

Examining the influence of regional-scale variability in temperature and light availability on the depth distribution of subtidal kelp forests

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Abstract

Foundation species play a disproportionate role in maintaining biodiversity and ecosystem functioning. Improved understanding of how environmental factors influence the distribution and population structure of foundation species therefore contributes to management and conservation of entire ecosystems. We surveyed subtidal kelp forests within four regions of the U.K., distributed over 9° of latitude and a mean sea temperature gradient of ~ 2.5°C. Our aims were: (1) to examine relationships between light availability and the structure and depth distribution of *Laminaria hyperborea* populations and (2) to determine whether depth-related patterns were consistent across regions with different temperature regimes. We recorded marked depth-related shifts in structure with decreasing light levels strongly correlated with declines in kelp density, cover, plant biomass, standing biomass, plant length, and age. We also recorded an effect of latitude; populations at our two colder, northernmost regions exhibited greater wet weight and length and higher standing biomass than populations in the warmer southern regions when under similar or even reduced light conditions, indicating an interactive effect of latitude, most likely related to temperature variability. We show that shifts in kelp population structure along depth gradients are strongly driven by light availability, although regional variability in the strength and nature of these relationships may be promoted by other factors such as temperature. Maximum depth penetration, standing biomass, plant density, and plant weight are useful indicators of light availability and, over time, could be monitored to detect changes in the quality of the overlying water column.

Understanding how physical and biological factors influence the distribution of organisms and the structure of populations is a fundamental goal of ecology, and a prerequisite for effective management and conservation of biodiversity (Bremner 2008; Kaiser et al. 2011). Coastal marine systems are often characterized by steep environmental gradients (in, e.g., wave exposure, light, and salinity) which in turn influence the structure and diversity of communities and the distribution of key habitats (Bonsdorff and Thomas 1999; Mann and Lazier 2013).

Benthic marine macrophytes (seagrasses and macroalgae) are foundation species that enhance local biodiversity in coastal ecosystems globally (Olafsson 2016). Kelp species are marine macrophytes that are distributed along > 25% of the world's coastlines (Wernberg et al. 2019; Jayathilake and

Costello 2020), and the forests they produce represent some of the world's most productive and diverse habitats (Steneck et al. 2002). They offer food and habitat for a high diversity of associated organisms (Christie et al. 2003; Tuya et al. 2011; Teagle et al. 2017), provide nursery habitat for a range of economically valuable fisheries species (Bertocci et al. 2015), alter local environmental conditions (Wernberg et al. 2005), and significantly contribute to primary productivity and carbon assimilation and transfer (Wilmers et al. 2012; Pessarrodona et al. 2018). Given their considerable ecological and socio-economic importance, a mechanistic understanding of the drivers of the distribution and structure of kelp (and other benthic macrophytes) is vital, especially considering the need to manage and conserve the habitats they underpin in a rapidly changing environment (Olafsson 2016).

Temperature is the key driver constraining the latitudinal distributions of kelps (Eggert 2012) and can influence the structure and performance of populations within a species' distribution (Wernberg et al. 2010; Smale et al. 2020). While both photosynthesis and respiration increase with increasing temperatures (up until maximum thermal thresholds), photosynthesis plateaus while respiration continues to rise (Hurd et al. 2014). This means above a certain temperature threshold

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for photosynthesis, finite resources are allocated toward maintenance and repair, and away from performance (Begon et al. 2005). Therefore, ecophysiological performance and resilience are often reduced in populations found toward warm water trailing edges. At a local level, the vertical extent of kelp populations is related to light penetration, with growth typically occurring at deeper depths in areas where water clarity is high, resulting in lower light attenuation with depth (Gattuso et al. 2006; Desmond et al. 2015; Deregibus et al. 2016). While light availability in coastal environments is highly variable over timescales of days to weeks and months, kelp plants can persist for many years and, as such, the structure and depth penetration of kelp populations may serve as an indicator of turbidity of the overlying water column over longer timescales (Anthony et al. 2004; Desmond et al. 2015). However, the shift in energy balance seen across latitudinal/temperature gradients may also affect local vertical distributions as the increased energy demand in warm populations may reduce the ability of individuals to persist under low light/energy conditions. Despite this potential interaction, studies investigating depth and latitudinal interactions are distinctly lacking.

Here, we examined the structure and distribution of kelp forests dominated by *Laminaria hyperborea*, the most common kelp species in the Northeast Atlantic, along a depth gradient (2–15 m below chart datum; bcd) at eight survey sites nested within four regions, which spanned 9° of latitude and > 1000 km of northeast Atlantic coastline. By conducting surveys across a large spatial scale, we were able to examine the influence of regional-scale processes, such as variability in ocean climate and light availability, on local depth-related patterns. These study sites have been the focus of an extensive field program over recent years, and latitudinal shifts in kelp forest structure, spatial variability in biodiversity, and rates of primary productivity are increasingly well understood (Smale et al. 2016, 2020; Smale and Moore 2017; Pessarrodona et al. 2018; Teagle et al. 2018; Bué et al. 2020; King et al. 2021). However, as with kelp forests in many regions, patterns of vertical distribution and shifts in structure along depth gradients remain unclear. As such, the aim of the current study was twofold: (1) to examine relationships between light (photosynthetically active radiation [PAR]) availability and the structure and depth distribution of *L. hyperborea* populations and (2) to determine whether depth-related patterns were consistent across regions with different temperature regimes.

Methods

Study area

We examined the structure of *L. hyperborea* populations along a depth gradient at eight sites, with paired sites nested within each of four adjacent regions situated between ~ 180 and 500 km apart (Fig. 1). The regions spanned a latitudinal gradient ranging from ~ 50° to ~ 59°N across the UK

coastline, corresponding to a gradient in average ocean temperature of ~ 2.5°C (Smale et al. 2016; Pessarrodona et al. 2018). The four regions were northern Scotland (hereafter “A”), west Scotland (B), southwest Wales (C), and southwest England (D), as shown in Fig. 1. Excluding latitude and temperature, key variables such as nutrient availability and grazing pressure generally do not vary across regions (Smale et al. 2016, 2020; Smale and Moore 2017; Pessarrodona et al. 2018).

Within each region, candidate study sites were selected based on the following criteria: (1) sites should include sufficient areas of subtidal rocky reef with steeply sloping gradient, stretching from 2 m bcd to at least 20 m depth; (2) sites should be representative of the wider region (in terms of coastal geomorphology) and not obviously influenced by localized anthropogenic activities (e.g., sewage outfalls, fish farms); and (3) sites should be “open coast” and moderately to fully exposed to wave action to ensure a dominance of *L. hyperborea*. From this pool of candidate sites, paired sites were selected for surveys; sites within regions were situated between ~ 1 and ~ 10 km apart, had similar wave fetch values, and were all characterized by dense, extensive stands of *L. hyperborea* (see Table 1 for environmental variables for the four regions). Previous intensive research within these study regions has shown that these populations have persisted and remained stable since 2014 (Pessarrodona et al. 2018; Smale et al. 2020), while historical surveys suggest that comparable *L. hyperborea* populations have persisted for decades (Jupp and Drew 1974). There is no evidence of deforestation events driven by, for example, warming, eutrophication, or overgrazing, as has been observed for kelp populations in some other regions (Watanabe and Harrold 1991; Moy and Christie 2012; Wernberg et al. 2016).

