Journal of Experimental Marine Biology and Ecology 592 (2025) 152129

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Seasonal response of respiration and thermal tolerance of PSII to sea surface temperature variation in two foundation seaweed species

Rosalie J. Harris [a,b,*], Callum Bryant [a], Pieter A. Arnold [a], Andrew P. Scafaro [a], Andrea Leigh [c], Melinda A. Coleman [d,e,f], Adrienne B. Nicotra [a]

[a] Research School of Biology, The Australian National University, Canberra, Australian Capital Territory, Australia
[b] Scripps Institution of Oceanography, Centre for Marine Biodiversity and Conservation, University of California San Diego, La Jolla, California, United States of America
[c] University of Technology Sydney, School of Life Sciences, PO Box 123 Broadway, NSW 2007, Australia
[d] Oceans Institute and School of Biological Sciences, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia
[e] Southern Cross University, National Marine Science Centre, 2 Bay Drive, Coffs Harbour, NSW 2450, Australia
[f] New South Wales Fisheries, National Marine Science Centre, 2 Bay Drive, Coffs Harbour, NSW 2450, Australia

ARTICLE INFO

Keywords:
Metabolic regulation
Respiration
Heat tolerance
Chlorophyll fluorescence

ABSTRACT

Amidst escalating sea surface temperatures, comprehending how marine organisms acclimate to temperature fluctuations is paramount. This understanding is not only needed to anticipate the ecological ramifications of future climatic conditions, but also forms the cornerstone of our efforts to effectively restore and safeguard these invaluable marine habitats. The mechanisms of acclimation in seaweed physiology in response to seasonal shifts in temperature have not yet been sufficiently explored. Here, we examined the physiological responses of two foundational seaweeds, *Ecklonia radiata* and *Phyllospora comosa*, to seasonal sea surface temperature (SST) variation. Our approach combined a fluorophore O_2-sensor system to measure respiration and chlorophyll fluorescence to assess critical heat thresholds (T_{crit}) with PSII. By measuring T_{crit} and respiration across a full year, we explored the metabolic costs and some of the trade-offs in seaweed acclimation and examined whether a higher T_{crit} entails a greater respiratory carbon cost, or, whether respiration acclimates as SST increases, reducing metabolic expenses. Our findings reveal significant seasonal shifts in T_{crit}, for both species. For metabolic activity, *Phyllospora* exhibited temporally stable respiration, indicating homeostatic regulation, while *Ecklonia* demonstrated potential energy deficits during warmer months. These findings are likely linked to the species' habitat differences, with *Phyllospora* occupying variable and extreme intertidal environments, and *Ecklonia* residing in more stable subtidal habitats. The relationship between the predicted temperature at maximum respiration (T_{max}) and T_{crit} indicated a coupling between thermal stability of respiration and photosynthesis within seaweeds. Our approach has uncovered important connections between thermal tolerance and respiration, providing new insights into seaweed physiology which offer a foundation for future research and conservation strategies under global warming.

1. Introduction

Ocean temperatures are expected to increase by up to 4 °C in 'worst-case' climate predictions (Cheng et al., 2022; IPCC, 2021); the ranges of marine species are already contracting and shifting poleward to escape the effects of warming seas (Hastings et al., 2020; Pecl et al., 2017; Smith et al., 2023). The ability of species to acclimate through plasticity or adapt through heritable responses will play a significant role in their survival and persistence in a warming world. Our current understanding of the physiological mechanisms underlying thermal tolerance and the capacity for acclimation to warming and extreme events are not adequate for assessing the vulnerability of marine species to climate change.

Seaweeds are sessile, foundational species, and are therefore particularly vulnerable to climatic changes (Wernberg et al., 2024). They not only provide critical structural habitat, but also support ecosystem services extending beyond their immediate environment (Cotas et al., 2023; Tano et al., 2017; Wernberg et al., 2011). As primary

---

* Corresponding author at: Scripps Institution of Oceanography, Centre for Marine Biodiversity and Conservation, University of California San Diego, La Jolla, California, United States of America.

E-mail address: r1harris@ucsd.edu (R.J. Harris).

https://doi.org/10.1016/j.jembe.2025.152129
Received 11 December 2024; Received in revised form 23 July 2025; Accepted 13 August 2025

producers, they play a crucial role in the health and productivity of marine ecosystems, offering essential habitat and food sources (Coleman and Wernberg, 2017; Wernberg et al., 2019b). However, climate change poses a direct threat to these vital species, with local extinctions already documented in regions such as New Zealand, Australia, and west coast of North America (Beas-Luna et al., 2020; Straub et al., 2019; Thomsen et al., 2019; Wernberg et al., 2013). Given these alarming trends, it is important to strengthen our understanding of how seaweeds acclimate to the continued escalation in sea surface temperatures, especially considering efforts to effectively restore and protect these invaluable habitats.

The ocean is characterised by seasonal sea surface temperature (SST) fluctuations, as it transitions from cool winters to warm summers. This temperature variation, along with other seasonal changes like irradiance, impacts the productivity of habitat-forming seaweeds (Flukes et al., 2015; Pessarrodona et al., 2022; Zarco-Perello et al., 2017), with seasonality as a major driver in seaweed growth, influencing biomass, carbon sequestration and reproduction (Fernández et al., 2020; Pfister et al., 2018; Veenhof et al., 2023). Seaweeds must acclimate to temperature changes to maintain their carbon balance, which is needed for growth, repair, and reproduction (Andersen et al., 2013; Wilson et al., 2015). Acclimation involves adjusting physiological processes, such as photosynthesis and respiration, to optimise performance under new environmental conditions (Lagerspetz, 2006; Way and Yamori, 2014). Previous studies have investigated the acclimation potential of seaweeds to changing temperatures, showing that some species maintain similar respiration rates when measured at the temperature they were recently growing in, suggesting they can acclimate to seasonal shifts in ambient temperature (Eggert and Wiencke, 2000). However, the extent and costs of acclimation in seaweed physiology to seasonal changes, especially under the pressures of increasing ocean temperatures and more frequent marine heatwaves (Cheng et al., 2022; Oliver et al., 2018) require further consideration. By investigating the capacity of seaweeds to acclimate thermal thresholds to these rapidly changing conditions and the costs of doing so, we are better able to assess their ability to cope with climate change. Although the general physiological responses of seaweeds to temperature are relatively well understood, particularly regarding carbon assimilation and growth (Bidwell and McLachlan, 1985; Díaz-Acosta et al., 2021; Franke et al., 2024; Graiff et al., 2025; Healey, 1972; Olischläger et al., 2017; Wernberg et al., 2016b), our understanding of how temperature specifically constrains the thermal limits of PSII and shapes respiration remains limited. Functional traits such as photosynthetic efficiency, thermal limits, carbon assimilation, and growth performance under varying thermal environments, can shed light on how seaweeds respond to temperature and how these traits vary across thermal environments.

Photosystem II (PSII), a key protein complex in the photosynthetic pathway, is particularly sensitive to thermal stress (Emmett and Walker, 1973; Gounaris et al., 1984). Fluorescence imaging can be used to derive a range of indicators of PSII condition including F_V/F_M and T_{crit}. F_V/F_M reflects the potential efficiency of PSII photochemistry and is widely used as a diagnostic tool for detecting stress or damage to the photosynthetic apparatus. T_{crit} provides a direct and quantifiable threshold of PSII impairment under heat stress. T_{crit} is derived using the minimum value of chlorophyll fluorescence (F_0) and its sudden rise at a temperature (T_{crit}) that indicates the temperature above which PSII cannot effectively employ non-photochemical quenching to prevent light damage Here we assess F_V/F_M for insight into overall photochemical health, and T_{crit} as our measure of PSII thermal limits.

