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INTRA-ANNUAL VARIABILITY IN RESPONSES OF A CANOPY FORMING KELP TO CUMULATIVE LOW TIDE HEAT STRESS: IMPLICATIONS FOR POPULATIONS AT THE TRAILING RANGE EDGE[1]

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Anthropogenic climate change is driving the redistribution of species at a global scale. For marine species, populations at trailing edges often live very close to their upper thermal limits and, as such, poleward range contractions are one of the most pervasive effects of ongoing and predicted warming. However, the mechanics of processes driving such contractions are poorly understood. Here, we examined the response of the habitat forming kelp, *Laminaria digitata,* to realistic terrestrial heatwave simulations akin to those experienced by intertidal populations persisting at the trailing range edge in the northeast Atlantic (SW England). We conducted experiments in both spring and autumn to determine temporal variability in the effects of heatwaves. In spring, heatwave scenarios caused minimal stress to *L. digitata* but in autumn all scenarios tested resulted in tissue being nonviable by the end of each assay. The effects of heatwave scenarios were only apparent after consecutive exposures, indicating erosion of resilience over time. Monthly field surveys corroborated experimental evidence as the prevalence of bleaching (an indication of physio logical stress and tissue damage) in natural populations was greatest in autumn and early winter. Overall, our data showed that *L. digitata* populations in SW England persist close to their upper physiological limits for emersion stress in autumn. As the intensity of extreme warming events is likely to increase with anthropogenic climate change, thermal conditions experienced during periods of emersion will soon exceed physiological thresholds and will likely induce widespread mortality and consequent changes at the population level.

Increased temperature associated with anthropogenic climate change has driven shifts in the distributions of many species as they track optimal thermal habitat (Parmesan et al. 1999, Chen et al. 2011, Poloczanska et al. 2013). While gradual, (mostly) poleward shifts in species' ranges may occur in response to decadal-scale warming trends, short-term extreme warming events can drive rapid stepwise shifts in species' distributions (Jentsch et al. 2007). Discrete extreme warming events (i.e., heatwaves), which are increasing in duration, frequency or intensity in many regions (Coumou and Rahmstorf 2012, Perkins et al. 2012, Oliver et al. 2018), are gaining recognition as forceful agents of ecological change. In terrestrial ecosystems atmospheric heatwaves have caused widespread mortality and consequent range contractions for trees and plant species (Ruthrof et al. 2018). Similarly, in ocean systems, marine heatwaves have decimated populations of seaweeds, invertebrates, fish, and sea birds (Garrabou et al. 2009, Pearce and Feng 2013, Smale and Wernberg 2013, Jones et al. 2018, Smale et al. 2019). However, despite their pervasive nature, a mechanistic understanding of how short-term warming events drive ecological change is lacking, which limits our ability to better predict the wider ecological consequences of climate change.

While adaptation to local conditions (Sanford and Kelly 2011, Valladares et al. 2014, Bennett et al.

2015, King et al. 2017a) or heterogeneous patterns of stress intensities (Helmuth et al. 2006, Lourenço et al. 2016) can complicate ecological responses to climatic changes, range-edge populations are generally the most vulnerable to warming (Hampe and Petit 2005, Chen et al. 2011, Smale et al. 2019). At trailing edges, temperatures experienced during heatwaves can often exceed a species' physiological limits, resulting in widespread mortality and stepwise range contractions (Wernberg et al. 2016, Hughes et al. 2017). Moreover, if the species affected by extreme temperatures is an ecologically important foundation species, indirect effects of local extirpation may manifest at the ecosystem level (Thomson et al. 2015, Wernberg et al. 2016). So far, experimental studies have overwhelmingly focused on summer extremes (e.g., Hamerlynck et al. 2000, Van Peer et al. 2004), as this is when any given species' absolute maximum thermal limit is most likely to be exceeded. However, periods of anomalously high temperatures relative to the seasonal climatological average can occur at any time of the year. This may be important as acclimation to lower ambient temperatures during cooler times of year, which could reduce thermal tolerance, is a well-known phenomenon that has been observed in a multitude of taxa (plants - Badger et al. 1982, seaweeds - Lüning 1984, fish - Bulger and Tremaine 1985, crustaceans - Layne et al. 1987, molluscs - Chapple et al. 1998, corals - Berkelmans and Willis 1999, insects - Hu and Appel 2004). Therefore, ecological responses to anomalously high temperatures could occur outside of periods of peak ambient temperatures (i.e., summer), but intra-annual variability in responses to realistic extreme warming events have rarely been examined.

Kelps (large brown seaweeds mostly of the order Laminariales) dominate temperate and subpolar rocky reefs and underpin some of the most productive and diverse ecosystems on Earth (Steneck et al. 2002). As their geographic distributions are largely constrained by temperature, kelps are particularly sensitive to warming trends (Eggert 2012). In recent decades both gradual increases in mean temperature (Viejo et al. 2011) and extreme warming events (Smale and Wernberg 2013) have caused high mortality, population declines and local extirpation at trailing edges for several species and in several regions (e.g., Cosson 1999, Raybaud et al. 2013). To date, most studies examining the responses of kelps to warming events, based on either controlled experiments or field observations, have focused on increased seawater temperatures (Wernberg et al. 2013, Reed et al. 2016, Hargrave et al. 2017). However, populations of several kelp species persist at the low intertidal fringe and are exposed to air temperatures multiple times over a spring-neap tidal cycle. Therefore, environmental conditions experienced during periods of emersion can also play a critical role in setting vertical (Flores-Molina et al.

2014, King et al. 2017b) and latitudinal (Martínez et al. 2012, López-Cristoffanini et al. 2013) distributions, and anomalously high air temperatures associated with atmospheric heatwaves could induce physiological stress, mortality and population declines.

