hoc pairwise tests were conducted. Res df: residual df

Response variable	Region			Site (Region)			Res df
	df	*F*	p	df	*F*	p	
Per m²							
Canopy density	3	2.31	0.187	8	2.83	**0.010**	84
Total density	3	0.59	0.629	8	21.38	**0.001**	84
Canopy biomass (l)	3	3.07	0.102	8	14.62	**0.001**	84
Sub-canopy biomass (l)	3	0.07	0.964	8	19.50	**0.001**	84
Per individual canopy-forming plant							
Biomass (l)	3	8.10	**0.010**[a]	8	16.21	**0.001**	172
Total length (l)	3	2.48	0.139	8	42.94	**0.001**	172
Stipe length (l)	3	1.48	0.302	8	66.52	**0.001**	172
Age	3	1.39	0.337	8	9.84	**0.001**	172
Standing stock carbon							
Canopy carbon (l)	3	2.66	0.131	8	18.05	**0.001**	84
Sub-canopy carbon (l)	3	0.12	0.930	8	23.41	**0.001**	84
Total carbon (l)	3	1.36	0.315	8	23.28	**0.001**	84

[a]Pairwise comparisons within region: A = B, A > C&D, B = C = D

0.4 (site B3) to 19.6 ± 1.1 kg FW m^{-2} (site A1) for canopy biomass and 0.2 ± 0.0 (site B3) to 2.8 ± 0.2 kg FW m^{-2} (site D1) for sub-canopy biomass.

Patterns of canopy plant biomass, stipe length and age were also spatially variable with significant 'between-site' variability observed in each case (Table 3, Fig. 3). Canopy plant biomass also varied significantly between regions (Table 3, Fig. 3), with sporophytes in the northernmost region (A) having greater biomass values than those in the southernmost regions (C and D). Indeed, the average canopy plant biomass for region A (1572 ± 208 g FW) was twice that of region D (702 ± 103 g FW) and 4 times that of region C (318 ± 65 g FW). Mean stipe length of canopy plants ranged from 54.6 ± 2.2 (C1) to 151 ±3.1 cm (B1), while the mean age ranged from 4.6 ± 0.2 (D3) to 7.75 ± 0.4 yr (B1). Mean total length of canopy plants did not vary significantly between regions or sites (Table 3), even though the minimum average length (119 ± 4 cm, C1) was less than half that of the maximum average length recorded (256 ± 4 cm, B1; Fig. 3).

In terms of spatial variability in standing stock of carbon, significant differences were observed between sites (but not regions) for canopy, sub-canopy and total carbon (Table 3, Fig. 4). Variability between sites was most pronounced for the northernmost regions (A, B), with canopy carbon and total carbon

varying by 500% amongst sites within region B and 350% within region A (Fig. 4). Between-site variability within the southernmost regions was less pronounced. Sub-canopy carbon was highly variable principally because of site-level differences in the density of sub-canopy plants (Table 3, Fig. 4). Overall, site-level averages of total standing stock of carbon ranged from 251 g C m^{-2} at site B3 to 1820 g C m^{-2} at site A1 (Fig. 4). Aside from site-level variability, regional averages for total standing stock of carbon differed markedly between the 2 northernmost regions and the 2 southernmost regions; A = 1146 ± 380, B = 808 ± 324, C = 355 ± 38, D = 575 ± 96 g C m^{-2}. The study-wide average for carbon contained within kelp forests was 721 ± 140 g C m^{-2}, with the vast majority (~86%) stored in canopy-forming, rather than sub-canopy, plants.