Quantifying environmental variables

At each survey site, an array of sensors was deployed to capture data on temperature, irradiance, and PAR. An anchor weight attached to a line and subsurface buoy was deployed at 18 m depth (bcd), in close proximity to the 15 m isobath surveyed as described below. A temperature and light sensor (Hobo pendant logger, Onset, USA), mounted to a small plastic frame held in an upward facing orientation was attached to the line at 15, 10, and 5 m depth (bcd). An additional sensor was attached to the subsurface buoy (again facing upward) at 2 m depth (bcd) at two of the sites within regions A and D, where this was practicable. At 5 and 15 m or 5 and 10 m (variable across sites), a radiometer that quantified PAR (Odyssey logger, Dataflow Systems PTY) was also attached to the line, adjacent to the temperature and light sensor, to allow for formal comparisons between irradiance (i.e., light intensity) and PAR (see below). Data on both sensors were recorded every 20 min. Sensor arrays were deployed in May 2017 and were retrieved some 4 months later, in September/October 2017. Measurements of irradiance and PAR were only examined for

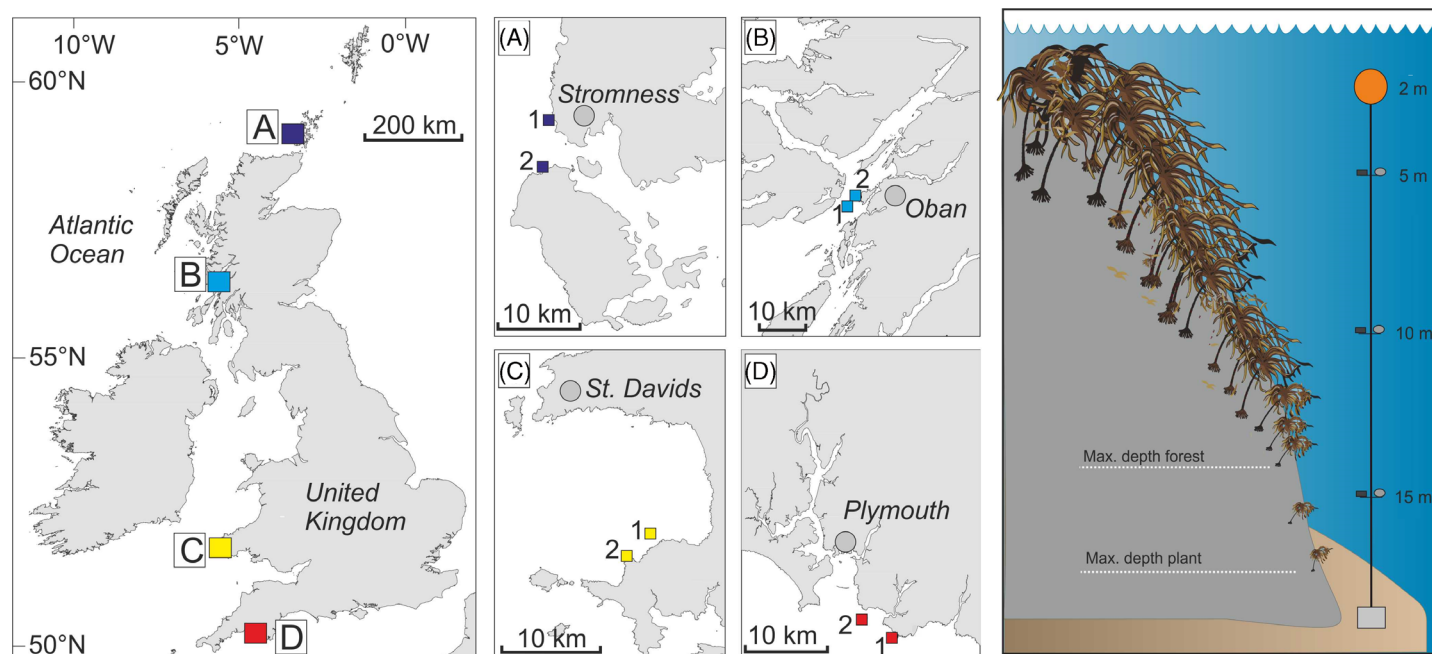


Fig. 1. Left: Map of U.K. displaying the four study regions: northern Scotland (A), western Scotland (B), southwest Wales (C), and southwest England (D). Middle: Inset maps show positions of paired study sites within each region. Right: Schematic of moorings deployed to collect temperature, irradiance, and PAR data.

Table 1. Summary of environmental conditions at each study site. This study included eight sites across four locations in the U.K. “Mean SST” is the annual mean temperature calculated from satellite-derived sea surface temperature (SST) data (2011–2020, 0.25° resolution data from NOAA Daily Optimum Interpolation Sea Surface Temperature [OISST], version 2.1; Huang et al. 2020). “Log Chl *a* mean” is the average annual concentration of chlorophyll *a* for each site ($\log_{10} \text{mg m}^{-3}$ from MODIS Aqua satellite data, 2011–2020). “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 (Burrows 2012). “ PO_4^{3-} ” and “ $\text{NO}_3^- + \text{NO}_2^-$ ” indicate average concentrations of phosphate and nitrite + nitrate respectively ($n = 2$ water samples taken from ~ 1 m above the kelp canopy in both spring and summer 2015) taken from Pessarrodona et al. (2018).

Location	Region	Mean SST (°C)	Log Chl <i>a</i> mean (mg m^{-3})	Log wave fetch (km)	PO_4^{3-} (μM)	$\text{NO}_3^- + \text{NO}_2^-$ (μM)
A	Northern Scotland	10.1	0.18	3.7	0.20	1.79
B	Western Scotland	10.7	0.76	3.2	0.28	2.73
C	Southwest Wales	12.3	0.48	3.6	0.19	2.93
D	Southwest England	13.1	0.39	3.8	0.14	2.73

the first 14 d of deployment, however, as beyond this time-frame biofouling of sensors could potentially influence light measurements (Smale et al. 2016).

Measures of surface irradiance for each location were retrieved for the same time period from NASA historical records (<https://power.larc.nasa.gov/data-access-viewer/>, accessed 2020 April 15). These records are derived from NASA’s CERES FLASHFlux project (version 3), a part of NASA POWER project

(see Acknowledgments). Briefly, measurements are gathered through NASA’s satellite systems and analyzed using MERRA-2 data product by the Global Modelling and Assimilation Office at NASA Goddard Space Flight Center. Averaged daily measurements are provided at a resolution of $0.5^\circ \times 0.5^\circ$. Solar radiation values (W m^{-2}) were converted to PAR ($\text{mol photons m}^{-2} \text{d}^{-1}$) using formulas cited in dos Reis and Ribeiro (2020) and are presented in Supplementary Table S1.

Kelp forest surveys

At each site, the structure of *L. hyperborea* populations was quantified along a depth gradient spanning 2–15 m (bcd) using traditional scuba diving techniques. Divers were deployed on the seaward-facing aspect of the sloping reef habitat and descended to 15 m (bcd) to commence survey work, after which divers ascended the slope and conducted surveys at 10, 5, and 2 m depth (bcd). At each depth increment, eight replicate 1 m² quadrats were haphazardly deployed on stable rocky substrata and the density of *L. hyperborea* was enumerated and recorded in situ. In each quadrat, the density and percent cover of both canopy-forming and subcanopy plants (defined as clearly identifiable digitated plants with stipe length > 5 cm) were recorded, as well as the density of sea urchins. Replicate quadrats were situated at least 3 m apart from one another, along the isobath of the targeted depth increment. To achieve the desired depth below chart datum, adjustments were made in situ using actual water depth and tidal height predictions for that place, date, and time. In addition, divers noted the maximum depth of the kelp forest (defined as continuous stands of plants where gaps between plants were < 1 m) and of individual kelp plants (i.e., solitary plants situated > 1 m from the margin of the forest). Where maximum depths exceeded the 15 m isobath for quadrat surveys, divers continued to descend the slope to record maximum depth limits (to a maximum operating depth of 22 m).