We examined the response of the kelp *Laminaria digitata* to realistic simulations of thermal stress experienced during atmospheric heatwaves occurring over periods of spring low tides. Across the North Atlantic, *L. digitata* functions as a foundation species on shallow rocky reefs by providing biogenic habitat, altering environmental conditions, and increasing benthic primary production (Schultze et al. 1990). In the northeast Atlantic, it is distributed from the Arctic southwards to its trailing range edge in northwest France, which is characterized by a similar thermal environment to southwest England (the location for the current study). *Laminaria digitata* has declined in abundance at the trailing range edge in recent decades and much of its southern extent is predicted to disappear by 2100 (Cosson 1999, Raybaud et al. 2013, Smale et al. 2013, Assis et al. 2018). In this region, *L. digitata* inhabits the low intertidal fringe and, as such, is typically exposed to air temperatures for 1-2 hours, twice a day, for ~4 consecutive days during periods of spring low tides. We used this as a basis to investigate the effects of realistic heatwave scenarios in both March (i.e., in spring, before annual maximum temperatures) and October (i.e., in autumn, after annual maximum temperatures) to examine temporal variability in responses to extreme warming events.

MATERIALS AND METHODS

Multiple, mature, medium-sized (stipe length > 20 cm) *Laminaria digitata* sporophytes were haphazardly collected from the low rocky shore at Wringcliff Bay, southwest England, United Kingdom (Fig. 1a), during low tide periods of emersion in both October 2016 and March 2017. Sporophytes were kept in cool, aerated seawater and immediately returned to the laboratory, where they were held in 150 L tanks for an acclimation period of 7 days. Holding tanks were maintained at ambient sea temperatures (10°C in March and 15°C in October) using aquarium chillers (DC- 750, Deltec, Delmenhorst). These ambient water temperatures were chosen to reflect actual sea temperatures that natural populations experience during each month (Fig. 1b). Our aim was to simulate realistic conditions with ecological relevance, rather than to repeat the same treatments at two different times. As such, *absolute* temperatures (both seawater and air) differed between the two experiments whereas the *relative* intensity of warming treatments were kept consistent (see below). March and October were chosen to represent typical conditions in spring and autumn, respectively. During these seasons, periods of emersion during low spring tides (and therefore exposure to air temperatures) are greatest. 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 freshwater as necessary; lamps (Reef Daylight T8 36 W, Interpret, Dorking)
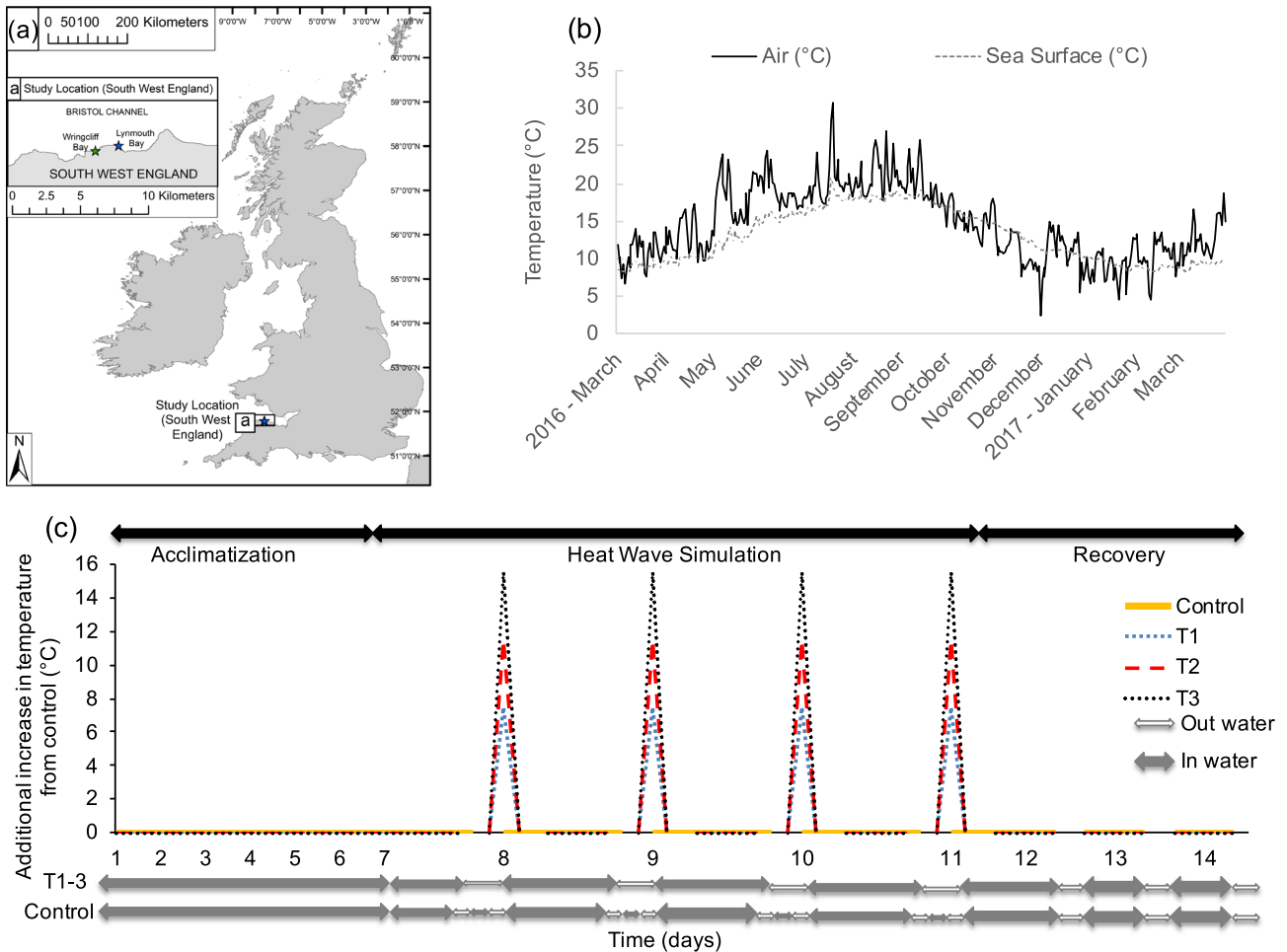
FIG. 1. Study location, climatology, and experimental approach. (a) Map indicates study region and specific location of study sites in North Devon, UK. (b) Maximum air temperature (daily mean temperature 0900-0900) and maximum sea surface temperature within the study region during the experimental period (air temperature data provided by the National Meteorological Library and Archive, Met Office, UK and sea surface temperature data courtesy of Channel Coastal Observatory, England, UK, www.channelcoast.org). (c) Graphical representation of experimental approach used to examine the effect of atmospheric heatwaves on *Laminaria digitata*. Experiments involved 7 days of acclimatization to seasonally adjusted ambient sea temperatures, followed by 4 days of heatwave simulation and a 3-day recovery period. During the heatwave simulation, *Laminaria digitata* tissue was consecutively exposed to one of four temperature treatments for 1 h before being returned to ambient seawater to simulate the returning tide.

