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Cool under heat: humidity moderates the tolerance of *Fucus vesiculosus* (Phaeophyceae) to changes in air temperature during emersion

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Abstract: Projections for climate change potentially mean that tidally exposed seaweeds will experience greater air temperature extremes than those that remain immersed. This study investigated the combined effects of temperature and humidity on the relative growth rate of *Fucus ves- iculosus* through two controlled experiments: (1) evaluating responses to various temperature and humidity regimes, and (2) assessing the impact of three consecutive days of heatwave conditions (25 °C). Samples from the upper and lower shore were subjected to 24, 30 and 40 °C at relative humidities of 30–90 % for 4 or 8 h, using an incubator oven to generate six vapour pressure deficit (VPD) levels (0.3– 5.3 kPa). A VPD of 5.3 kPa proved detrimental to the seaweeds regardless of duration. In contrast, *F. vesiculosus* tolerated a VPD of 2.4 kPa for up to 8 h. Little difference was detected between upper and lower shore residing specimens. Heat- wave conditions did not negatively affect *F. vesiculosus* growth irrespective of shore location. Blades could recover from proportional water biomass loss of up to 0.6 but not from a loss of 0.7 regardless of VPD. Nonetheless, greater VPD values tended to coincide with increased water biomass loss and decreased post-exposure growth. These findings suggest that increased humidity may mitigate thermal stress, enhancing resilience under projected climate scenarios.

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Keywords: climate change; desiccation; fucoid; heatwave; intertidal zone; macroalgae

1 Introduction

In 2018, the Intergovernmental Panel on Climate Change (IPCC) estimated that human activity has already caused approximately 1 °C of climate change above pre-industrial levels, with global warming likely to reach 1.5 °C between 2030 and 2052 if current rates continue (IPCC 2018). A common area of concern is the impacts of climate change on our marine ecosystems including increasing water and air temperatures (IPCC 2018; Nolan et al. 2010). Extreme weather events such as droughts and heatwaves have also become more intense and frequent since the 1950s (IPCC 2021). Heatwaves pose a particular threat to many species of seaweed which live in the intertidal zone (i.e., extended periods of atypically high temperature exposure during emersion, lasting for ≥3 days), as the considerable temper- ature and desiccation regimes imposed by tidal fluctuations may be further exacerbated by heatwave events during daily exposure periods (Davison and Pearson 1996; Harley et al. 2012; Hurd et al. 2014).

In particular, temperature dictates the performance of seaweeds at a fundamental level, as it determines the rate of enzymatic processes and metabolic function, such as those involved in photosynthesis and respiration (Harley et al. 2012; Raven and Geider 1988). As a result, seaweeds have evolved biochemical and physiological adaptations to optimize performance in the temperature ranges in which they reside (Eggert 2012). However, due to current rates of environmental change, these temperature ranges are predicted to drastically change, leading to water and air temperatures sufficiently high, or low enough, to cause disruptive stress from cellular and sub-cellular damage (Davison and Pearson 1996). This damage, along with the resources used for repair and protection of cells, can reduce development through reduced growth, decreased photosynthetic activity and even induce mortality

(e.g., Bell 1993; Davison and Pearson 1996; Eggert 2012; Harley et al. 2012).

For intertidal seaweed species, many studies have focused on understanding their response to climate-related stressors during both immersion (e.g., Breeman 1988; Serisawa et al. 2004; Simonson et al. 2015; Yotsukura et al. 2011) and emersion (e.g., Chu et al. 2012; Fernández et al. 2015; Flores-Molina et al. 2014; Martínez et al. 2012; Román et al. 2020). In some instances, dehydration or desiccation of macroalgae inhabiting the upper intertidal zones can lead to the loss of over 90 % of the seaweed's cellular water content, meaning the desiccation is essentially an osmotic stress (Contreras-Porcia et al. 2017). The level of desiccation experienced by a seaweed can be related to self-shading where blade material may overlap removing material from direct contact with the environ- ment (Fernández et al. 2015), as well as its surface-area to volume ratio (Schonbeck and Norton 1979). In both cases, the duration of exposure is considered a critical factor. Short exposure periods to hot air temperatures may have minimal effects for some seaweed species, whilst a long continuous exposure may result in severe stress (Hurd et al. 2014; Whalen et al. 2023). The severity of air temperature and desiccation exposure can relate to the position of seaweed across the intertidal zone, meaning seaweeds residing at the upper shoreline can experience greater durations of exposure to climatic stressors than those found inhabiting the lower shore. Yet it is possible that upper shore residing seaweeds will recover quicker from desiccation compared to the those residing on the lower shore as a result of natural selection to longer emersion times (Dring and Brown 1982).

