

RESEARCH ARTICLE

Marine heatwaves and decreased light availability interact to erode the ecophysiological performance of habitat-forming kelp species

 Alissa V. Bass  | Kathryn E. Smith  | Dan A. Smale 

Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth, UK

Correspondence

Dan A. Smale, Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth, England, UK.
Email: dansma@mba.ac.uk

Present address

Alissa V. Bass, Simon F.S. Li Marine Science Laboratory, The Chinese University of Hong Kong, Sha Tin, New Territories, Hong Kong, China

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Abstract

Coastal marine ecosystems are threatened by a range of anthropogenic stressors, operating at global, local, and temporal scales. We investigated the impact of marine heatwaves (MHWs) combined with decreased light availability over two seasons on the ecophysiological responses of three kelp species (*Laminaria digitata*, *L. hyperborea*, and *L. ochroleuca*). These species function as important habitat-forming foundation organisms in the northeast Atlantic and have distinct but overlapping latitudinal distributions and thermal niches. Under low-light conditions, summertime MHWs induced significant declines in biomass, blade surface area, and F_v/F_m values (a measure of photosynthetic efficiency) in the cool-water kelps *L. digitata* and *L. hyperborea*, albeit to varying degrees. Under high-light conditions, all species were largely resistant to simulated MHW activity. In springtime, MHWs had minimal impacts and in some cases promoted kelp performance, while reduced light availability resulted in lower growth rates. While some species were negatively affected by summer MHWs under low-light conditions (particularly *L. digitata*), they were generally resilient to MHWs under high-light conditions. As such, maintaining good environmental quality and water clarity may increase resilience of populations to summertime MHWs. Our study informs predictions of how habitat-forming foundation kelp species will be affected by interacting, concurrent stressors, typical of compound events that are intensifying under anthropogenic climate change.

KEYWORDS

ecophysiology, kelp, *Laminaria*, light limitation, marine heatwaves, season

INTRODUCTION

Anthropogenic climate change is altering the structure and functioning of ecosystems globally (Hoegh-Guldberg & Bruno, 2010; Walther et al., 2002). In the marine realm, shifts in species' ranges in response to recent ocean warming have been widely reported

(Lenoir et al., 2020; Poloczanska et al., 2013), often leading to novel communities shaped by distinct ecological interactions (Lurgi et al., 2012; Vergés et al., 2014). Predicting biological responses to future climatic changes remains challenging, particularly as the experimental evidence base is lacking for many taxa (Bass et al., 2021; Wernberg et al., 2012).

Abbreviations: MHW, marine heatwaves; PAR, photosynthetically active radiation.

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Responses may vary between populations and species (Gilman et al., 2006; Kelly et al., 2012; King et al., 2018), and climatic changes are often compounded by other stressors (Halpern et al., 2015). When occurring simultaneously, stressors in the marine environment, such as increased temperature and decreased light and oxygen availability, may cause additive, synergistic, or antagonistic responses in marine organisms (Crain et al., 2008). Moreover, biological responses may differ seasonally depending on phenology, ambient conditions, and the number and intensity of concurrent stressors (Henson et al., 2017; Wahl et al., 2020).

In addition to the gradual warming trends observed across most of the global coastal ocean (Johnson & Lyman, 2020; Lima & Wetthey, 2012), marine ecosystems are also subjected to increasing occurrences of extreme climatic events, such as marine heatwaves (MHWs or discrete periods of anomalously warm water; see Hobday et al., 2016) and tropical storms (Coumou & Rahmstorf, 2012; Oliver et al., 2018). MHWs in particular are emerging as pervasive stressors for entire marine ecosystems (Smale et al., 2019; Smith et al., 2021, 2023; Wernberg et al., 2016) and are predicted to intensify in coming decades as a consequence of anthropogenic climate change (Frölicher et al., 2018; Oliver et al., 2019). As the frequency of extreme climatic events increases, the likelihood of marine ecosystems experiencing multiple climatic and/or nonclimatic events concurrently (compound events) also rises, with the potential to exacerbate biological impacts. For example, stressors such as decreased water clarity (Tait et al., 2021), harmful algal blooms (Trainer et al., 2020), or deoxygenation events (Espinoza-Morriberón et al., 2019; Tassone et al., 2022) commonly occur simultaneously with MHWs. Moreover, many regions that experience multiple nonclimate stressors are also areas of MHW intensification (Smale et al., 2019). While research on biological impacts of MHWs has risen dramatically in recent decades, relatively few studies have examined the combined effects of multiple stressors on multiple species (reviewed by Bass et al., 2021).

Kelp species are distributed along approximately one-quarter of the world's coastlines (Jayatilake & Costello, 2020), where they function as foundation organisms by providing food and shelter for a wide range of associated organisms, contributing significantly to coastal primary productivity and underpinning a number of ecosystem services (Duarte et al., 2022; Pessarrodona et al., 2018; Smale et al., 2013; Steneck et al., 2002). Two environmental variables that are key in determining the distribution and performance of kelp and other marine macrophytes are temperature and light availability (Bearham et al., 2013; Lüning, 1980). The distribution of kelp species is strongly constrained by temperature, and recent warming trends and discrete MHWs have driven large-scale loss of kelp forest habitat in several regions (Arafeh-Dalmau et al., 2019;

Smale, 2020; Thomsen et al., 2019; Wernberg et al., 2016). Moreover, light availability, which is directly related to water clarity and quality, strongly influences kelp distribution and abundance (Desmond et al., 2015; Smith et al., 2022), and reduced light availability due to the increased turbidity of coastal waters can decrease kelp distribution, abundance, and productivity (Blain et al., 2021; Mabin et al., 2019; Tait et al., 2021). The interaction between temperature and light availability may become increasingly important as oceans warm and MHWs intensify while, simultaneously, decreased water quality and clarity has already led to “coastal darkening” in many regions (Blain et al., 2021; Capuzzo et al., 2015; Frigstad et al., 2013; Mangan et al., 2020). Despite this, very few studies so far have examined the combined effects of extreme warming events and reduced light availability on the performance of multiple macrophyte species experimentally (but see Kim et al., 2020 and Sánchez-Barredo et al., 2020 for single species studies).

In this study, we examined the individual and interactive effects of MHWs and reduced light availability across two seasons on the ecophysiological performance of three kelp species widely distributed across the northeast Atlantic (*Laminaria digitata*, *L. hyperborea*, and *L. ochroleuca*). These species have overlapping distributions in the southwest UK and coexist under some conditions, yet they have clear and distinct thermal niches and environmental requirements. The overall aim of the study was to examine the influence of temperature and light availability on the ecophysiological performance of these species to better understand likely responses to MHW intensification and reduced light availability. We conducted a realistic, ecologically relevant manipulation and monitored a range of critical response variables across two seasons to address this aim.