specifically designed for aquatic plants were used to generate a 12:12 h light:dark regime with PAR irradiance levels of ~100 μmol photons · m^{-2} · s^{-1} (recorded with an Odyssey PAR meter). For experimentation, discs of tissue (area 8 cm^2) were excised from epiphyte-free sections of blade tissue found immediately above the meristematic region, using a cork borer. All stress assays described below were performed on individual discs, with responses assumed to reflect that of the wider sporophyte; a well-established approach in phycological research (García-Mendoza and Colombo-Pallotta 2007, Henkel and Hofmann 2008, Pearson et al. 2009, Rothäusler et al. 2009, Jueterbock et al. 2014). Discs were placed in individual sampling pots with holes in the lids to allow free water movement for the duration of the experiment.

From each individual sporophyte four discs were excised, with each being assigned to one of four experimental treatments. Treatments were designed to simulate stress from short-term exposure to air temperatures during periods of low tide emersion, experienced over consecutive days, interspersed with longer periods of immersion in seawater held at typical temperatures. As such, the experiment tested for the effects of consecutive exposures to an atmospheric heatwave, rather than a marine heatwave (sensu Hobday et al. 2016). Treatments involved short-term exposure to one of three air temperatures (Fig. 1c); T1 (7.5°C above control), T2 (11.5°C above control) and T3 (15.5°C above control), as well as a control set of discs (C; held in seawater except briefly to take measurements described below). The experiments described below were repeated in both March and October, which differ in terms of climatological average temperatures (Fig. 1b). As such, in March the absolute temperatures used were: ambient control = 10.5°C, T1 = 18.0°C, T2 = 22.0°C and T3 = 26.0°C; whereas in October absolute temperatures were: ambient control = 14.5°C, T1 = 22.0°C, T2 = 26.0°C and T3 = 30.0°C. Both the absolute and relative increases in temperature were chosen to represent realistic conditions experienced by natural populations in the study region during atmospheric heatwaves (Fig. 1b; Hereward et al. 2018). For example, air temperatures can exceed 20°C and 27°C in both March and October respectively (Fig. 1b).

For each treatment, discs were removed from seawater tanks, blotted dry and placed in incubators held at the temperatures described above for one hour, simulating low tide emersion stress ($n = 5$ discs for each treatment). Discs were then returned to seawater tanks for 24 h to simulate the returning tide. Exposure to the air temperature treatments was repeated for four consecutive days, to simulate emersion patterns during periods of spring low tides. Following 4 days of emersion treatments, a 3-day 'recovery' phase was conducted whereby discs were held in seawater tanks at control temperatures to monitor post-heatwave response patterns. Response variables (F_v/F_m and fresh weight, see below) were measured immediately before and after exposure treatments and once a day during the recovery phase. Stress was measured as maximum quantum yield (F_v/F_m) of photosystem II (PSII) using a Pocket PEA chlorophyll fluorimeter (Hansatech Instruments Ltd, Norfolk, UK). The maximum quantum yield of PSII (i.e., the ratio of photochemical quenching, F_v, to total fluorescence from closed PSII reaction centers, F_m) is proportional to its efficiency (Butler 1978). F_v/F_m is an established method to quantify physiological responses of seaweeds, with a value of < 0.6 indicative of stress (Pearson et al. 2009, Jueterbock et al. 2014, Saada et al. 2016, King et al. 2017b). Before all F_v/F_m measurements were taken, discs were dark adapted for 15 minutes. At the end of the experiment, each disc was photographed, and the area of bleached material quantified using Image J (National Institutes of Health, USA). If the whole disc was no longer a healthy color (i.e., light green) it was scored as 100% bleached. Discs were then dried (60°C for 48 h) to determine the dry weight, from which desiccation rates and relative water content (RWC) were determined using:

$$RWC = [(TW - DW)/(FW - DW)] \times 100$$

where TW is wet weight of treated kelp; FW is initial fresh weight of fully hydrated kelp (pre-treatments); DW is dry weight of kelp disc.

To place experimental results into a wider context, field surveys of natural *Laminaria digitata* populations were also conducted at two sites in southwest England (Wringcliff Bay and Lynmouth Bay; Fig. 1a). Both sites support dense and extensive stands of *L. digitata* (Hereward et al. 2018). Surveys were conducted each month (i.e., on spring low tides) over a year to quantify levels of in situ bleaching. Ten sporophytes were haphazardly chosen during each survey; bleaching levels were determined using a semiquantitative severity index (Table 1). We developed and used the index as it allowed for rapid nondestructive assessment of bleaching of entire plants. Surveys were conducted at the same tidal height and within a similar area on the shore (fixed using GPS), but different sporophytes were sampled each time to achieve independence.

TABLE 1. Semiquantitative bleaching severity index used to quantify in situ bleaching of mature *Laminaria digitata* sporophytes at two study sites in North Devon, UK.

Level of bleaching	Description of bleaching
0	No bleaching
1	Tinge – tinges of bleaching
2	Edge - <25% bleached from edge of some blade fronds
3	Edge – ≥ 50% bleached from edge of some blade fronds
4	Patchy bleaching across whole kelp blade
5	Totally bleached

Statistical analysis. As the absolute temperatures used for each treatment varied between months, data from the two experiments were analyzed separately. We formally tested for the effects of Temperature (4 levels: C, T1, T2 and T3) and Time (11 time points) within each experiment, and then informally compared the magnitude of responses between experiments. F_v/F_m and RWC values were analysed separately using Repeated Measures Analysis of Variance (RM ANOVA) in SPSS v.25 (IBM). Models had two factors: Temperature treatment (4 levels: C, T1, T2 and T3) and Time (11 time points). Residuals were first visually examined to check for normality. Where the assumption of sphericity was violated (Mauchly's test), degrees of freedom were modified with Greenhouse–Geisser corrections. Where significant differences were detected, post hoc pair-wise tests were conducted to facilitate interpretation of the RM ANOVA results (t-test with Bonferroni correction). Data on the proportion of discs bleached at the end of the experiments were arcsine transformed and then analysed with a one-way ANOVA with the single factor of Temperature (4 levels: C, T1, T2 and T3).