These photosynthetic responses are closely tied to the overall mitochondrial respiration that underlies the energy demands of photosynthesis (Bennett et al., 2022). Respiration is involved in the maintenance of cellular functions and growth (Burris, 1977; O'Leary et al., 2019). It is closely tied to the rate of photosynthesis, which provides the necessary carbohydrates that are used in respiration (Falkowski and Raven, 2013). Respiration is often strongly temperature-dependent, meaning that its rate increases with rising temperatures but can be reduced under excessively high temperatures (Gent and Enoch, 1983; O'Sullivan et al., 2017; Sharpe, 1983). This temperature sensitivity of respiration underlies its importance in metabolic regulation, especially under varying thermal conditions. However, how respiration acclimates in response to heat and whether this adjustment supports shifts in thermal tolerance is not thoroughly understood, particularly in seaweeds. Thus, while photosynthetic and respiratory processes are interconnected, the specifics of how they influence each other under different environmental conditions are not well understood.

The adaptation of seaweeds to temperature changes likely necessitates a significant energetic balancing act, where allocating resources for enhanced heat tolerance might compete with the demands of growth and reproduction (Camp et al., 2019; Perez et al., 2023). However, most photosynthetic organisms can acclimate both photosynthesis and respiration so that carbon assimilation and growth are maximised at the prevailing growth temperature (Davison et al., 1991; Eggert and Wiencke, 2000; Zou and Gao, 2014). At exceedingly high temperatures, the ability to optimise growth through acclimation of carbon net assimilation may be impaired by the added costs of protecting biochemical processes such as proteins and membranes from heat damage (Scafaro et al., 2021). While there is evidence for the acclimation of carbon metabolism to temperature in other systems (e.g., terrestrial plants and phytoplankton), whether seaweeds demonstrate similar capacities, particularly in response to long-term changes in SST, remains unclear. While rising temperatures can boost metabolic rates, enhancing growth and productivity, excessively high temperatures may disrupt the balance between respiratory demands and carbon assimilation. This can result in disproportionately high respiration rates required for repair and maintenance, which may exceed the carbon gained through photosynthesis. Such an imbalance imposes significant metabolic costs, leading to cellular stress and damage (Berry and Bjorkman, 1980; Danaraj et al., 2021). Furthermore, acclimation to higher temperatures often involves reallocating resources to cellular maintenance processes, such as repairing heat-induced damage to proteins and membranes and enhancing antioxidant or heat shock protein production. These stress-response mechanisms can divert energy away from growth and reproduction, potentially limiting these functions under prolonged thermal stress (Way and Yamori, 2014). Additionally, thermal acclimation within a narrow temperature range may reduce physiological flexibility, diminishing an organism's capacity to tolerate broader environmental fluctuations (Bunce, 2007).

On short time scales (hours), elevated temperatures drive up respiration rates (Atkin and Tjoelker, 2003), potentially depleting energy reserves vital for maintenance and repair, thus affecting health, but on longer time scales (seasonally), for example, respiration is expected to acclimate (Padilla-Gamiño and Carpenter, 2007). It is also important to compare respiration rates of seaweeds at SST to that at the temperature where respiration is maximised, as we can better understand acclimation processes and species underlying metabolic capacity to cope with thermal stress. Understanding short and long term fluctuations in respiration provides insight into the overall energy dynamics of responses to temperature shifts and serves as a productivity indicator, with photosynthetic rate ultimately determining the energy available for respiration (Posch et al., 2019). The temperature dependence of carbon gain and loss via photosynthesis and respiration respectively, will be key to predicting the sensitivity of seaweeds to warming (Eggert and Wiencke, 2000; Kübler and Davison, 1995; Staehr and Wernberg, 2009). This approach offers a promising avenue for understanding the potential impacts of climate change on seaweed communities and their future distribution.

Here, we investigate seasonal variation in the metabolic costs of thermal tolerance. To assess the extent to which habitat-forming seaweeds acclimate to seasonal temperature variation, we sampled two ecologically important foundation species: *Ecklonia radiata* (C.Agardh) J.Agardh.

and *Phyllospora comosa* (Labillardière) C. Agardh, hereafter called *Ecklonia* and *Phyllospora*, every second month for one year. *Ecklonia* is found exclusively in the more stable subtidal zone whereas *Phyllospora* is found in the more variable and more seasonally exposed intertidal and shallow subtidal zones. We measured their F_V/F_M, the heat tolerance threshold (T_{crit}) for the photochemical machinery, and respiration at four standardised temperatures: 14, 21, 26 and 32 °C across the course of one year. Our hypotheses were: 1) $F_{V/}F_M$ would remain stable throughout the year, as stability in this metric suggests that species are able to maintain photochemical function despite seasonal temperature fluctuations, 2) Thermal tolerance (T_{crit}) would vary across the seasons, consistent with sea surface temperature change, 3) Respiration would acclimate to SST such that we would see no relationship between SST and respiration at a given SST and finally, 4) As heat tolerance increased in warmer months, so too would maximum potential respiration, as increased energy would be required to maintain healthy PSII such that we predict a positive correlation with the temperature at which maximum was reached (T_{max}).

2. Methods

2.1. Sampling and site selection

To capture seasonal fluctuations in heat tolerance and respiration, two sites 45 km apart were sampled bi-monthly beginning on the 27th of April 2022 ending on the 16th of February 2023, resulting in six time points across the year. The first site was Horseshoe Bay Beach, Bermagui, New South Wales Australia (36°25′29.6"S 150°04′45.7″E) and the second was at Tathra Beach, New South Wales (36°43′37.0"S 149°59′05.8″E). The two sites were included to capture a measure of spatial variability. Samples were collected at low tide at about 2 m depth. At each visit 15 individuals each of *Phyllospora* and *Ecklonia* were sampled by harvesting 30 cm of thallus. Samples were placed into a black catch bag. During collection, water temperature was recorded for 20 min at two meters depth. Upon collection, seaweed samples were immediately transferred to wet cotton bags and placed in a cooler, then driven back to the laboratory at the Australian National University which took 3 h (this length of time post-harvest does not affect F_V/F_M values; Harris et al., 2022). Heat tolerance measurements were performed within half an hour after return to lab and respiration was measured in the following hour (as per protocols from Coast et al., 2022 and Scafaro et al., 2021; Scafaro et al., 2017)).

2.2. Heat tolerance measurements

We measured the critical temperatures (T_{crit}) of PSII for each seaweed sample following the method of Harris et al. (2022). This approach measures the variation in basal chlorophyll fluorescence (F_0) in response to gradually increasing temperatures and is a robust indicator of thermal limits to PSII and overall photochemical health (Arnold et al., 2021; Bryant et al., 2024; Knight and Ackerly, 2002; O'Sullivan et al., 2017; Schreiber and Berry, 1977). Any epiphytes on the tissue were deliberately avoided and samples were wiped clean with paper towel. For each assay, samples were cut them into squares of 1 cm × 1 cm using a razor blade, then placed on a gridded paper matrix. To prevent drying, the squares were immediately covered with cling film. Prior to initiating the temperature assay, samples underwent a dark adaptation period of 20 min, after which we measured the initial maximum quantum yield of PSII (F_V/F_M) to verify the health of each sample. A thermocouple was positioned atop each sample and temperature was steadily elevated at a rate of 15 °C per hour, commencing from the native seawater temperature corresponding with the month of collection. We deployed a modulating blue light of minimal intensity, incapable of driving photosynthesis, to continuously measure the basal fluorescence every 20 s throughout the assay. Simultaneously, temperature data were logged every five seconds using a dataTaker DT85 (Lontek, Glenbrook, New South Wales, Australia). The T_{crit} values, indicative of the onset of thermal stress of PSII, were calculated by analysing the temperature-dependent fluorescence curves. Following Harris et al. (2022), we identified the breakpoint in these curves, marking the transition point between the slow and rapid phases of fluorescence change. This breakpoint is indicative of the temperature threshold at which functional impairment of the photosynthetic apparatus begins, thus serving as a proxy for thermal stress expressed as a value in °C.

