



Photophysiological Responses of Canopy-Forming Kelp Species to Short-Term Acute Warming

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Specialty section:

This article was submitted to
Marine Ecosystem Ecology,
a section of the journal
Frontiers in Marine Science

Received: 15 February 2019

Accepted: 06 August 2019

Published: 27 August 2019

Citation:

Burdett HL, Wright H and
Smale DA (2019) Photophysiological
Responses of Canopy-Forming Kelp
Species to Short-Term Acute
Warming. *Front. Mar. Sci.* 6:516.
doi: 10.3389/fmars.2019.00516

The frequency of short-term oceanic warming events [“marine heatwaves” (MHWs) or heat spikes] has increased over the past century and is projected to further increase because of anthropogenic climate change. Given that marine organisms are strongly influenced by temperature, an increased occurrence of warming events could alter the structure of populations, communities, and ecosystems. The distribution and ecophysiological performance of kelp species – globally important foundation species that play significant roles in nutrient cycling and habitat creation in temperate coastal systems – is particularly constrained by temperature. However, their photophysiological responses to warming events remains unclear, which hinders attempts to understand, and predict the effects of ocean warming on kelp populations and the ecosystems they underpin. Here, we experimentally simulated a heat spike (+2°C and +4°C in magnitude, 3 days in duration, and compared with ambient controls) and examined the photophysiological responses of two canopy-forming kelp species widely distributed across the northeast Atlantic – *Laminaria digitata* and *Laminaria hyperborea*. Both species were resilient to the realistic warming treatments in terms of their photosynthetic characteristics. However, we found that *L. digitata* individuals, which were collected from populations found toward the upper limit of this species’ thermal range, exhibited increased oxygen production at higher temperatures, particularly after multiple days of exposure to the warming event. *L. digitata* also exhibited a greater poise for dissipating excess energy through non-photochemical pathways. In contrast, *L. hyperborea*, which extends further south into warmer waters and tends to occupy deeper reefs that are almost constantly submerged, appeared to be photo-physiologically insensitive to the heat spike. This study enhances our mechanistic understanding of the photophysiological and photoprotective responses of kelps to short-term acute warming events – features which are likely to emerge as important drivers of ecological change in coming decades.

Keywords: kelp, photophysiology, PAM fluorescence, marine heatwave, *Laminaria digitata*, *Laminaria hyperborea*, macroalgae

INTRODUCTION

The upper layers of the global ocean have warmed at a rate of $\sim 0.1^{\circ}\text{C}$ per decade since the mid-20th century, albeit with pronounced regional, and seasonal variability (IPCC, 2013). Recent climatic changes have caused changes in the distribution of species (Pinsky et al., 2013; Poloczanska et al., 2013), the structure of communities and ecosystems (Vergés et al., 2014; Wernberg et al., 2016), and the provision of ecosystem services (Pecl et al., 2017). Superimposed onto gradual warming trends are discrete extreme warming events – “marine heatwaves” [MHWs] or “heat spikes” – during which sea temperatures are anomalously high for periods of days to months or even years (Hobday et al., 2016, 2018). Recent research has shown that over the past century MHW frequency and duration increased by 34 and 17%, respectively, and that many regions have experienced rapid intensification of MHWs (Oliver et al., 2018). Moreover, it is likely that MHWs will intensify in coming decades, as a result of anthropogenic climate change (Frölicher et al., 2018). As the distribution of marine species is highly constrained by temperature, with many populations persisting toward the upper limits of species’ thermal niches (Sunday et al., 2012), continuation of both long- and short-term warming will drive redistribution of species, and reconfiguration of communities and ecosystems at the global scale (García Molinos et al., 2016; Hughes et al., 2017).

Kelps (macroalgae of the Order Laminariales) are distributed along approximately one-quarter of the world’s coastlines, across temperate and subpolar latitudes in both hemispheres, where they function as foundation species in nearshore marine ecosystems (Steneck and Johnson, 2013; Teagle et al., 2017). By providing complex biogenic habitat and exhibiting high rates of primary productivity, kelps enhance local biodiversity, fuel inshore food webs, and elevate secondary productivity (Steneck et al., 2002; Teagle et al., 2017, 2018). With regards to inshore carbon cycling, kelps fix and transfer globally significant amounts of carbon (Krause-Jensen and Duarte, 2016) that may eventually become trapped and stored in sediments, and thus contribute toward natural carbon sequestration (Krause-Jensen and Duarte, 2016; Smale et al., 2018). However, the ecophysiology and spatial distribution of kelp species is strongly influenced by temperature (Eggert, 2012); recent ocean warming trends have been linked with major shifts in the structure and functioning of some kelp populations and their associated communities (Wernberg et al., 2016). Increased temperature may also impact rates of primary productivity and carbon assimilation and transfer, with knock-on effects for interconnected habitats (Pessarrodona et al., 2019). That said, a recent global analysis (Krumhansl et al., 2016) showed that temporal trends in kelp populations are highly variable between different species and biogeographical regions. Whilst there is a general consensus that continued ocean warming will drive shifts in the geographical ranges of kelp species and changes in kelp-dominated communities (Harley et al., 2012; Brodie et al., 2014), the underlying physiological mechanisms and the

drivers of observed variability in contemporary responses are poorly understood.