Fucus vesiculosus (Phaeophyceae), otherwise known as 'bladder wrack' is a common macroalga on intertidal shores of the northeastern Atlantic. Interestingly, Joyce et al. (2019) observed that thallus samples of *F. vesiculosus* exposed to the harsh conditions of steam treatments (≥100 °C) to prevent biofouling did not significantly influence *F. vesiculosus* biomass. This is a remarkable result, which sets the premise for the need to develop an improved understanding of the extent to which *F. vesiculosus* can withstand thermal stressors associated with climate change, such as exposure to atmospheric heatwaves during emersion (Fernández et al. 2015; Martínez et al. 2012). Species resistance or susceptibility to climate driven escalation in atmospheric temperature during intertidal emersion may affect, among others, shifts in species distributions, altered community dynamics, and potential impacts on species abundance and diversity (Harley et al. 2012). In the present study, the effect of various air temperature and humidity (i.e. desiccation regimes) regimes on *F. vesiculosus* are considered for macroalgae dwelling at different shore heights (upper and lower shore) of the intertidal zone over short and long exposure periods (4 h and 8 h) reflecting typical emersion periods for many shore locations of the northeast Atlantic. Selected air temperatures reflect those at the lower and upper bands of air temperatures associated with heatwave conditions (24, 30 and 40 °C). The criteria used to define the occurrence of a heatwave varies across geopolitical jurisdictions, including national and even at regional and county levels within a country (e.g., United Kingdom; McCarthy et al. 2019). In general, temperatures between 24.5 and 28 °C would be considered the minimal thermal threshold, and the daily maximum temperature would normally need to exceed the designated minimal thermal threshold for three or more consecutive days to be declared a heatwave. To date, the highest recorded air temperatures in northeastern Atlantic regions have tended to be between 33 and 40 °C (e.g., Met Office 2022).

In the present study, to assess the impact of desiccation as well as heatwaves on *F. vesiculosus*, two experiments were carried out. In the first experiment, upper and lower shore specimens were exposed to desiccation regimes over short and long durations (4 h or 8 h). Combined temperature and humidity levels used for the formulation of desiccation regimes were expressed as vapour-pressure deficit (VPD), which is the difference between the actual moisture content and the total saturation point for air at a given temperature. Relative humidity (RH) expresses the amount of water vapour present in air as a percentage of the maximum possible carrying capacity at a given temperature (i.e., absolute humidity), with absolute humidity varying for different temperatures, therefore making comparison of RH across different temperatures inadequate to compare specific hu- midity of air (Coughlan et al. 2015). In general, greater VPD corresponds to decreased relative humidity and increases desiccation, while a VPD of zero means the air is 100 % saturated at a given temperature. In the second experiment, the influence of a heatwave effect was also considered for both upper and lower shore specimens and high and low relative humidity regimes over three consecutive days (i.e., three days above 24 °C). It was hypothesised that greater VPD would result in a reduced growth rate due to increased desiccation at higher VPDs. In turn, while increased humidity can moderate desiccation, increased humidity may also pre- vent transpiration and therefore efficient cooling. Accord- ingly, the highest air temperature (40 °C) was expected to induce mortality in all specimens regardless of humidity. Finally, it was hypothesised that samples from the upper intertidal zone would better tolerate increased VPD, higher temperatures, and longer exposure times due to natural exposure to longer daily emersion times.

2 Materials and methods

2.1 *Sample collection and maintenance*

Blade samples of *F. vesiculosus* L. were harvested from the intertidal zone of Walter Shore, Strangford Lough, Northern Ireland (54°22′56.59″N; 5°33′12.07″W). Strangford Lough ex- periences a maximum change in tidal elevation of approxi- mately 4 m (Kregting and Elsäßer 2014), therefore samples were collected from the highest and lowest band during suitable low tides (<0.5 m above chart datum) between 20 July and 12 August 2020. Samples were transported in a cooler- box, within source water, to the Queen's University Marine Laboratory (QML), Portaferry, Northern Ireland, which is located approximately 200 m from the sampling site. Samples were cleaned of any visible adhering organ- isms such as algae and molluscs. Following this, blade sam- ples were cut so that lengths ranged from 135 to 263 mm and measured from the distal tip toward the base of the thallus to incorporate the apical meristematic region). Samples were then maintained in uncovered, outdoor, seawater flow- through tanks at 12.8 ± 2.1 °C for a 24-h period before being used within experiments.

2.2 *Experiment 1: the impact of temperature and humidity on the relative growth rate of* F. vesiculosus