Linking the environment with kelp forest structure

Three separate multiple linear regression analyses were conducted to examine links between 10 environmental variables and kelp canopy density, canopy biomass and standing stock of carbon (Table 4, marginal tests are presented in Table S2 in the Supplement). For canopy density, the environmental variables included in the most parsimonious solution
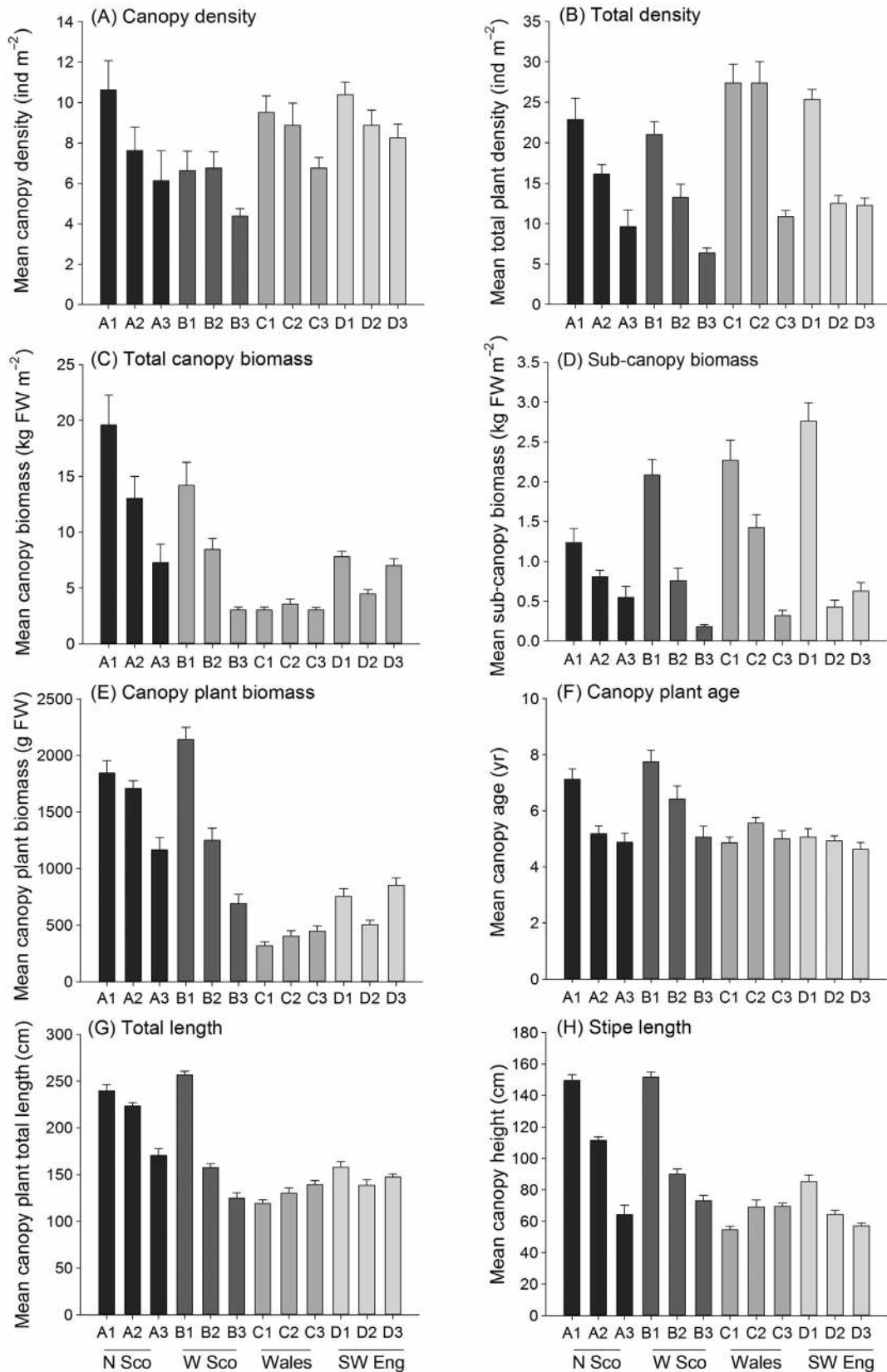
Fig. 3. Structure of *Laminaria hyperborea* populations at each study site. Bars represent mean values ± SE (n = 8 for quadratlevel variables: A–D; n ≥ 12 for plant-level variables: E–H). See Fig. 2 for locations of study sites. FW: fresh weight
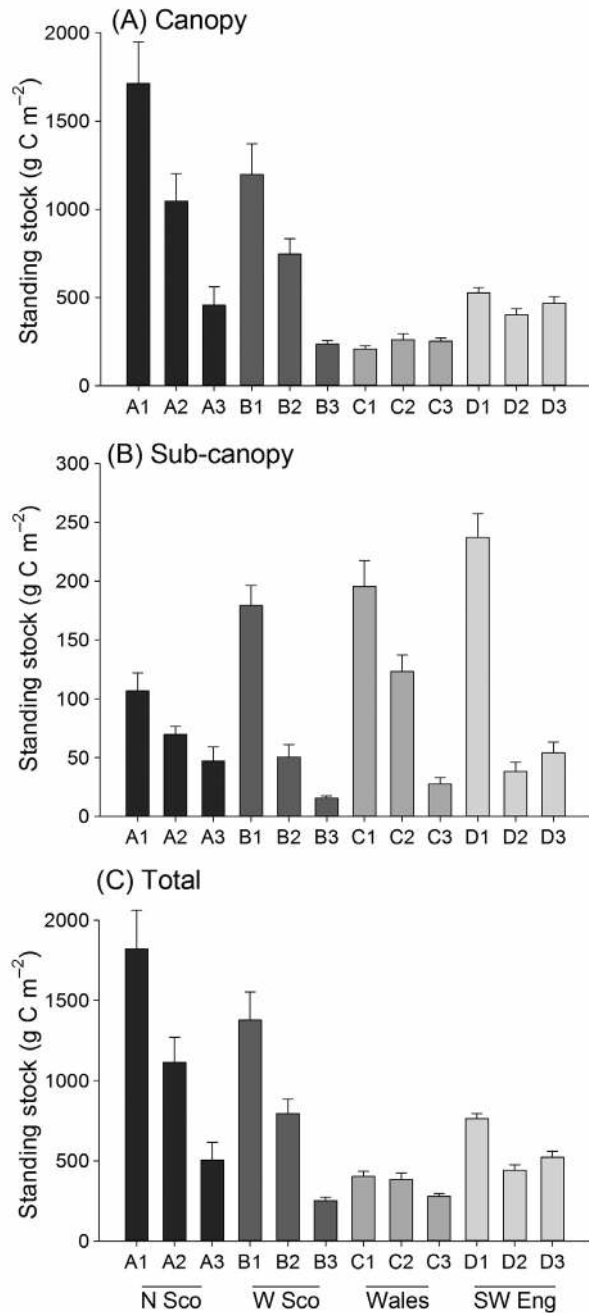
Fig. 4. Estimated standing stock of carbon (g C m^{-2}) provided by (A) the kelp canopy, (B) sub-canopy plants and (C) the total population of *Laminaria hyperborea* at each study site. Bars represent mean values ± SE, n = 8. See Fig. 2 for locations of study sites