METHODS

Environmental context

Satellite-derived Sea Surface Temperature data (OISST v.2) were downloaded from the ERDDAP data server (<https://coastwatch.pfeg.noaa.gov/erddap/>). Pixels between the latitudinal and longitudinal boundaries of the Southwest UK (49° N to 51°3' N and 3°2' W to 6° W, respectively) were averaged per time point between 1982 and the end of September 2020 (just before the first experiment). Using the “heatwaveR” package in R, we identified 88 MHW events that occurred between 1982 and 2020, with 34 summer MHWs (July to September) and 17 in spring (March to May; Figure S1A in the Supporting Information). MHWs were either categorized as moderate or strong using the MHW categorization criterion of Hobday et al. (2018). The duration

of these MHW events spanned from 5 d (minimum duration as categorized by Hobday et al., 2016) to 78 d (Figure S1B), with an average of 13 d. Mean MHW intensity over the whole period was 1.6°C, and the highest maximum intensity for a MHW was 3.6°C (Figure S1B). Therefore, our experiment consisted of a control temperature (nonheatwave scenario), a current MHW scenario (moderate/strong), and a future MHW scenario (extreme).

Study species

The kelp congeneric species *Laminaria digitata*, *L. hyperborea*, and *L. ochroleuca* were the focus of the study. *L. digitata* and *L. hyperborea* are both cold-temperate species with similar latitudinal distributions, extending from northern Norway and Iceland southward to France and northern Portugal, respectively (Kain, 1979; Smale et al., 2013). *L. digitata* tends to dominate the low intertidal and shallow subtidal zones of wave-exposed rocky shores, whereas *L. hyperborea* dominates subtidally (Hereward et al., 2018; Smale & Moore, 2017). Conversely, *L. ochroleuca* is a warm-temperate species distributed from the southwest of England and Ireland southward to Morocco and the Mediterranean (Pessarrodona et al., 2019; Schoenrock et al., 2019). *L. ochroleuca* is found both subtidally and in the extreme low intertidal areas, and despite being first recorded in the United Kingdom in the late 1940s (Parke, 1948), it is now widespread and can be locally dominant in this region (Teagle & Smale, 2018). All three species persist in the southwest UK and can coexist along moderately wave-exposed coastlines. Crucially, these species are responding to recent warming trends, declining in abundance and extent at their southern trailing range edges, while some are proliferating at their northern leading range edges (Casado-Amezúa et al., 2019; Raybaud et al., 2013; Smale et al., 2015). *L. ochroleuca*, in particular, has extended its range edge northward and is predicted to continue to do so throughout the coming decades (Assis et al., 2018; Pessarrodona et al., 2019; Teagle & Smale, 2018).

Collection and experimental set-up

Thirty juvenile sporophytes of approximately the same size (~10 cm stipe length; hereafter “plants”) of each of *Laminaria digitata*, *L. hyperborea*, and *L. ochroleuca* were collected at extreme low tide from the rocky shores off Cawsand Bay, southwest UK (N50°19'26.1" N, W004°11'17.1"; Figure S2A in the Supporting Information). Kelp plants were brought back to the laboratory where three individuals (one of each species) were placed immediately into one of 30 separate 37-L

aerated experimental tanks (Figure S2B). Plants were attached by the holdfast to ceramic tiles, using cable ties to maintain an upright orientation. The tanks were large enough to ensure that there was no shading of the kelps by each other and that all had similar amounts of light.

We conducted a fully crossed factorial experiment with three temperature treatments and two light levels resulting in six experimental treatments, with five replicate tanks per treatment. Temperature treatments were comparable to mean sea temperature for the collection month (18°C and 10°C in October and March, respectively), +2°C (approximate mean MHW intensity), and +4°C (maximum MHW intensity). Water temperature was controlled by aquarium bar heaters (300W 3619, EHEIM) and refrigerated chillers (DC750, D-D The Aquarium Solution) connected to temperature controllers (Inkbird ITC-308) that maintained treatment levels of $\pm 0.3^\circ\text{C}$. Bar heaters and the chiller outlets were placed into three 64-L tanks (one for each temperature treatment), and the water from each of the sumps provided water to the five replicate tanks. Five rows of full spectrum waterproof LED strip lights mounted onto polystyrene sheets (for low light) or fascia board (for high light) were fixed above the rows of tanks and set on a 12:12 light:dark cycle. Nonlimiting (high) light treatment was provided by waterproof 24 V LED strips (5700–6500 k Studioflex, LED technologies) connected to a 150 W LED driver (LED technologies) at a PAR of approximately $100 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$, whereas 12 V LEDs (6000 k Daylight white, Le Innovation) and plastic black mesh fitted over the tanks were used to create the light-limited (low) treatment at one-tenth the intensity of the high-light treatment, with an overall PAR of $\sim 10 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Light saturation for photosynthesis in mature *Laminaria* plants is around $10\text{--}150 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Egan et al., 1989; Lüning, 1979); however, gametophytes and young plants have much lower light requirements due to photoacclimation to lower light levels beneath canopies and, therefore, can grow at light levels of just $1 \mu\text{mol photon} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Han & Kain, 1996). As such, the treatments selected here were intended to represent light-limited and light-saturated conditions as opposed to stressful light conditions that can cause photoinhibition. Light conditions were also comparable to those recorded in kelp-dominated shallow subtidal habitats in the study region (Smith et al., 2022).

Temperature and light sensors (Hobo pendant logger, Onset) were placed in each tank and programmed to take recordings every 30 min, while spot measurements of light intensity were taken toward the top of the tank where unshaded kelp lamina were situated, using a calibrated multiple parameter meter (Seneye Reef, Seneye). At the start of each experiment, kelp plants were held at the lower temperature (i.e., ambient control) for 2 days while processing to acclimate

to laboratory conditions before increasing experimental temperatures by 1°C per day to mimic the onset of a MHW.