Kelps are distributed along rocky coastlines throughout the NE Atlantic from Portugal and Morocco to northern Norway and Iceland (Bolton, 2010). Multiple kelp species are found within this region, each with varying environmental requirements, so that different species persist and dominate under different environmental conditions (Smale et al., 2013). Recent warming trends have driven some shifts in kelp distributions, with cool-affinity species declining at their warm trailing range edge (Raybaud et al., 2013; Tuya et al., 2014) and warm-affinity species expanding at their cool leading range edge (Smale et al., 2015), resulting in changes in local diversity (Teagle and Smale, 2018), and ecosystem functioning (Pessarrodona et al., 2019). Conversely, some kelp populations have remained relatively constant and stable over time (Krumhansl et al., 2016). At the physiological level, the temperature range within which kelps can carry out critical processes such as photosynthesis varies between species, life stages and the processes themselves (Delebecq et al., 2016), so that determining the thermal niche is complex. Even so, the extreme temperatures that macroalgal populations are exposed to during MHWs can exceed thermal thresholds, inducing protective responses (e.g., heat shock proteins, see King et al., 2019) and leading to impaired performance (Hargrave et al., 2017), altered physiology (Gouvêa et al., 2017), and ultimate mortality (Wernberg et al., 2013). Inter-specific variability in photophysiological mechanistic responses to short-term acute warming events remains unclear, but would allow for improved predictions of the future effects of ocean warming on kelp populations and the communities they underpin.

Here, we examined photosynthetic characteristics (as net oxygen flux in the light and chlorophyll-a fluorescence) of two critical habitat-forming kelp species – *Laminaria digitata* and *Laminaria hyperborea* – during a short-term acute warming event. These kelp species dominate wave exposed rocky reef habitats along much of the NE Atlantic coastline. Both species have a northern Boreal distribution: *L. hyperborea* is distributed from the Arctic to northern Portugal while *L. digitata* is distributed from the Arctic to a southerly range limit in northern France in the NE Atlantic. The current warm water limit of *L. digitata* is ~ 100 nautical miles south of the location of the current study; range edge populations are subjected to a similar climatic environment as those examined here. As well as differences in latitudinal ranges, these species differ in their vertical distributions as *L. digitata* is primarily found in the low intertidal zone whereas *L. hyperborea* tends to dominate deeper reefs, extending from the extreme low intertidal to subtidal reefs. Differences in latitudinal extensions and vertical distributions may manifest in differing responses to contemporary and predicted future ocean warming, although previous experimental work suggests they have similar upper thermal tolerances (Bolton and Lüning, 1982; tom Dieck, 1993). The aim of this study was to determine photophysiological responses of populations of these ecologically important species to short-term warming events.

MATERIALS AND METHODS

Experimental Set-Up

Both *Laminaria digitata* and *L. hyperborea* were collected by removing whole plants from their *in situ* environment; individuals were carefully removed by prising the holdfast from the rocky substratum. Both species were collected from within Plymouth Sound – *L. digitata* was collected from the shore during a low spring tide and *L. hyperborea* was collected by SCUBA divers at ~1 m depth (BCD). In total, 24 mature, medium sized (stipe length 30–50 cm) individuals of each species were collected, stored in seawater containers and immediately returned to the laboratory. The experiment described below was first conducted with *L. digitata* and subsequently with *L. hyperborea* using exactly the same approach. Kelp specimens were collected immediately prior to their respective experiment so the length of time between field collection and the start of the experiment was the same for both species. All experimentation was completed during a 16-day period in July 2017.

During each experiment, two plants were placed into each of 12 individual 130 L tanks filled with local filtered seawater within a recirculating system. Plants were orientated in an upright position by securing holdfasts to rocks using cable ties; duplicate plants were placed at opposite ends of the tanks, ~50 cm apart, to simulate actual densities recorded in the field (e.g., Smale et al., 2016; Hereward et al., 2018). Two plants were placed in each tank to reflect natural populations (i.e., plants are generally found in stands rather than individually) and to capture between-plant variability. Seawater was maintained at the desired temperature (see below) with aquarium chillers (DC-750, Deltec, Delmenhorst) or heaters (300W DR-9300, Boyu, Guangdong) as necessary. Turbulent water flow was generated with a wave maker in each tank (WM-6000, All Pond Solutions, Uxbridge). Salinity was maintained at 35 with the addition of fresh water as necessary. Lamps specifically designed for aquatic plants (Reef Daylight T8 36 W, Interpret, Dorking) were used to generate a 14:10 h light–dark regime with PAR irradiance levels of ~100 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (recorded with an Odyssey PAR meter). Average daily light intensity (measured with a Hobo pendant logger, 15 min intervals, daytime only) during the experiment was 1970 ± 163 Lux. As such, levels of PAR and light intensity, as well as the daylight regime used in the study were comparable to those experienced by natural populations *in situ* during typical summer months (Pedersen et al., 2014; Smale et al., 2016).

Plants were held at ambient water temperature for 60 h to acclimate to tank conditions. Ambient temperature was set at ~16°C, which is typical of local summer sea temperatures from the surface to >20 m depth – well within the depth ranges inhabited by the study species (Smyth et al., 2009; Brewin et al., 2017). Following this, the water temperature of four replicate tanks was gradually increased by ~2°C over a 48-h period. The water temperature of four other replicate tanks was increased over the same 48-h period by ~4°C. The water temperature of the remaining four tanks was maintained at ambient temperature. These temperature treatments were selected as they are representative of the magnitude of actual

warming events, both generally (Hobday et al., 2016) and specifically within the study location (Joint and Smale, 2017). Each set of four tanks were fed by a larger header reservoir, so that water temperature in each tank within each treatment was consistent. Water changes were conducted daily (~10% of total volume) using local filtered seawater. Experimental temperatures were maintained for a further 3 days to simulate short-term acute warming events of differing magnitude (i.e., ~+2°C and ~+4°C); the temperature treatments of ambient conditions, low magnitude and high magnitude warming are hereafter referred to as T_0 , T_1 , and T_2 , respectively (**Supplementary Figure S1**). Temperature was monitored in each set of tanks using Hobo pendant loggers, which recorded temperature every 15 min throughout the experiment. Net daytime oxygen flux was measured on days 1–3 of the heat spike period, whilst photosynthetic characteristics were measured on days one and two only (analytical details below).