Table 4. DISTLM Pseudo-*F*-values for the environmental predictors selected for the most parsimonious model for each kelp response variable. Displayed are the environmental variables selected by DISTLM as part of the best models; '–' indicates the variable was available for the analysis, but not selected as part of the best model. Marginal tests for all predictor variables are presented in Table S2 in the Supplement

Environmental variable	Pseudo-*F*-values		
	Canopy density	Canopy biomass	Total carbon
Summer max. temperature	–	4.34	2.89
Summer daytime light	–	1.75	0.84
Water motion (tides)	4.32	–	7.31
Water motion (waves)	7.34	–	–
Depth	–	–	–
Nitrate + nitrite	–	–	–
Phosphate	–	–	–
Urchin density	–	–	–
Mean chl *a*	–	–	–
Wave fetch	35.20	7.52	8.65

(Table 4). For standing stock of carbon, the most parsimonious solution (R^2 = 0.83, RSS = 0.70) included summer maximum temperature, large-scale fetch, summer daytime light and water motion (tides) (Table 4). Marginal tests for all variables are shown in Table S2.

Scatterplots and simple linear regressions were used to further examine relationships between these key environmental variables and kelp canopy structure and carbon stock. Plots showed that wave fetch and wave-related water motion were strongly positively correlated with canopy density (wave fetch: r^2 = 0.77, p < 0.001; water motion [waves] r^2 = 0.52, p < 0.001; Fig. 5). Summer daytime light values were significantly positively correlated with kelp canopy biomass (r^2 = 0.53, p < 0.001), while summer maximum temperatures were significantly negatively related to canopy biomass (r^2 = 0.37, p < 0.001). Finally, total standing stock of carbon was significantly positively correlated with summer daytime light (r^2 = 0.42, p < 0.001) and tended to decrease with temperature and increase with wave fetch, but these relationships were not significant (Fig. 5).

DISCUSSION

Kelp canopy biomass, stipe length and age (but not density) were, in general, greatest at the wave-exposed sites within the northern and western regions of Scotland, where water temperature was relatively low and light levels comparatively high.