The morphology and biomass of kelp plants were also examined by destructive sampling of individuals. At each depth increment, 10 canopy-forming plants were randomly collected and labeled appropriately. Kelp plants were returned to the laboratory, upon which morphometric measurements were immediately taken (e.g., length and fresh weight biomass of the holdfast, stipe and blade, the age of individuals as estimated by cross-sectioning of the base of the stipe and counting growth rings). Quadrat surveys were conducted at each site in May 2017 and collections for biomass and morphology measurements were conducted in September–October 2017.

Statistical approach

The relationship between irradiance and PAR was examined for all paired measurements taken from the same depth and location using linear regression. Prior to analysis, both variables were log transformed. For each site, the proportion of surface irradiance penetrating to each depth was calculated based on measures of surface irradiance gathered from NASA historical records. The relationships between irradiance recorded at each adjacent depth (i.e., 2 and 5 m, 5 and 10 m, 10 and 15 m) were modeled, with region and site included as factors (see Supplementary Information for details). In each case, the relationship between adjacent depths was highly significant (adjusted $R^2 > 0.86$), with no effect of region or site. Consequently, where irradiance data were not available due to occasional failure of loggers (across the study, light data were unavailable for 13 of the 32 depth/site combinations), values

for these depths and sites were interpolated using the irradiance values recorded from other depths at the same site.

For all kelp forest response variables and environmental variables, nested ANOVAs (site nested within region) were first carried out to compare paired sites surveyed within a region. Kelp forest response variables included population structure (i.e., canopy plant density and total *L. hyperborea* density) and plant-level metrics (i.e., total fresh weight, blade fresh weight, total length, blade length, blade width, and age). Environmental variables included temperature (averaged per 24 h) and irradiance (averaged from 07:00 to 19:00 UTC). In all cases, no difference was observed between the two sites from within any one region (Supplementary Table S2). Consequently, the data from paired sites were pooled for all further analyses. Two-way ANOVAs were then used to explore the main effects of region and depth and the interaction effects of these two factors on each kelp forest response variable and environmental variable. Where differences were observed (at $p < 0.05$), post hoc tests were conducted to examine the differences between individual levels of each factor. For each region and depth, the average total plant biomass was multiplied by average canopy density to give an estimated biomass per m². Two-way ANOVAs were then carried out on these data using the calculated mean, standard error of the mean, and n for each region/depth. All response variables were checked for homoscedasticity prior to analyses and data were transformed where necessary.

To investigate the relationships between kelp forest response variables and environmental variables, logarithmic regression analyses were carried out comparing the proportion of surface irradiance penetrating to each depth to the kelp forest response variable recorded at that depth. Regions with similar temperature profiles (dictated by post hoc analyses) were grouped together for analyses while those with significantly different temperature profiles were analyzed independently. Bonferroni correction was used to adjust for multiple individual tests to ensure an overall type I error rate of $\alpha = 0.05$ was maintained. All statistical analyses were conducted in RStudio v. 1.2.5042 (R Core Team 2020) using the packages “car,” “stats,” “graphics,” “ggpubr,” and “emmeans.” Figures were produced using Graph-Pad PRISM v8.4.2 for windows, GraphPad Software, www.graphpad.com.

Results

Environmental variables

Overlapping temperature data were collected from 02 June 2017 to 23 August 2017. Summer seawater temperatures varied significantly with region; there was a clear latitudinal distinction between the two northernmost regions and the two southernmost regions (pairwise comparisons within region: $A = B$, $A \& B < C \& D$, $C = D$; see Supplementary Fig. S1 for longer term SST time series). Within each region, there was no significant variability in temperature between depth

increments (Tables 2, 3). On any single day, the difference in water temperature between 2 and 15 m averaged 0.12°C and 0.29°C in regions A and D, respectively; in regions B and C (where temperature sensors were not deployed at 2 m), the temperature differed by 0.03°C and 0.11°C, respectively, between 5 and 15 m. On average, summer mean and maximum temperatures were 2.64°C and 2.73°C lower in the northernmost regions than the southernmost regions, respectively (Table 2; Fig. 2A).

Measures of irradiance were more variable and differed significantly between both regions and depths. The highest levels of irradiance were recorded in regions A and D while the lowest levels were observed in region C (Tables 2, 3; Figs. 2B–E, 3). In all regions, light levels decreased with depth, with each separate depth strata being significantly different to all others. At the shallowest 2-m-depth increment, mean irradiance ranged from 5493 lumens m⁻² in region A to 2209 in region C. At 15 m depth, mean irradiance ranged from 966.9 lumens m⁻² in region A to 161.5 lumens m⁻² in region C. The average proportion of surface irradiance penetrating to 2 m depth ranged from between 9.16% in region A to 3.40% in region C, while penetration to 15 m ranged from 1.53% in region A and 0.23% in region C (Table 2; Fig. 3). Paired data for illumination and PAR were collected at five sites at 5 m, three sites at 10 m and two sites at 15 m (Supplementary Fig. S2). Linear regression indicated a strong relationship between the two variables following log transformation (Adj. $R^2 = 0.957$, $p < 0.001$).

Kelp forest structure

The structure of *L. hyperborea* forests was highly variable across both regions and depth increments. In the northernmost regions (A, B), where water temperatures were lower, kelp was present to depths greater than 15 m; in region A, both the kelp forest and kelp individuals extended to ~ 24 m depth, whereas in region B the kelp forest extended to 13 m depth with the deepest *L. hyperborea* individual recorded at 16 m. In contrast, in the southernmost regions the kelp forest extended to only 9 and 10 m depth (despite comparable levels of irradiance to the northern regions) and the deepest individual was recorded at 11 and 12 m for regions C and D, respectively (Fig. 3). The percent cover of canopy forming plants also varied between regions. At 2 m, percent cover was almost identical across regions (97–100%). A high cover (> 93%) continued at 5 m in regions A, B, and D, while cover declined to 78% in region C. In region A, the percent cover of canopy forming plants remained high at 10 m (99%) and decreased slightly at 15 m, to 81%. In all other regions, a larger reduction in percent cover was observed with increasing depth; by 10 m depth, cover was 65%, 16%, and 30% in regions B, C, and D, respectively, and by 15 m, kelp was only present at site B (3% cover). The percent cover of subcanopy plants was lower but followed a similar trend with cover decreasing with increasing depth in all regions. Between 2 and 15 m, percent cover of subcanopy plants ranged from 81% to 41% in region A and 63% to 3% in region B. In regions C and D, subcanopy plant coverage ranged from 58% to 9% (C) and from 70% to

Table 2. Summary of temperature and light conditions at each region and depth. Summer temperatures were recorded from 02 June to 23 August 2017. Light data were obtained for 14 d following sensor deployment at each region; light intensity and PAR values shown are daytime measurements (07:00–19:00 h). Proportion of surface irradiance is based across 24 h.

