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

Running title: Kelp forest structure along environmental gradients

Dan A. Smale[1*], Michael T. Burrows[2], Ally J. Evans[3], Nathan King[3], Martin D. J. Sayer[2,4], Anna L. E. Yunnie[5], Pippa J. Moore[3,6]

[1]Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

[2]Scottish Association for Marine Science, Dunbeg, Oban, Argyll, Scotland PA37 1QA

[3]Institute of Biological, Environmental and Rural Sciences, Aberystwyth University, Aberystwyth, SY23 3DA, UK.

[4]NERC National Facility for Scientific Diving

[5]PML Applications Ltd, Prospect Place, Plymouth, PL1 3DH, UK

[6]Centre for Marine Ecosystems Research, School of Natural Sciences, Edith Cowan University, Joondalup 6027, Western Australia, Australia

*Correspondence: Email: dansma@mba.ac.uk Fax: +44(0)1752633102; Phone: +44(0)1752633273

ABSTRACT

Kelp forests represent some of the most productive and diverse habitats on Earth. Understanding drivers of ecological pattern 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, Wernberg et al. 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*, which is distributed from its equatorward range edge in northern Portugal to it 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 equator-ward 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, Pedersen et al. 2012, Bekkby et al. 2014, Rinde et al. 2014). Comparatively 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, Moore 1973, Jupp & Drew 1974, Kain 1975) 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. 2014) 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 & Bremmer 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 Status (GES) for UK marine habitats (see Borja et al. 2010 for discussion of 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 four regions in the UK, spanning ~50°N to ~59°N (Fig. 2). Regions encompassed a temperature gradient of ~2.5°C (mean annual sea surface temperature 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 were selected based on the following criteria: (i) sites should include sufficient areas of subtidal rocky reef at ~5 m depth (below chart datum); (ii) 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); (iii) sites should be 'open coast' and moderately to fully exposed to wave action to ensure a dominance of *L. hyperborea* (rather than *Saccharina latissima* which dominates sheltered coastlines typical of Scottish sea lochs, for example); and (iv) 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 eight 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 by 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 five-week period in August-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 weights (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 (Fig. S1), 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 below). 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 hrs 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-week period in July-August 2014 and retrieved ~6 weeks later. To quantify water motion induced by waves or tidal flow, an accelerometer ('HOBO' Pendant G Logger) 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) and the accelerometer recorded its position in three axes every 5 minutes (see Evans & Abdo 2010 for similar approach and method validation). A temperature and light level sensor ('HOBO' Temperature/Light weatherproof Pendant Data Logger 16k) was also attached to the buoy and captured data every 15 minutes (Fig S2). The sensor array was deployed for >45 days 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 and 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). Then the range of water motion values recorded within each 12 hour period, which encapsulated ~1 complete cycle of ebbing and flowing tide, was calculated and averaged over the 45-day 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 days during peak summer temperatures where all sensor array deployments overlapped (26th July – 18th 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 days 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 0800 and 2000 hrs) 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) indicated that light sensors at each site were stationary and horizontally-orientated for 51.8-88.1% of the light logging events (mean across 12 sites = 72.1% ± 10.4). 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 months) 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* and wave exposure. Temperature data used were monthly means for February and August (i.e. monthly minima and maxima), averaged from 2000-2006, using 9-km resolution data from the Pathfinder AVHRR satellite (obtained from the NASA Giovanni Data Portal). 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 chlorophyll *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 2002-2012 (see Burrows 2012 for 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). All relationships were highly significant ($P<0.001$), and had R^2 values ≥ 0.80 (Fig. S3). Study-wide averages showed that FW to DW ratios varied between parts of the plant, with mean percentage values of dry to fresh weight being 29.8, 16.8 and 21.4% for basal blade, distal blade and stipe, respectively (Fig. S3). 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 FW:DW 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).