The experiment was run twice, in early spring (March 2021) and late summer (September 2020), to determine whether the influence of temperature and light was consistent across seasons, particularly given seasonality in kelp species growth rates (Kain, 1989; Lüning, 1979). Each experiment ran for 4 weeks postacclimation (5 weeks in total) to simulate a prolonged warming event. Spring temperatures were on average $9.8^{\circ}\text{C} \pm 0.4^{\circ}\text{C}$, $11.8^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$ and $14.2^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$ after acclimation while average light intensity was 2460 ± 266 lux and 286.5 ± 65 lux for the high and low treatments, respectively (Figures S3 and S4 in the Supporting Information). During the summer experiment, average temperatures were $18.1^{\circ}\text{C} \pm 0.1^{\circ}\text{C}$, $20.0^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$, and $22.5^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$ for the three treatments after acclimation while average light intensity was 2517 ± 260 lux and 263 ± 63 lux for the high- and low-light treatments, respectively (Figures S3 and S4). By converting these lux measurements to PAR using established relationships (e.g., Long et al., 2012), approximate average PAR values were $\sim 75 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for the high light and $\sim 8 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for the low-light treatments. Tank cleans and water changes took place every other day to replete nutrient levels and maintain salinity, which was measured using a temperature and salinity meter (YSI EcoSense EC 300A, Xylem Analytics). Approximately one-third of the water within the experimental system was replaced with seawater pumped from an intake in the adjacent waters of Plymouth Sound, which is then held within a large below-ground reservoir. Salinity and nutrient levels in this wider system remained relatively constant throughout the year (salinity: ~ 35 , nitrate: $\sim 20 \mu\text{M} \cdot \text{L}^{-1}$, phosphate: $\sim 5 \mu\text{M} \cdot \text{L}^{-1}$) and did not become limiting and/or stressful.

Response variables

On the day of collection and once a week during the experiment, plants were removed from the tanks and blotted with tissue paper before being weighed. The weight of the tile was subtracted after weighing the whole plants (i.e., blade and stipe/holdfast) with the tiles attached. At the beginning of the experiment, any blades over 20 cm in length from the meristem were clipped back in order to prevent shading of other kelps in the same tank. Plants were then photographed against a white background with a scale bar (Figure S2C). The surface area of the blade was later calculated from images using ImageJ (FIJI package extension, Schindelin et al., 2012). In addition, dark-adapted maximum quantum yield (F_v/F_m) values were taken using a continuous excitation chlorophyll fluorimeter (Pocket

PEA, Hansatech Instruments Ltd) at an illumination of $2500 \mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ with 1-s pulses to assess health and photosynthetic performance. F_v/F_m values relate to the photosynthetic efficiency of photosystem II in a dark-adapted state, with healthy unstressed tissue yielding values >0.70 and lower ratios indicating lower efficiency and higher physiological stress (Butler & Kitajima, 1975; Kitajima & Butler, 1975). Two measurements of F_v/F_m were taken for each plant following dark adaptation using dark adaptation leafclips for 20 min, with values then averaged for analysis. Any bleaching, tissue necrosis, or mortality (i.e., loss of all photosynthetic components: blades and meristem) of plants was also recorded. The change in fresh weight biomass, surface area, and F_v/F_m between week 1 (postacclimation to experimental temperatures) and week 4 (end of experimental period) was calculated for each plant. Prior to analysis, changes in biomass and surface area were standardized by calculating percentage change for each individual.

Statistical approach

Differences in percentage change in biomass, surface area, and F_v/F_m between treatments, were statistically analyzed in R statistical software (R Core Team, 2021) using the package “car.” Before analyses, we performed a Levene's test to check for homogeneity of variance, and residuals were inspected and were log-transformed if required to ensure normality. Only changes in biomass for *Laminaria ochroleuca* did not require transformation. When the data met these assumptions, we then performed 2-way ANOVAs with fixed factors “light” and “temperature” for each species and experiment/season separately and for each response variable. Post hoc Tukey tests were carried out on main effects or interaction where significant ($p < 0.05$) to determine which treatment levels differed from one another. Where data did not meet the assumptions of ANOVA even after transformation (changes in biomass and surface area in the summer experiment, changes in F_v/F_m in both seasons) a more conservative p -value (< 0.01) was adopted for significance. Mean values of response variables are presented \pm standard error (SE).

RESULTS

Spring experiment

Under high-light conditions, all three species exhibited significant increases in biomass in spring, regardless of the warming treatment, with average gains of $50.5\% \pm 2.8\%$, $58.0\% \pm 4.5\%$, and $39.7\% \pm 2.7\%$ for *Laminaria digitata*, *L. hyperborea*, and *L. ochroleuca*, respectively across all temperature treatments

(Figure 1). Under low-light conditions, all three species again increased in mean percentage biomass, but to a lesser degree, with average increases of $10.3\% \pm 1.0\%$,

$15.2\% \pm 0.9\%$, and $1.3\% \pm 2.0\%$ for *L. digitata*, *L. hyperborea*, and *L. ochroleuca*, respectively, across all temperature treatments (Figure 1). ANOVA detected