Region	Depth (m)	Summer temp (°C)		Light intensity (lumens m ⁻²)		PAR (mol photons m ⁻² d ⁻¹)		% surface irradiance	
		Mean	Max	Mean	Max	Mean	Max	Mean	Max
N Scotland (A)	2	12.30	13.79	5493	9240	4.156	6.855	9.16	14.16
	5	12.28	13.79	4353	7267	3.431	6.337	7.09	10.93
	10	12.30	13.83	1822	3399	1.764	3.518	2.88	5.26
	15	12.22	13.76	966.9	1884	0.967	1.991	1.53	3.05
W Scotland (B)	2	—	—	3594	7078	2.763	5.314	6.41	7.92
	5	12.49	14.16	2876	5585	2.149	3.914	4.99	6.12
	10	12.51	14.19	768.7	1435	0.633	1.157	1.30	1.88
	15	12.50	14.18	356.9	704.5	0.303	0.586	0.60	0.94
SW Wales (C)	2	—	—	2209	4866	1.733	3.715	3.40	6.97
	5	14.95	16.56	1799	3865	1.367	2.982	2.67	5.44
	10	14.91	16.52	504.7	1435	0.429	1.157	0.74	2.01
	15	14.89	16.60	161.5	513.18	0.141	0.433	0.23	0.62
SW England (D)	2	15.13	16.48	5213	8884	3.956	6.602	6.90	9.74
	5	15.22	17.20	4071	6990	2.978	5.230	5.33	7.52
	10	15.06	17.16	1696	3149	1.336	2.451	2.22	3.51
	15	14.94	16.30	780.1	1376	0.641	1.180	1.01	1.64

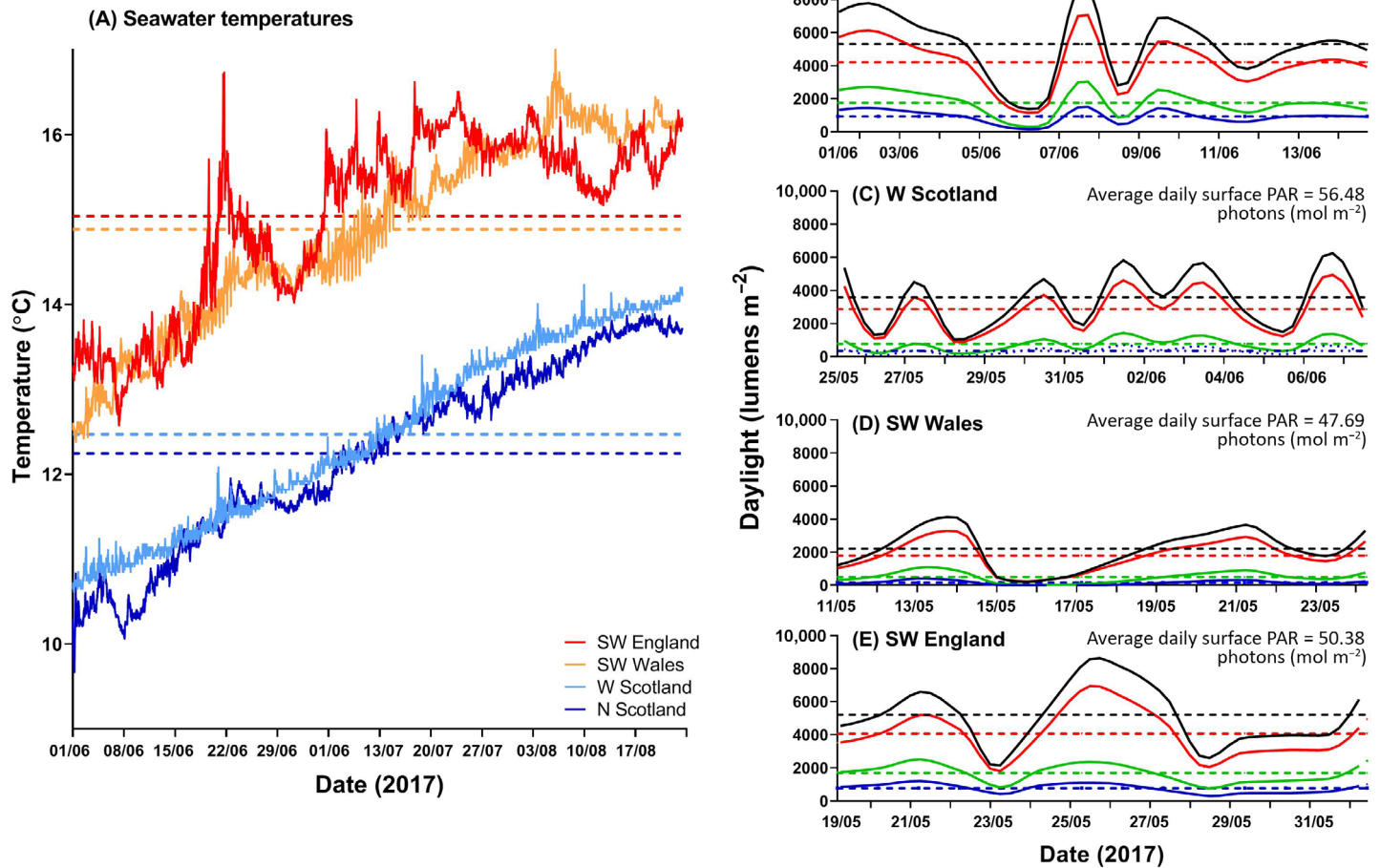


Fig. 2. Seawater temperature and daytime light intensity recorded during the study period. **(A)** Overlapping summer temperatures were recorded for 82 d; mean values for each region are shown as actual values did not vary significantly between depths and sites within each region. Dashed lines indicate mean temperature observed during the measurement period for each region. **(B–E)** Daytime (07:00–19:00 h) light intensity across a 14-d deployment of light sensors, deployed at 2 m (black line) 5 m (red line), 10 m (green line), and 15 m (blue line) bcd. Solid lines represent daily mean values for light intensity; dashed lines represent the mean intensity across the 14-d period. Measurements were not obtained at 15 m in region B or at 2 m in region B and C; therefore values shown for these depth/locations are modeled estimates based on strong relationships between adjacent depths across sites (adjusted $R^2 > 0.86$). Data were averaged across both sites within each region, as between-site variability was minimal and nonsignificant. Mean surface irradiance data derived from NASA historical records (<https://power.larc.nasa.gov/data-access-viewer/>, accessed 2020 April 15).

9% (D) between 2 and 10 m (Fig. 3; Supplementary Table S3). Urchins were present in very low and relatively consistent densities in all regions. The greatest density observed was 0.56 ind. m⁻² at 10 m depth in region B. In all regions, no urchins were recorded in at least one depth increment (Supplementary Table S3).

All population-structure metrics (i.e., total *L. hyperborea* density, canopy plant density, and canopy standing biomass) varied significantly with the interaction term and by the main factors of region and depth (two-way ANOVAs, $p \leq 0.003$ in all cases; Fig. 4; Table 3). In all cases, measurements decreased with increasing depth. However, the effect of depth on population metrics was more pronounced in the warmer, southern regions than in the cooler, northern regions (Fig. 4). This was particularly evident at 10 m, where total density, canopy

density, and canopy standing stock in regions C and D were very low or negligible but markedly higher in regions A and B.