In a fully factorial experiment (see Table S1) the relative growth rate of *F. vesiculosus* as a proxy for survival to desiccation was assessed at three air temperatures (24, 30 and 40 °C) and both high and low RH levels (mean ± SE: 39.1 ± 0.9 and 83.1 ± 0.9) over short and long durations of exposure (4 h or 8 h). The simulated exposure times to air are typical of upper and lower shore emersion. Combined tem- perature and humidity pairings resulted in VPD values of 0.3, 0.6, 1.7, 1.8, 2.4, and 5.3 kPa (Table S1). Control samples were placed directly into uncovered, outdoor, seawater flow- through tanks at 12.8 ± 2.1 °C (i.e., controls were not desic- cated). All treatment and control combinations were repli- cated five times (i.e., $n = 5$). Blade samples were placed on two stainless steel metal grids inside an incubator oven where climatic regimes could be achieved (Gallenkamp Model IH- 150 Size Two Incubator). While air temperature was established via the device's temperature control system, humidity regimes were achieved by placing additional seaweed biomass in trays within the oven on the bottom, to release water vapour, or using silica gel beads as a desic- cator. Both temperature and humidity in the incubator were monitored using a temperature and humidity logger (MSR 145, MSR® data-loggers and measuring instruments, Switzerland), with seaweed biomass and/or silica beads added on an *ad hoc* basis to ensure maintenance of a consistent humidity. Light was not provided to remove any additional stress that light can cause (Fernández et al. 2015). To record biomass loss, immediately prior to commencement of the experiment, samples were blotted dry with paper towels and their wet-weight biomass was recorded using a precision weighing-scale (Mettler Toledo XP603S Delta Range scales; $d = 1$ mg). Post treatment, the wet- weight biomass was once again recorded for each sample after a 15-min cool-down period prior to returning the samples to the seawater flow-through tanks for a 14-day period.

Relative growth rate (RGR) was calculated as an indi- cator of the long-term response to each treatment (Equa- tion (1)), where Equation (1) does not account for tissue erosion. Prior to the experiments, a needle and thread was used to tag one blade of each specimen in the meristematic region, ~2–3 cm from the apical tips. This allowed the elon- gation of the apical region to be measured with calipers in the same location throughout the experiment (i.e., distance from location of the thread to blade tip). Sample length was re- measured for each specimen at the end of the 14-day post- treatment recovery period. Relative growth rate (RGR) was then calculated using the initial length (L_i) of the meriste- matic region (i.e., distance from thread to tip) in mm, final length (L_f) in mm, and time (t) in days, according to Equa- tion (1) (Evans 1972).

$$\mathrm{RGR} = \frac{\ln(L_f) - \ln(L_i)}{t} \quad (1)$$

VPD in kPa was calculated using RH and air temperature (T) in °C according to Equation (2) (adapted from Murray 1967).

$$\mathrm{VPD} = [610.78 \times e^{(T/(T+238.3)\times 17.2694)}] \times [(1 - \mathrm{RH})/100] \quad (2)$$

2.3 *Experiment 2: heatwave effects on relative growth rate of* F. vesiculosus

Samples were prepared following the protocol outlined in Experiment 1. Both lower and upper shore samples were exposed to a simulated heatwave (24.5 ± 0.02 °C) at either low or high RH levels (45.2 ± 0.2 and 92.9 ± 0.03, respectively) using an incubator drying oven (Gallenkamp Model IH-150 Size Two Incubator). Combined temperature and humidity pairings resulted in VPD values of 0.2 and 1.7 kPa. Samples were exposed to the desiccation regimes for an 8-h period

for either a single day or for three consecutive days. Between experimental days, the samples were placed into the seawater flow-through tanks at 12.8 ± 2.1 °C simulating one immersion and emersion during a 24-h period. Control samples were placed directly into seawater flow-through tanks (i.e., controls were not desiccated). All treatment and control combinations were replicated five times (i.e., n = 5). Temperature and humidity were continuously monitored within the chamber using a temperature and humidity logger (MSR145, MSR® data-loggers and measuring in- struments, Switzerland). Sample wet-weight biomass, as well as the length of blade apical sections, were recorded pre- and post-treatment using the same methods as outlined in Experiment 1.

2.4 *Data analysis*

Statistical analyses were conducted using R software (R Core Team 2021; R 4.4.1). Logistic regression in the form of generalised linear models (GLM: car) (Fox and Weisberg 2019) were employed for non-normal data and/or hetero- scedastic residuals (Gamma), and normal distributed data with homoscedastic residuals (gaussian). A stepwise deple- tion approach was used to remove non-significant terms when appropriate (i.e., $p > 0.05$), while overall model sig- nificance was determined using likelihood ratio tests in all cases (lmtest) (Zeileis and Hothorn 2022). Where p-values were significant ($\alpha < 0.05$), Tukey's LSD adjustments for multiple pairwise comparisons were used for post-hoc analysis (emmeans) (Lenth 2017). Normality of residual distributions and homoscedasticity of variances were tested using Shapiro-Wilk tests ($p > 0.05$) and Levene's tests ($p > 0.05$), respectively.

For Experiment 1, RGR and change in water content of *F. vesiculosus* samples were assessed as a function of VPD (seven levels: 0.3, 0.6, 1.7, 1.8, 2.4, 5.3, control – i.e., 0.0 kPa), exposure time (two levels: 4 h and 8 h) and shore location (two levels: high and low). As RH is dependent on air tem- perature, the combined measure of VPD facilitates an assessment of the climatic regimes. For Experiment 2, the RGR and change in water content of *F. vesiculosus* were assessed as a function of VPD (three levels: 0.2, 1.7, control – i.e., 0.0 kPa), exposure time (three levels: 1 day, 3 days, control – i.e., 0 days) and shore location (two levels: high and low).