(R^2 = 0.92, residual sum of squares [RSS] = 2.78) were (in order of importance) large-scale wave fetch, wave-driven water motion and tide-driven water motion (Table 4). For canopy biomass, the variables included in the most parsimonious model (R^2 = 0.69, RSS = 1.37) were summer maximum temperature, large-scale fetch and summer daytime light
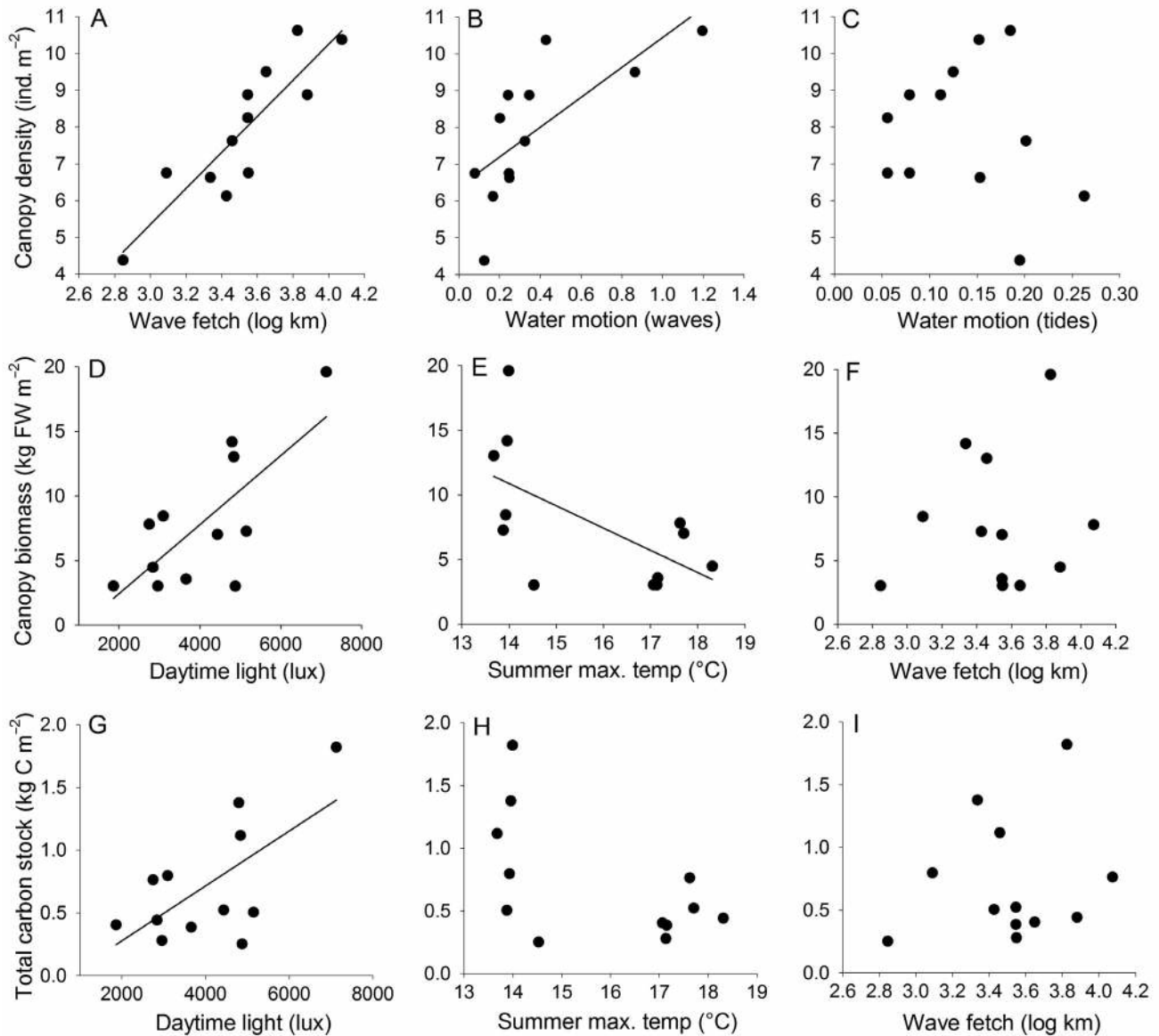
Fig. 5. Relationships between key environmental predictor variables (as determined by DISTLM, see Table 4) and (A–C) kelp canopy density, (D–F) canopy biomass and (G–I) standing stock of carbon. Significant linear regressions (at $p < 0.05$) are shown (r^2 values: plot A = 0.77, B = 0.52, D = 0.53, E = 0.37, G = 0.42). FW: fresh weight