All plant-level metrics (i.e., total fresh weight, blade fresh weight, total length, blade length, blade width, and age) also varied significantly with the interaction term and by the main factors of region and depth (two-way ANOVAs, $p \leq 0.001$ in all cases; Fig. 5; Table 3). Within a region, kelp forest response variables typically decreased with increasing depth. Between regions there was a distinction between the two northernmost regions (A, B) and the two southernmost regions (C, D), with greater values recorded in the northernmost regions for all variables except blade length which was variable across regions and depths (Fig. 5). Across depths, the total fresh weight of an individual canopy-forming plant in the northern regions was more than double the total fresh weight recorded in southern

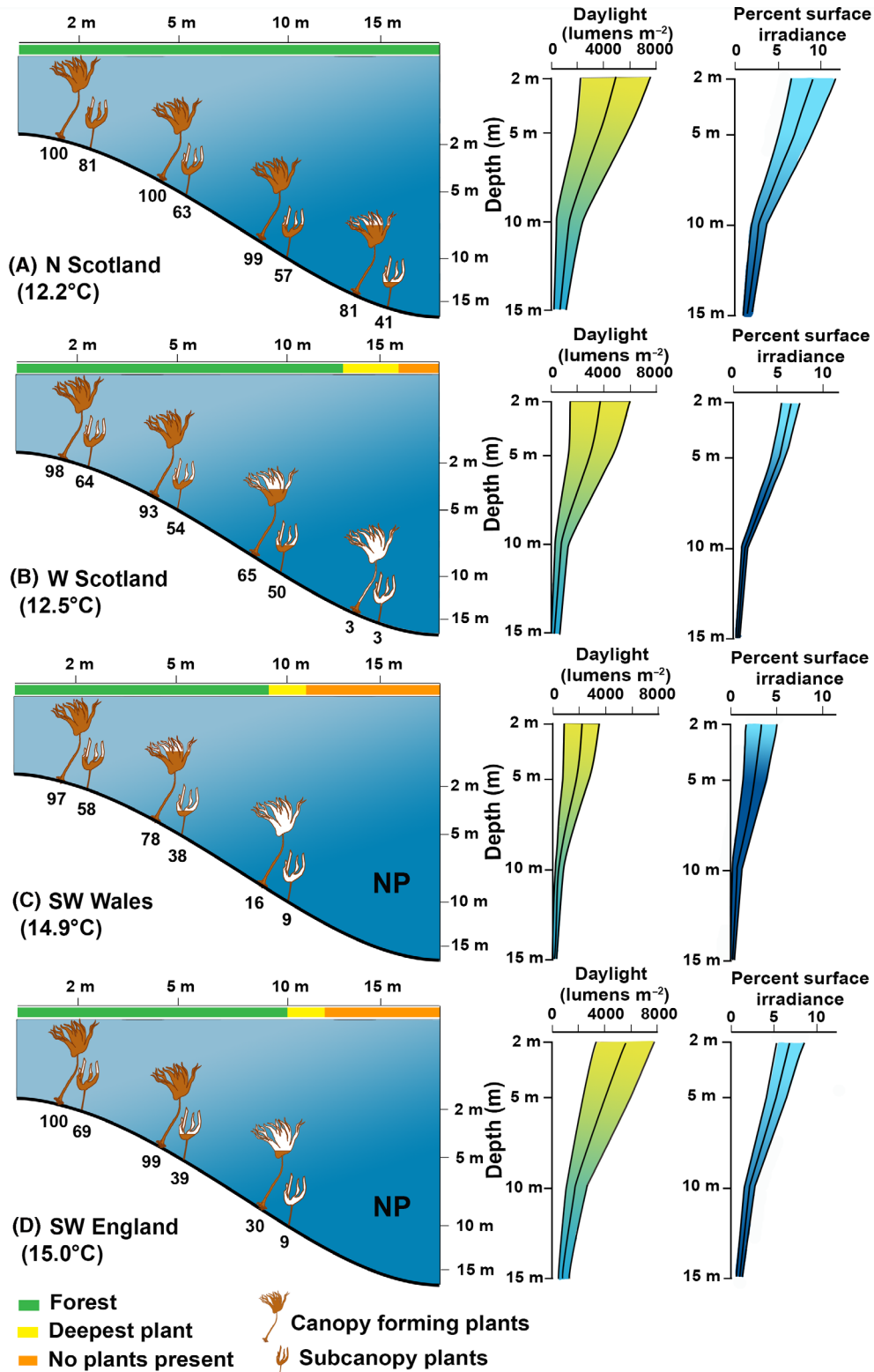


Fig. 3. Schematic of vertical distribution of kelp populations in each region (left). The brown-colored fill of each plant (canopy-forming or subcanopy), and the numerical value below each plant, both indicate the percent cover of plants recorded at that depth. The colored line at the top of each plot represents the presence of kelp forest (plants < 1 m apart) and extent of individual plants. Change in light intensity (middle) and surface irradiance penetration with depth (right) are also presented for each region (mean ± SD). Temperatures below each location name represent average sea temperature over the study period. NP, no plants present.

Table 3. Results of ANOVAs to test for differences in environmental variables, and kelp individuals, and populations, between regions and depths.

Response variable	Region			Depth			Region × depth			Res df
	df	F	p	df	F	p	df	F	p	
Environmental variables										
Light intensity (lumens m ⁻²)	3	42.67	0.001	3	136.64	0.001	9	0.59	0.807	208
Seawater temperature	3	483.56	0.001	2	0.53	0.588	6	0.45	0.843	979
Kelp variables										
Per m ²										
Canopy density	3	74.03	0.001	3	390.17	0.001	9	21.75	0.001	232
Total density	3	97.74	0.001	3	527.05	0.001	9	25.08	0.001	239
Canopy biomass	3	24.03	0.001	3	37.87	0.001	9	3.68	0.003	240
Per individual canopy-forming plant										
Total length	3	613.84	0.001	3	576.50	0.001	9	58.42	0.001	239
Blade length	3	143.51	0.001	3	461.96	0.001	9	52.01	0.001	239
Blade width	3	498.71	0.001	3	229.32	0.001	9	331.18	0.001	232
Total fresh weight	3	559.53	0.001	3	663.07	0.001	9	39.74	0.001	240
Blade fresh weight	3	136.49	0.001	3	347.79	0.001	9	9.99	0.001	238
Age	3	187.55	0.001	3	108.00	0.001	9	14.48	0.001	240

regions. Blade fresh weight was at least 70% greater in northern regions than in southern regions. Blade width was at least 50% greater, and total plant length and age were both more than 37% higher in northern regions compared to those in southern regions. Typically, the magnitude of differences between measurements recorded in northern vs. southern regions increased with increasing depth, thus suggesting an interplay between temperature and light attenuation. Post hoc analyses indicated that overall, the two northernmost regions were most similar in kelp population structure (Supplementary Fig. S3).