RESULTS

In March, the 18°C (T1) and 22.0°C (T2) treatments had very little effect on F_v/F_m values, which remained markedly similar to control values before and after each emersion period, as well as during the recovery phase (Fig. 2). The 26.0°C (T3) treatment had a notable effect following emersion on Day 3 and Day 4, but F_v/F_m values for experimental discs returned to control values during the recovery phase (Fig. 2). In October, however, responses differed markedly, as F_v/F_m declined sharply after Day 3 of emersion shock in all treatments (T1 = 22.0°C, T2 = 26.0°C and T3 = 30.0°C). All the tissue discs failed to recover and F_v/F_m declined to zero by the end of the experiment in all treatments, indicating that tissue was non-viable (Fig. 2). Statistically, we recorded highly significant effects of all main factors and their respective interactions (Table 2). The 2-way interactions were highly significant in both months, as time effects (i.e., before/after emersion shock, start/end of experiment) varied between temperature treatments but the magnitude of this pattern varied between seasons (Table 3).

In March, all temperature treatments had a notable effect on RWC, which decreased with time, particularly in the 22.0°C (T2) and 26.0°C (T3) treatments (Fig 3). The consecutive emersion shocks had a marked effect on RWC, with water content dropping to ~60% and ~40% in the 22.0°C (T2) and 26.0°C (T3) treatments, respectively (Fig. 3). Although some recovery was apparent, RWC values did not return to control levels following cumulative shocks (Fig. 3). In October, a similar pattern was observed although the magnitude of impact and decline in RWC was more pronounced in all 3 treatments (T1 = 22.0°C, T2 = 26.0°C and T3 = 30.0°C; Fig. 3). Statistically, we again recorded highly significant effects of all main factors and their respective interactions (Table 4). The 2-way interactions were indicative of time effects varying
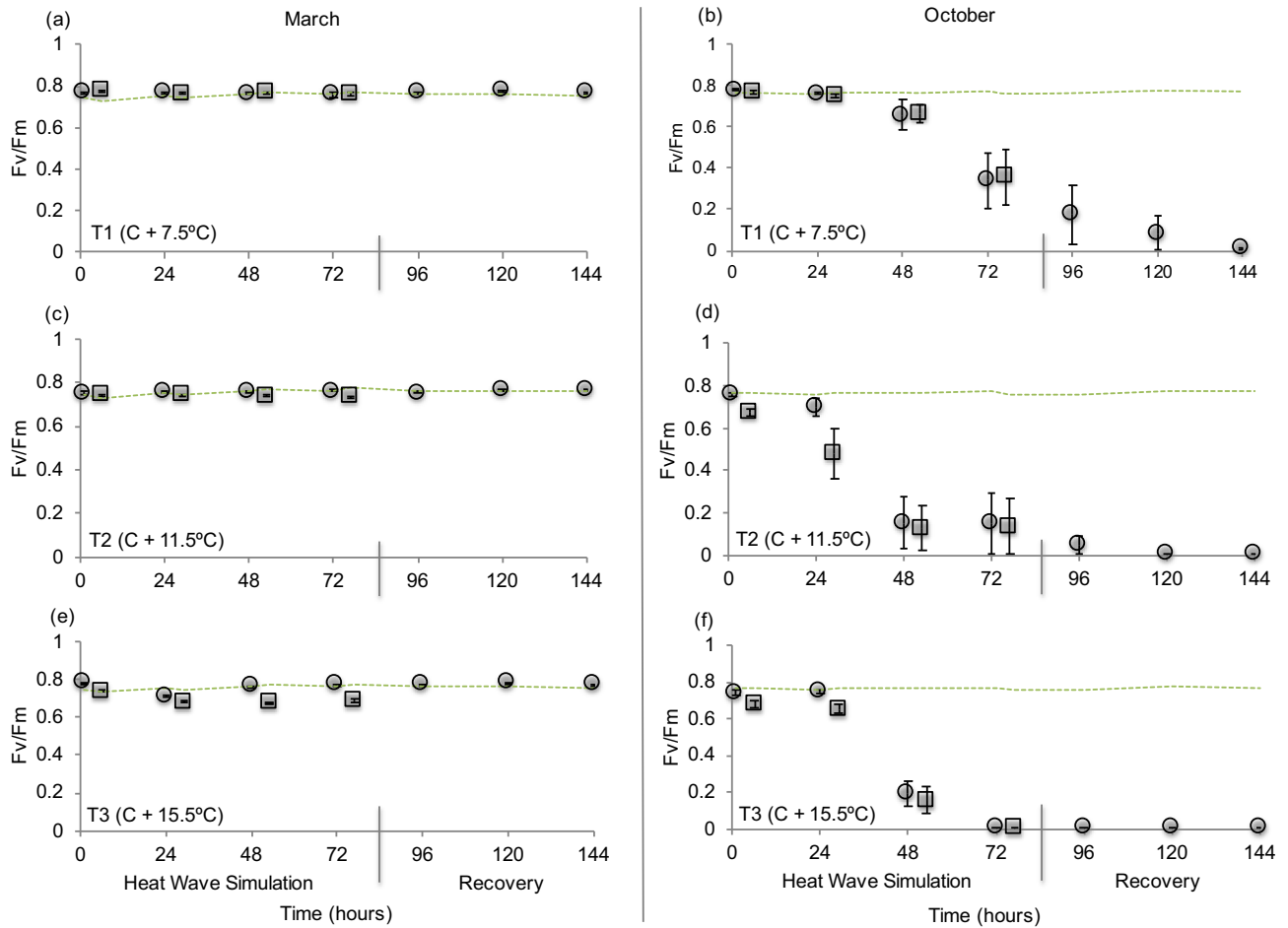
Fig 2. Mean F_v/F_m values ($n = 5$, $\pm$ SE) recorded during spring (left) and autumn (right) experiments, whereby tissue discs were exposed to consecutive 1 h emersion treatments: (a + b) T1 (control temperature + 7.5°C), (c + d) T2 (control temperature + 11.5°C) and (e + f) T3 (control temperature + 15.5°C). Square symbols indicate measurements taken immediately after emersion periods. Initial open symbol represents F_v/F_m prior to any experimental treatment. Subsequent open symbols are taken 24 h after treatments to monitor recovery. Dotted line represents F_v/F_m for controls, which were maintained at ambient temperature.