2.3. Respiration assays

To assess the respiration, we employed a Q2 O_2-sensor system (Astec Global, Maarssen, The Netherlands), which was initially designed for seed germination assays but more recently has been adapted for plant leaf and root respiration (O'Leary et al., 2017; Scafaro et al., 2017). The Q2 uses automated, high-throughput fluorophore measurements of oxygen consumption for estimation of respiration. We followed protocols outlined in Scafaro et al. (2017). Cut seaweed material was patted dry to remove any surface water droplets with paper towel and placed in 1 ml tubes, each of which was hermetically sealed with specialised caps provided by Astec Global. These caps incorporate a fluorescent metal-organic dye sensitive to oxygen (O_2) quenching. (Note that given tubes were airtight, minimal desiccation occurred to samples, also confirmed from no drop in sample weight post assay This method was chosen after trial comparisons between seawater and air showed greater stability and consistency in oxygen flux signals in air than in submerged conditions, likely due to reduced variability from boundary layer effects and diffusion gradients).

The samples were housed in a custom-built frame, draped in black cloth to ensure a dark environment, essential for accurate respiration measurements. The Q2 O_2-sensor utilises a blue-spectrum LED to emit an excitation pulse (approximately 480 nm), followed by the detection of emission in the red spectrum (approximately 580 nm). This process allows for the quantification of O_2-dependent fluorescence decay. A fiber-optic fluorescence detection unit, mounted on a robotic arm, sequentially measured the oxygen consumption from the vials. Respiration rates were recorded at intervals of approximately 4 min, which was determined to be the optimal frequency for measuring our seaweed samples, but total time run was 12 h to obtain a linear rate of consumption. The sensor was calibrated before each assay using both a tube with ambient air (set as 100 % O_2) and a tube devoid of O_2 created by purging with N_2 gas (set as 0 % O_2). The rate of O_2 depletion was reported as a fraction of O_2 relative to these calibration standards and converted to molar concentrations following the ideal gas law as outlined by Scafaro et al. (2017). We conducted respiration measurements at four temperatures; 14 °C, 21 °C, 26 °C, and 32 °C, allowing us to explore the effects of temperature on seaweed respiration.

Oxygen levels were recorded at regular intervals, and these data were used to generate oxygen depletion curves for each sample. The total oxygen concentration of gas in the tube was calculated at each time point using known constants such as temperature, pressure, and the ideal gas law. Respiration rates were derived from the slope of the oxygen depletion curves, representing the rate of oxygen consumption over time. This slope, calculated as micromoles of oxygen consumed per second, was then normalised to the fresh weight, dry weight, and area of the seaweed samples. The final respiration rates were calculated for each sample at varying temperature conditions. R scripts for extraction are available in Scafaro et al. (2017).

Note: We acknowledge that the absolute respiration rates reported here may underestimate true rates of oxygen consumption. This is likely due to the absence of agitation during incubation, which can allow oxygen gradients to develop around the thallus surface, and the use of air rather than seawater as the measurement medium. These conditions may reduce the diffusion of oxygen and mask faster rates of respiration. Furthermore, the extended incubation period (4–5 h) required to detect linear oxygen depletion may allow some acclimatory processes to initiate during measurement. Therefore, while absolute rates should be interpreted cautiously, the relative responses of respiration to temperature and seasonal variation remain robust and biologically meaningful within the context of this study.

2.4. Statistical analyses

We fit linear mixed-effects regression models to determine the responses of F_V/F_M and heat threshold (T_{crit}) to seasonal variation across both species using the `LMER` function from the `LMERTEST` package in R version: 4.0.2 (R Core Team, 2018). For the response variables T_{crit} and F_V/F_M, we tested for non-linear patterns by fitting season as a second-degree (quadratic) polynomial term, as well as species, and their interaction as fixed factors and included site as a random factor.

We analysed variation in respiration patterns across temperature, across seasons, and between the species, using respiration data obtained from the dry weight of samples measured at the 14, 21, 26 and 32 °C temperatures. We fit an LMER model with respiration as the response variable, second-degree polynomial term of measurement temperature, along with season and species, and all interactions as fixed effects, and unique sample ID as a random factor to account for repeated measures. The model was then used to generate predicted values of respiration between 14 and 32 °C at 0.1 °C intervals across all seasons using the *predict.merMod* function. From the curve (all R^2 were above 0.4, see Fig. 2), we calculated the predicted respiration at a given SST (R_{SST}) across a range of SSTs observed across the year, the maximum respiration and the temperature at which maximum was reached (T_{max}). To analyse the change in respiration with SST, we fit models with a second-degree polynomial term for SST, species, and their interactions as fixed effects, without random effects. We then investigated the relationship between T_{max} and T_{crit} as predicted from the curve. Here T_{crit} was the response variable, with T_{max} and species as fixed effects with sample ID as random effect.

We used Akaike Information Criterion (AIC) for all analyses and compared the linear relationships of season or temperature against models that included second-degree polynomial of those predictors. In all cases, the polynomial fit explained substantially more variance. We report Analysis of Deviance tables using Type II Wald F tests with Kenward-Roger degrees of freedom (df) for all models.

3. Results

3.1. Heat tolerance

Counter to our prediction, F_V/F_M varied significantly across the year, where values were lowest in summer months and highest in winter (Fig. 1a, Table 1). Species exhibited different patterns): *Ecklonia* maintained a more consistent F_V/F_M across the year whereas *Phyllospora* had a stronger decline in F_V/F_M heading into the warmer months, particularly December (Fig. 1a). Note that although F_V/F_M varied significantly, these values were never so low to be indicative of sustained damage in seaweeds (average values >0.5).

As predicted, heat tolerance thresholds of T_{crit} varied significantly across the year, following a non-linear pattern that was highest in the warmer months and lowest in winter (Fig. 1b). Again, species did not respond uniformly to these seasonal changes resulting in a significant species by season interaction: *Ecklonia* had an average T_{crit} that was 1.5 °C lower than *Phyllospora* based on the mean difference across the year (Table 1, Table S1). Additionally, T_{crit} generally tracked changes in SST at time of sampling for both species (Fig. 1b).

3.2. Respiration

Respiration increased with temperature up to an optimum that peaked between 20 and 25 °C, regardless of season. The model fit the observed data well ($R^2 = 0.66$; Fig. 2) and showed significant effects of season and species (Table 2). *Ecklonia* had a consistently significantly higher respiration across every season and measurement temperature compared to *Phyllospora*. Respiration was greatest in February which also correlated with the warmest SST of 23.3 °C, regardless of measurement temperature.

Table 1
ANOVA results from a linear mixed-effects regression model to determine if T_{crit} and F_V/F_M vary with season (fit as a second-degree polynomial term) and species.