Linking the environment with kelp-forest structure

Across the eight sites, we observed significant relationships between light availability (proportion of surface irradiance reaching 15 m) and the maximum depth penetration of both the kelp forest ($R^2 = 0.61$, $p < 0.05$) and individual plants ($R^2 = 0.54$, $p < 0.05$). However, the relationships between these variables were stronger when the colder northern sites (regions A and B) when examined separately from the warmer southern sites (regions C and D). To explore this further, for each kelp forest response variable, two separate logarithmic regression analyses were carried out to examine links between the proportion of surface irradiance penetrating to each depth and the response variable. Logarithmic functions were used as these provided the best fit for the data. The similarity in seawater temperatures observed in the two northernmost regions and in the two southernmost regions enabled the data to be

combined from regions A and B (low temperature), and regions C and D (high temperature), for these analyses. There was a significant relationship between almost all response variables and the proportion of surface irradiance penetrating to each depth, which shifted with seawater temperature (Fig. 6; Supplementary Table S4). Measurements were generally greater under higher light and lower temperature conditions, with the exception of plant density, which increased with both increasing light and temperature. The strength of the relationship varied between response variables; the strongest relationships observed were for canopy density (Adj. $R^2 = 0.765$ for northern regions, Adj. $R^2 = 0.723$ for southern regions) and blade biomass (Adj. $R^2 = 0.864$ for northern regions, Adj. $R^2 = 0.667$ for southern regions). Significant relationships were observed between irradiance and total density, canopy density, canopy standing biomass, total fresh weight, blade fresh weight, and blade length in both northern and southern regions, and for total length, blade width, and age in southern regions.

Discussion

We recorded consistent and marked shifts in the structure of *L. hyperborea* populations along depth gradients across the study regions. At all our study sites, total plant density, canopy plant density, canopy standing biomass, total plant biomass, and blade biomass decreased with depth, in alignment with decreasing light availability. However, relationships

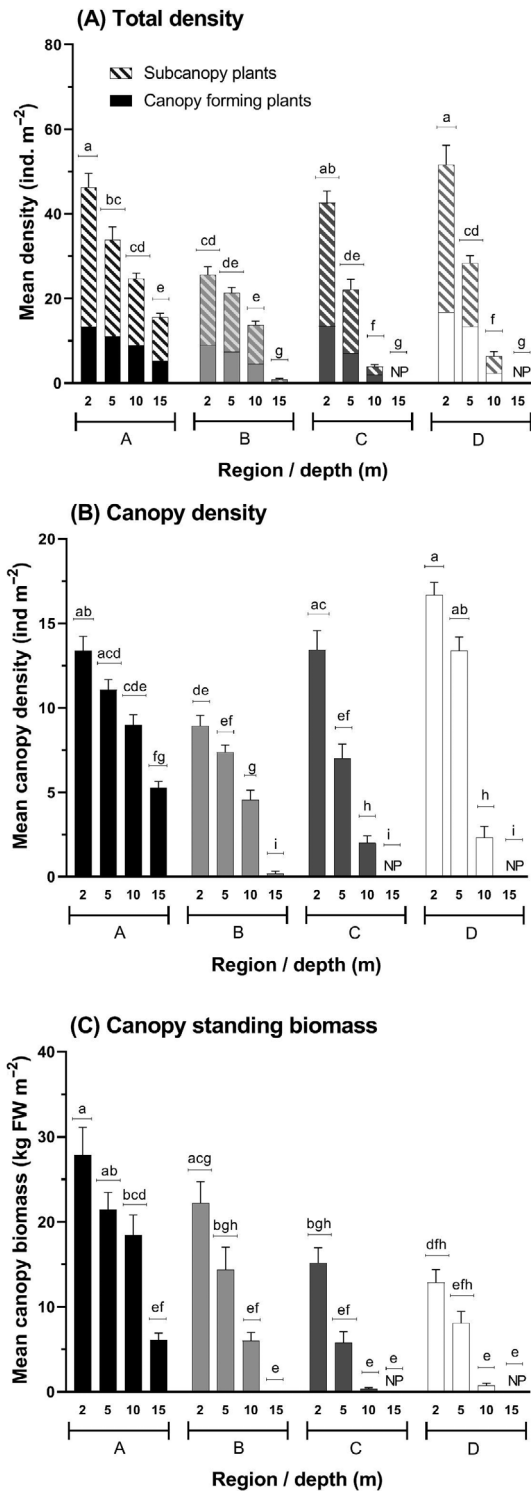


Fig. 4. Density and standing biomass of *L. hyperborea* populations at each depth increment in each region (values are means \pm SE, $n = 16$ for all variables). **(A)** Total plant density. **(B)** Density of canopy formers only. **(C)** Standing biomass of kelp canopy (n.b. mean canopy biomass at 15 m at each site in region B was 0.03 and 0.02 kg FW m⁻² and, consequently, values are not visible on plot). NP, not present. Depths are below chart datum. Lower case letters relate to post hoc analyses (Tukey tests); bars that share the same letter are not significantly different to each other.

between light availability and metrics of population structure were not consistent across all four regions. Rather, they varied to some extent between the two northern and the two southern regions, which differ in their thermal regimes with the northern regions being significantly cooler than the southern regions. When regions were pooled by thermal regime (cool A + B; warm C + D) strong negative relationships of differing strengths between kelp forest response variables and the proportion of surface irradiance reaching each depth were also identified. Together, this indicates that the influence of light availability on kelp population structure is not entirely consistent across latitude, suggesting that differences in temperature or some other factor(s) are also important in driving depth-related patterns.

It is likely that differences in temperature mediated stress and energy budgets can account for the majority of the differences in depth relationships between regions, which vary by $\sim 2.5^{\circ}\text{C}$ between the northern and southern areas. Other key variables such as wave exposure, nutrient availability, and grazing pressure are similar across the latitudinal gradient examined in this study and, although they may contribute to some differences, they are less influential drivers of ecological structure (Smale et al. 2016, 2020; Smale and Moore 2017; Pessarrodona et al. 2018). Differences in temperature scaling between photosynthesis and respiration mean that more energy is required for maintenance in our southern, warmer populations. Gametophyte stages are particularly sensitive to temperature and light interactions with light requirements for successful gametogenesis increasing exponentially with temperature (Luning 1980). Maximum temperatures recorded in our southern regions are also known to be stressful for *L. hyperborea* sporophytes and gametophytes (Bolton and Luning 1982; Müller et al. 2009 and references therein). Therefore, conditions in our southern regions are more energetically costly, and the resulting energy budget may decrease performance and persistence at lower depths. Indeed, regions A (cool) and D (warm) had similar light and energy profiles yet depth penetration was considerably greater in the cooler region. It should also be noted that summer day length also covaries with latitude, with our northern regions experiencing ~ 2 h additional daylight during the summer months (Smale et al. 2016). The importance of day lengths on growth rates relates to the increased capacity to store carbohydrates in advance of the following year's growth period (Luning 1971; Rinde and Sjøtun 2005). Indeed, Drew (1983) argued that day length and temperature may be more important than actual irradiance levels in determining photosynthetic rates of several kelp species. Further work should characterize the annual light budget at different latitudes, which may be particularly important for long-lived perennial species such as *L. hyperborea*. Clearly, additional research to disentangle the effects of photoperiod, irradiance, and temperature on growth and productivity is warranted.