TABLE 2. Results of a repeated measures ANOVA (with a Greenhouse-Geisser correction for the within-subject effects) to test for differences in F_v/F_m values in response to consecutive 1 hour emersion heat shocks (C, T1, T2, T3). The model had two factors: Temperature and Time. Significant values ($P < 0.05$) are highlighted in bold.

	Source	df	SS	MS	F	P
March	Temperature	3.00	0.028	0.009	41.411	**<0.001**
	Time	3.49	0.039	0.011	49.014	**<0.001**
	Temperature x Time	10.48	0.073	0.007	30.673	**<0.001**
October	Temperature	3.00	8.248	2.750	31.843	**<0.001**
	Time	2.42	9.845	4.056	81.876	**<0.001**
	Temperature x Time	7.28	4.633	0.636	12.843	**<0.001**

between temperature treatments and the magnitude of this pattern varying somewhat between seasons (Table 5). For example, after 24 h recovery, the RWC of tissue in the October stress treatments did not reach the levels observed at comparable time points in March (Fig. 3).

At the end of the experiment, following the recovery phase, the percentage area of bleaching observed on the tissue discs was highly variable between treatments and between experiments (Fig. 4). In both March and October, we observed a clear effect of temperature treatment, with greater

TABLE 3. Results of post-hoc pair-wise comparisons between Time points within each Temperature treatment. Comparisons for the March experiment shown in top right of matrix, those for the October experiment in the bottom left. A black circle indicates pair-wise comparisons were significant (at $P < 0.01$).

T1

October \ March	1	2	3	4	5	6	7	8	9	10	11
1											
2				●	●	●					
3											
4										●	
5										●	
6											
7	●	●	●	●	●	●				●	
8	●	●	●	●	●	●					
9	●	●	●	●	●	●				●	
10	●	●	●	●	●	●	●	●			
11	●	●	●	●	●	●	●	●			

T2

October \ March	1	2	3	4	5	6	7	8	9	10	11
1		●				●					●
2	●		●		●	●			●	●	●
3				●		●		●			●
4	●	●			●					●	●
5	●	●	●			●		●			●
6	●	●	●	●			●		●	●	●
7	●	●	●	●				●			●
8	●	●	●	●					●		●
9	●	●	●	●						●	●
10	●	●	●	●							●
11	●	●	●	●							

T3

October \ March	1	2	3	4	5	6	7	8	9	10	11
1		●	●	●	●	●		●			
2	●		●	●	●	●	●	●	●	●	●
3				●	●	●	●		●	●	●
4					●		●		●	●	●
5	●	●	●	●		●		●	●		●
6	●	●	●	●			●		●		●
7	●	●	●	●				●			●
8	●	●	●	●					●	●	●
9	●	●	●	●							●
10	●	●	●	●							●
11	●	●	●	●							

bleaching observed in the higher intensity treatments (Fig. 4). However, the magnitude of the effect varied between experiments, with high rates of bleaching (up to 100% in T3, 30.0°C) in October compared with moderate bleaching rates (~50% in T3, 26.0°C) in March (Fig. 4). When comparing across the same absolute temperatures (i.e., T3 in March and T2 in October, both 26°C), bleaching rates were almost double in October compared with March (Fig. 4). Statistically, we recorded a highly significant effect of Temperature treatment in both experiments (one-way ANOVA; March: $F_{3,16} = 116.3$, $P < 0.001$; October; $F_{3,16} = 58.3$, $P < 0.001$), with post-hoc tests indicating that all treatments differed from one another in both experiments.

The rates of in situ bleaching we observed in natural populations also varied markedly through the year (Fig. 5). At Wringcliff Bay, we recorded negligible bleaching rates in March (in 2016 and 2017), April and May. Similarly, at Lynmouth Bay, minimal bleaching occurred during March (2016 and 2017), May, June, July and August. In contrast, the highest

bleaching rates were recorded between October and December at both sites (Fig. 5).