Net Oxygen Flux

Net O₂ flux from kelp individuals was measured using unstirred benthic chambers placed over the basal meristematic area of the blade, which were weighed down to avoid movement during the incubation (270 ml volume, 95 cm² surface area, and transparent to incoming PAR). At the start of the incubation, the oxygen concentration of the water inside the chamber was measured using an oxygen optode system (PreSens Fibox 3), with optode sensor spots fixed to the inside chamber wall. Incubations lasted for ~2 h (exact time noted for each incubation), following which a second O₂ concentration measurement was made. Net change in O₂ concentration from the start to the end of the incubation was used to determine the net O₂ flux between the kelp frond and the overlying water column (i.e., net increase in O₂ concentration over time = net O₂ production by the kelp). Net O₂ flux of each plant within each tank was measured on days 1, 2, and 3 of the warming treatments at the same time of day for each sample.

Photophysiological Responses

Chlorophyll-a fluorescence measurements were conducted using Pulse Amplitude Modulation fluorometry, with a Diving-PAM instrument (Walz GmbH) and used to calculate photosynthetic characteristics of the kelp plants. Measurements were taken following previous methodologies and notations (Burdett et al., 2012, 2014). Notation and parameter calculations are provided in **Supplementary Table S1**. A 5-mm-diameter fiber optic probe was used for all measurements, positioned 10 mm from the surface of the kelp plant. Quasi-dark acclimation (Hennige et al., 2008) was achieved by using the “Surface holder” Walz accessory and placing this over the kelp plant for 10 s prior to taking rapid light curve (RLC) measurements – this is known to be sufficient time to achieve results statistically similar to full dark acclimation in a range of marine photosynthetic organisms (Hennige et al., 2008; Burdett et al., 2012). PAM settings were: measuring light intensity = 3, damping = 3, gain = 8, saturation pulse intensity = 2, saturation pulse width = 1.0, and actinic light intensity = 1.

Rapid light curves, where organisms are exposed to pulses of saturating actinic light interspersed with short periods of

increasing levels of irradiance, were conducted on both the basal (meristematic) area and distal (“old” growth) area of the blade. Measurements were obtained (at approximately the same time of day) from each plant on days 1 and 2 of the warming. RLCs have become well established within PAM fluorometry and provide information on energy dissipation from light-limiting through to light-saturating conditions (Ralph and Gademann, 2005). However, due to the short exposure time at each irradiance step, steady-state conditions are not achieved (Ralph and Gademann, 2005). Thus, in contrast to traditional light curves, results from RLCs reflect actual, rather than optimal, photosynthetic state (Ralph and Gademann, 2005), yielding data on dark/light-acclimated minimum fluorescence (F_o and F_o' , respectively), dark/light acclimated maximum fluorescence (F_m and F_m' , respectively), fluorescence under actinic light (F'), and quenched fluorescence [F_q' , defined as $(F_m - F')$]. In this experiment, the RLCs used eight irradiance steps each of 10 s duration ranging from 1 to 569 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$.

Maximum photosynthetic efficiency, F_v/F_m , was defined as $(F_m - F_o)/F_m$. The minimum saturating intensity (E_k – the irradiance level at which light shifts from being photosynthetically limiting to photosynthetically saturating; units = $\mu\text{mol photons m}^{-2}\text{s}^{-1}$) and initial photosynthetic rate [α (no units)] were calculated by fitting RLC data to the irradiance-normalized non-linear least squares regression model of Jassby and Platt (1976) in the R package Phytotools (Silsbe and Malkin, 2015) to describe the light response of quantum efficiency using the following equation:

$$y = (1/x) * \alpha * E_k * \tanh(x/E_k)$$

Where x = PAR levels of each RLC step and $y = F_q'/F_m'$ at each RLC step. All model fits were statistically significant (model p -value < 0.0001 for all). Maximum relative electron transport rate ($rETR_{\text{max}}$) was calculated as $E_k * \alpha$. Effective photochemical efficiency under actinic light (F_q'/F_m') was defined as $F_q'/F_m' = (F_m - F')/F_m'$. Quasi-non-photochemical quenching (NPQ) was defined as $\text{NPQ} = F_m - F_m'/F_m'$ (Bilger and Björkman, 1990) under peak RLC irradiance. A second non-photochemical quenching parameter (qN) is defined as $\text{qN} = F_v'/F_m'$ at each RLC step. Photochemical quenching (qP) is defined as $\text{qP} = F_q'/F_v'$ at each RLC step. F_q'/F_m' , NPQ, qN, and qP were expressed against E/E_k (where E = RLC light level) to assess sample response relative to limiting/optimal/saturating irradiance for photosynthesis when $E/E_k < 1/ = 1/ > 1$, respectively.

Statistical Analysis

Duplicate plants within each tank were treated as subsamples and response variable measurements were averaged across plants to yield a single value per tank; all analyses were conducted with tanks as true replicates. Repeated measure analysis of variance was conducted to examine the effects of temperature treatment (3 levels, fixed), tank (repeated, nested within temperature), and experimental day (3 levels, fixed) on net oxygen production. As each species was experimented on separately in serial manipulations, data on each was analyzed

separately and informal comparisons across species were made. Data were first tested for normality and homogeneity of variance and transformed were necessary. Where significant main effects or interactions were detected (at $p < 0.05$), further pairwise tests (SNK) were conducted to explore further. A similar approach was adopted to examine variability in photophysiological response variables. Data from the basal and distal sections of the blade were analyzed separately using a model similar to that described above: temperature treatment (3 levels, fixed), tank (repeated, nested within temperature), and experimental day (2 levels, fixed).