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 ± standard error (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 (Tables 1 and 2) and Pearson's correlation co-efficient was used to test for co-linearity 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 ($r > 0.9$), of these only maximum summer 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 max. temp., summer mean light, tidal water motion, wave water motion, depth, nitrate + nitrite (NO_3^-+NO_2^-), phosphate (PO_4^{3-}), urchin density, mean log chlorophyll *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 the AIC_c model selection criterion (McArdle & Anderson 2001, Anderson et al. 2008). AIC_c is a modified version of Akaike's 'An Information Criterion' 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 clear distinction between the two northernmost regions (A&B) and the two southernmost (C&D) based on summer mean, summer maximum and annual mean temperatures (Table 1, Fig. S4). 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 two 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 four 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 (Fig. S5, S6). 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 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 '*X*1' the most exposed and site '*X*3' 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 four 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 two southernmost regions (C&D; ~8°C) compared with the two northernmost regions (A&B;

~6°C). Mean chlorophyll *a* concentration was comparable between regions although values were notably higher within the west Scotland (B) region (Table 2).

Kelp forest structure

All sites were dominated by *L. hyperborea* (>80% relative abundance of all canopy-forming macroalgae), although *Saccharina latissima, Saccorhiza polyschides*, *Laminaria ochroleuca, Laminaria digitata* and *Alaria escuelenta* 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 three 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 inds. m^{-2} (site A1), while mean total plant density ranged from 6.4 ± 0.6 (site B3) to 27.4 ± 2.6 inds. m^{-2} (site C2). Similarly, biomass per unit area was highly variable between sites (Table 3. Fig. 3) and ranged from 3.0 ± 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&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 four 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 C 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). For canopy density the environmental variables included in the most parsimonious solution ($R^2 = 0.92$, 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 (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. *L. hyperborea* is a cold-temperate species; the growth and maintenance of both the gametophyte and sporophyte is compromised at sea temperatures 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 temperatures 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. Sjøtun et al. 1998, Bartsch et al. 2008 and references therein). As such, a combination of cooler temperatures 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 inversely related to seawater temperature in the current study, may also be important. At higher latitudes, longer summer day lengths (a proxy for photoperiod) may benefit kelp performance by facilitating 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 *E. 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 *S. 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 stream-lined 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 inter-specific 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 C (1820 g C m^{-2} at the most wave-exposed site in N 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 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*, as well as drive changes in kelp species distributions, with 'cold'-water species being replaced by 'warm'-water species along some coastlines (Smale et al. 2014). Concurrently, intensified and altered human activities along coastal margins may combine with changes in rainfall and runoff to increase turbidly, 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 one (salt marshes) or two (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 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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Table 1. Summary of environmental and biological predictor variables recorded at each study site. This study included 12 sites within 4 distinct regions in the UK. ‘Peak summer mean temp.’ is the average daily temperature (°C) recorded *in situ* during a period of 24 days (26th July – 18th August 2014), where all sensor array deployments overlapped. ‘Peak summer max. temp.’ is the maximum daily average recorded during the observation period (°C). ‘Summer day light’ is the average daytime light intensity (between 0800 and 2000 hours) recorded during a 14-day deployment of light loggers at each site. ‘Tidal water motion’ is a proxy for water movement driven by tidal flow, which was derived from the range in water motion values recorded during a 24 hr period, averaged over the 45-day accelerometer deployment. ‘Wave water motion’ is a proxy for water movement driven by waves, which was derived from averaging the 3 highest-magnitude water motion values observed during the 45-day accelerometer deployment (following correction for tidal-induced movement). ‘Depth’ indicates average depth (below chart datum) of each study site. ‘NO_3^-+NO_2^-’ and ‘PO_4^{3-}’ indicate average concentrations of nitrite + nitrate and phosphate (n = 2 water samples collected *in situ* 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 mean temp. (°C)**	**Peak summer. max .temp. (°C)**	**Summer day light (lumens m^{-2})**	**Tidal water motion (ms^{-1})**	**Wave water motion (ms^{-1})**	**Depth (m)**	**NO_3^-+NO_2^- (µM)**	**PO_4^{3-} (µM)**	**Urchin density (inds 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

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

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

Table 3. Results of univariate permutational ANOVAs to test for differences in kelp individuals and populations between regions and sites. 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 (at P<0.05) are indicated in bold and where significant differences between Regions were observed posthoc pairwise tests were conducted (region A = northern Scotland; B = western Scotland; C = southwest Wales; and D = southwest England).

Response	**Region**			**Site(Region)**			**Res**
variable	**df**	***F***	**P**	**df**	***F***	**P**	**df**
Per square meter							
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***	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

*pairwise comparisons within region: A=B, A>C&D, B=C=D

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.