F_V/F_M	*F-value*	*df*	*P-value*
Season	24.168	2	< 0.001
Species	44.210	1	< 0.001
Season * Species	4.051	2	0.01
T_{crit}	*F-value*	*df*	*P-value*
Season	29.951	2	< 0.001
Species	13.875	1	< 0.001
Season * Species	6.291	2	0.002

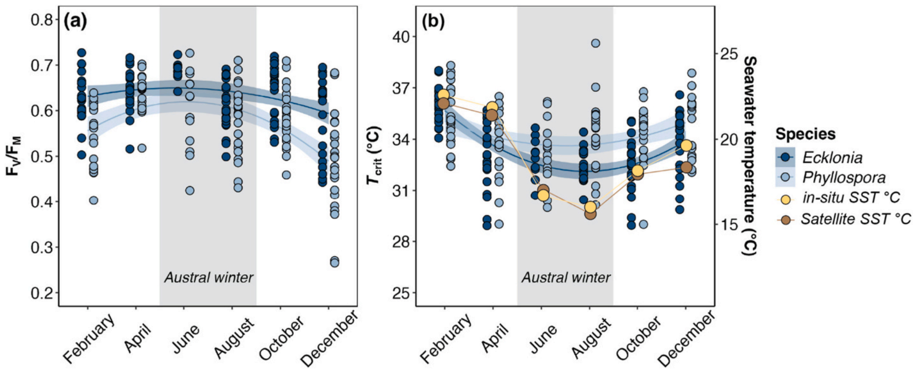

Fig. 1. Variation in thermal tolerance of photosystem II across a year for *Ecklonia* and *Phyllospora* with (a) maximum quantum yield of PSII (F_V/F_M) and (b) critical temperatures derived from *T*-F_0 curves (T_{crit}). Points are raw values with both sites included. Solid lines are a second-degree polynomial regression. Note the secondary axis for (b) where yellow points and yellow line represent measured in situ sea surface temperature (°C) at the location of sampling at time of measurements using HOBOs, whilst brown points are satellite derived daily means averaged for the respective month, sourced from NOAA NCDC OISST version2p1 AVHRR SST. Shaded section depicts the time of Austral winter. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

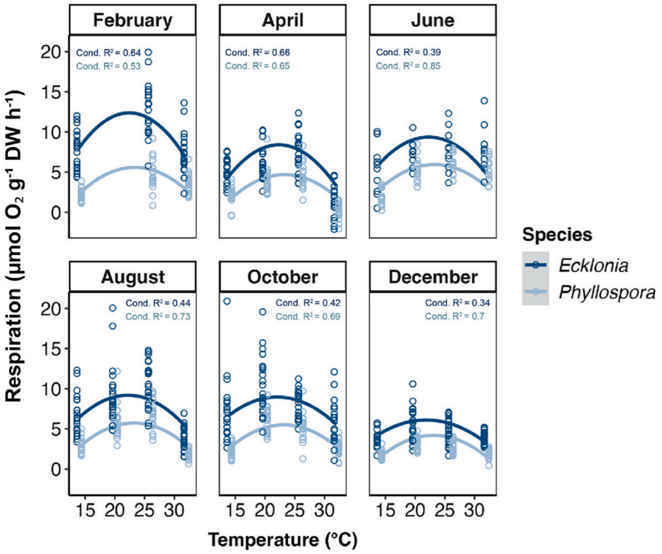

Fig. 2. Respiration by dry weight measured at four temperatures at six time points across the year. Raw values are shown by open circles, and fitted curves are predicted values from linear mixed-effects models for both species across months at 0.1 °C intervals. Note that the 21 °C measurement temperature in February was removed due to a technical issue with the Q2. Conditional R^2 shown for each curve for each species for each sampling period, top row in each panel in dark blue is *Ecklonia*, below in light blue is *Phyllospora*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
ANOVA results from a linear mixed-effects regression model to determine if R_{dark} varies with the effects of temperature treatments (14, 21, 26 and 32 °C; fit as a second-degree polynomial term) and season and species and interactions thereof.

Respiration	F-value	df	P-value
Measurement temperature	237.523	2	< 0.001
Season	20.875	1	< 0.001
Species	190.531	1	< 0.001
Measurement temperature * Season	6.181	2	0.002
Measurement temperature * Species	11.669	2	< 0.001
Season * Species	10.271	1	0.001
Measurement temperature * Season * Species	3.998	2	0.018

We anticipated that the predicted respiration rate at sea surface temperature (R_{SST}) would demonstrate acclimation to sea surface temperature (SST), leading us to predict an absence of a direct relationship between R_{SST} and SST. Instead, we found that R_{SST} followed a non-linear pattern showing higher predicted respiration values at both the lower and upper ends of SST, and much lower respiration values at the median SST, around 19 °C (Fig. 3). There were significant two-way species * SST interactions for this model, where the non-linear pattern was far more amplified for *Ecklonia*, whereas *Phyllospora* remained relatively more stable throughout the changes in SST (Fig. 3, Table 3).

Finally, we hypothesised that as photosynthetic heat tolerance (T_{crit}) increased in warmer months, there would also be a corresponding increase in the temperature at which respiration was maximised (T_{max}), as carbon assimilation and metabolic energy demand for that carbon would be presumably linked. To test this, we used predicted values from the model above and found a strong positive correlation between T_{crit} and the predicted temperature where respiration was maximal (T_{max}) for both species (Fig. 4, Table 4). The T_{max} differed significantly between the species (*Ecklonia* = 22.2 °C ± 0.007, *Phyllospora* = 23.2 °C ± 0.003). There was no significant interaction, which demonstrated that T_{crit} increased with increasing T_{max} in the same manner for both species

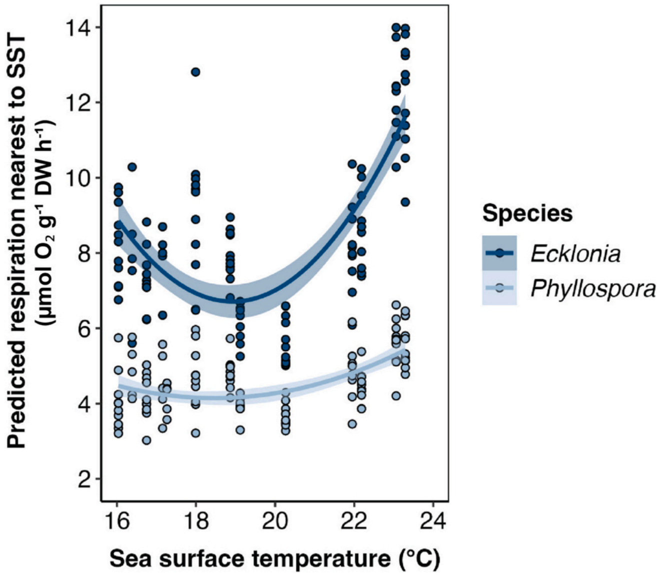

Fig. 3. Relationships between sea surface temperature (SST) and predicted respiration that is nearest to the sea surface temperature (R_{SST}) at time of collection, overall model $R^2 = 0.79$. *Ecklonia* shows increased metabolic requirements (greater respiration) at both high and low SST whilst *Phyllospora* suggests a more stable homeostatic regulation of respiration to prevailing SST. Model is fit as a second-degree polynomial term ± SE.

Table 3
ANOVA results from a linear model to determine predicted respiration closest to the SST (R_{SST}) at time of collection (fit as a second-degree polynomial term).

R_{SST}	F-value	df	P-value
SST	96.401	2	< 0.001
Species	654.991	1	< 0.001
SST * Species	34.683	2	< 0.001

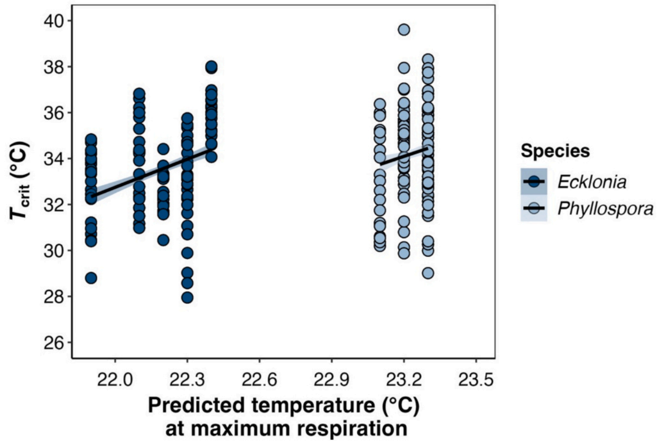

Fig. 4. The relationship between photosynthetic heat tolerance (T_{crit}) and the predicted temperature at maximum respiration (T_{max}) in *Ecklonia* and *Phyllospora*. This correlation suggests an interdependent thermal stability between the processes within PSII and respiration in these species. These predictions are derived from the main model, here there are 12 different curves being fit to estimate T_{max}. The points show that there were five different T_{max} values for *Ecklonia* and only three for *Phyllospora* as T_{max} was the same for multiple seasons. Linear model fit ± SE.