RESULTS

Experimental Conditions of the Simulated Heat Spike

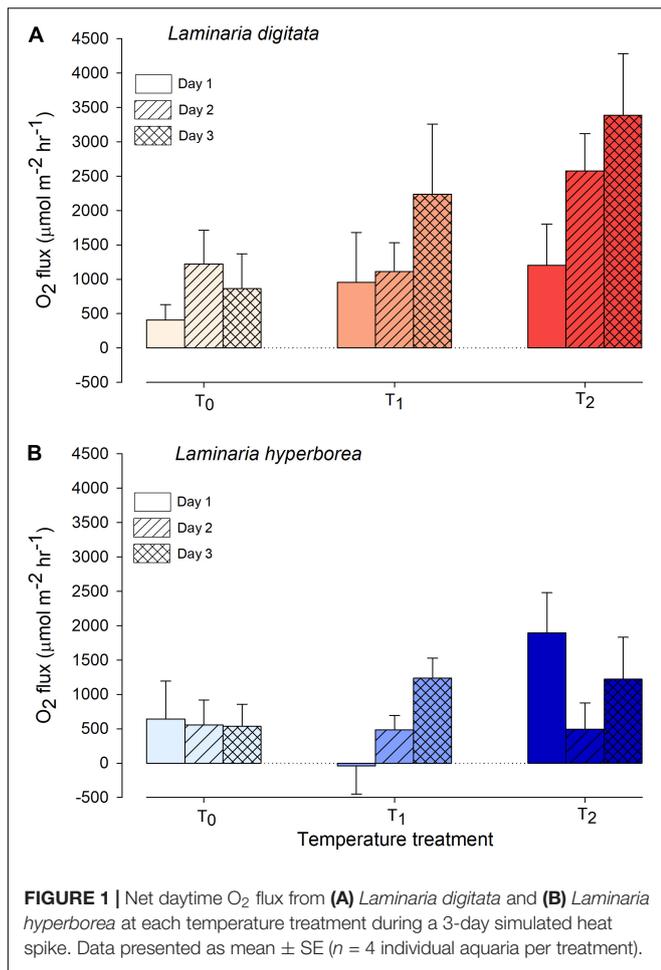
During the first experiment, on *L. digitata*, daily mean temperatures in the treatments during the 3-day warming event were: $T_0 = 15.7 \pm 0.1^\circ\text{C}$, $T_1 = 18.4 \pm 0.0^\circ\text{C}$, and $T_2 = 19.9 \pm 0.0^\circ\text{C}$, which corresponded to ambient conditions, $+2.7^\circ\text{C}$ and $+4.2^\circ\text{C}$ treatments, respectively. In the second experiment, on *L. hyperborea*, daily mean temperatures in the three treatments were: $T_0 = 15.6 \pm 0.1^\circ\text{C}$, $T_1 = 18.3 \pm 0.1^\circ\text{C}$, and $T_2 = 20.1 \pm 0.1^\circ\text{C}$, corresponding to ambient conditions, $+2.7^\circ\text{C}$ and 4.5°C , respectively (Supplementary Figure S1).

Net Oxygen Flux

For *Laminaria digitata*, O_2 production tended to increase with increased temperature and with experimental day (Figure 1). By the third day, net O_2 flux was more than four times greater in the T_2 treatments compared with T_0 (Figure 1). The effect of temperature was statistically significant: pairwise tests showed that O_2 production was greater at T_2 compared with T_0 and T_1 (Table 1). Duration of exposure was also important, as O_2 production was greater on experimental Day 3 compared with Day 1 (Table 1). For *L. hyperborea*, the effect of warming on O_2 production was less evident, with no consistent responses to either temperature treatment or experimental day (Figure 1). Statistically, the interaction term between the main factors was significant (Table 1), with pairwise tests indicating that the effect of temperature treatment was significant on Day 1, but not on Day 2 and 3. By Day 3 of the warming, no differences in net O_2 production between treatments were recorded (Table 1). Informal comparison between the species indicated that O_2 production rates for *L. digitata* were generally greater than *L. hyperborea*, particularly under the higher warming treatments (Figure 1).

Photophysiological Responses

For *Laminaria digitata*, photosynthetic efficiency (F_v/F_m) values were relatively consistent between factors, with mean values ranging from ~ 0.72 to ~ 0.74 (Figure 2). For basal blade tissue, we recorded a significant effect of experimental day as F_v/F_m values were lower, overall, on Day 2 (Table 2). For distal blade tissue, no significant variability was detected (Table 2). For *L. hyperborea*, mean F_v/F_m was higher, ranging from ~ 0.74



to 0.76 (Figure 2). For both basal and distal blade tissue, no significant effects of time or temperature were recorded (Table 2). Overall, F_v/F_m values were slightly lower for *L. digitata* compared with *L. hyperborea* (Figure 2). A similar pattern was observed for alpha (α), a measure of initial photosynthetic rate, in that the basal blade tissue of *L. digitata* exhibited the greatest response, with a general decline in α with increasing temperature and significantly lower values on Day 2 of experimentation (Supplementary Table S2 and Supplementary Figure S2).

For *Laminaria digitata*, saturation intensity (E_k) measured on basal blade tissue varied markedly between experimental days, with overall values on Day 2 being significantly higher than on Day 1 (Figure 3 and Table 2). There was a general increase in E_k with increasing temperature treatment, although between-sample variability meant that this trend was not significant. For distal blade tissue, E_k values were relatively consistent between temperature treatments and days (Figure 3). For *L. hyperborea*, E_k values measured in basal blade tissue were relatively consistent across treatments and days, and no significant effects were detected (Figure 3 and Table 2). In contrast, E_k values measured in distal blade tissue varied markedly between days, with overall values on Day 2 being significantly lower than on Day 1 (Figure 3 and Table 2). A similar pattern was observed for maximum relative electron transport rate (rETR_{max}; Supplementary Table S2 and Supplementary Figure S3).

When $E/E_k = 1$, the RLC light level is “optimal” and neither saturating nor limiting. Under limiting light levels (and up to $E/E_k \sim 0.5$), effective photochemical efficiency under actinic light (F_q'/F_m') was between 0.7 and 0.8, suggesting a 70–80% photosynthetic efficiency. When $E/E_k = 1$, despite being theoretically optimal, F_q'/F_m' and photochemical quenching (qP) had decreased from initial values by ~20–30% reaching a minimum when RLC light levels were $\sim 10 \times E_k$ (Figure 4). For non-photochemical quenching (qN and NPQ), a slight increase began at $E/E_k = 0.1$, rising rapidly at $E/E_k > 1$ and reaching a maximum at $E/E_k = \sim 10$, although this was characterized by a wide variability (Figure 4). *L. digitata* tended to have higher qN and NPQ values across a wider range of E/E_k (Figure 4).