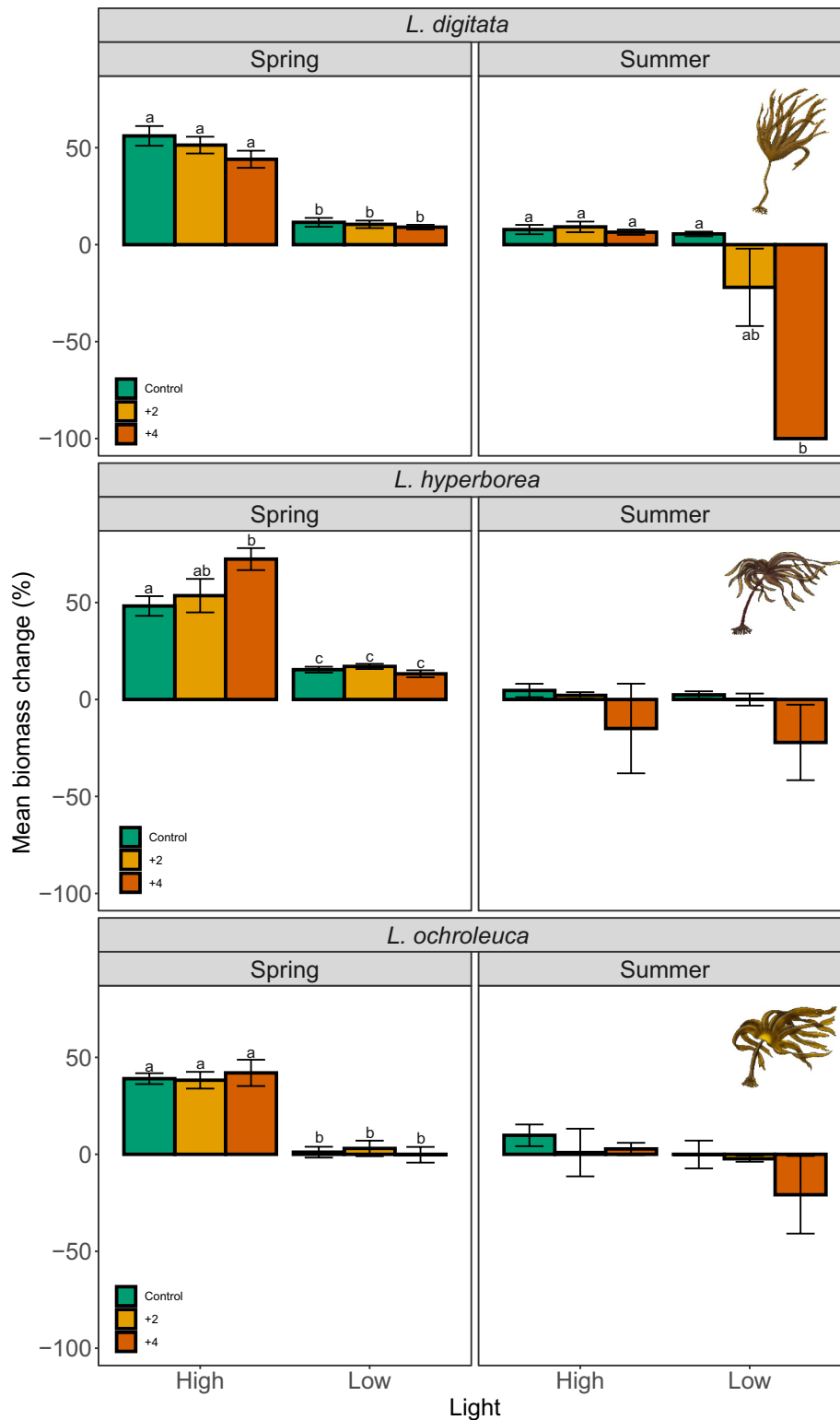


FIGURE 1 Percentage change in fresh weight biomass of each whole plant for each species under each treatment between the start and end of the experimental phase ($n=5$). Values are means \pm SE. Lowercase letters represent results of Post hoc tests (Tukey); bars that share the same letters are not significantly different to each other (absolute temperatures in spring: $9.8^{\circ}\text{C} \pm 0.4^{\circ}\text{C}$, $11.8^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$ and $14.2^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$; in summer: $18.1^{\circ}\text{C} \pm 0.1^{\circ}\text{C}$, $20.0^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$, and $22.5^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$).

significant variability in percentage changes in biomass between light treatments for all species (Table 1; $p < 0.001$). There was also a significant interactive effect between light and temperature for *L. hyperborea* (Table 1; $p = 0.023$), whereby post hoc tests indicated that growth rates increased significantly with temperature under high-light conditions but not under low-light conditions (Figure 1; Figure S5 in the Supporting Information).

Percentage changes in the surface area of kelp blades showed a similar pattern to biomass in that all species exhibited positive responses at both high- and low-light levels, regardless of temperature, with the magnitude of responses markedly greater under high-light conditions versus limited light conditions (Figure 2). Average change in surface area across the three temperature treatments was $167.5\% \pm 16.5\%$, $294\% \pm 23.0\%$, and $83.3\% \pm 15.5\%$ under high light for *Laminaria digitata*, *L. hyperborea*, and *L. ochroleuca*, respectively, compared with the much lower $28.0\% \pm 6.0\%$, $132.0\% \pm 18.2\%$, and $14.0\% \pm 21.2\%$ under low light. ANOVA again detected highly significant variability between light levels for each species (Table 1), with greater increases in blade surface area under high-light conditions compared to light-limited plants (Figure 1; Figure S6 in the Supporting Information).

Absolute F_v/F_m values, which ranged from 0.82 to 0.69 by the end of the experiment, did not change markedly for any species or treatment (Figure 3; Figure S7 in the Supporting Information). In general, F_v/F_m declined under high-light levels slightly more than under low light (mean changes of 0.02, -0.044 , -0.012 vs. -0.011 , -0.019 , -0.064 for *Laminaria digitata*, *L. hyperborea*, and *L. ochroleuca*, respectively), but all values indicated "healthy" tissue. The decline in F_v/F_m values was greater under high light compared with low-light conditions for *L. hyperborea*, but no other significant differences were detected (Table 1). While no mortality was recorded during the spring experiment, some *L. ochroleuca* plants exhibited signs of bleaching, and at low-light levels some tissue loss was observed (Table 2).

Summer experiment

Under high-light conditions in summer, all three species exhibited minimal change in biomass at any temperature, with average percentage change values of $7.8\% \pm 2.0\%$, $-2.7\% \pm 7.6\%$, and $4.5\% \pm 4.4\%$ for *Laminaria digitata*, *L. hyperborea*, and *L. ochroleuca*, respectively (Figure 1). At low-light levels, however, all species lost biomass, with the magnitude of loss generally increasing at higher temperatures (Figure 1; Figure S5). Notably, *L. digitata* plants held at $+4^\circ\text{C}$ (i.e., absolute temperature of 22.6°C) had disintegrated by the end of the experiment, losing all biomass. Across

the temperature treatments, average change in fresh weight biomass was $-39.0\% \pm 13.4\%$, $-6.6\% \pm 6.7\%$, and $-7.7\% \pm 7.0\%$ for *L. digitata*, *L. hyperborea*, and *L. ochroleuca*, respectively. Statistically, ANOVA detected a significant effect of light ($p < 0.001$), temperature ($p < 0.001$), and the interaction term ($p = 0.007$) on biomass change for *L. digitata*, but not for the other species (Table 1). Post hoc tests showed that the negative effects of increasing temperatures were greater under low-light conditions than high-light conditions (Figure 1; Figure S5).

Changes in surface area of blade tissue showed similar patterns in that under high-light availability, all three species showed minimal responses, with the exception of *Laminaria ochroleuca* at the lowest temperature treatment, which exhibited a $\sim 50\%$ increase in surface area (Figure 1). Conversely, under low-light conditions, all species exhibited decreases in surface area, particularly at the higher temperature treatments (Figure 2; Figure S6). Average change in surface area across the three temperature treatments was $7.6\% \pm 2.6\%$, $-12.3\% \pm 8.6\%$, and $16.3\% \pm 11.2\%$ under high light for *L. digitata*, *L. hyperborea*, and *L. ochroleuca*, respectively, compared with $-45.0\% \pm 13.0\%$, $-6.3\% \pm 6.8\%$, and $-24.8\% \pm 9.8\%$ under low-light levels. ANOVA detected significant effects of light ($p < 0.001$) and temperature ($p = 0.003$) for *L. digitata*, with greater declines under the highest temperature treatment and under low-light conditions (Table 1, Figure 1).