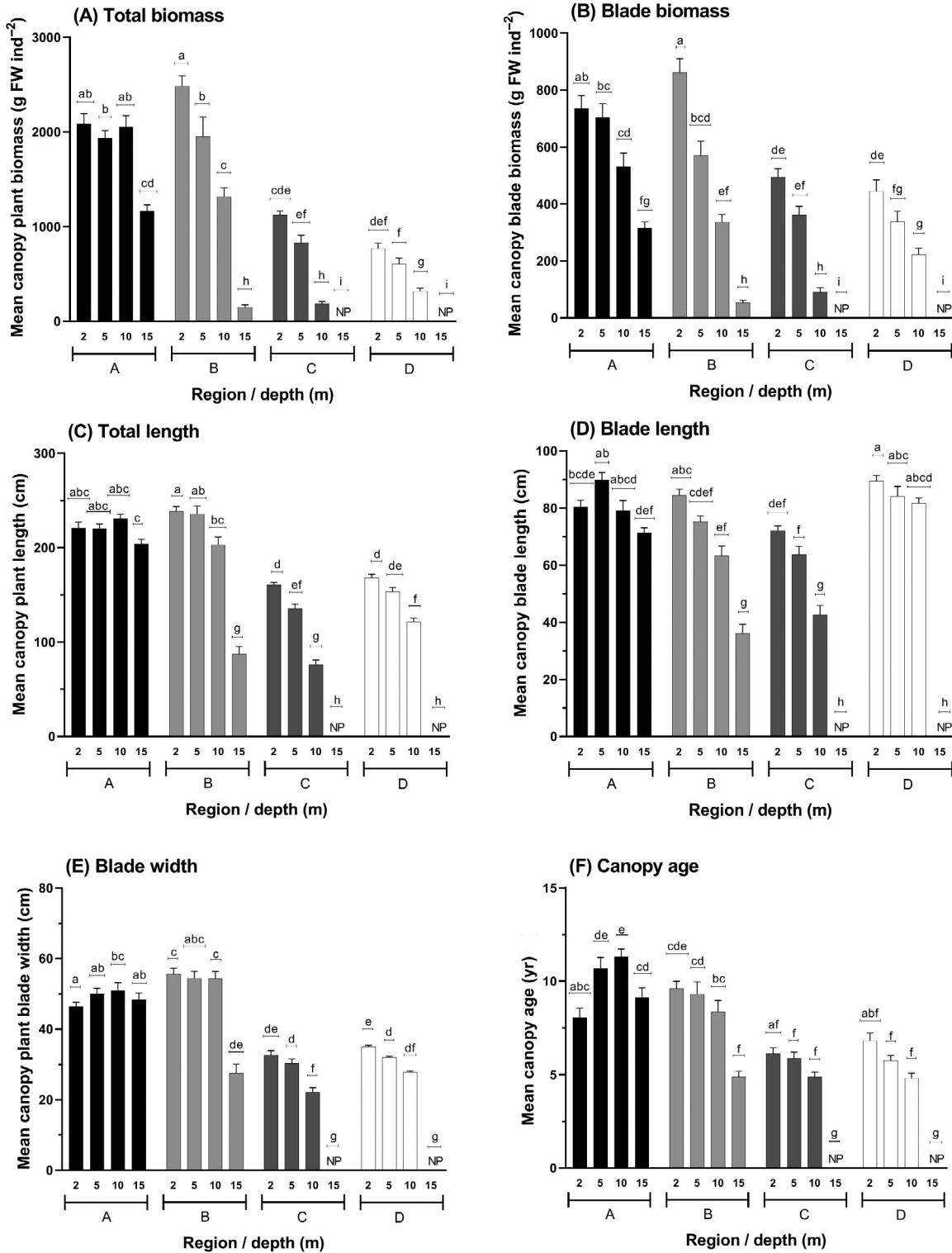


Fig. 5. Differences in response variables (A-F) for *L. hyperborea* populations in each region. Bars represent mean values \pm SE. $n = 16$ for all variables. NP, no plants present. Depths are below chart datum. Letters above bars represent results of post hoc analyses (Tukey). Bars that share the same letter are not significantly different to each other.

Clearly, light is a limiting resource for subtidal kelp populations and, as such, both plant-level (e.g., plant biomass, size) and population-level (standing biomass, percent cover)

metrics change markedly with depth. While we recognize that a range of other factors can also influence kelp population structure and plant morphology, our sites were carefully selected to

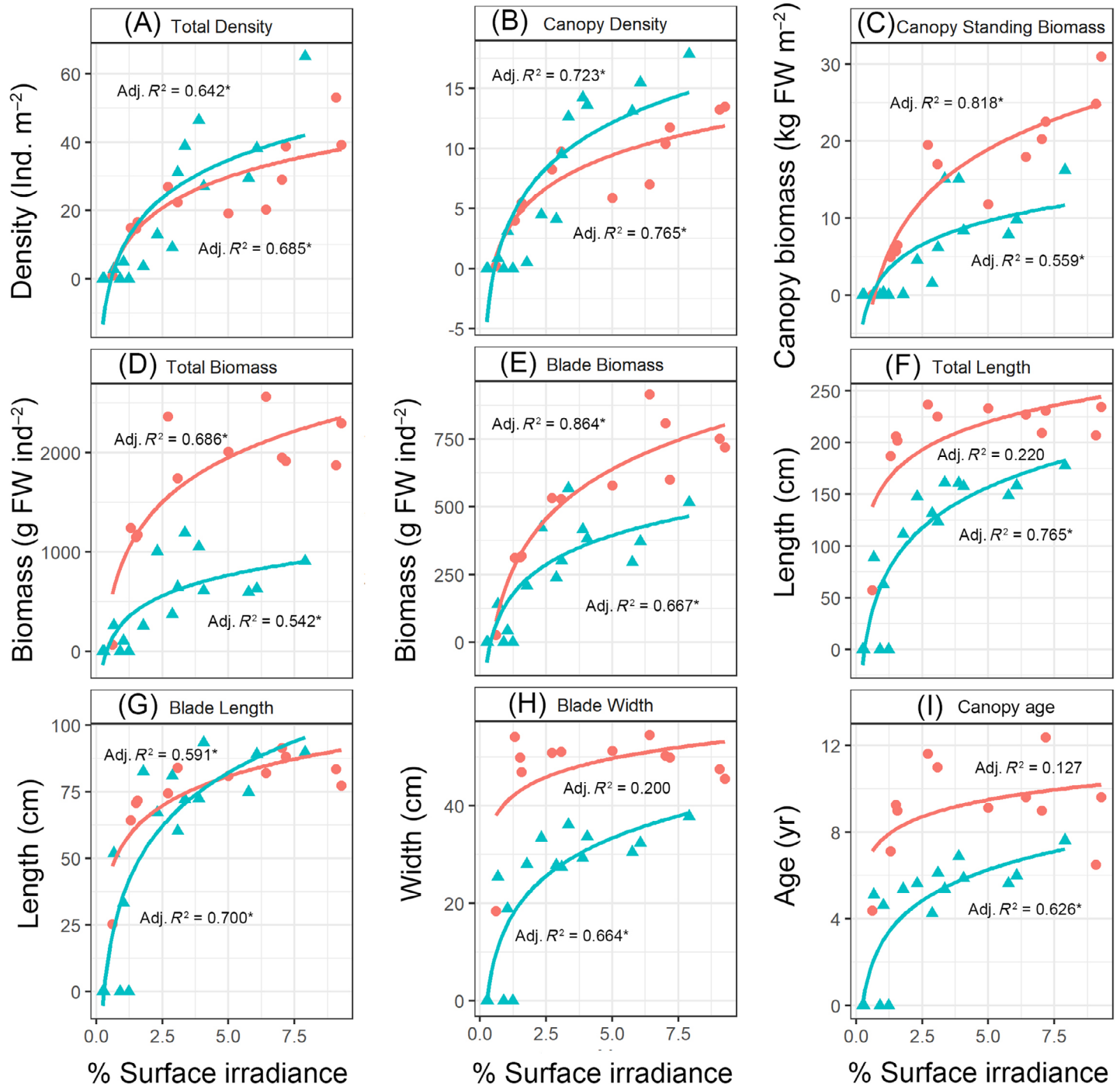


Fig. 6. Shifts in kelp-forest response variables (A-I) with percent surface irradiance in cooler northern regions (A and B; closed circles) and warmer southern regions (C and D; open circles). Logarithmic regression analyses were used to explore all relationships. Asterisks after the R^2 value represent significant relationships following Bonferroni corrections.

ensure similar wave exposure conditions and substratum type, while other key variables such as nutrient availability and grazing pressure do not vary markedly across the study regions (Smale et al. 2016, 2020; Smale and Moore 2017; Pessarrodona et al. 2018). As such, the variability patterns described here are

likely to be primarily driven by light and temperature. The range of maximum depth penetration recorded in this study (11–24 m) aligns with previous observations of kelp depth limits, although maximum depth limits can occasionally exceed 40 m at comparable latitudes (see fig. 2 in Krause-Jensen et al. 2019).