Table 4
ANOVA results from a linear mixed-effects model to determine if T_{crit} varies with T_{max} and species.

T_{crit}	*F-value*	*df*	*P-value*
T_{max}	80.704	1	< 0.001
Species	44.016	1	< 0.001
T_{max} * Species	0.001	1	0.972

(Fig. 4, Table 4).

4. Discussion

Our study examining seasonal variation in thermal tolerance and the metabolic costs thereof in seaweeds, revealed remarkable physiological adjustments in both *Ecklonia radiata* and *Phyllospora comosa* in response to seasonal changes. We found that both species exhibited higher heat tolerance (T_{crit}) during summer and lower values in winter, while F_V/F_M showed the opposite pattern with lowest values in summer and highest in winter. Together, these results point to a clear seasonal trend in the physiological status of these seaweeds with changing temperatures. Likewise, rates of respiration varied across the year, with peaks in the warmest month of February when SST reached a maximum at 23.3 °C. We also found the predicted respiration rates at SST exhibited a quadratic relationship, indicating increased energy demands at both the lowest and highest seasonal SST, relative to more moderate temperatures. Finally, we found a positive linear relationship between thermal tolerance of PSII (T_{crit}) and the temperature at which respiration was at a maximum (T_{max}) for both species, illustrating that the heat response of respiration and PSII are coupled to one another. The observed differences in acclimation of thermal tolerance and respiration between *Ecklonia* and *Phyllospora* are likely attributable to their distinct habitat preferences. *Phyllospora*, which inhabits the more variable intertidal/shallow subtidal zone, demonstrated greater physiological plasticity, reflected in its capacity to acclimate heat tolerance while maintaining stable metabolic respiratory costs in response to seasonal changes. This likely reflects the evolutionary pressures of coping with fluctuating temperatures, high irradiance, and aerial exposure during low tides. In contrast, *Ecklonia*, which occupies the more stable subtidal environment, exhibited less pronounced seasonal acclimation, likely due to the relatively consistent thermal conditions of its habitat. This limited seasonal adjustment in *Ecklonia*'s thermal tolerance and respiration may indicate a reduced capacity to cope with future increases in SST and the thermal variability associated with marine heatwaves.

4.1. *Species differences in heat tolerance and seasonal acclimation: implications for climate resilience*

Seasonal variation in thermal tolerance and photosynthetic efficiency revealed clear differences between species. The energetic costs of maintaining elevated critical temperatures (T_{crit}) particularly in summer, could be substantial for both species and may lead to trade-offs with growth, reproduction, or maintenance, especially at the range edges where spore production declines (Forbord et al., 2020; Straub et al., 2022; Veenhof et al., 2023). If high T_{crit} translates to improved resilience under prolonged warming, this could help buffer ecological decline. (Coleman et al., 2008; Posch et al., 2022; Vergés et al., 2016; Wernberg et al., 2016a).

Phyllospora exhibited higher average T_{crit} and greater seasonal variability in F_V/F_M than *Ecklonia*, suggesting stronger thermal acclimation capacity. This aligns with previous work showing that some seaweeds exhibit dynamic and highly acclimatory heat tolerance thresholds across environmental gradients (Becheler et al., 2022; Umanzor et al., 2019). The response of *Phyllospora* likely reflects its exposure to fluctuating and extreme conditions in the intertidal and shallow subtidal zones. During low tides, it experiences direct sunlight, desiccation, and wide temperature shifts, all of which can stress photosynthetic systems (Davison and Pearson, 1996). These challenges may drive the need for more flexible adjustments to its photochemistry and thermal tolerance across seasons. The higher F_V/F_M ratios observed in winter indicate enhanced PSII efficiency during cooler, less stressful conditions (Padilla-Gamiño and Carpenter, 2007).

In contrast, *Ecklonia* displayed lower and a more stable T_{crit} and less seasonal variation in F_V/F_M, consistent with its residence in more thermally stable subtidal environments. This reduced seasonal responsiveness may suggest narrower physiological plasticity and, potentially, greater vulnerability under warming scenarios, particularly at the warmer edge of its distribution (Davis et al., 2022; Hernández et al., 2023; IPCC, 2021). Its relatively consistent F_V/F_M throughout the year may reflect allocation towards maintaining baseline PSII efficiency, rather than dynamically adjusting to seasonal extremes (Wernberg et al., 2019a).

Thermal acclimation will also reflect the changing role of light and nutrients across seasons (Jeffers et al., 2025; Thomsen et al., 2019). Variation in irradiance can directly affect photo-physiological metrics such as F_V/F_M, as light history influences non-photochemical quenching capacity and overall photochemical efficiency (Kalaji et al., 2012; Ruban, 2016). In high-light conditions, increased photoprotective mechanisms may depress F_V/F_M, while lower-light conditions may enhance PSII efficiency due to reduced photoinhibition (Endo et al., 2023). Similarly, nutrient availability can regulate metabolism, affecting both photosynthetic efficiency and respiration rates (Mueller et al., 2016). Future studies incorporating rapid light-response (P—I) curves or oxygen production under natural irradiance could provide more direct estimates of photosynthetic output, enabling better integration of light-use efficiency into assessments of thermal acclimation. The effect of changes in light regime on thermal acclimation of T_{crit} is at present unknown but is likely to be significant for predicting species responses to future warming. Integrating light and nutrient dynamics into future assessments of thermal tolerance will be crucial for capturing the full complexity of acclimation in natural systems.

4.2. *Carbon costs of thermal tolerance: links between respiration and heat tolerance*

The decline in respiration observed at higher SST (e.g. in summer months Fig. 2) may seem beneficial at first glance, as it implies lower carbon loss to metabolic processes. It is possible that this reflects a physiological adaptation to reduce respiratory carbon loss under conditions of reduced photosynthetic input. However, given the thermal stress context and the concurrent declines in photochemical performance, we interpret this reduction as more likely indicative of cellular damage or metabolic failure rather than an active downregulation strategy (Zahra et al., 2021). At high SSTs, critical structures such as membranes and enzymes may begin to fail, compromising photosynthesis and other metabolic processes that require respiratory energy (Wernberg et al., 2016b). This breakdown likely results in the observed reduction in respiration but may also signal a relative reduction in capacity to sustain essential functions, reflecting a tipping point beyond which metabolic processes can no longer keep pace with thermal stress (Kumar et al., 2020). Thus, while *Phyllospora* shows some capacity for homeostatic regulation at intermediate temperatures, both species may face increasing metabolic constraints as ocean temperatures rise, particularly if seasonal peaks begin to exceed their current thermal operating range.