DISCUSSION

We examined sub-lethal photophysiological responses of two canopy-forming kelp species to a short-term acute warming event. In terms of net oxygen flux in the light (i.e., net photosynthesis), *L. digitata* exhibited a significant ecophysiological response, whilst *L. hyperborea* appeared less sensitive with no apparent effect on net photosynthesis. Investigation of the associated photosynthetic characteristics revealed no significant trends in either species as a result of warming, despite the significant increase in net oxygen release in *L. digitata*. This suggests these kelp species exhibit a degree of photophysiological resilience to short-term acute warming.

TABLE 1 | The effect of temperature treatment, tank and experimental day on net oxygen flux as determined by RM ANOVA for both *Laminaria digitata* and *Laminaria hyperborea*.

Spp	Temp [2]			Tank (Temp) [9]		Day [2]			Temp × Day [4]			Res [18]
	MS	F	P	MS	MS	F	P	MS	F	P	MS	
LD	7.3×10^6	9.73	0.006	7.6×10^5	5.1×10^6	4.39	0.028	1.1×10^6	0.97	0.446	1.2×10^6	
	Pairwise tests; temp: $T_0 = T_1 < T_2$. Day: $3 > 1, 3 = 2, 2 = 1$											
LH	1.6×10^6	2.76	0.116	5.7×10^5	7.3×10^5	1.89	0.109	1.4×10^6	3.72	0.007	2.9×10^5	
	Pairwise tests; interaction: Day 1: $T_0 = T_1 < T_2$. Day 2: $T_0 = T_1 = T_2$. Day 3: $T_0 = T_1 = T_2$											

P-values shown in bold are significant (at $P < 0.05$); pairwise tests (SNK) were conducted as necessary. “Spp,” species (LD, *Laminaria digitata*; LH, *Laminaria hyperborea*); “Res,” residual. Degrees of freedom (df) associated with each factor are shown in squared brackets.

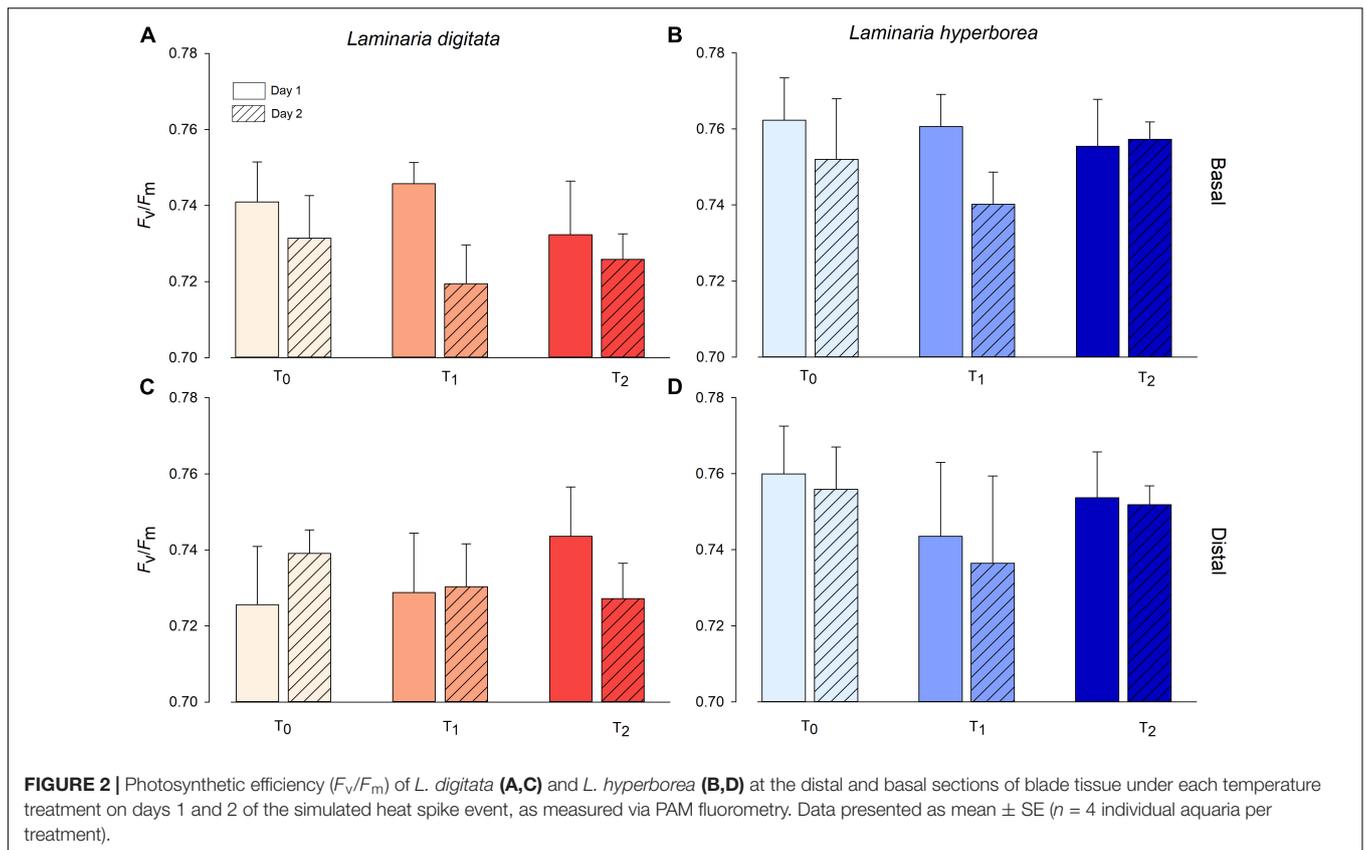


TABLE 2 | The effect of temperature treatment, tank and experimental day on F_v/F_m and E_k , as determined by RM ANOVA for *Laminaria digitata* and *Laminaria hyperborea* for both basal and distal blade tissue.