DISCUSSION

We recorded pronounced variability in the vulnerability of a key habitat-forming kelp to heatwave scenarios between our experiments. The trailing range edge population of *Laminaria digitata* exhibited little resilience to simulated terrestrial heatwaves in October, whereas ecophysiological responses to similar magnitude warming events in March were minimal. In October, all tissue was non-viable by the end of the experiment, even at the lowest-magnitude treatment tested. This suggests that when autumnal heatwaves coincide with periods of high-magnitude low tides, individuals within natural populations are likely to become highly stressed, exhibiting symptoms of tissue bleaching and necrosis, potentially leading to mortality of the sporophyte. Even if physiological damage was non-lethal, adverse ecophysiological effects could manifest at the individual and
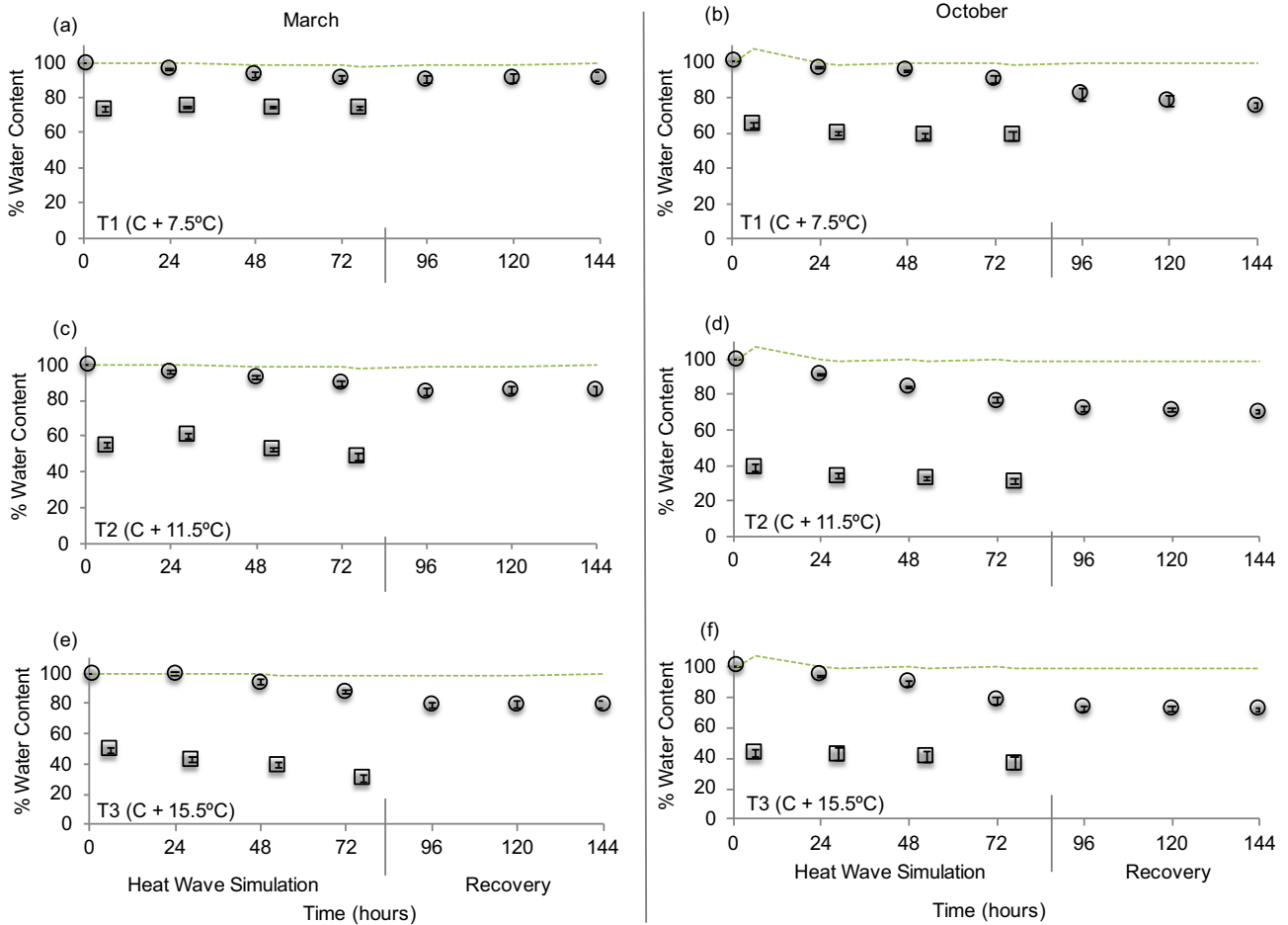
FIG. 3. Mean Relative Water Content (RWC) values ($n = 5$, $\pm$ SE) recorded during spring (left) and autumn (right) experiments, whereby tissue discs were exposed to consecutive 1 h emersion treatments: (a + b) T1 (control temperature + 7.5°C), (c + d) T2 (control temperature + 11.5°C) and (e + f) T3 (control temperature + 15.5°C). Square symbols indicate measurements taken immediately after emersion periods. Initial open symbol represents RWC prior to any experimental treatment. Subsequent open symbols are taken 24 h after treatments to monitor recovery.

TABLE 4. Results of a repeated measures ANOVA (with a Greenhouse-Geisser correction for the within-subject effects) to test for differences in relative water content values in response to consecutive 1 hour emersion heat shocks (C, T1, T2, T3). The model had two factors: Temperature and Time. Significant values ($P < 0.05$) are highlighted in bold.

	Source	df	SS	MS	F	P
March	Temperature	3.00	24682.376	8227.459	110.307	**<0.001**
	Time	2.17	38127.662	17544.335	713.022	**<0.001**
	Temperature x Time	6.52	18834.219	2888.837	117.406	**<0.001**
October	Temperature	3.00	43487.540	14495.847	146.312	**<0.001**
	Time	3.16	50700.001	16028.348	877.288	**<0.001**
	Temperature x Time	9.48	20764.694	2188.190	119.767	**<0.001**

population levels. For example, during autumn, actual growth rates of *L. digitata* are low and photosynthetic products are stored as carbohydrates that can be mobilized in the following spring when nutrients become available (Black 1950, Adams et al. 2011). Therefore, sublethal stress caused by bleaching and resource reallocation to cellular repair would restrict capacity to produce and store carbohydrates, with the potential to severely impair

productivity and ecological performance (Davison and Pearson 1996).

Our study suggests that *Laminaria digitata* populations at the trailing range edge are particularly susceptible to autumn heatwaves because: (i) sea temperatures are highest in late summer/autumn (Smyth et al. 2010, Pessarrodona et al. 2018), (ii) air temperatures can exceed 26°C (Fig. 1), which was consistently shown to be stressful during our

TABLE 5. Results of post-hoc pair-wise comparisons between time points within each temperature treatment. Comparisons for the March experiment shown in top right of matrix, those for the October experiment in the bottom left. A black circle indicates pair-wise comparisons were significant (at $P < 0.01$).

T1

October	March	1	2	3	4	5	6	7	8	9	10	11
	1		●	●	●	●	●	●	●	●	●	●
	2	●		●		●		●		●	●	●
	3	●	●		●	●	●	●	●	●	●	●
	4	●	●	●		●		●		●	●	●
	5	●		●	●			●		●		
	6	●		●		●		●		●	●	●
	7	●	●	●	●		●		●			
	8	●	●	●	●	●	●	●		●	●	●
	9	●	●	●	●	●	●	●	●			●
	10	●	●	●	●	●	●	●	●	●		
	11	●	●	●	●	●	●	●	●	●	●	

T2

October	March	1	2	3	4	5	6	7	8	9	10	11
	1		●	●	●	●	●	●	●	●	●	●
	2	●		●	●	●	●	●	●	●	●	●
	3	●	●		●	●	●	●	●	●	●	●
	4	●	●	●		●		●	●	●	●	●
	5	●	●	●	●					●	●	●
	6	●	●	●	●	●				●	●	●
	7	●	●	●	●	●	●		●	●	●	●
	8	●	●	●	●	●	●	●		●	●	●
	9	●	●	●	●	●	●	●	●			
	10	●	●	●	●	●	●	●	●			
	11	●	●	●	●	●	●	●	●			