Variation in photosynthetic efficiency, as measured by F_v/F_m , was markedly greater in summer compared with spring, with absolute values ranging from 0.82 to 0.0. On average, we recorded changes in F_v/F_m values of -0.33 , -0.05 , and -0.04 under low light for *Laminaria digitata*, *L. hyperborea*, and *L. ochroleuca*, respectively, and -0.06 , -0.11 and -0.1 under high light. For *L. digitata*, ANOVA detected significant effects of light, temperature, and the interaction term (Table 1). Post hoc tests showed that declines in F_v/F_m with increasing temperature were more pronounced under low-light conditions (Figure 1; Figure S7). ANOVA also detected a significant effect of temperature for *L. hyperborea* (Table 1), with greater reductions in F_v/F_m under the $+4^\circ\text{C}$ treatment (Figure 1; Figure S7).

For all three species, some level of mortality was observed under low-light conditions and $+2^\circ\text{C}$ and $+4^\circ\text{C}$ treatments, as well as under high-light conditions at $+4^\circ\text{C}$ (Table 2). However, *Laminaria digitata* had the highest mortality rates under the $+4^\circ\text{C}$ treatment, with all five replicate plants disintegrating by the end of the experiment. In comparison, *L. hyperborea* and *L. ochroleuca* suffered only 20% mortality at this treatment combination. Some bleaching was observed for *L. ochroleuca* across most treatment combinations, while for all species, tissue loss was more commonly recorded at low-light and high-temperature treatments (Table 2).

TABLE 1 Results of two-way ANOVA (conducted for each *Laminaria* species and seasonal experiment separately) to test for differences in response variables between light and temperature treatments and their interaction.

	<i>L. digitata</i>			<i>L. hyperborea</i>			<i>L. ochroleuca</i>			Residuals (df)
	Light	Temp	Light x Temp	Light	Temp	Light x Temp	Light	Temp	Light x Temp	
Spring										
Biomass										
df	1	2	2	1	2	2	1	2	2	24
F	235.7	1.84	0.35	97.03	2.06	5.38	117.96	0.019	0.336	
p	<0.001	0.38	0.98	<0.001	0.2	0.023	<0.001	0.981	0.718	
Surface area										
df	1	2	2	1	2	2	1	2	2	24
F	125	2.39	1.31	28.04	0.69	0.72	7.962	0.22	0.115	
p	<0.001	0.113	0.288	<0.0001	0.51	0.5	<0.0001	0.8	0.89	
Fv/Fm										
df	1	2	2	1	2	2	1	2	2	24
F	1.461	0.277	0.371	10.049	1.413	0.140	0.646	0.96	1.791	
p	0.238	0.761	0.694	0.004	0.263	0.87	0.429	0.397	0.188	
Summer										
Biomass										
df	1	2	2	1	2	2	1	2	2	24
F	32.64	10.3	6.02	0.1427	1.86	0.264	2.965	0.954	0.08	
p	<0.001	<0.001	0.007	0.709	0.176	0.974	0.098	0.399	0.923	
Surface area										
df	1	2	2	1	2	2	1	2	2	24
F	21.664	7.423	2.639	0.037	0.577	0.629	6.669	0.942	0.349	
p	<0.001	0.003	0.09	0.849	0.569	0.541	0.016	0.4	0.7	
Fv/Fm										
df	1	2	2	1	2	2	1	2	2	24
F	22.925	28.16	9.864	0.86	6.553	0.485	0.96	1.57	0.174	
p	<0.001	<0.001	<0.0001	0.363	0.005	0.621	0.337	0.229	0.841	

Note: Significant p-values ($p < 0.05$) are shown in bold; tests where preconditions were not met and a more conservative significance value of 0.01 was adopted are shown with an underlined p ("p").