Spp	Var	Sect	Temp [2]			Tank (Temp) [9]			Day [1]			Temp \times Day [2]			Res [9]
			MS	F	P	MS	MS	F	P	MS	F	P	MS		
LD	F_v/F_m	Basal	9.0×10^{-5}	0.54	0.599	1.7×10^{-4}	1.2×10^{-3}	15.07	0.004	2.2×10^{-4}	2.79	0.114	8.0×10^{-5}		
		Distal	5.0×10^{-5}	0.19	0.834	2.8×10^{-4}	3.7×10^{-7}	0.01	0.969	3.0×10^{-4}	1.28	0.323	2.3×10^{-4}		
	E_k	Basal	118.3	1.26	0.327	93.2	954.7	17.61	0.002	21.0	0.38	0.689	54.2		
		Distal	199.1	1.63	0.248	121.9	104.6	2.63	0.139	118.8	2.99	0.101	39.6		
Pairwise tests: F_v/F_m basal; Day: 1 > 2															
E_k basal; Day: 1 < 2															
LH	F_v/F_m	Basal	1.1×10^{-4}	0.31	0.741	3.7×10^{-4}	4.2×10^{-4}	3.00	0.117	3.4×10^{-4}	2.38	0.147	4.2×10^{-4}		
		Distal	6.8×10^{-4}	2.46	0.140	2.7×10^{-4}	1.1×10^{-4}	0.23	0.644	1.3×10^{-5}	0.02	0.973	4.9×10^{-4}		
	E_k	Basal	108.5	0.87	0.452	124.7	18.9	0.51	0.492	2.7	0.07	0.929	36.9		
		Distal	490.0	3.42	0.078	143.2	1036.7	39.48	0.001	72.3	2.75	0.117	160.2		
Pairwise tests: E_k distal; Day: 1 > 2															

P-values shown in bold are significant (at $P < 0.05$); pairwise tests (SNK) were conducted as necessary. "Spp," species (LD, *Laminaria digitata*; LH, *Laminaria hyperborea*); "Var," response variable; "Sect," section; "Res," residual. Degrees of freedom (df) associated with each factor are shown in squared brackets.

Temperature Responses

Up to a certain threshold, increasing temperature is expected to increase macroalgal oxygen production, due to higher electron transport rate through the photosystems (Delebecq et al., 2016). This trend was clearly observed for *L. digitata*, even after just 3 days of acute exposure to the high-magnitude T_2 warming treatment. Chronic, longer-term exposure to the absolute temperatures used here for the warming treatments

(i.e., ~ 18 – 20°C) is known to result in reduced ecophysiological performance (Simonson et al., 2015; Hargrave et al., 2017), increased mortality (Bartsch et al., 2013; Wilson et al., 2015), and consequent population-level impacts (Raybaud et al., 2013) for *L. digitata*, reinforcing the sensitivity of this species to elevated temperature. In contrast to *L. digitata*, a consistent oxygen production response was not observed in *L. hyperborea*, suggesting a degree of variability and/or insensitivity to