T3

October	March	1	2	3	4	5	6	7	8	9	10	11
	1		●		●	●	●	●	●	●	●	●
	2	●		●	●	●	●	●	●	●	●	●
	3	●	●		●	●	●	●	●	●	●	●
	4	●		●		●	●	●	●	●	●	●
	5	●	●		●		●	●	●	●	●	●
	6	●	●	●	●	●		●	●	●	●	●
	7	●	●	●	●	●	●		●	●	●	●
	8	●	●	●	●	●	●	●		●	●	●
	9	●	●	●	●	●	●	●	●			
	10	●	●	●	●	●	●	●	●			
	11	●	●	●	●	●	●	●	●			

experiments, and (iii) high-magnitude equinox spring tides result in relatively long periods of exposure to air temperatures, thereby increasing the potential for heat and desiccation stress for low shore organisms (Colman 1933). As such, if air temperatures continue to increase or atmospheric heatwaves intensify in autumn, as has been suggested (Coumou et al. 2015, Kendon et al. 2018), *L. digitata* populations at the trailing edge will be subjected to adverse thermal conditions, with likely consequences for individuals and populations. It should be noted that our ecologically-relevant approach necessitated that different absolute temperature treatments (both seawater and air temperature) were used in March and April, in order to simulate realistic conditions experienced by natural populations. As such, the greater impact and lower recovery observed in October compared with March may have been due to stressful air temperatures, suboptimal water temperatures during the recovery period or an erosion of resilience to thermal stress

following a period of chronic high temperatures. Although the relative importance of each mechanism is unclear, the realized combined effects of autumnal heat stress on trailing edge *L. digitata* populations are significant.

Our experimental findings were corroborated by our field surveys of natural populations, as rates of bleaching of blade tissue (indicative of physiological stress) were low in spring/summer and markedly higher in autumn/winter. This increased population-level stress response was likely due to a combination of the chronic effects of high sea temperatures during late summer/autumn, longer periods of emersion stress during spring low tides in autumn and intrinsic biological properties (e.g., lower growth rates in autumn and less replenishment of damaged tissue, Kain 1979, and seasonal variation in biochemistry, Hereward et al. 2018).

Loss of *Laminaria digitata* at the trailing range edge will perhaps have wider consequences for reef communities along the intertidal fringe, especially
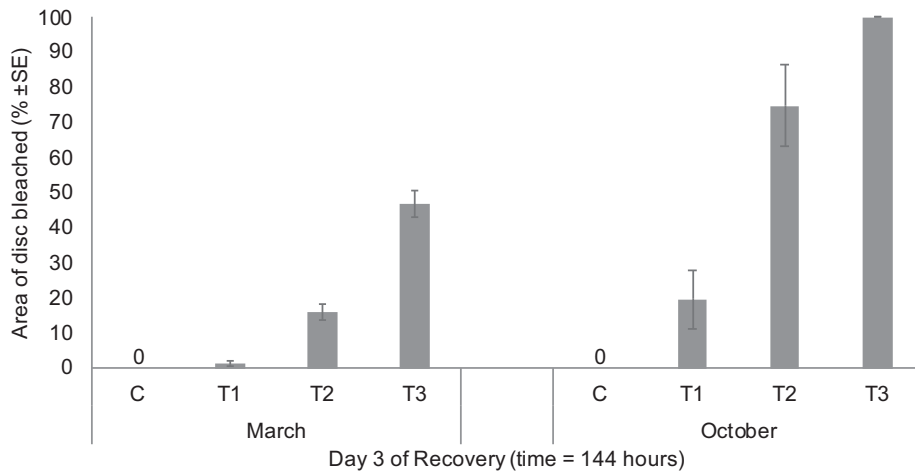
Fig. 4. Mean percentage of bleached tissue ($n = 5$, ±SE) recorded on *Laminaria digitata* discs on day three of recovery (the final day of monitoring) following experiments conducted in spring (left) and autumn (right) for each treatment: C (controls held at ambient temperature; T1 (control temperature + 7.5°C); T2 (control temperature + 11.5°C) and T3 (control temperature + 15.5°C).
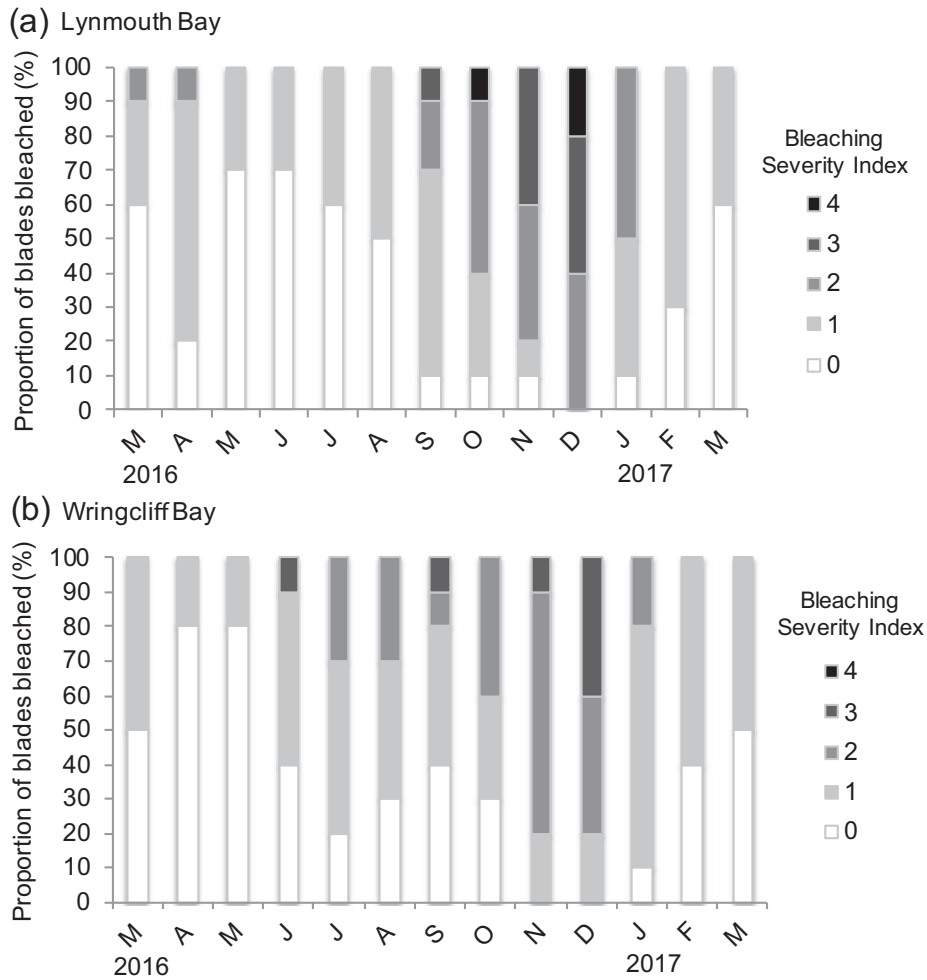