3 Results

For Experiment 1, the RGR significantly differed for *F. vesiculosus* subjected to different climatic regimes (see Table S2; Figure S1). VPD and exposure time both had a significant effect on RGR, while shore location did not have a statistically apparent effect. Post-hoc analysis of RGR indicated that samples exposed to VPD values ≥1.8 kPa were significantly decreased compared to the RGR of samples exposed to VPD values ≤1.7 kPa for both exposure times (all $p < 0.0001$; Figure 1A and B), except samples exposed to 2.4 kPa for 4 h ($p > 0.05$; Figure 1A). Growth of *F. vesiculosus* was reduced (<0.01 d^{-1}) when blades were exposed to VPD values ≥ 1.8 kPa for both exposures (4 h or 8 h) compared to a RGR of >0.03 d^{-1} for samples exposed to VPD values ≤1.7 kPa with the exception of VPD values of 2.4 kPa (Figure 1A and B). The RGR of *F. vesiculosus* blades exposed for 4 h to a VPD value of 2.4 was similar to samples exposed to VPD values ≤1.7 kPa for both the 4 h and 8 h exposures. When blades were exposed to VPD values of 2.4 kPa for 8 h, RGR was lower than samples exposed to VPD values ≤1.7 kPa, but higher than either 1.8 or 5.3 kPa for both exposures (Figure 1A and B).

The proportion of biomass loss of *F. vesiculosus* subjected to different climatic regimes significantly increased following desiccation exposure (Table S2; Figure S2). VPD and exposure time both had a significant effect on biomass loss, while shore location did not have a statistically apparent effect. In general, *F. vesiculosus* subjected to greater VPD values showed greater proportional biomass loss with post-hoc analysis showing significant differences between treatments (Figure 1C and D).

For Experiment 2, the RGR of *F. vesiculosus* subjected to different heatwave conditions significantly differed (Table S2; Figure 2A and B). Shore location and exposure time both had a significant effect on RGR, while VPD did not have a statistically apparent effect. Post-hoc analysis indicated that the RGR of upper shore control samples was signifi- cantly greater than the RGR for upper shore samples exposed to the simulated heatwave treatment for three consecutive days ($p < 0.01$; Figure 2A). In turn, the RGR of low shore control samples was also significantly greater than the RGR for lower shore samples exposed to the heatwave for three days ($p < 0.01$; Figure 2B). The RGRs of the lower shore control samples were also significantly higher than the up- per shore control samples ($p < 0.01$). The RGR between upper shore samples exposed to heatwave conditions for either one or three days did not differ ($p > 0.05$; Figure 2A). Similarly, low shore samples also did not differ between exposure periods of one and three days ($p > 0.05$; Figure 2B). The RGR of upper shore samples exposed to heatwave conditions for one day was significantly greater than for low shore samples maintained under heatwave conditions for one day ($p < 0.01$; Figure 2A and B) but did not differ to low shore samples kept under heatwave conditions for three days ($p > 0.05$). In turn,