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

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 C (g C m^{-2})**	**References**
Laminaria hyperborea	United Kingdom	721	This study
Laminaria hyperborea[1]	United Kingdom	594	Kain (1977)
Laminaria hyperborea[1]	United Kingdom	682	Jupp & Drew (1974)
Laminaria hyperborea[1]	Norway	800	Sjøtun et al. (1998)
Laminaria digitata	Rhode Island	49	Brady-Campbell et al. (1984)
Laminaria digitata/*Saccharina latissima*	France	162	Gevaert et al. (2008)
Saccharina latissima	Rhode Island	243	Brady-Campbell et al. (1984)
Macrocystis pyrifera[2]	California	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[3]	New Zealand	208	Salomon et al. (2008)
Ecklonia radiata[3]	W. Australia	820	Kirkman (1984)

[1] Calcuated from a ratio of fresh weight to dry weight (22 %) and dry weight to carbon (31%) for *Laminaria hyperborea* reported by this study and Sjøtun et al. (1996).
[2] Calculated from a ratio of fresh weight to dry weight (10 %) and dry weight to carbon (30%) suggested for *Macrocystis pyrifera* by Reed & Brzezinski (2009)
[3] Calculated from ratios of fresh weight to dry weight (19 %) and dry weight to carbon (36%) for *Ecklonia radiata* reported by de Bettignies et al. (2013).

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

Habitat	**Standing stock C (g C m^{-2})**	**Extent in UK (km^2)**	**Total C (t C x 10^3)**	**References**
Kelp forest[1]	665	8151[2]	5250	Kain (1977); Jupp & Drew (1974); 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	Nafilyan (2015); Alonso et al. (2012)
Coniferous forest	7000	15060	105420	Nafilyan (2015); Alonso et al. (2012)
Heathland	200	21120	4224	Nafilyan (2015); Alonso et al. (2012)

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

[2] Yesson et al. (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 estimate 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 8151km^2.

Figure Legends

Figure 1. Extensive kelp canopies formed by *Laminaria hyperborea* in northern Scotland (A). A wide range of fauna and flora, including sub-canopy kelp plants, is found beneath the canopy (B).

Figure 2. Map of UK indicating 4 study regions: northern Scotland (A), western Scotland (B) southwest Wales (C) southwest England (D). Inset maps indicate locations of 3 study sites within each region.

Figure 3. Structure of *Laminaria hyperborea* populations at each study site. Bars represent mean values ± SE (n = 8 for quadrat-level variables: A, B, C, D); $n \geq 12$ for plant-level variables: E, F, G, H).

Figure 4: Estimated standing stock of carbon (g C m^{-2}) provided by the kelp canopy (A), sub-canopy plants (B) and the total population of *Laminaria hyperborea* at each study site (C). Bars represent mean values ± SE, n = 8.

Figure 5: Relationships between key environmental predictor variables (as determined by DISTLM, see Table 4) and kelp canopy density (A-C), canopy biomass (D-F) and standing stock of carbon (G-I). 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).