Laminaria hyperborea is a cold-temperate species; the growth and maintenance of both the gameto-phyte and sporophyte is compromised at sea temper-atures in excess of 20°C (see Müller et al. 2009 and references therein), and the cooler climate typical of the northernmost regions of the UK is likely to be more favourable for *L. hyperborea* populations than the climate farther south, where maximum tempera-tures exceeded 18°C. In addition, average light levels were generally greater in the northernmost regions, and increased light availability is associated with faster growth and greater size of kelp plants (e.g. Sjø-

tun et al. 1998, Bartsch et al. 2008 and references therein). As such, a combination of cooler tempera-tures and higher light levels may explain the greater biomass, canopy height (i.e. stipe length) and age at the northernmost regions, particularly at wave-exposed sites. Summer day length, which was in-versely related to seawater temperature in the current study, may also be important. At higher lati-tudes, longer summer day lengths (a proxy for pho-toperiod) may benefit kelp performance by facilitat-ing greater synthesis and storage of carbohydrates, which can then fuel faster and/or prolonged growth

in the following winter/spring active growth season (see Rinde & Sjøtun 2005 and references therein). It is important to note that the density of sea urchins (exclusively *Echinus esculentus*) was consistently low and was not a useful predictor for any of the ecological response variables. Although sea urchin grazing is an important driver of kelp forest structure in some regions around the world (reviewed by Steneck et al. 2002), as well as locally within some restricted areas of the British Isles (Jones & Kain 1967, Kitching & Thain 1983), such 'top-down' pressure is likely to be of less importance than 'bottom-up' factors along much of the UK coastline, as has been shown to be the case in other kelp-dominated systems around the world (Wernberg et al. 2011).

Population structure of *L. hyperborea* was highly variable at the site level, demonstrating the importance of exposure to waves and tides in determining kelp density, biomass and morphology. Canopy density and biomass were greatest at the most exposed sites, reflecting the tolerance of *L. hyperborea* to high-energy environments (Smale & Vance 2015). On exposed coastlines, *L. hyperborea* formed dense stands with well-defined canopy tiers, unlike under sheltered conditions where smaller plants formed a sparser canopy, often mixed with *Saccharina latissima.* Within a region, total plant density and canopy biomass more than quadrupled from the most sheltered to the most exposed site, while individual plants were generally taller, longer and older under wave-exposed conditions. Our study agrees with previous work on *L. hyperborea* populations, which has demonstrated the positive influence of wave exposure on kelp density and biomass (Sjøtun & Fredriksen 1995, Sjøtun et al. 1998, Pedersen et al. 2012, Gorman et al. 2013). Many kelp species show morphological adaptations to wave exposure, including a larger holdfast, a shorter thicker stipe and a more streamlined blade with much-reduced drag (Gaylord & Denny 1997, Wernberg & Thomsen 2005). However, *L. hyperborea* populations exhibit a greater stipe length, blade length and total biomass under more exposed conditions, at least within the range of wave exposure conditions captured by the current study. Having a greater stipe length and blade area may be competitively advantageous within dense canopies where shading may limit light levels and prevent growth of smaller plants (Sjøtun et al. 1998). Clearly, kelp plant morphology is a trade-off between maximising light and nutrient absorption and minimising drag and wave-induced dislodgement and mortality. As canopy-forming *L. hyperborea* plants can tolerate extreme hydrodynamic forces

(Smale & Vance 2015), and the abundance of *L. hyperborea* is positively related to wave exposure (Burrows 2012), maintaining a greater stipe length and biomass may not substantially increase the likelihood of wave-induced mortality. Rather, wave-exposed conditions may facilitate growth of *L. hyperborea* by releasing sporophytes from interspecific competition, reducing epiphyte loading and limiting self-shading (Pedersen et al. 2012).