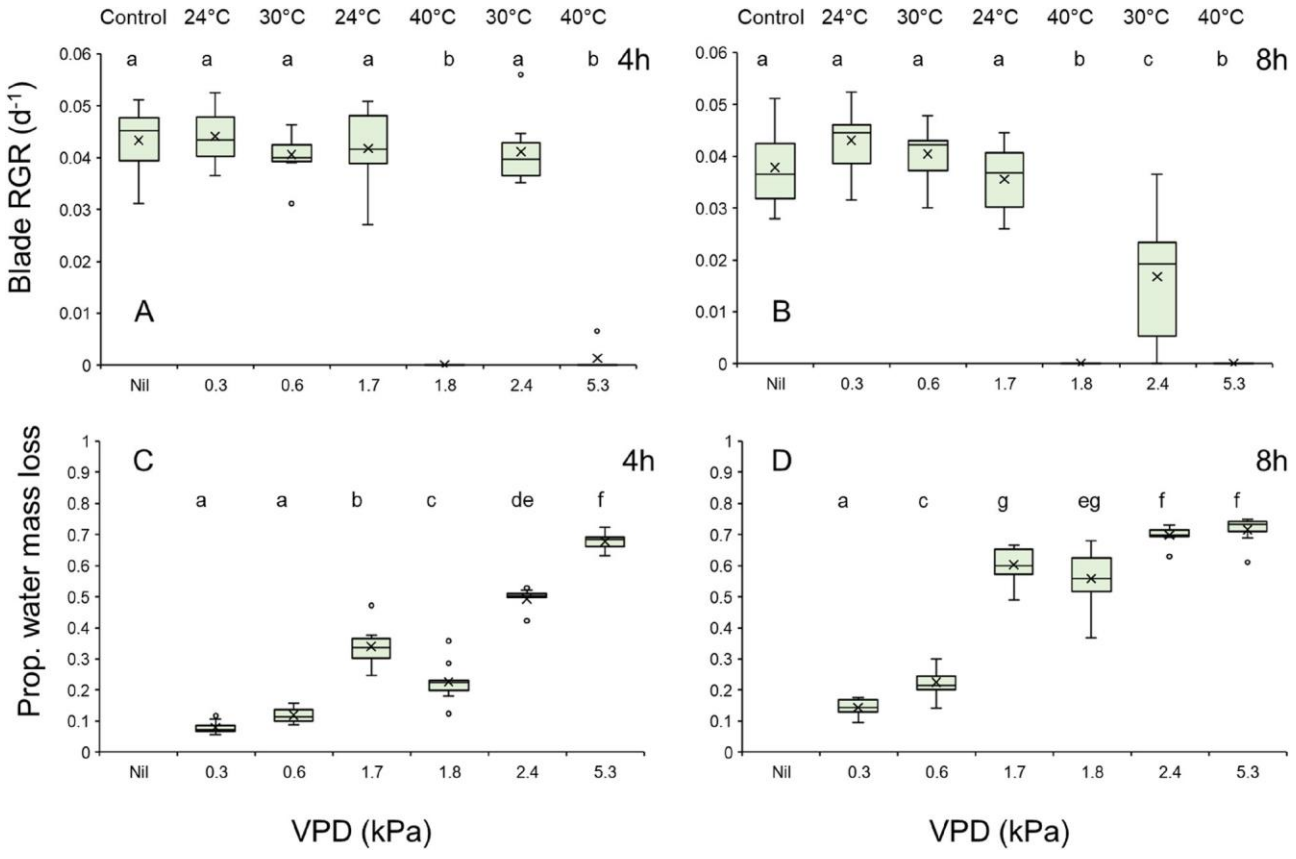


Figure 1: Median relative growth rate (RGR: A, B) and proportional biomass loss (C, D) for *Fucus vesiculosus* samples (n = 10) following exposure to desiccation regimes. Interquartile ranges (IQR), maximum and minimum IQR values, and outliers (◦) are also shown, while × denotes mean values. Samples were exposed to various air temperature (24 °C, 30 °C and 40 °C) and a series of low and high relative humidities (30–90 % RH) for either 4 h (A, C) or 8 h (B, D). Temperature and humidity combinations provided for categories of vapour pressure deficit (VPD: 0.3, 0.6, 1.7, 1.8, 2.4, and 5.3 kPa). A VPD of zero means the air is 100 % saturated at a given temperature. Nil = control samples. Samples were collected from the upper and lower shore (n = 5; see Figures S1 and S2), but pooled due to non-significance (α = 0.05). Shared letters indicate statistical similarity among pairwise comparisons across panels A and B, and separately C and D (i.e. $p > 0.05$).

the RGR of upper shore samples exposed to the simulated heatwave for three days was significantly reduced compared to low shore samples likewise exposed to the three-day treatment ($p < 0.01$; Figure 2A and B), as well as compared to low shore samples exposed for a single day ($p < 0.01$).

The proportion of water biomass loss of *F. vesiculosus* subjected to different heatwave conditions for one day compared to those exposed to heatwave conditions for three days significantly differed following desiccation exposure (Table S2). VPD significantly affected biomass loss, while exposure time and shore location did not have a significant effect (Figure 3). The proportional biomass loss for samples exposed to the same VPD level did not differ between exposure times (i.e., 0.2 or 1.7 kPa for either 1 or 3 days; both $p > 0.05$). Biomass change was significantly different between samples exposed to 0.2 kPa and 1.7 kPa for 1 day ($p < 0.0001$). In turn, biomass change also was significantly different between samples exposed to 0.2 kPa and 1.7 kPa for 3 days ($p < 0.0001$).

The proportion of water biomass loss of *F. vesiculosus* subjected to different heatwave conditions for up to three days significantly differed following daily desiccation expo- sure (Table S2; Figure 4). VPD significantly affected the proportion of biomass loss, while exposure time and shore location did not have a significant effect. The biomass of samples exposed to 0.2 kPa significantly differed between day 1 and day 3 ($p < 0.0001$), as well as between day 2 and day 3 ($p < 0.0001$). No statistically apparent effects were detected between days 1 and 2 ($p > 0.05$) (Figure 4). In turn, biomass of samples exposed to 1.7 kPa did not significantly differ between days 1, 2 or 3 (all $p > 0.05$; Figure 4). Proportional biomass loss also differed between VPD levels subjected to the same exposure period (i.e., 0.2 vs. 1.7 kPa assessed within each daily exposure period; all $p < 0.0001$). All other com- parisons for biomass change among the two VPD levels and three exposure times were all significantly different (all $p < 0.0001$).