Fig. 5. Level of in situ bleaching observed in natural populations of *Laminaria digitata* at two sites in North Devon, UK (a = Lynmouth Bay, b = Wringcliff Bay), across 13 months (March 2016-March 2017). Each month, 10 mature sporophytes were randomly collected and bleaching levels were quantified using a semi-quantitative bleaching severity index described in Table 1.

as there are no warm-adapted functionally equivalent species to replace it (King et al. 2017b). As a foundation species, *L. digitata* generates habitat for a diverse array of associated flora and fauna (Schultze et al. 1990, Blight and Thompson 2008), provides organic matter for inshore food webs (Schaal et al. 2009) and is an important contributor to overall benthic primary production (Krumhansl and Scheibling 2012). As such, a climate-driven range contraction would likely alter the wider ecological structure and functioning of low intertidal communities in this region.

Trailing edge population losses may also result in the loss of unique genotypic and phenotypic diversity below the species level (e.g., Nicastro et al. 2013). Like many northern hemisphere species, trailing edge populations of seaweeds often acted as refugia during the Quaternary glaciations, and as a result, can harbor the bulk of a species' contemporary genetic diversity (e.g., Assis et al. 2013, Neiva et al. 2016). Trailing edges are also subject to high selective pressures that promote the development of unique phenotypic variation (Kawecki 2008). King et al. (2019) observed reduced genetic diversity but distinct adaptive ecotypes at the trailing edge of *Laminaria digitata*. Therefore, while climate induced range contractions may not compromise *L. digitata*'s genepool the loss of unique phenotypic variation may still threaten the adaptive potential of a species as a whole (Reed and Frankham 2003).

Extreme warming relative to seasonal climatologies can occur year-round, yet intra-annual variability in the impacts of extreme climatic events upon organisms, populations, and communities is poorly understood (De Boeck et al. 2010). Here, heatwave scenarios of a similar relative magnitude in spring had little impact on the ecophysiology of *Laminaria digitata*, as we observed complete recovery in terms of F_v/F_m and water content, and only moderate levels of bleaching. This is perhaps counter-intuitive, as seasonal acclimation to lower ambient temperature can lower absolute thermal tolerances (Lüning 1984). This could be explained if thermal set points due to acute stress are more fixed than set points for chronic temperature stress that have generally been employed when measuring thermal tolerance (e.g., Lüning 1984). For example, the heat shock response, which is a key physiological mechanism for dealing with acute thermal stress, has been found to be fixed regardless of incubation temperature (Barua and Heckathorn 2004).

The high vulnerability of *Laminaria digitata* range edge populations to atmospheric heatwaves in autumn is particularly interesting, as exposure to air temperature is not considered to be a key factor constraining its latitudinal distribution. Unlike most temperate kelps, the peak reproductive period for *L. digitata* occurs in summer, and a major demographic constraint relates to the summer inhibition of gametogenesis (Bartsch et al. 2013). As a result,

its latitudinal distribution follows the 17°C summer isotherm in sea temperature, which is situated in the Western English Channel. In reality, mature sporophytes are able to grow and survive in sea temperatures far higher than those that natural populations actually experience (Bolton and Luning 1982; N.G. King, unpub. data). However, this does not seem the case for low tide emersion stress, as current climatological conditions are very close to thermal thresholds for *L. digitata*. Therefore, while decadal scale warming may result in a gradual range contraction for *L. digitata* (Raybaud et al. 2013), mediated by inhibition of reproduction, acute stress imposed by exposure to atmospheric heatwaves may invoke more abrupt population declines in the near future.

Our findings highlight some limitations regarding common approaches for measuring stress responses in intertidal organisms. Due to their steep environmental gradients, accessibility and diverse floral and faunal communities, intertidal rocky shores are amongst the world's best-studied ecosystems. In particular, stress physiology has a rich history, with early ecologists attempting to link physiological limits with vertical distributions (e.g., McMahon and Russell-Hunter 1977, Schonbeck and Norton 1978) and more recently to understand future changes in latitudinal distributions (e.g., Harley 2011, King et al. 2017b). However, stress physiology has almost solely focused on critical limits from single exposures, which does not replicate the repeated periods of emersion stress intertidal organisms experience over the course of consecutive spring low tides. King et al. (2017b) found key interspecific differences in thermal tolerance between *Laminaria digitata* and the congener, *L. ochroleuca*, which were only revealed through realistic consecutive stress treatments. The current study suggests that consecutive stress exposures are also needed to fully understand responses to atmospheric heatwaves. Assuming that the observed erosion of resilience with consecutive exposures is a common pattern for macroalgae, this means that critical thermal limits have likely been previously underestimated. As Environmental Niche Models (ENMs) move away from correlations with mechanistic cause and effect relationships (Kearney and Porter 2009, Jordà et al. 2012, Sunday et al. 2012, Martínez et al. 2015), identification of accurate physiological limits will become even more critical. Moreover, an accurate understanding of how short-term warming events affect populations will also be critical as ENMs begin to incorporate climatic extremes. As ENMs represent the most widely used tool to predict species redistributions under climate change the incorporation of accurate critical limits will be paramount to increase confidence in projected redistributions.

Understanding species redistributions under climate change is one of the most pressing challenges in contemporary ecology. We have shown

that populations of an important habitat-forming kelp persist very close to physiological limits for environmental challenges not previously considered. For intertidal organisms, sensitivity to extreme sea temperatures experienced during marine heatwaves needs to be coupled with sensitivity to stressful air temperatures experienced during atmospheric heatwaves. Moreover, it is important to note that these warming trends are not occurring in isolation. Decadal scale gradual warming, marine heatwaves and atmospheric heatwaves constitute different aspects of climate warming, which may interact with each other and with non-climatic stressors (e.g., eutrophication) to erode the resilience of populations and communities in coming decades. To accurately predict future distribution and abundance patterns of intertidal kelp species, such as *Laminaria digitata,* a deeper mechanistic understanding of these concurrent processes is needed.

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