Respiration rates peaked at T_{max} values of 22.2 °C (*Ecklonia*) and 23.2 °C (*Phyllospora*), closely matching the highest recorded SST of 23.3 °C during February. This proximity suggests that both species operate near their physiological limits during summer. At T_{max}, elevated respiration represents a significant carbon cost, potentially redirecting resources from growth and reproduction to maintenance (Eggert, 2012). For *Ecklonia*, the lower T_{crit} and higher respiration indicates a less efficient balance between thermal tolerance and energy use, increasing its vulnerability to prolonged warming. The decline in respiration at higher measurement temperatures (Fig. 2) may be indicative of a metabolic downregulation, potentially signalling a reduction in growth rate (Atkin and Tjoelker, 2003; Davison, 1991; Zou and Gao, 2014). *Phyllospora*, however, demonstrated a capacity to modulate its respiration across changes in SST (Fig. 3). This modulation suggests a potential for homeostatic regulation, maintaining stable metabolic activity despite environmental temperature shifts (Atkin et al., 2000). These findings are consistent with Eggert and Wiencke (2000), who reported that several Antarctic red algae exhibited respiration rates that acclimated to cold environments, helping to maintain carbon balance under persistently low temperatures. We found evidence that respiration was acclimated to seasonal SST in *Phyllospora*, with similar rates observed when measured at the species' growth temperature. This level of resilience was less apparent in *Ecklonia*, which instead exhibited increased respiration at prevailing SST, potentially indicating a lower capacity for acclimation in this species, and a higher risk of biomass loss under warmer conditions with climate change (Wernberg et al., 2016b; Martínez et al., 2018). Davison and Davison (1987) found that at higher growth temperatures, the brown seaweed *Laminaria saccharina* exhibited increased respiration and reduced growth, suggesting a limited capacity to adjust to warming compared to its performance at cooler temperatures or to other, more thermally flexible species. Yet, without concurrent data on carbon assimilation in our study, it is speculative to conclude that these higher rates necessarily lead to decreased net biomass accumulation. Therefore, exploring the relationship between assimilation, respiration, and thermal tolerance in seaweeds represents a compelling area for future research.

The relationship between the predicted T_{max} of respiration and T_{crit}, appears to be linear and positive (Fig. 4). This suggests a coupling between the thermal response of respiration and photosynthetic thermal tolerance such that as the photosynthetic apparatus of seaweed acclimates to higher temperatures, their respiration rate also adjusts, maintaining a balance between these two physiological processes. Martínez et al. (2012) found that the intertidal seaweed *Fucus serratus* was highly sensitive to the combined effects of high solar radiation, temperature, and low humidity during low tide, leading to growth inhibition and photosynthetic damage. The increased exposure to these stressors in the intertidal zone may drive *Phyllospora* to require more frequent adjustments to its photosynthetic machinery and respiratory processes to maintain optimal performance (Harley et al., 2012). In contrast, *Ecklonia* inhabits the more stable subtidal zone (Wernberg et al., 2011) and has likely been selected for consistency in its respiratory response, rather than flexibility. This results in a less plastic respiration and potentially greater carbon costs during thermal stress, which could increase its susceptibility under future climate scenarios. This distinction highlights the influence of habitat-specific selection pressures on the evolution of both mean thermal strategies and potential plasticity. *Phyllospora*'s lower and more stable respiration during summer suggests an adaptive strategy to conserve energy under heat stress, potentially at the cost of growth. This long-term acclimation reflects thermal stability and may confer resilience under climate warming (Flukes et al., 2015; Lapointe and Duke, 1984). In contrast, *Ecklonia*'s respiration increased in line with SST, indicating a different form of plasticity, one that may be less efficient under sustained thermal stress due to higher metabolic costs and potential carbon imbalance. Note that our experiments were conducted at the mid-latitude in the range of these species. Seaweed populations at the warm range edge can exhibit lower genetic diversity and higher vulnerability to climatic stress compared to those in cooler regions (Wernberg et al., 2018), as well as potential adaptations to warmer conditions, such as higher thermal tolerance but lower growth rates (Coleman et al., 2011; King et al., 2019; Vranken et al., 2021; Wood et al., 2020). Phenotypic plasticity and physiological responses can also vary geographically (Flukes et al., 2015; Staehr and Wernberg, 2009). Thus, broader assessments across both species' range via common garden and reciprocal transplant experiments are needed to understand variability in acclimation capacity. Long-term studies of chronic heat exposure will further clarify persistence potential under future warming.

5. Conclusions

Our examination of metabolic trade-offs in heat tolerance of two foundation species in Australia's temperate marine ecosystems demonstrated species-specific differences in seasonal acclimation patterns of importance to predicting their potential response to climate change induced changes in SST. Our findings demonstrate a link between the ability of seaweeds to maintain functional respiration rates and photosynthetic efficiency under increasing temperatures. From here, a deeper understanding between photosynthetic carbon assimilation and respiration in relation to thermal tolerance of seaweed species more broadly is needed. Investigating how these physiological processes co-vary and influence each other under different thermal regimes could provide invaluable insights into the adaptive strategies and potential for rapid natural or assisted evolution of these species. Future research should also focus on identifying genetic variants within populations that exhibit both high heat tolerance and stable or efficient respiration. Such individuals could be prime candidates for use in restoration efforts, as they may possess enhanced survival capabilities in increasingly warm ocean conditions (Coleman et al., 2020).

CRediT authorship contribution statement

Rosalie J. Harris: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Callum Bryant:** Visualization, Software, Resources, Methodology, Investigation, Data curation, Conceptualization. **Pieter A. Arnold:** Writing – review & editing, Supervision, Software, Methodology, Investigation, Formal analysis, Conceptualization. **Andrew P. Scafaro:** Writing – review & editing, Supervision, Software, Resources, Data curation. **Andrea Leigh:** Writing – review & editing, Visualization, Validation, Supervision, Project administration, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Melinda A. Coleman:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Adrienne B. Nicotra:** Writing – review & editing, Supervision, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis.

Funding

Our work received support from the Ecological Society of Australia via The Holsworth Wildlife Research Endowment and from the Australian Government Research Training Program, which were granted to Rosalie Harris.

Declaration of competing interest

Rosalie Harris reports financial support was provided by Holsworth Wildlife Research Endowment. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We acknowledge the Yuin and Ngunnawal First Nations peoples, the Traditional Custodians of the lands where our research was conducted. Thanks to Lara Hedley and Owen Atkin and John Mackenzie for field and laboratory assistance.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jembe.2025.152129.

Data availability

Data will be archived in an open access database on publication.

References

Andersen, G.S., Pedersen, M.F., Nielsen, S.L., 2013. Temperature acclimation and heat tolerance of photosynthesis in Norwegian Saccharina latissima (Laminariales, Phaeophyceae). J. Phycol. 49, 689–700. https://doi.org/10.1111/jpy.12077.

Arnold, P.A., Briceño, V.F., Gowland, K.M., Catling, A.A., Bravo, L.A., Nicotra, A.B., 2021. A high-throughput method for measuring critical thermal limits of leaves by chlorophyll imaging fluorescence. Funct. Plant Biol. 48, 634–646. https://doi.org/10.1071/FP20344.

Atkin, O.K., Tjoelker, M.G., 2003. Thermal acclimation and the dynamic response of plant respiration to temperature. Trends Plant Sci. 8, 343–351. https://doi.org/10.1016/S1360-1385(03)00136-5.

Atkin, O.K., Edwards, E.J., Loveys, B.R., 2000. Response of root respiration to changes in temperature and its relevance to global warming. New Phytol. 147, 141–154. https://doi.org/10.1046/j.1469-8137.2000.00683.x.

Beas-Luna, R., Micheli, F., Woodson, C.B., Carr, M., Malone, D., Torre, J., Boch, C., Caselle, J.E., Edwards, M., Freiwald, J., Hamilton, S.L., Hernandez, A., Konar, B., Kroeker, K.J., Lorda, J., Montaño-Moctezuma, G., Torres-Moye, G., 2020. Geographic variation in responses of kelp forest communities of the California current to recent climatic changes. Glob. Chang. Biol. 26, 6457–6473. https://doi.org/10.1111/gcb.15273.

Becheler, R., Haverbeck, D., Clerc, C., Montecinos, G., Valero, M., Mansilla, A., Faugeron, S., 2022. Variation in thermal tolerance of the giant Kelp's gametophytes: suitability of habitat, population quality or local adaptation? Front. Mar. Sci. 9.

Bennett, S., Vaquer-Sunyer, R., Jordá, G., Forteza, M., Roca, G., Marbà, N., 2022. Thermal performance of seaweeds and seagrasses across a regional climate gradient. Front. Mar. Sci. 9.