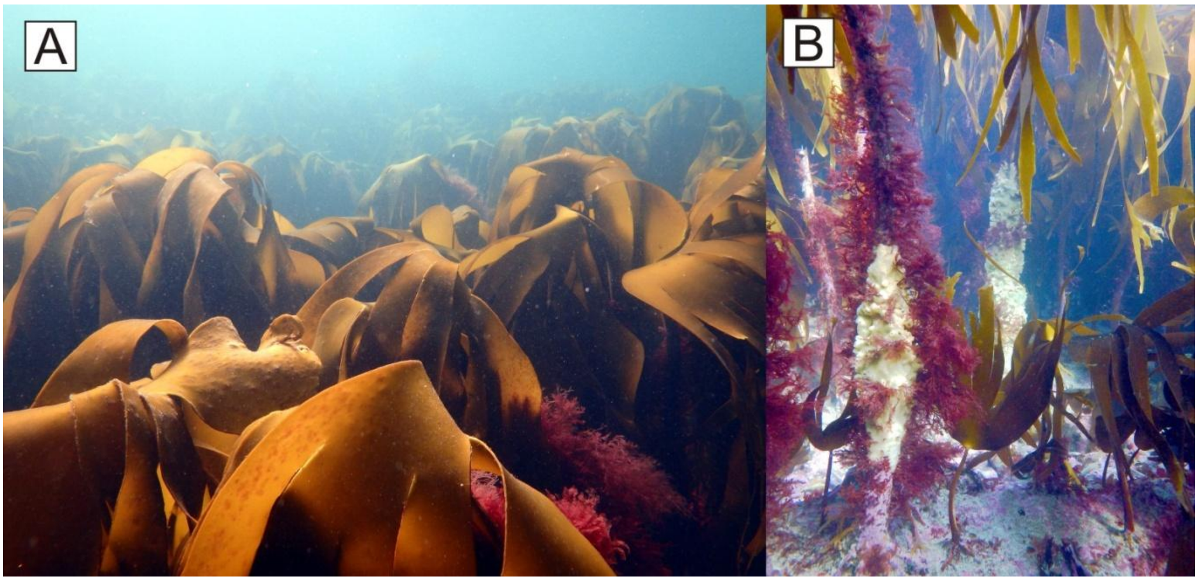

Fig. 1

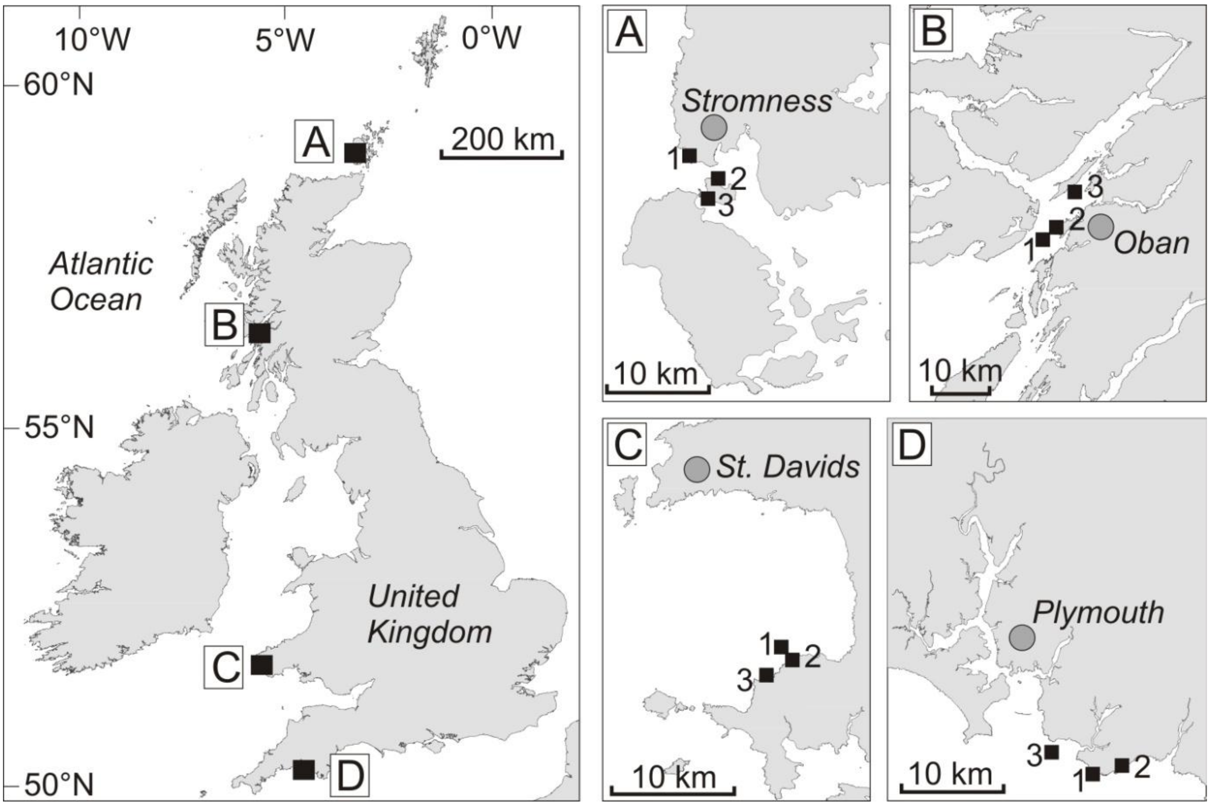
10°W
5°W
0°W
60°N
55°N
50°N
200 km
A
B
C
D
Atlantic Ocean
United Kingdom
Stromness
1
2
3
10 km
Oban
St. Davids
Plymouth