The range of values for kelp biomass and density presented here are comparable to previous studies on *L. hyperborea* in the northeast Atlantic, which have included study sites at similar depths in Norway (Sjøtun et al. 1993, Rinde & Sjøtun 2005, Pedersen et al. 2012), Ireland (Edwards 1980), Scotland (Jupp & Drew 1974), the Isle of Man (Kain 1977) and Russia (Schoschina 1997). There have been far fewer robust assessments of the standing stock of carbon, so contextualising our carbon stock values is challenging. However, by using our study average ratio of DW:FW of 22%, and assuming that 30% of dry weight is carbon, previous reports of standing biomass can be used for comparison. This approach suggests that our maximum mean value for the standing stock of carbon (1820 g C m^{-2} at the most wave-exposed site in northern Scotland) is greater than previous estimates for UK kelp stands, which have reported maximum mean values of 924 (Kain 1977) and 1350 g C m^{-2} (Jupp & Drew 1974) from the Isle of Man and western Scotland, respectively. As such, the maximum standing stock of carbon within UK kelp forests may have been previously underestimated.

Our study-wide average for standing stock of carbon (721 g C m^{-2}) is comparable to previous estimates for *L. hyperborea* in the UK and Norway (Table 5). Reported values of standing stock of carbon contained within kelp forests dominated by various species around the world are highly variable, most likely due to different survey techniques, methodologies and inherent natural variability and patchiness (Table 5). Even so, values for *L. hyperborea* forests compare favourably with those for other kelp canopies, perhaps because *L. hyperborea* has a large, robust stipe structure and forms dense aggregations. It is evident that kelp plants 'lock up' a considerable amount of carbon within shallow-water marine ecosystems (Table 5).

A principal finding of the current study is the observed variation in standing stock of carbon, which varied by an order of magnitude between sites. This variability was related to summer light levels, maximum sea temperature (which was correlated with other variables, including summer day length and

Table 5. Reported estimates of standing stock of carbon in kelp-dominated systems from around the world. Estimates are given as mean values per study, averaged over seasons, sites and years as appropriate

Kelp	Region	Standing stock (g C m^{-2})	References
Laminaria hyperborea	UK	721	This study
Laminaria hyperborea[a]	UK	594	Kain (1977)
Laminaria hyperborea[a]	UK	682	Jupp & Drew (1974)
Laminaria hyperborea[a]	Norway	800	Sjøtun et al. (1998)
Laminaria digitata	Rhode Island, USA	49	Brady-Campbell et al. (1984)
Laminaria digitata/Saccharina latissima	France	162	Gevaert et al. (2008)
Saccharina latissima	Rhode Island, USA	243	Brady-Campbell et al. (1984)
Macrocystis pyrifera[b]	California, USA	273	Foster & Schiel (1984)
Macrocystis pyrifera	Subantarctic	670	Attwood et al. (1991)
Lessonia nigrescens	Chile	487	Tala & Edding (2007)
Lessonia trabeculata	Chile	1120	Tala & Edding (2007)
Ecklonia radiata[c]	New Zealand	208	Salomon et al. (2008)
Ecklonia radiata[c]	W. Australia	820	Kirkman (1984)

[a]Calculated from ratios of dry weight (DW) to fresh weight (FW) (22%) and C:DW (31%) for *Laminaria hyperborea* reported by this study and Sjøtun et al. (1996)
[b]Calculated from ratios of DW:FW (10%) and C:DW (30%) suggested for *Macrocystis pyrifera* by Reed & Brzezinski (2009)
[c]Calculated from ratios of DW:FW (19%) and C:DW (36%) for *Ecklonia radiata* reported by de Bettignies et al. (2013)

mean temperature), wave fetch, tidal-driven water motion and depth, which explained almost all of the observed variation. These environmental variables are also critical for predicting the presence of *L. hyperborea* in Norway (Bekkby et al. 2009), suggesting broad-scale consistency in the key drivers of population structure. Clearly, kelps play a key role in nutrient cycling in coastal marine ecosystems, and the uptake, storage and transfer of carbon through kelp forests represents an important ecosystem service (Mann 1972b, Salomon et al. 2008). The observed and predicted increases in seawater temperature in the northeast Atlantic (Belkin 2009, Philippart et al. 2011), however, may diminish the carbon storage capacity of *L. hyperborea*, and may drive changes in kelp species distributions, with 'cold'-water species being replaced by 'warm'-water species along some coastlines (Smale et al. 2015). Concurrently, intensified and altered human activities along coastal margins may combine with changes in rainfall and runoff to increase turbidity, sediment and nutrient loads in coastal waters (Gillanders & Kingsford 2002). Reduced light and water quality will reduce the extent of kelp forests in temperate seas and diminish the standing stock of carbon held at any one time. The best approach to conserve this ecosystem service would be to adopt a combination of both improved local-scale catchment management and regional-to-global scale action to alleviate the underlying causes and impacts of ocean warming (Strain et al. 2015).