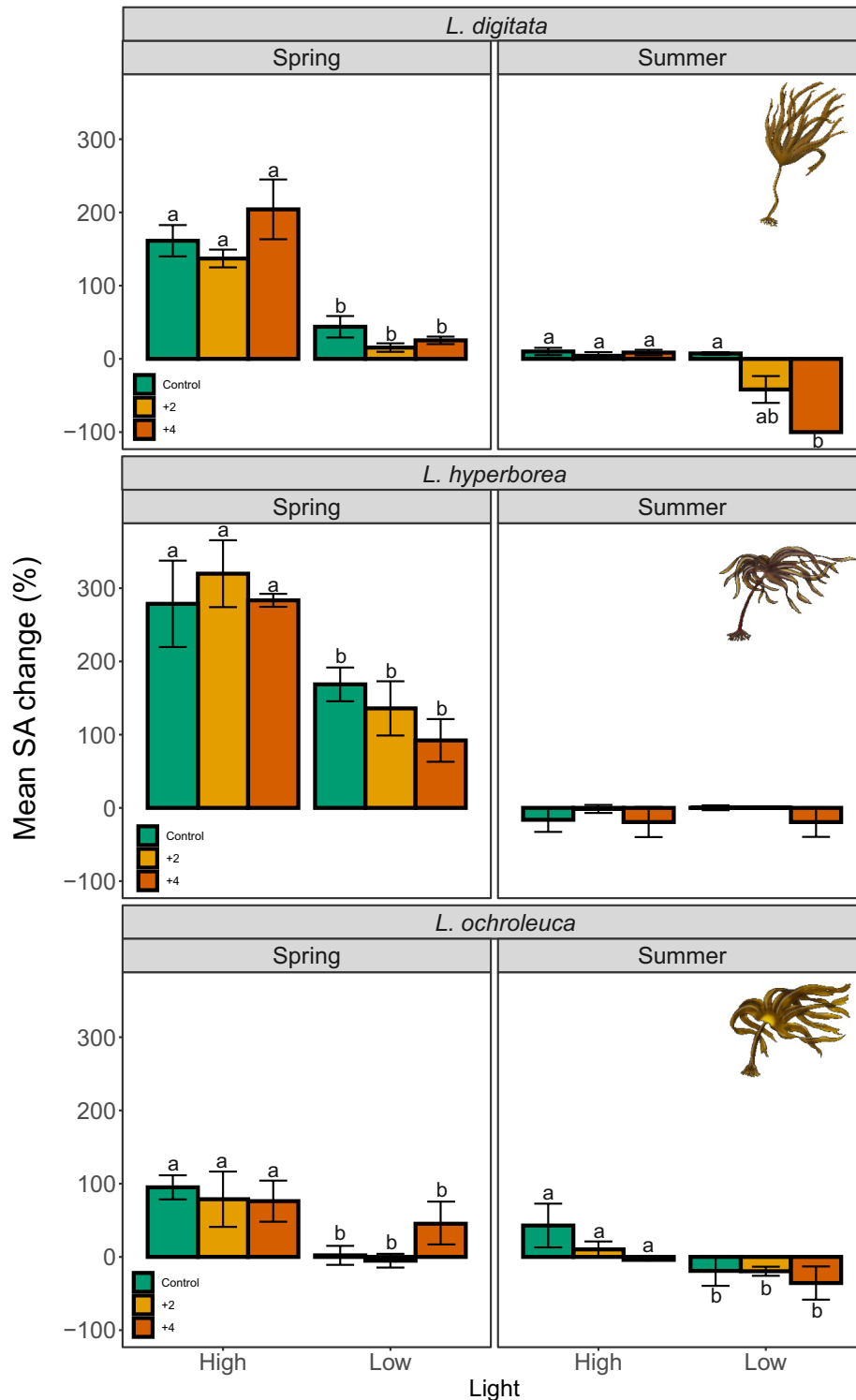


FIGURE 2 Percentage change in blade surface area for each species under each treatment between the start and end of the experimental phase. Values are means \pm SE. Lowercase letters represent results of Post hoc tests (Tukey); bars that share the same letters are not significantly different to each other (absolute temperatures in spring: $9.8^{\circ}\text{C} \pm 0.4^{\circ}\text{C}$, $11.8^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$ and $14.2^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$; in summer: $18.1^{\circ}\text{C} \pm 0.1^{\circ}\text{C}$, $20.0^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$, and $22.5^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$).

DISCUSSION

Our study showed that realistic summertime MHWs occurring at low-light levels can have major deleterious impacts on multiple habitat-forming kelp species

in the Northeast Atlantic. The frequency and intensity of MHWs are projected to increase over the coming decades as a consequence of anthropogenic climate change (Frölicher et al., 2018; Oliver et al., 2018, 2019), with widespread implications for marine ecosystems

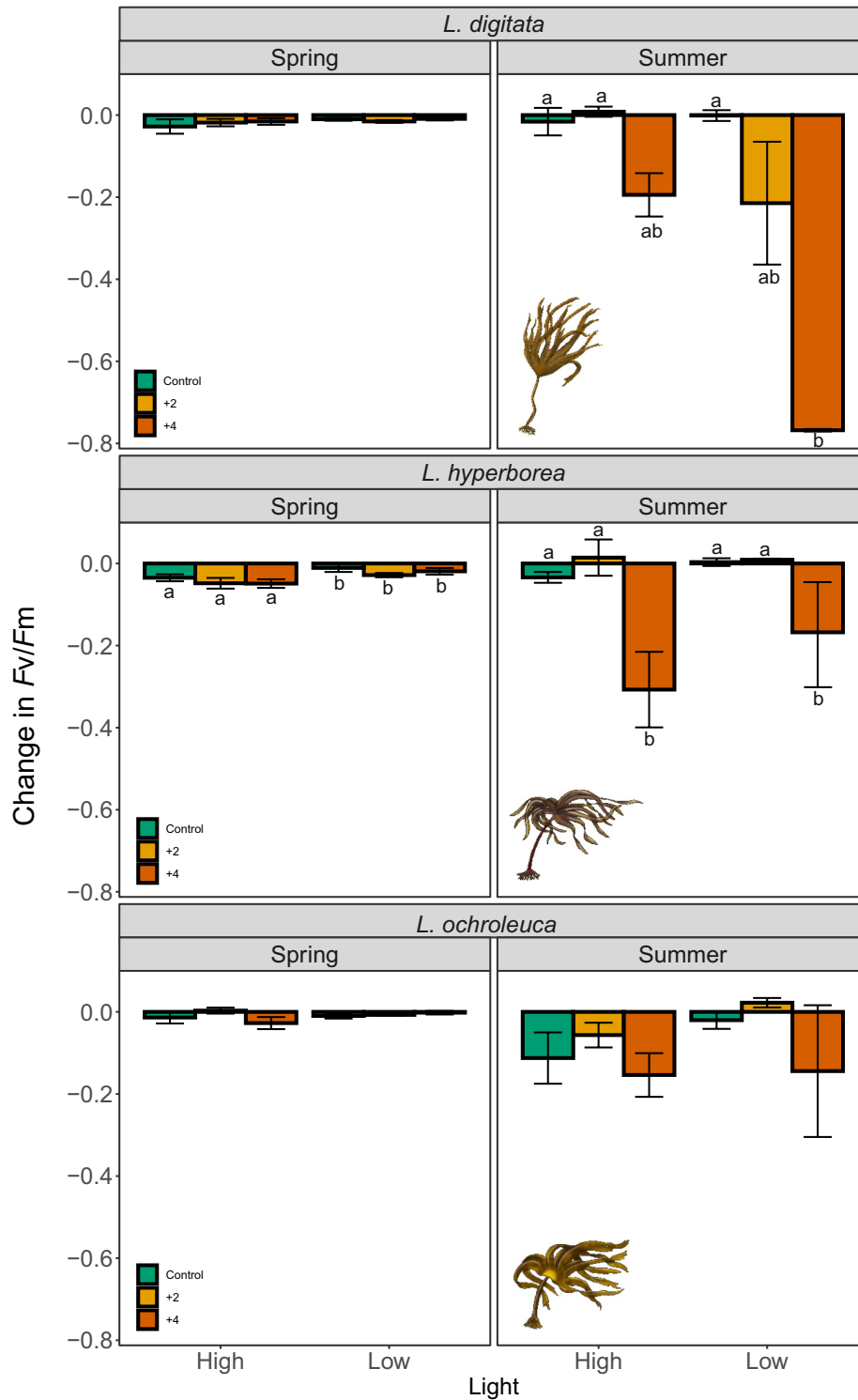


FIGURE 3 Change in F_v/F_m values for each *Laminaria* species under each treatment between the start and end of the experimental phase. Values are means \pm SE. Lowercase letters represent results of Post hoc tests (Tukey); bars that share the same letters are not significantly different to each other (absolute temperatures in spring: $9.8^{\circ}\text{C} \pm 0.4^{\circ}\text{C}$, $11.8^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$ and $14.2^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$; in summer: $18.1^{\circ}\text{C} \pm 0.1^{\circ}\text{C}$, $20.0^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$, and $22.5^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$).

and the services and benefits they underpin (Smale et al., 2019; Smith et al., 2021, 2023). Kelp species are predicted to shift their distributions in response to decadal-scale warming and MHW intensification (Assis et al., 2016, 2018), with populations that exist toward

species' trailing (warm) range edges particularly vulnerable to increasing temperatures (Smale, 2020; Smale et al., 2019). Concurrently, in many systems, local-to-regional stressors, including eutrophication, reduced sea ice cover, and increased sedimentation

TABLE 2 Rates of mortality, bleaching, and tissue loss recorded for each *Laminaria* species, treatment, and experiment, expressed as a percentage of replicate plants for each combination ($n=5$).