Patterns of decreased productivity with decreased irradiance are unsurprising given the inherent need of macroalgae for light to photosynthesis. For *L. hyperborea*, higher light availability has been linked with larger size and faster growth (Sjötun et al. 1998; Smale et al. 2020). Even across small spatial scales, light attenuation has been identified as an important predictor of kelp occurrence and cover (Gorman et al. 2013). In Loch Linnhe, close to our survey sites in west Scotland (i.e., region B), the maximum depth penetration of *L. hyperborea* forests and individual canopy-forming plants is 6.5 and 10.7 m, respectively (Tsiamis et al. 2020), compared to 13 and 16 m recorded in this study. Sedimentation rates are relatively high within the Loch Linnhe system (Overnell and Young 1995) and the resultant increased light attenuation is likely to cause comparatively low productivity and depth penetration. Direct relationships between water clarity and macroalgal vertical distribution have also been shown for newly ice-free areas of the South Shetland Islands (Deregibus et al. 2016) and in inshore habitats in New Zealand where coastal land use influences water clarity (Desmond et al. 2015). The notably deep penetration of kelp forests and plants in both low and high latitude areas (> 60 m) has also been attributed to the particularly high clarity of water in these environments (Graham et al. 2007; Krause-Jensen et al. 2019). Temporal changes in light availability also directly affect kelp population structure; for example, in Helgoland, a ~30% increase in vertical distribution limits of *Laminaria* forests was observed between 1970 and 2005, thought to be a direct response to increased water quality (Pehlke and Bartsch 2008). It should be noted that, due to logistical constraints, we did not measure other physical parameters that can vary with depth in shallow subtidal systems. Most notably, sedimentation rates and turbulence have been shown, along with light availability, to influence the structure of rhodolith assemblages in subtidal habitats at Gran Canaria Island (Otero-Ferrer et al. 2020). Our sites were highly exposed to wave action and generally steeply sloping and we observed little evidence of sediment deposition on the reef. However, relatively higher turbulence at shallower depths could influence kelp populations by increasing plant motion, leading to enhanced nutrient transfer and increased light availability via reduced intraspecific competition (Pedersen et al. 2012). This could promote biomass accumulation relative to deeper plants with less motion, although a previous study found limited effects of moderate changes in water motion on growth rates of this species (Kregting et al. 2013).

Ecological interactions could, in addition to the physical factors of temperature and light, also influence depth-related shifts in population structure and maximum depth penetration. Specifically, grazing by the omnivorous sea urchin *Echinus esculentus* has been implicated in controlling maximum depth penetration of *Laminaria* populations in the Isle of Man, UK, although other factors were also important (Jones and Kain 1967), while a further study in west Scotland

recorded highest urchin densities at 15 m depth but little evidence of grazing control over kelp populations (Comely and Ansell 1988). Here, urchin densities were generally low, even at our deeper stations, and did not vary between regions or depths. It may be that urchin grazing is more important in more wave-sheltered locations, where densities tend to be greater (Sivertsen 1997; Rinde et al. 2014) but, even so, urchin grazing is not considered a major structuring process within this system (Smale et al. 2013). However, at lower latitudes, for the same or similar kelps, herbivory by fishes and sea urchins is a key process influencing kelp populations (Franco et al. 2015). Perhaps more importantly, in our warmer southern regions, kelp stands are more mixed with *Saccorhiza polyschides* and *Laminaria ochroleuca* forming mixed stands with the dominant *L. hyperborea* (Smale and Moore 2017). In southwest England (region D), occasional *S. polyschides* and *L. ochroleuca* plants were observed in slightly deeper waters than *L. hyperborea* and, although densities were low, some inter-specific competition between either the microscopic gametophyte or the macroscopic sporophyte stages may influence maximum depth penetration. Moreover, the relatively short period (~4 months) over which our study was conducted did not allow temporal variability in kelp population structure to be examined at these sites. While these kelp forests are thought to be relatively stable across seasons and years (Pedersen et al. 2012), it is possible that historical disturbances (e.g., from intense freshening or storm events) could have influenced depth-related patterns and recovery is ongoing. That said, during >5 years of regular observations in these regions there has been no evidence of atypical “resetting” events (authors pers. obs.).

Our study formally examined the relationship between PAR and light intensity at our survey sites. In situ irradiance measurements obtained from wave-exposed shallow-water coastal habitats are comparatively rare and can be used to develop and validate remote sensing products and assess different monitoring approaches. Across our study, we found a very strong relationship between PAR and light intensity, suggesting that light sensors (which are generally more affordable and easier to deploy and maintain than PAR sensors) can be used to collect in situ data on the light environment in an ecologically meaningful way when studying benthic primary producers in this region. Strong relationships between PAR and light intensity have previously been observed in other regions and habitats, such as seagrass meadows in the U.S. (Long et al. 2012) and subtidal reefs in New Zealand (Desmond et al. 2015), and have now been demonstrated for rocky reefs around the U.K.

More generally, our study has shown that light availability and sea temperature are critical factors influencing the structure of kelp populations in the U.K. Given that the habitats these kelp species underpin have considerable socioeconomic importance, for targeted finfish and crustaceans (Bertocci et al. 2015), inshore food webs (Bué et al. 2020), and carbon

cycling (Pessarrodona et al. 2018), improved understanding of the effects of environmental change is vital for their conservation and management. Any reductions in coastal water quality leading to increased turbidity and light attenuation will likely lead to declines in depth penetration, plant size and standing biomass, while also facilitating the spread and competitiveness of non-native kelps (Epstein et al. 2019a,b). Trends in water quality in coastal habitats in the U.K. are highly variable among systems, catchments, and regions, being influenced by a number of policy drivers operating across the land–sea interface (Maier et al. 2009). Even so, any changes in light attenuation related to coastal development or agricultural practices, for example, will negatively impact kelp forests at local to regional scales, as has been observed for canopy-forming macroalgae elsewhere (Connell et al. 2008; Scherner et al. 2013). Similarly, the geographical distributions of macroalgal species are strongly constrained by temperature (Müller et al. 2009) and recent warming trends have impacted kelp forests across many regions (Smale 2020). For example, increased sea temperatures in southwest U.K. have been linked with shifts in species' distributions, reductions in local diversity, and changes in rates and timings of primary production (Teagle and Smale 2018; Pessarrodona et al. 2019; Moore and Smale 2020). Moreover, population losses and range contractions at the equatorward distribution limit of *L. hyperborea* and predicted to occur throughout coming decades in response to predicted warming (Assis et al. 2018). Our study shows that the interactive effects of warming and decreased light availability would lead to less productive and extensive kelp forests in the U.K., with implications for ecological functioning and the provision of ecosystem services.

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Conflict of Interest

None declared.

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