We compared our estimates of the total standing stock of carbon within *L. hyperborea* forests with reported values for other vegetated habitats in the UK (Table 6). Interestingly, because of the comparatively low spatial extents of seagrass beds and salt marshes, the total amount of carbon contained within kelp forests at any point in time is 1 (salt marshes) or 2 (seagrass meadows) orders of magnitude greater than in these other vegetated coastal marine habitats (Table 6). Intuitively, the standing stock of carbon contained within terrestrial forests is substantially greater, although the estimate for heathland ecosystems is comparable to kelp forests in UK waters (Table 6). Although the values are subject to several sources of error and uncertainty and should be interpreted with some caution, the relative contribution of each habitat type highlights the critical importance of kelp forests with respect to the ecosystem service of carbon assimilation, storage and transfer. The important difference between kelp forests and other vegetation types is that turnover of organic matter is relatively rapid and carbon is not sequestered 'below ground' (as it is in salt marshes and seagrass meadows, where it may remain buried for hundreds of years; see Fourqurean et al. 2012), which therefore limits the capacity of kelp forests as long-term carbon sinks in their own right. However, the vast majority of kelp-derived matter (>80%) is processed as detritus, rather than through direct consumption (Krumhansl & Scheibling 2012), and exported detritus may be transported many kilometres away from source into

Table 6. Estimated total standing stock of carbon in vegetated UK habitats. The standing crop of carbon for kelp forests is an average of 3 independent studies on *Laminaria hyperborea* in the UK

Habitat	Standing stock (g C m^{-2})	Extent in UK (km^2)	Total C (t C × 10^3)	References
Kelp forest[a]	665	8151[b]	5250	Jupp & Drew (1974), Kain (1977), this study
Seagrass meadow	161	50–100	8–16	Garrard & Beaumont (2014) and refs therein
Salt marsh	440	453	199	Garrard & Beaumont (2014) and refs therein
Broadleaf forest	7000	13730	96110	Alonso et al. (2012), Nafilyan (2015)
Coniferous forest	7000	15060	105420	Alonso et al. (2012), Nafilyan (2015)
Heathland	200	21120	4224	Alonso et al. (2012), Nafilyan (2015)

[a]This value is derived only from forests dominated by *L. hyperborea* and does not include the contribution of other kelp-dominated habitats (e.g. *Saccharina latissima* beds in wave-sheltered habitats)

[b]Yesson et al. (2015a) predicted the area of UK habitat suitable for the presence of *L. hyperborea* to be 15 984 km^2. Based on Burrows (2012), we estimated that *L. hyperborea* will be abundant (and therefore form kelp forest rather than isolated stands or individuals) on 51 % of this suitable habitat, giving an estimated total area of kelp forest of 8151 km^2

receiver habitats that do have long-term carbon storage capacity, such as seagrass beds, salt marshes and the deep sea (Duggins & Estes 1989, Wernberg et al. 2006). Recent work has shown that macroalgae can function as 'carbon donors', as they produce and export material that is later assimilated by 'blue carbon' habitats as allochthonous organic matter (reviewed by Hill et al. 2015). In seagrass beds, for example, up to 72 % of buried carbon may originate from allochthonous sources (Gacia et al. 2002), of which macroalgal detritus may constitute a significant proportion (Trevathan-Tackett et al. 2015).

Given the high rates of biomass and detritus production of kelps (Krumhansl & Scheibling 2012), the extensive spatial coverage of kelp populations in the UK (Yesson et al. 2015a) and the intense hydrodynamic forces that influence exposed coastlines dominated by *L. hyperborea* (Smale & Vance 2015), it is likely that export of kelp-derived carbon to receiver habitats is an important process that warrants further investigation. What is clear is that kelp forests in the UK represent a significant carbon stock, play a key role in energy and nutrient cycling in inshore waters and provide food and habitat for a wealth of associated organisms, including socioeconomically important species. Enhanced valuation and recognition of these ecosystem services may promote more effective management and mitigation of anthropogenic pressures, which will be needed to safeguard these habitats under rapid environmental change.

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