Fig. 2

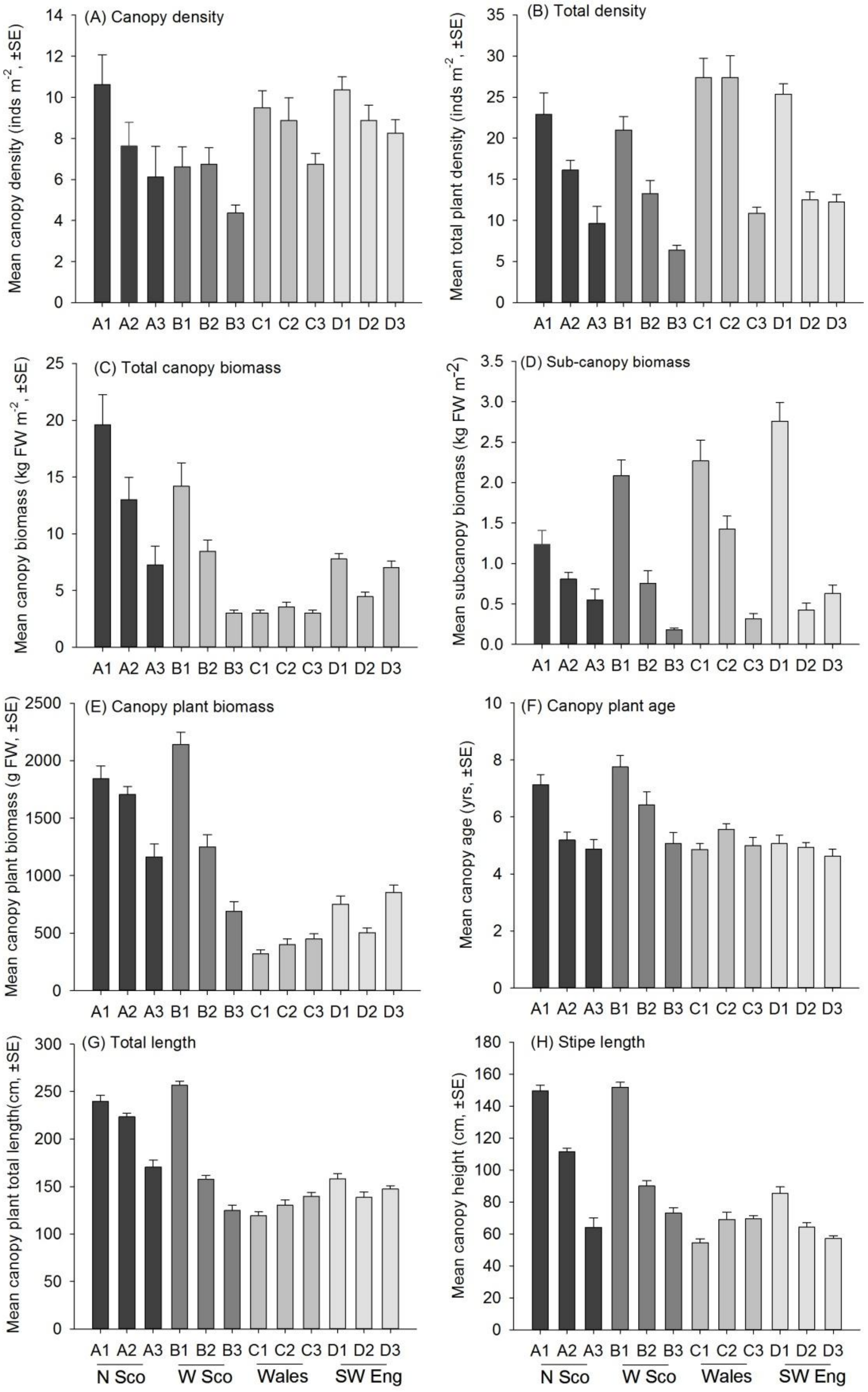
(A) Canopy density
Mean canopy density (inds m^{-2}, ±SE)
0
2
4
6
8
10
12
14
(B) Total density
Mean total plant density (inds m^{-2}, ±SE)
0
5
10
15
20
25
30
35
(C) Total canopy biomass
Mean canopy biomass (kg FW m^{-2}, ±SE)
0
5
10
15
20
25
(D) Sub-canopy biomass
Mean subcanopy biomass (kg FW m^{-2})
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
(E) Canopy plant biomass
Mean canopy plant biomass (g FW, ±SE)
0
500
1000
1500
2000
2500
(F) Canopy plant age
Mean canopy age (yrs, ±SE)
0
2
4
6
8
10
(G) Total length
Mean canopy plant total length(cm, ±SE)
0
50
100
150
200
250
300
(H) Stipe length
Mean canopy height (cm, ±SE)
0
20
40
60
80
100
120
140
160
180
A1 A2 A3 B1 B2 B3 C1 C2 C3 D1 D2 D3
N Sco
W Sco
Wales
SW Eng