Berry, J., Bjorkman, O., 1980. Photosynthetic response and adaptation to temperature in higher plants. Annu. Rev. Plant Physiol. 31, 491–543. https://doi.org/10.1146/annurev.pp.31.060180.002423.

Bidwell, R.G.S., McLachlan, J., 1985. Carbon nutrition of seaweeds: photosynthesis, photorespiration and respiration. J. Exp. Mar. Biol. Ecol. 86, 15–46. https://doi.org/10.1016/0022-0981(85)90040-1.

Bryant, C., Harris, R.J., Brothers, N., Bone, C., Walsh, N., Nicotra, A.B., Ball, M.C., 2024. Cross-tolerance: salinity gradients and dehydration increase photosynthetic heat tolerance in mangrove leaves. Funct. Ecol. 38, 897–909. https://doi.org/10.1111/1365-2435.14508.

Bunce, J.A., 2007. Direct and Acclimatory responses of dark respiration and translocation to temperature. Ann. Bot. 100, 67–73. https://doi.org/10.1093/aob/mcm071.

Burris, J.E., 1977. Photosynthesis, photorespiration, and dark respiration in eight species of algae. Mar. Biol. 39, 371–379. https://doi.org/10.1007/BF00391940.

Camp, E.F., Edmondson, J., Doheny, A., Rumney, J., Grima, A.J., Huete, A., Suggett, D.J., 2019. Mangrove lagoons of the great barrier reef support coral populations persisting under extreme environmental conditions. Mar. Ecol. Prog. Ser. 625, 1–14. https://doi.org/10.3354/meps13073.

Cheng, L., von Schuckmann, K., Abraham, J.P., Trenberth, K.E., Mann, M.E., Zanna, L., England, M.H., Zika, J.D., Fasullo, J.T., Yu, Y., Pan, Y., Zhu, J., Newsom, E.R., Bronselaer, B., Lin, X., 2022. Past and future ocean warming. Nat. Rev. Earth Environ. 3, 776–794. https://doi.org/10.1038/s43017-022-00345-1.

Coast, O., Posch, B.C., Rognoni, B.G., Bramley, H., Gaju, O., Mackenzie, J., Pickles, C., Kelly, A.M., Lu, M., Ruan, Y.-L., Trethowan, R., Atkin, O.K., 2022. Wheat photosystem II heat tolerance: evidence for genotype-by-environment interactions. Plant J. 111, 1368–1382. https://doi.org/10.1111/tpj.15894.

Coleman, M.A., Wernberg, T., 2017. Forgotten underwater forests: the key role of fucoids on Australian temperate reefs. Ecol. Evol. 7, 8406–8418. https://doi.org/10.1002/ece3.3279.

Coleman, M.A., Kelaher, B.P., Steinberg, P.D., Millar, A.J.K., 2008. Absence of a large Brown macroalga on urbanized rocky reefs around Sydney, Australia, and evidence for historical Decline1. J. Phycol. 44, 897–901. https://doi.org/10.1111/j.1529-8817.2008.00541.x.

Coleman, M.A., Roughan, M., Macdonald, H.S., Connell, S.D., Gillanders, B.M., Kelaher, B.P., Steinberg, P.D., 2011. Variation in the strength of continental boundary currents determines continent-wide connectivity in kelp. J. Ecol. 99, 1026–1032. https://doi.org/10.1111/j.1365-2745.2011.01822.x.

Coleman, M.A., Wood, G., Filbee-Dexter, K., Minne, A.J.P., Goold, H.D., Vergés, A., Marzinelli, E.M., Steinberg, P.D., Wernberg, T., 2020. Restore or redefine: future trajectories for restoration. Front. Mar. Sci. 7. https://doi.org/10.3389/fmars.2020.00237.

Cotas, J., Gomes, L., Pacheco, D., Pereira, L., 2023. Ecosystem services provided by seaweeds. Hydrobiology 2, 75–96. https://doi.org/10.3390/hydrobiology2010006.

Danaraj, J., Ayyappan, S., Mariasingarayan, Y., Packiyavathy, I.A.S.V., Sweetly Dharmadhas, J., 2021. Chlorophyll fluorescence, dark respiration and metabolomic analysis of Halodule pinifolia reveal potential heat responsive metabolites and biochemical pathways under ocean warming. Mar. Environ. Res. 164, 105248. https://doi.org/10.1016/j.marenvres.2020.105248.

Davis, T.R., Champion, C., Coleman, M.A., 2022. Ecological interactions mediate projected loss of kelp biomass under climate change. Divers. Distrib. 28, 306–317. https://doi.org/10.1111/ddi.13462.

Davison, I.R., 1991. Environmental effects on algal photosynthesis: temperature. J. Phycol. 27, 2–8. https://doi.org/10.1111/j.0022-3646.1991.00002.x.

Davison, I.R., Davison, J.O., 1987. The effect of growth temperature on enzyme activities in the brown alga *Laminaria saccharina*. Br. Phycol. J. 22, 77–87. https://doi.org/10.1080/00071618700650101.

Davison, I.R., Pearson, G.A., 1996. Stress tolerance in intertidal seaweeds. J. Phycol. 32, 197–211. https://doi.org/10.1111/j.0022-3646.1996.00197.x.

Davison, I.R., Greene, R.M., Podolak, E.J., 1991. Temperature acclimation of respiration and photosynthesis in the brown alga *Laminaria saccharina*. Mar. Biol. 110, 449–454. https://doi.org/10.1007/BF01344363.

Díaz-Acosta, L., Barreiro, R., Provera, I., Piñeiro-Corbeira, C., 2021. Physiological response to warming in intertidal macroalgae with different thermal affinity. Mar. Environ. Res. 169, 105350. https://doi.org/10.1016/j.marenvres.2021.105350.

Eggert, A., 2012. Seaweed responses to temperature. In: Wiencke, C., Bischof, K. (Eds.), Seaweed Biology: Novel Insights into Ecophysiology, Ecology and Utilization, Ecological Studies. Springer, Berlin, Heidelberg, pp. 47–66. https://doi.org/10.1007/978-3-642-28451-9_3.

Eggert, A., Wiencke, C., 2000. Adaptation and acclimation of growth and photosynthesis of five Antarctic red algae to low temperatures. Polar Biol. 23, 609–618. https://doi.org/10.1007/s003000000130.

Emmett, J.M., Walker, D.A., 1973. Thermal uncoupling in chloroplasts. Inhibition of photophosphorylation without depression of light-induced pH change. Arch. Biochem. Biophys. 157, 106–113. https://doi.org/10.1016/0003-9861(73)90395-0.

Endo, H., Moriyama, H., Okumura, Y., 2023. Photoinhibition and photoprotective responses of a Brown Marine macroalga acclimated to different light and nutrient regimes. Antioxidants 12, 357. https://doi.org/10.3390/antiox12020357.

Falkowski, P.G., Raven, J.A., 2013. Aquatic Photosynthesis, Second edition. Princeton University Press.

Fernández, P.A., Gaitán-Espitia, J.D., Leal, P.P., Schmid, M., Revill, A.T., Hurd, C.L., 2020. Nitrogen sufficiency enhances thermal tolerance in habitat-forming kelp: implications for acclimation under thermal stress. Sci. Rep. 10, 3186. https://doi.org/10.1038/s41598-020-60104-4.

Flukes, E.B., Wright, J.T., Johnson, C.R., 2015. Phenotypic plasticity and biogeographic variation in physiology of habitat-forming seaweed: response to temperature and nitrate. J. Phycol. 51, 896–909. https://doi.org/10.1111/jpy.12330.