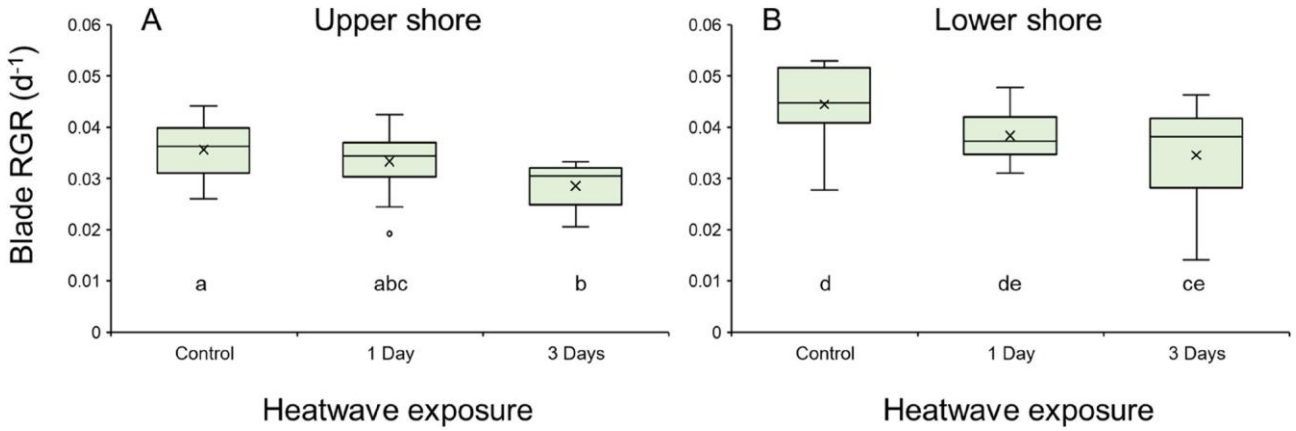


Figure 2: Median relative growth rate (RGR: A, B) for *Fucus vesiculosus* samples (n = 10) following exposure to a heatwave desiccation regime. Interquartile ranges (IQR), maximum and minimum IQR values, and outliers (◦) are also shown, while × denotes mean values. Samples were exposed to simulated heatwave (24.5 °C) at either low or high relative humidity levels (45.2 ± 0.2 and 92.9 ± 0.03, respectively). Air temperature and humidity combinations provided for two categories of vapour pressure deficit (VPD: 0.2 and 1.7 kPa), however samples exposed to different VPD levels (n = 5) were pooled due to non-significance (α = 0.05). Shared letters indicate statistical similarity among pairwise comparisons across both panels (i.e. $p > 0.05$).

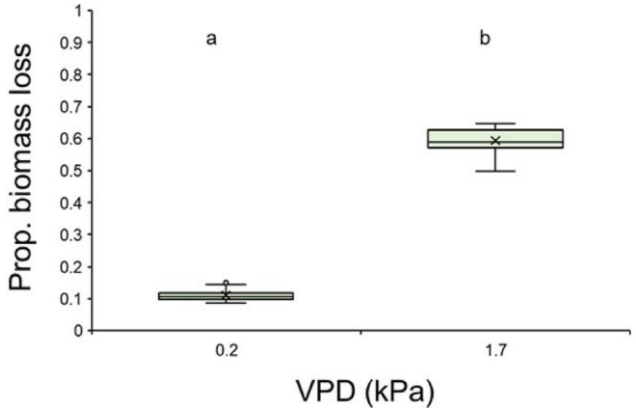


Figure 3: Median proportional biomass loss for *Fucus vesiculosus* samples (n = 20) following exposure to desiccation regimes. Interquartile ranges (IQR), maximum and minimum IQR values, and outliers (◦) are also shown, while × denotes mean values. Samples were exposed to a simulated heatwave (24.5 °C) at either low or high relative humidity levels (45.2 ± 0.2 and 92.9 ± 0.03). Air temperature and humidity combinations provided for two categories of vapour pressure deficit (VPD: 0.2 and 1.7 kPa). A VPD of zero means the air is 100 % saturated at a given temperature. Samples were collected from the upper and lower shore (n = 5) and exposed to desiccation regimes for either one or three days (n = 5). Data for shore location and exposure time were pooled due to non-significance (α = 0.05; see Figure S3). Letters indicate a statistical pairwise difference (i.e. $p < 0.0001$).

4 Discussion

When exposed to a range of air temperatures and relative humidity, the individual blade samples of *F. vesiculosus* were able to tolerate high temperatures and low relative humidity of 30 °C and 44 % RH respectively for up to 8 h. In turn, it is suggested that 40 °C has a detrimental effect on *F. vesiculosus* with no growth recorded regardless of exposure time or humidity. Blades could recover from proportional water biomass loss of up to 0.6 but not from a loss of 0.7 regardless of VPD. Despite the difference in natural emer- sion times between the upper and lower shore residing specimens, little difference was detected in their tolerance to desiccation. Even with persistent heatwave conditions for multiple successive days, no detrimental impact on RGR was detected. Unexpectedly, specimens originating from the lower shore displayed greater RGRs than those obtained from the upper shore, including controls, following expo- sure to heatwave conditions for up to three days. Reduced growth by upper shore specimens may reflect greater in- vestment in energy storage (e.g., mannitol production), as the optimal temperature for photosynthetic activity by *F. vesiculosus* appears to be higher than their optimal water temperature for growth (Graiff et al. 2015), with the physiological responses of upper shore specimens being possibly aligned to energy conservation compared to those obtained from the lower shore. The results of this study indicate that *F. vesiculosus* is capable of coping with current air temperatures and the predicted 1.5 °C increase in temperatures regardless of humidity or exposure time, as well as heatwave conditions lasting for up to three-days.