Fig. 3

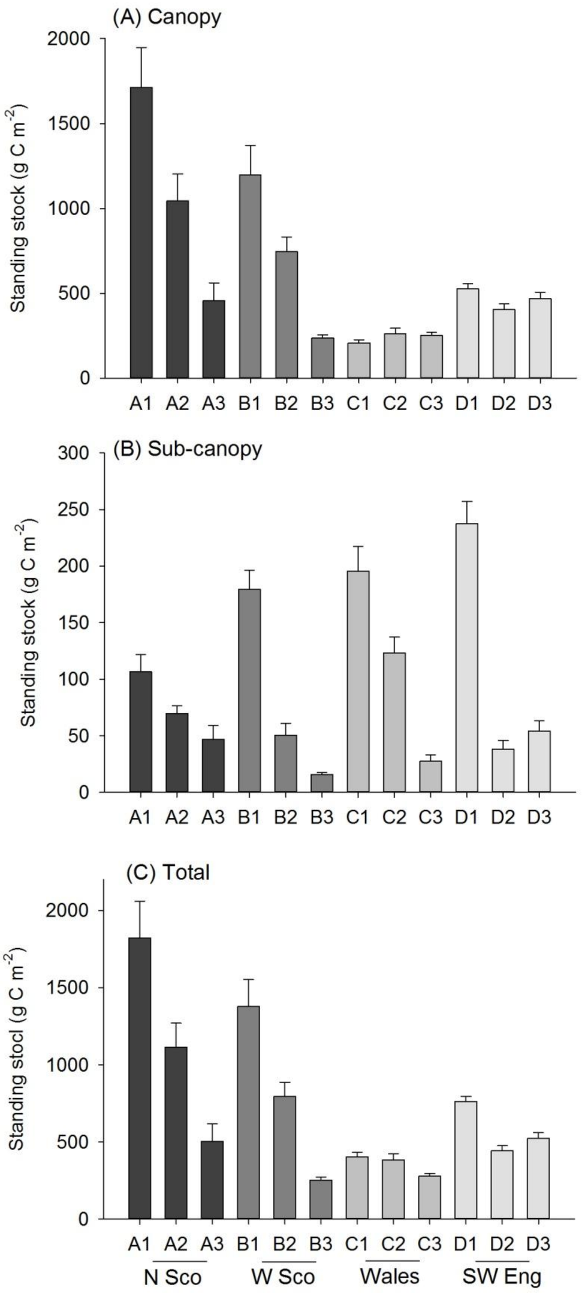
(A) Canopy
Standing stock (g C m^{-2})
0
500
1000
1500
2000
A1 A2 A3 B1 B2 B3 C1 C2 C3 D1 D2 D3
(B) Sub-canopy
Standing stock (g C m^{-2})
0
50
100
150
200
250
300
A1 A2 A3 B1 B2 B3 C1 C2 C3 D1 D2 D3
(C) Total
Standing stocl (g C m^{-2})
0
500
1000
1500
2000
A1 A2 A3 B1 B2 B3 C1 C2 C3 D1 D2 D3
N Sco
W Sco
Wales
SW Eng