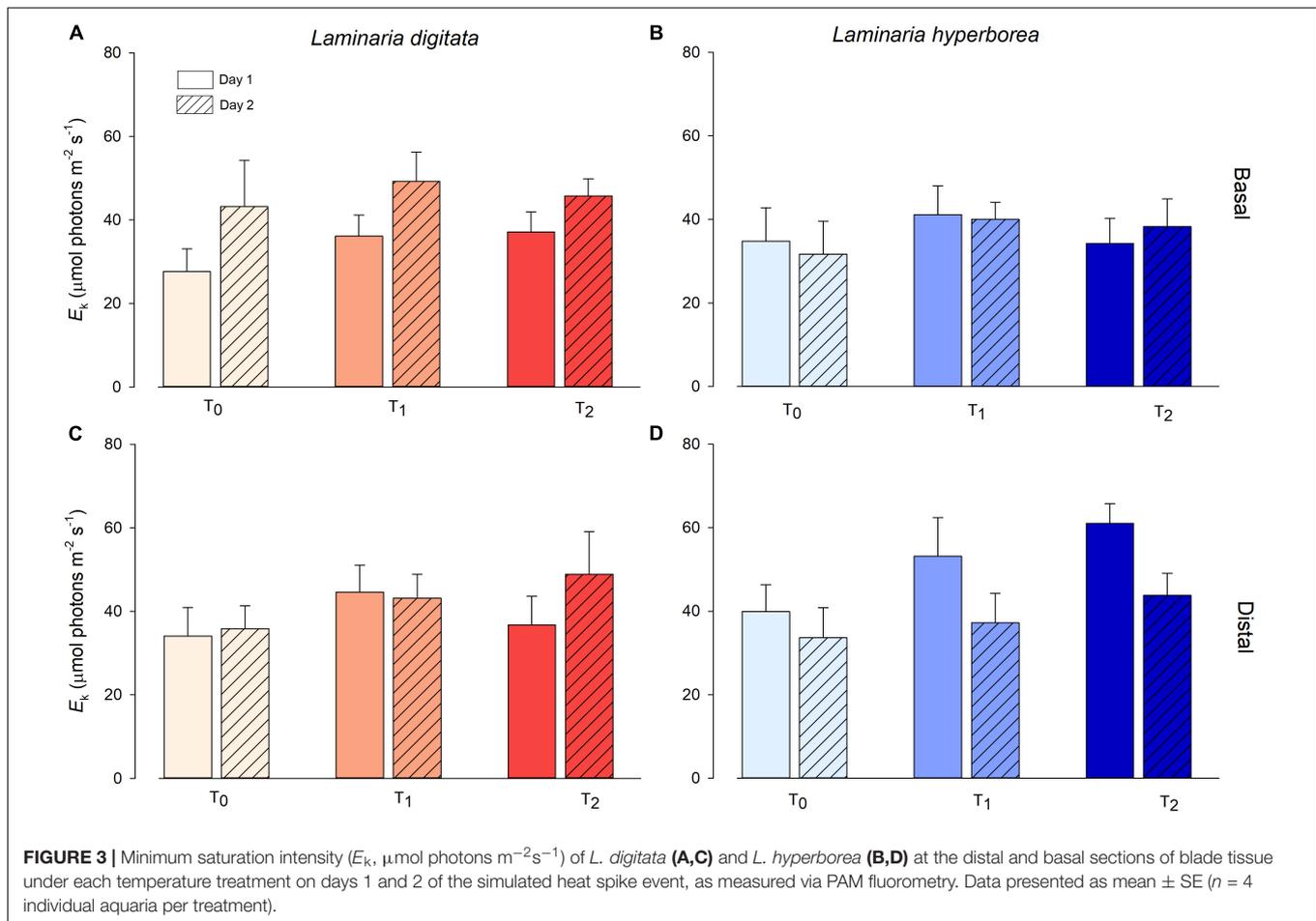


FIGURE 3 | Minimum saturation intensity (E_k , $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) of *L. digitata* (A,C) and *L. hyperborea* (B,D) at the distal and basal sections of blade tissue under each temperature treatment on days 1 and 2 of the simulated heat spike event, as measured via PAM fluorometry. Data presented as mean \pm SE ($n = 4$ individual aquaria per treatment).

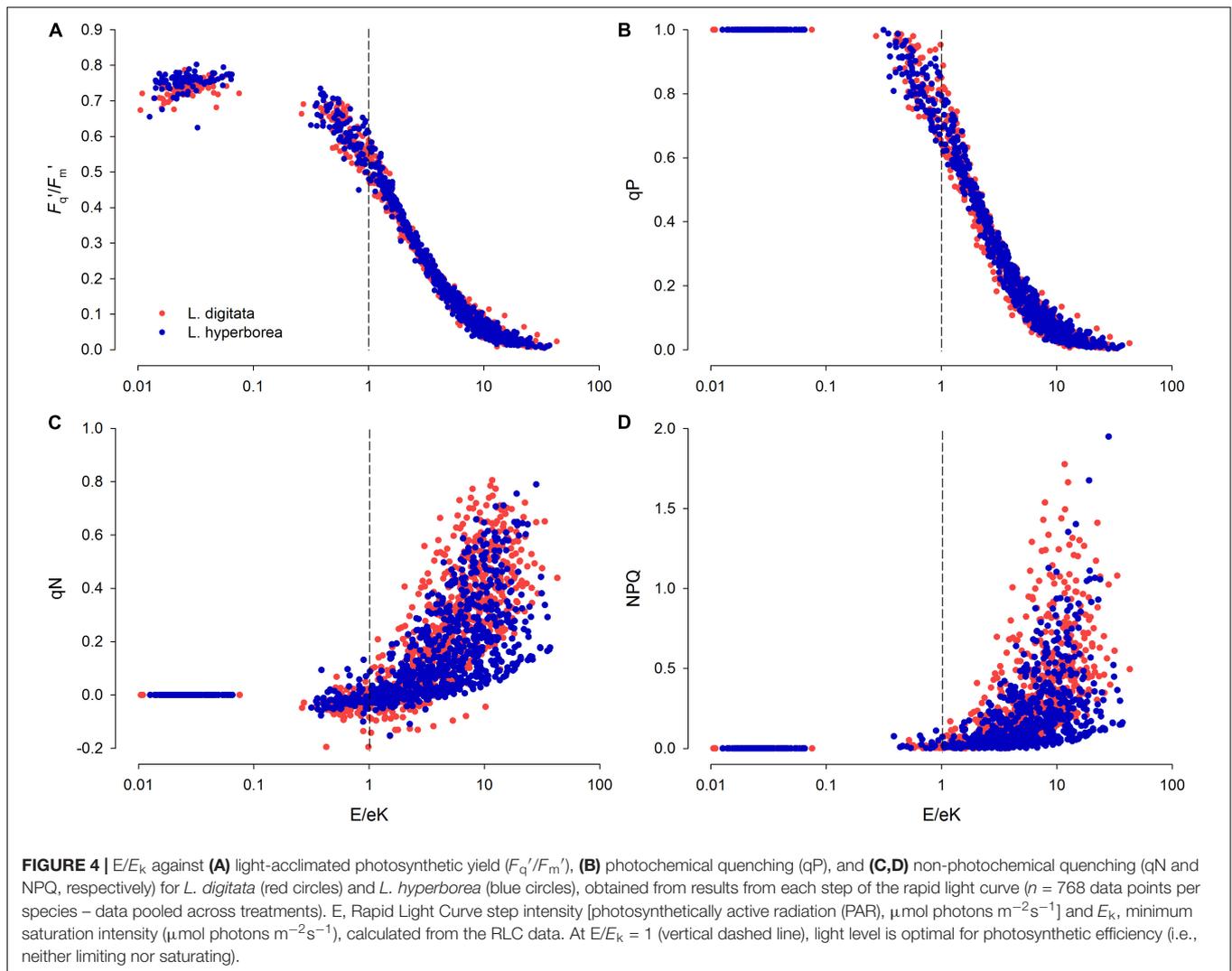
the temperature increases tested in this study. Oxygen flux measurements are only available in the light, preventing an assessment of net respiration rates. While this limits the extent of physiological insight, it does not diminish the significant trends in daytime net oxygen flux under simulated warming event. In the field, this physiological response could have significant biogeochemical implications since macrophytic photosynthesis is also major driver of daytime oxygen elevation in coastal systems (Burdett et al., 2013; Attard et al., 2015). In the absence of dark net respiration rates it is not yet possible to determine the full effect a warming event might have on the magnitude of diel oxygen variation. Interestingly, despite a significant response in net daytime oxygen production, no significant response in photosynthetic characteristics were observed in either species, suggesting that during acute, short-term warming events core photophysiological processes can be maintained with only a physiological response. Trends in F_v/F_m , E_k and rETR_{max} suggest that increased temperature may have increased the electron transport rate through photosystem II and reduced photosynthetic, but not to such an extent as to be beyond the natural between-plant variability and temperature-driven increase in oxygen-flux kinetics.