Vapor pressure deficit (VPD) plays a critical role in the desiccation stress experienced by macroalgae in upper intertidal zones, with implications for growth and survival. Intense desiccation can lead to the loss of over 90 % of seaweeds' cellular water content (Contreras-Porcia et al. 2017; Schagerl and Möstl 2011). Desiccation rates are linked to both air temperature and humidity in terms of the maximum

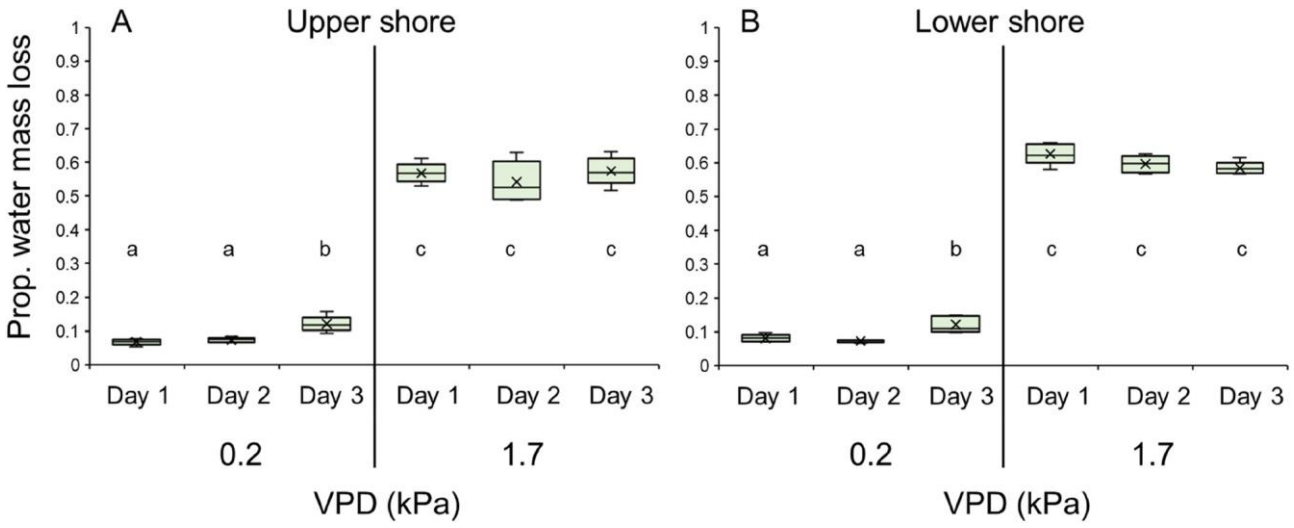


Figure 4: Median proportional biomass loss for *Fucus vesiculosus* samples (n = 5) following exposure to desiccation regimes for up to three days. Interquartile ranges (IQR), maximum and minimum IQR values, and outliers (◦) are also shown, while × denotes mean values. Samples were exposed to a simulated heatwave (24.5 °C) at either low or high relative humidity levels (45.2 ± 0.2 and 92.9 ± 0.03). Air temperature and humidity combinations provided for two categories of vapour pressure deficit (VPD: 0.2 and 1.7 kPa). A VPD of zero means the air is 100 % saturated at a given temperature. Shared letters indicate statistical similarity among pairwise comparisons across both panels (i.e. $p > 0.05$).

possible air moisture content at a given air temperature (Williams and Dethier 2005). In this study, VPD was calculated to determine the air moisture content experienced by *F. vesiculosus* specimens during desiccation treatments. Greater VPD values tended to lead to a decreased RGR and greater water biomass loss. The observed decrease in RGR as VPD values increased is likely a result of tissue damage as metabolic resources must be diverted from growth to tissue repair (Davison and Pearson 1996). These data agree with previous findings that both temperature and desiccation stress are influential on the growth rate, and therefore survival of seaweed species (Fernández et al. 2015; Martínez et al. 2012). Although mostly overlooked in favor of water and air temperature-based assessment for heat stress and desiccation, VPD is a primary determinant of desiccation stress rather than air temperature alone (Chu et al. 2012; Coughlan et al. 2018). For example, the proportional water biomass loss shows little variation between samples exposed to high humidity at 40 °C and those exposed to low humidity at 24 °C, conditions which generate a similar VPD despite the drastic difference in air temperature. These results under- score the importance of VPD as a more reliable indicator of desiccation stress than air temperature alone.

Species desiccation tolerances and the associated vertical shoreline distribution of intertidal organisms is considered to be determined by an ability to quickly recover from desiccation during rehydration rather than an ability to retain water and avoid desiccation (Davison and Pearson 1996; Flores-Molina et al. 2014). Accordingly, heatwaves are of particular concern for intertidal organisms as, although heatwave conditions pose little or no threat on the timescale of a single day, extended exposure over consecutive days could detrimentally impact littoral residing organisms. Detrimental effects may occur from resource depletion, for example reduced growth likely occurs if *F. vesiculosus* cannot replace the metabolic resources used to repair damaged tissues faster than the rate of resource depletion. Alternatively, if the rate of desiccation exceeds recovery through rehydration, desiccation stress may eventually cause significant damage to *F. vesiculosus* (Hurd and Dring 1991). Accordingly, detrimental effects would likely become particularly apparent under heatwave conditions, where recovery time between exposure to harmful conditions is limited. While it appears *F. vesiculosus* is unlikely to be damaged by heatwave conditions for up to three days of exposure, the impact of longer heatwave exposure periods should be assessed (Brown 2020), as heatwaves lasting for longer durations or warmer air temperatures may cause damage to *F. vesiculosus*.