Fig. 4

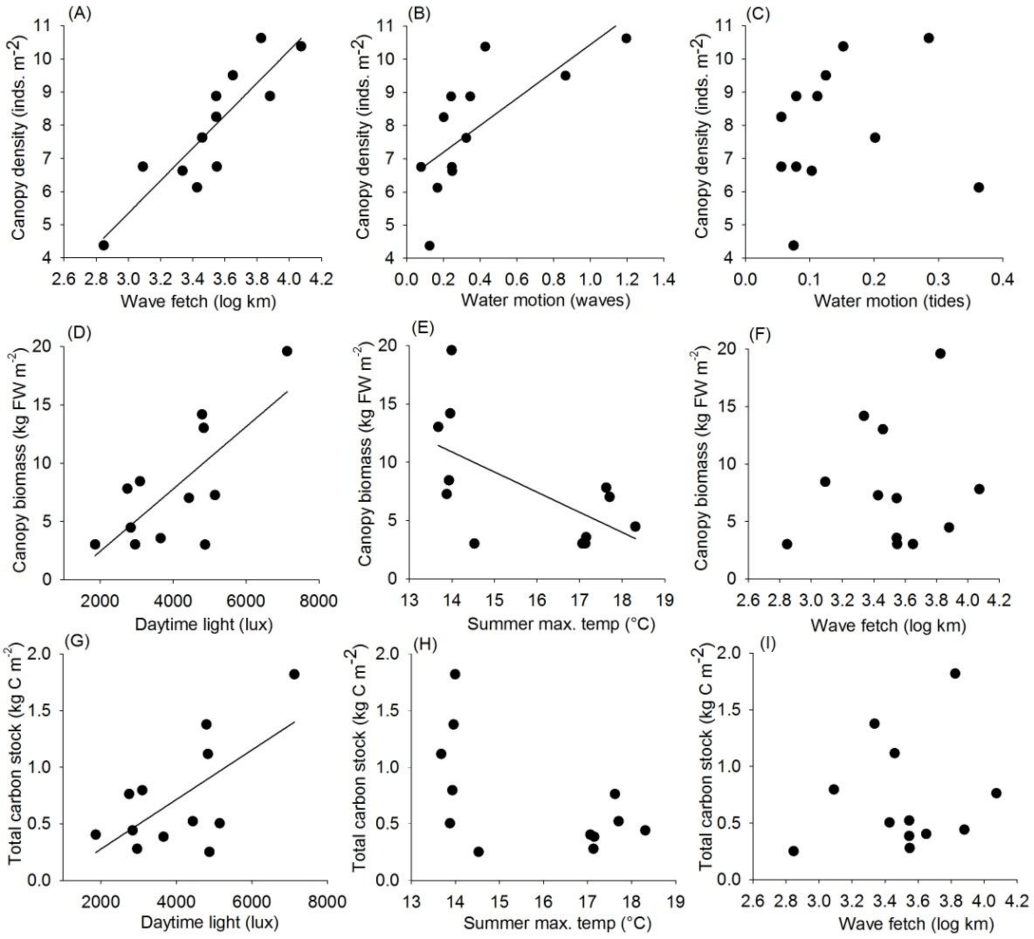
(A)
Canopy density (inds. m^{-2})
4 5 6 7 8 9 10 11
2.6 2.8 3.0 3.2 3.4 3.6 3.8 4.0 4.2
Wave fetch (log km)
(B)
Canopy density (inds. m^{-2})
4 5 6 7 8 9 10 11
0.0 0.2 0.4 0.6 0.8 1.0 1.2 1.4
Water motion (waves)
(C)
Canopy density (inds. m^{-2})
4 5 6 7 8 9 10 11
0.0 0.1 0.2 0.3 0.4
Water motion (tides)
(D)
Canopy biomass (kg FW m^{-2})
0 5 10 15 20
2000 4000 6000 8000
Daytime light (lux)
(E)
Canopy biomass (kg FW m^{-2})
0 5 10 15 20
13 14 15 16 17 18 19
Summer max. temp (°C)
(F)
Canopy biomass (kg FW m^{-2})
0 5 10 15 20
2.6 2.8 3.0 3.2 3.4 3.6 3.8 4.0 4.2
Wave fetch (log km)
(G)
Total carbon stock (kg C m^{-2})
0.0 0.5 1.0 1.5 2.0
2000 4000 6000 8000
Daytime light (lux)
(H)
Total carbon stock (kg C m^{-2})
0.0 0.5 1.0 1.5 2.0
13 14 15 16 17 18 19
Summer max. temp (°C)
(I)
Total carbon stock (kg C m^{-2})
0.0 0.5 1.0 1.5 2.0
2.6 2.8 3.0 3.2 3.4 3.6 3.8 4.0 4.2
Wave fetch (log km)

Fig. 5