The insensitivity of photosynthetic characteristics to elevated temperature allows us to compare the two species responses.

Via an elevated and more light-responsive non-photochemical quenching response (an effective method for dissipating excess absorbed energy), *L. digitata* may have a greater potential capacity for photo-protection. This was driven by an elevated maximal fluorescence (F_m') – which can also correspond to an up-regulation of photo-protective xanthophyll cycling (Lavaud et al., 2002). Further pigment-level analyses would be required to confirm this mechanism. For *L. digitata*, experimental day also had an effect on the photosynthetic characteristics of the basal tissue. The meristoderm of kelps (the peripheral layer of photosynthetically active cells of the basal tissue) is known to be highly biogeochemically active and capable of accumulating significant iodine concentrations (Küpper and Carrano, 2019). Such biogeochemical activity may increase the sensitivity of this tissue to altered environmental conditions (whether via experimental treatment or laboratory conditions) leading to the integrated observational response seen in this study.

Ecological Implications

Laminaria digitata and *Laminaria hyperborea* are critical components of coastal marine ecosystems in the NE Atlantic, as they provide complex habitat for a wide range of associated flora and fauna (Blight and Thompson, 2008; Schaal et al., 2016; Teagle et al., 2018) and exhibit high rates of carbon



capture and release (Schaal et al., 2009; Hereward et al., 2018; Pessarrodona et al., 2018). Recent and projected warming trends have been linked with population losses and range contractions at the equatorward limit of the distributions of both *L. digitata* (Raybaud et al., 2013) and *L. hyperborea* (Voerman et al., 2013; Casado-Amezúa et al., 2019) in France and Spain/Portugal, respectively. Prolonged exposure to warmer-than-average sea temperatures can manifest in responses at the organism level, such as decreased growth (Hargrave et al., 2017), and at the population level, such as reproductive failure (Bartsch et al., 2013). Similarly, exposure to acute air temperature stress during periods of low-tide emersion can have impacts at the physiological and individual level (King et al., 2018b). Ultimately, warming can lead to the loss of kelp populations at the range edge, with subsequent shifts in the structure of communities (Voerman et al., 2013) and even ecosystems (Wernberg et al., 2016).

The scale of the heating spike simulated in this study (in terms of duration and magnitude) is frequently observed in the study region, which experiences short-term temperature variability as

well as longer-lasting MHW events (Joint and Smale, 2017; Brewin et al., 2018). Both species exhibited photophysiological resilience to an acute period of high temperature; short-lived warming events may therefore not physiologically impact these kelp species. The significant increase in net daytime oxygen flux by *L. digitata* suggests that this species has a lower sensitivity threshold, perhaps because it is near the southerly range edge of its distribution, and already under physiological pressure. It is likely that increased exposure to acute warming events (whether seawater or air temperatures) combined with longer-term exposure to gradual increases in mean sea temperature, will negatively impact range edge populations, leading to shifts in the species distribution and altered community structure (Raybaud et al., 2013; Filbee-Dexter et al., 2016). However, it should be noted that this study was conducted on single populations over a single event and did not account for any local adaptation that could lead to between-population variability in thermal tolerance. Indeed, thermal divergence between populations has been shown for several kelp species (Gerard and Du Bois, 1988; King et al., 2019) and may be commonplace in marine macrophyte

species more generally (King et al., 2018a). Clearly, further work comparing photophysiological responses to temperature across multiple populations within these species' ranges and in response to varied temperature regimes is needed to confirm the photophysiological resilience of these species to the chronic and acute ocean warming projected for the coming decades. Recent advances *in situ* experimentation via manipulation of environmental conditions within an incubation chamber (e.g., Gattuso et al., 2014; Burdett et al., 2018) provide the opportunity to conduct comparable experiments with reduced laboratory artifacts and the capacity to investigate these questions at the organism to community scale.

Canopy-forming kelp species are vital components of mid and high-latitude coastal ecosystems, underpinning core ecological processes such as primary productivity, trophic connectivity and habitat provision (Blight and Thompson, 2008; Smale et al., 2013). As macroalgal species' distributions are strongly constrained by temperature, recent warming trends have driven shifts in their geographical ranges (e.g., Raybaud et al., 2013; Schaal et al., 2016; Pessarrodona et al., 2018) and projected warming will continue drive changes in the coming decades (Müller et al., 2009; Hereward et al., 2018). MHW events further compound decadal-scale ocean warming by exerting acute and intense stress onto organisms, populations, communities, and ecosystems. Projected increases in MHW activity in coming decades (Frölicher et al., 2018) will likely coincide with current kelp population distributions. This study suggests that those populations near their upper thermal limit may be most affected (i.e., equator range edge – *L. digitata* in this study) because of a slight increase in photophysiological sensitivity. Prolonged or repeated responses in terms of net oxygen production may provide short-term metabolic benefits in some species (via increased oxygen production), but also increased energy use and

demand in the longer term. A deeper mechanistic understanding of ecophysiological responses to increased temperature is needed to better predict near-future impacts of ocean warming on kelp populations and communities.

DATA AVAILABILITY

All datasets generated for this study are included in the manuscript and/or the **Supplementary Files**.

AUTHOR CONTRIBUTIONS

HB and DS co-designed the experiment and analyzed the data. All authors performed the experiment, took the samples, made measurements, and wrote the manuscript.

FUNDING

This research was supported by a Marine Biological Association Ray Lankester Investigatorship awarded to HB and was conducted whilst DS was in receipt of a Natural Environment Research Council Independent Research Fellowship (NE/K008439/1).

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2019.00516/full#supplementary-material>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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