	Light	Temp	% Mortality			% Bleached			% Tissue loss		
			<i>L. dig</i>	<i>L. hyp</i>	<i>L. och</i>	<i>L. dig</i>	<i>L. hyp</i>	<i>L. och</i>	<i>L. dig</i>	<i>L. hyp</i>	<i>L. och</i>
Spring	High	Control	–	–	–	–	–	–	–	–	–
		+2	–	–	–	–	–	40	–	–	–
		+4	–	–	–	–	–	20	–	–	–
	Low	Control	–	–	–	–	–	40	–	–	20
		+2	–	–	–	–	–	–	–	–	40
		+4	–	–	–	–	–	20	–	–	40
Summer	High	Control	–	–	–	–	–	20	–	20	–
		+2	–	–	–	–	–	40	–	20	–
		+4	–	20	–	–	–	40	20	20	–
	Low	Control	–	–	–	–	–	40	–	40	60
		+2	20	–	–	–	–	20	20	–	40
		+4	100	20	20	–	–	–	–	–	20

and freshwater run-off, has led to higher turbidity and “coastal darkening” (Blain et al., 2021; Seers & Shears, 2015), which, in turn, influences the distribution and productivity of benthic macrophytes, including kelp species (Desmond et al., 2015; Smith et al., 2022). Moreover, as MHWs are often compound events (Dzwonkowski et al., 2020) wherein increased temperatures occur simultaneously with other stressors (e.g., decreased oxygen, reduced light, and lower nutrient levels; Rogers-Bennett & Catton, 2019; Sen Gupta et al., 2020), understanding the interactive effects of multiple concurrent stressors is needed to improve predictions of MHW impacts.

Following a high-intensity summertime MHW (i.e., +4°C, absolute temperature of ~22.5°C) and under low-light conditions, *Laminaria digitata* and (to a lesser extent) *L. hyperborea* exhibited declines in biomass, surface area, and photosynthetic efficiency. The declines in biomass and area, along with increased prevalence of bleaching and mortality, are indicative of thermal stress as physiological limits are exceeded. Temperature stress has the potential to disrupt cellular biological processes (Davison & Pearson, 1996), such as functioning of the photosynthetic apparatus (Bischof & Rautenberger, 2012). In general, photosynthesis and respiration are positively correlated with increasing temperature, although photosynthesis may reach a maximum threshold sooner before declining rapidly, while respiration rates continue to rise before reaching a critical threshold (Hurd et al., 2014). As such, where increases in respiration rates are not tracked by increases in photosynthesis due to limited light availability, tissue necrosis, and mortality can occur (Davison et al., 1991). This was observed in our cool-water species, and exacerbated effects of temperature under low-light conditions have also been observed for other kelp species (Mabin et al., 2019; Sánchez-Barredo et al., 2020).

Under high-light conditions—representative of low turbidity/favorable water quality—the effects of the summertime MHW were comparatively benign, with all species exhibiting some resistance to the warming treatments (notwithstanding a marked decrease in Fv/Fm in *Laminaria digitata*). Here, when light is not limiting, photosynthesis rates may track increasing respiration for longer and to higher temperatures, supporting maintenance and protective mechanisms (Davison et al., 1991). Additionally, the annual patterns of metabolism, growth, and development of macrophytes is controlled by endogenous rhythms and has also been documented in the Laminariales (Bartsch et al., 2008). During summer *L. hyperborea* is in a dormant phase with limited growth observed between May and December (Sjøtun et al., 1996), while *L. digitata* and *L. ochroleuca* enter low-growth phases (Pessarrodona et al., 2019) during which blade elongation is minimal and biomass gain is driven by storage compound production (Lüning, 1979). Therefore, any responses in biomass or surface area during late summer and autumn months are related to tissue necrosis or the inability to produce and store compounds.

Laminaria digitata fared markedly worse than the other two species during the high-intensity summertime MHW, particularly under low-light conditions. Indeed, *L. digitata* exhibited 100% mortality with all replicates losing all biomass through tissue necrosis. Under high-light conditions, some negative responses to warming were observed for *L. digitata* and *L. hyperborea*, but not *L. ochroleuca*. Variation between these species in their responses to short-term warming has been reported previously (Burdett et al., 2019; Hargrave et al., 2017; King et al., 2018) and likely relates to differing thermal tolerances and latitudinal distributions. *L. digitata* has the most northerly distribution of the three species, extending from the Arctic

toward the equator to its trailing (warm) range edge in Brittany, France, where it has recently undergone population declines and a range contraction (Raybaud et al., 2013). The upper thermal limit of mature sporophytes is 20°C–22°C (Bolton & Lüning, 1982; tom Dieck, 1992), although reproduction in natural populations may be impaired at summer temperatures of ~18°C (Bartsch et al., 2013). Interestingly, in our study, *L. digitata* was able to survive under high-light conditions at temperatures in excess of 22°C, maintaining tissue biomass while exhibiting slight declines in *Fv/Fm*, but was obliterated by such temperatures under low-light conditions. Moreover, of the three species, *L. digitata* exhibits the shallowest depth distribution in the northeast Atlantic, typically being restricted to the low intertidal/shallow subtidal fringe, and local populations may be acclimatized to higher light availability than the other species or to the local conditions at the sampling site (Delebecq et al., 2013). As such, a combination of a lower upper thermal threshold and acclimation to higher light levels are likely to have caused the greater adverse impacts observed for *L. digitata*.

In contrast to *Laminaria digitata*, *L. ochroleuca* has a distinctly Lusitanian distribution, extending from the United Kingdom and Ireland toward the equator to the Mediterranean and Morocco (Assis et al., 2018), although it has also recently exhibited climate-driven range shifts (Casado-Amezúa et al., 2019; Teagle & Smale, 2018). The upper thermal limit of mature sporophytes is around 23°C–24°C (Franco et al., 2018; tom Dieck, 1992), greater than the temperature treatments employed in our study. *L. hyperborea* also extends further south than *L. digitata*, onto the Iberian Peninsula, where it has also exhibited population declines in response to recent warming (Casado-Amezúa et al., 2019; Voerman et al., 2013), and the stated upper thermal limit of juvenile *L. hyperborea* sporophytes is around 21°C–22°C (Bolton & Lüning, 1982; tom Dieck, 1992). A combination of slightly higher upper thermal limits and acclimation to lower light levels may have underpinned the observed lower-magnitude responses. Even so, while *L. hyperborea* plants were largely resistant to the high-intensity summertime MHW treatment under high light, when light was limiting, they were negatively impacted, with some mortality recorded. This suggests that upper thermal limits are reduced under low-light levels, which are typical of decreased coastal water quality. Variability in responses to experimental MHWs between habitat-forming seaweeds has been reported from other systems (Atkinson et al., 2020; Straub et al., 2019, 2022) and is an important consideration in predicting MHW impacts at the community and ecosystem levels.