Desiccation can be influenced by, among other things, surface-area to volume ratio and shoreline composition of the seaweed, which were not taken into account in this study. Smaller organisms have a greater surface-area to volume ratio and are therefore more prone to desiccation (Hurd et al. 2014). All specimens tested in this experiment were cut with lengths ranging from 135 to 263 mm. Actual size of *F. vesiculosus* found *in situ* will considerably vary, with mature samples regularly being of much greater length.

Hence, the smaller samples of seaweed used for experimentation were more likely to show signs of desiccation than their larger counterparts. Further, while experimental conditions were consistently maintained, *in situ* VPD will change throughout the duration of emersion under varying conditions of wind, sunlight and closeness of the ebb and flood tides. In addition, specimens were laid flat and spread- out during experimentation to ensure no overlap between samples. Naturally occurring *F. vesiculosus* on the shore tends to be found in clusters, usually with significant over- lapping of blades and with other seaweed species, frequently growing in or around damp crevices or pools. The shelter and proximity to moisture sources will likely act as a natural means of desiccation reduction, with the outermost over- lapping seaweed blades essentially shielding the inner seaweeds from desiccation upon emersion. Additionally, any water vapour generated from the desiccation of the sea- weeds, or from nearby pools, will likely increase relative humidity around specimens, further reducing the rate of moisture loss. Yet our data clearly indicate both upper and lower shore *F. vesiculosus* can resist desiccation under heatwave conditions, with specimens continuing to grow following three days of exposure, with *in situ* conditions likely in part to mitigate desiccation exposure to levels lower than those assessed by the present study.

In this study, the tolerance of *F. vesiculosus* to changes in air temperature, humidity and exposure time was deter- mined through examining their impacts on sample biomass change and RGR. This approach involved quantifying re- sponses on a whole sample scale incorporating all cellular processes. In order to further investigate the exact damage caused to the seaweed by the various stressors, observations should be made at a cellular level, classifying molecular and biochemical markers for each individual stressor (Davison and Pearson 1996). For example, Flores-Molina et al. (2014) investigated effects of desiccation on naturally hydrated, dehydrated and rehydrated fronds and found that species with higher intertidal distributions displayed greater activ- ity of the antioxidant enzyme catalase. The authors suggest that seaweeds growing on the upper shore were more capable of buffering excess reactive oxygen species induced during desiccation. This would be particularly beneficial in determining the exact cause of both temperature-induced and desiccation-induced mortality in *F. vesiculosus* but re- quires further investigation.

Throughout both the air temperature and humidity experiments and the heatwave experiment, samples were treated in a temperature-controlled oven in complete darkness. This was primarily for consistency and also because light can be an added stressor (Fernández et al. 2015). However, future work should include the influence of light on the recovery of the blade to desiccation given the importance of light and desiccation on the biochemical processes of photosynthesis (e.g. Dring and Brown 1982). In addition, the effects of air temperature will not be the same on all metabolic processes because of the sensitivities of enzymes and the influence of other factors including light and nutrients (Hurd et al. 2014). Therefore, it would be useful to determine the relationship between the level of desiccation, light and internal nutrient status of the blade and thallus growth rate.

Given the current extent of global warming, and concerning predictions for unprecedented levels in the future, climate change has become a prominent global issue now more than ever. Understanding the tolerance of different macroalgal species to changes brought about by climate change, such as rising temperatures, is vital in predicting impacts on factors such as local biodiversity and ecosystem function, and allowing us to develop strategies to reduce these impacts or adapt to them. When *F. vesiculosus* was exposed to air temperatures of 40 °C or desiccation resulting in biomass loss exceeding approximately 71 %, there were clear damaging effects. This reduction in biomass likely mostly equates to water loss during desiccation. When specimens were exposed to a simulated heatwave scenario for three days there was no difference among subsequent *F. vesiculosus* growth rates when compared with specimens exposed for a single day. Although the present study has not tested the effect of increased ocean temperatures, extended heatwaves lasting in excess of three days, or repeated heatwave events temporally separated by a return to typically expected seasonal temperatures, as well as the potential acclimatisation or localised adaptation of *F. vesiculosus* to changes in global desiccation regimes, it appears *F. vesiculosus* can tolerate temperatures of up to 40 °C, with desiccation regimes governing water loss. Under a potential further 1.5 °C warming, it seems unlikely that *F. vesiculosus* in the North- ern Hemisphere will be negatively impacted by climate change in the next 10–30 years.

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