All species were resistant to the simulated MHWs in springtime, with no observed reductions in biomass, area, or *Fv/Fm*. Indeed, under high-light conditions all

species increased significantly in biomass and surface area, regardless of temperature treatment. Given those absolute temperatures during the maximum intensity MHW in springtime (i.e., 14°C) were unlikely to be thermally stressful, it is perhaps unsurprising that kelp species did not exhibit negative responses to simulated MHW activity. Indeed, increasing temperatures experienced during MHWs are likely to lead to increased metabolism, growth, and performance until conditions become thermally stressful (Smith et al., 2023). This was evidenced, to some degree, by greater biomass gain at the warmest treatment for *Laminaria hyperborea* and *L. ochroleuca*, although in general springtime MHWs elicited minimal responses. More generally, it should be noted that our findings relate specifically to sporophytes collected from single populations, and that life stage, as well as location and timing of kelp material collections, could influence temperate tolerances and thermal responses (e.g., Heinrich et al., 2016).

Most MHW studies conducted to date have focused on summer MHWs when absolute temperatures are most likely to be stressful, yet MHWs can occur in different seasons and even across seasons and years (Di Lorenzo & Mantua, 2016; Diehl et al., 2021; Thorl et al., 2022). It is evident that MHW impacts will vary seasonally due to the absolute temperatures experienced, the phenology and ecology of the species and communities involved, and seasonality of other environmental factors (e.g., nutrient/food availability). Previous work on macroalgae has demonstrated both consistency (Atkinson et al., 2020) and variability (Hereward et al., 2020) in responses to extreme warming events across seasons. Intuitively, when temperatures experienced during MHWs are nonstressful and do not exceed thermal thresholds, organisms may improve ecophysiological performance as temperatures near optima for cellular processes and metabolic rates (Smith et al., 2023). Here, MHWs occurring in springtime, when ambient sea temperatures are low, induced no negative impacts and, in some cases, induced low-magnitude positive responses in kelp performance. Clearly, seasonality in MHW activity is an important factor determining the impacts of MHWs on individuals, populations, and communities. With respect to ecological interactions between *Laminaria ochroleuca* and *L. digitata* in the intertidal zone and *L. hyperborea* in the subtidal, sublethal MHWs in winter could reduce the competitive advantage of the cold-adapted species over the warm-adapted one that performs poorly at temperatures below ~10°C (Izquierdo et al., 2002).

In conclusion, under high-light conditions typical of favorable coastal water quality, habitat-forming kelp species were largely resistant to realistic, ecologically meaningful simulated MHWs, even during summer when ambient temperatures were highest. However, under low-light conditions typical of coastal waters influenced by high rates of sedimentation, nutrient input,

or physical disturbance, cool-adapted kelp species were negatively impacted by summertime MHWs, albeit to varying extents. The warm-adapted species, *Laminaria ochroleuca*, was largely resistant to MHW activity occurring in both spring and summer and under high- and low-light conditions. With increasing MHW activity, this species may continue to proliferate in the study region, partially replacing cool-adapted kelp species, with implications for ecological structure and functioning (Pessarrodona et al., 2019; Smale et al., 2015, 2022). Clearly, reducing local stressors, maintaining favorable environmental conditions, and prioritizing areas of cooler, clearer water for biodiversity conservation may be useful management approaches. Such actions may, to some extent, reduce the susceptibility of habitat-forming kelp species and their associated communities and ecosystems to MHW intensification in coming decades.

AUTHOR CONTRIBUTIONS

Alissa Bass: Conceptualization (equal); data curation (equal); formal analysis (equal); investigation (equal); writing – original draft (equal); writing – review and editing (equal). **Kathryn Smith:** Formal analysis (equal); writing – original draft (equal); writing – review and editing (equal). **Dan Smale:** Conceptualization (equal); formal analysis (equal); funding acquisition (equal); project administration (equal); supervision (equal); writing – original draft (equal); writing – review and editing (equal).

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ORCID

Alissa V. Bass  <https://orcid.org/0000-0002-6809-3261>

Kathryn E. Smith  <https://orcid.org/0000-0002-7240-1490>

Dan A. Smale  <https://orcid.org/0000-0003-4157-541X>

<https://orcid.org/0000-0003-4157-541X>

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. MHW climatology in the study region in southwest UK, using “heatwaveR” package in statistical software R. (A) The frequency of MHW events of differing severity (categorized by MHW intensity

– Hobday et al., 2018) in different seasons. Moderate MHWs lie within 1–2x the 90th percentile, while strong MHWs lie within 2–3x the 90th percentile. (B) The number of MHW events in the study region since 1982, their maximum intensity, and observed duration (blue line).

Figure S2. (A) Location in decimal degrees of collection site (red square) and the area of sea surface temperature extraction for MHW analysis (blue square). (B) Image of experimental set-up showing tanks each containing three kelps (one of each species), exposed to two light levels (high and low) and three temperatures; control and MHW intensities of +2°C and +4°C. Image shows one of five replicates. (C) Example of picture of kelp plant with clipped blades and kelp identification on cable tie, taken against a white background for blade surface area analysis. Photos were taken at a set distance, and scale bar was included in every picture.

Figure S3. Light data from Hobo loggers (averaged between loggers from all temperature treatments; $n=3$)

Figure S4. Temperature data from all Hobo loggers ($n=6$)

Figure S5. Changes in mean biomass over time (weeks) for each species, experiment, and treatment. Values are means \pm SE. Spring absolute temperatures were $9.8^{\circ}\text{C} \pm 0.4^{\circ}\text{C}$, $11.8^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$ and $14.2^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$, and summer temperatures were $18.1^{\circ}\text{C} \pm 0.1^{\circ}\text{C}$, $20.0^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$, and $22.5^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$.

Figure S6. Changes in mean surface area over time (weeks) for each species, experiment, and treatment. Values are means \pm SE. Spring absolute temperatures were $9.8^{\circ}\text{C} \pm 0.4^{\circ}\text{C}$, $11.8^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$ and $14.2^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$, and summer temperatures were $18.1^{\circ}\text{C} \pm 0.1^{\circ}\text{C}$, $20.0^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$, and $22.5^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$.

Figure S7. Changes in mean F_v/F_m over time (weeks) for each species, experiment, and treatment. Values are means \pm SE. Spring absolute temperatures were $9.8^{\circ}\text{C} \pm 0.4^{\circ}\text{C}$, $11.8^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$ and $14.2^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$, and summer temperatures were $18.1^{\circ}\text{C} \pm 0.1^{\circ}\text{C}$, $20.0^{\circ}\text{C} \pm 0.2^{\circ}\text{C}$, and $22.5^{\circ}\text{C} \pm 0.3^{\circ}\text{C}$.

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