Forbord, S., Matsson, S., Brodahl, G.E., Bluhm, B.A., Broch, O.J., Handå, A., Metaxas, A., Skjermo, J., Steinhovden, K.B., Olsen, Y., 2020. Latitudinal, seasonal and depth-dependent variation in growth, chemical composition and biofouling of cultivated Saccharina latissima (Phaeophyceae) along the Norwegian coast. J. Appl. Phycol. 32, 2215–2232. https://doi.org/10.1007/s10811-020-02038-y.

Franke, K., Bartsch, I., Karsten, U., Graiff, A., 2024. Seasonality influences the effect of warming on kelp photosynthesis. Mar. Ecol. Prog. Ser. 739, 15–29. https://doi.org/10.3354/meps14623.

Gent, M.P.N., Enoch, H.Z., 1983. Temperature dependence of vegetative growth and dark respiration: a mathematical model. Plant Physiol. 71, 562–567. https://doi.org/10.1104/pp.71.3.562.

Gounaris, K., Brain, A.R.R., Quinn, P.J., Williams, W.P., 1984. Structural reorganisation of chloroplast thylakoid membranes in response to heat-stress. Biochim. Biophys. Acta BBA - Bioenerg. 766, 198–208. https://doi.org/10.1016/0005-2728(84)90232-9.

Graiff, A., Franke, K., Karsten, U., Liesner, D., Gordillo, F.J.L., Iñiguez, C., 2025. Differential effects of warming on carbon budget, photosynthetic yield and biochemical composition of cold-temperate and Arctic isolates of *Laminaria digitata* (Phaeophyceae). J. Plant Physiol. 306, 154436. https://doi.org/10.1016/j.jplph.2025.154436.

Harley, C.D.G., Anderson, K.M., Demes, K.W., Jorve, J.P., Kordas, R.L., Coyle, T.A., Graham, M.H., 2012. Effects of climate change on global seaweed communities. J. Phycol. 48, 1064–1078. https://doi.org/10.1111/j.1529-8817.2012.01224.x.

Harris, R.J., Bryant, C., Coleman, M.A., Leigh, A., Briceño, V.F., Arnold, P.A., Nicotra, A. B., 2022. A novel and high-throughput approach to assess photosynthetic thermal tolerance of kelp using chlorophyll α fluorometry. J. Phycol., jpy.13296 https://doi.org/10.1111/jpy.13296.

Hastings, R.A., Rutterford, L.A., Freer, J.J., Collins, R.A., Simpson, S.D., Genner, M.J., 2020. Climate change drives poleward increases and equatorward declines in marine species. Curr. Biol. 30, 1572–1577.e2. https://doi.org/10.1016/j.cub.2020.02.043.

Healey, F.P., 1972. Photosynthesis and respiration of some Arctic seaweeds. Phycologia 11, 267–271. https://doi.org/10.2216/i0031-8884-11-3-267.1.

Hernández, S., García, A.G., Arenas, F., Escribano, M.P., Jueterbock, A., De Clerck, O., Maggs, C.A., Franco, J.N., Martínez, B.D.C., 2023. Range-edge populations of seaweeds show niche unfilling and poor adaptation to increased temperatures. J. Biogeogr. 50, 780–791. https://doi.org/10.1111/jbi.14572.

IPCC, 2021. Working Group I Contribution to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Camb. Univ. Press, p. 13.

Jeffers, M., Chapman, C.C., Sloyan, B.M., Bostock, H., 2025. Control of spatio-temporal variability of ocean nutrients in the East Australian Current. J. Ocean Sci. 21 (2), 537–554.

Kalaji, H.M., Carpentier, R., Allakhverdiev, S.I., Bosa, K., 2012. Fluorescence parameters as early indicators of light stress in barley. J. Photochem. Photobiol. B 112, 1–6. https://doi.org/10.1016/j.jphotobiol.2012.03.009.

King, N.G., McKeown, N.J., Smale, D.A., Wilcockson, D.C., Hoelters, L., Groves, E.A., Stamp, T., Moore, P.J., 2019. Evidence for different thermal ecotypes in range Centre and trailing edge kelp populations. J. Exp. Mar. Biol. Ecol. 514–515, 10–17. https://doi.org/10.1016/j.jembe.2019.03.004.

Knight, C.A., Ackerly, D.D., 2002. An ecological and evolutionary analysis of photosynthetic thermotolerance using the temperature-dependent increase in fluorescence. Oecologia 130, 505–514. https://doi.org/10.1007/s00442-001-0841-0.

Kübler, J.E., Davison, I.R., 1995. Thermal acclimation of light-use characteristics of *Chondrus crispus* (Rhodophyta). Eur. J. Phycol. https://doi.org/10.1080/09670269500650971.

Kumar, Y.N., Poong, S.-W., Gachon, C., Brodie, J., Sade, A., Lim, P.-E., 2020. Impact of elevated temperature on the physiological and biochemical responses of *Kappaphycus alvarezii* (Rhodophyta). PLoS ONE 15, e0239097. https://doi.org/10.1371/journal.pone.0239097.

Lagerspetz, K.Y.H., 2006. What is thermal acclimation? J. Therm. Biol. 31, 332–336. https://doi.org/10.1016/j.jtherbio.2006.01.003.

Lapointe, B.E., Duke, C.S., 1984. Biochemical strategies for growth of Gracilaria Tikvahiae (rhodophyta) in relation to light intensity and nitrogen Availability1. J. Phycol. 20, 488–495. https://doi.org/10.1111/j.0022-3646.1984.00488.x.

Martínez, B., Arenas, F., Rubal, M., Burgués, S., Esteban, R., García-Plazaola, I., Figueroa, F.L., Pereira, R., Saldaña, L., Sousa-Pinto, I., Trilla, A., Viejo, R.M., 2012. Physical factors driving intertidal macroalgae distribution: physiological stress of a dominant fucoid at its southern limit. Oecologia 170, 341–353. https://doi.org/10.1007/s00442-012-2324-x.

Martínez, B., Radford, B., Thomsen, M.S., Connell, S.D., Carreño, F., Bradshaw, C.J.A., Fordham, D.A., Russell, B.D., Gurgel, C.F.D., Wernberg, T., 2018. Distribution models predict large contractions of habitat-forming seaweeds in response to ocean warming. Divers. Distrib. 24, 1350–1366. https://doi.org/10.1111/ddi.12767.

Mueller, B., den Haan, J., Visser, P.M., Vermeij, M.J.A., van Duyl, F.C., 2016. Effect of light and nutrient availability on the release of dissolved organic carbon (DOC) by Caribbean turf algae. Sci. Rep. 6, 23248. https://doi.org/10.1038/srep23248.

O'Leary, B.M., Lee, C.P., Atkin, O.K., Cheng, R., Brown, T.B., Millar, A.H., 2017. Variation in leaf respiration rates at night correlates with carbohydrate and amino acid supply. Plant Physiol. 174, 2261–2273. https://doi.org/10.1104/pp.17.00610.

O'Leary, B.M., Asao, S., Millar, A.H., Atkin, O.K., 2019. Core principles which explain variation in respiration across biological scales. New Phytol. 222, 670–686. https://doi.org/10.1111/nph.15576.

Olischläger, M., Iñiguez, C., Koch, K., Wiencke, C., Gordillo, F.J.L., 2017. Increased pCO2 and temperature reveal ecotypic differences in growth and photosynthetic performance of temperate and Arctic populations of Saccharina latissima. Planta 245, 119–136. https://doi.org/10.1007/s00425-016-2594-3.

Oliver, E.C.J., Donat, M.G., Burrows, M.T., Moore, P.J., Smale, D.A., Alexander, L.V., Benthuysen, J.A., Feng, M., Sen Gupta, A., Hobday, A.J., Holbrook, N.J., Perkins-Kirkpatrick, S.E., Scannell, H.A., Straub, S.C., Wernberg, T., 2018. Longer and more frequent marine heatwaves over the past century. Nat. Commun. 9, 1324. https://doi.org/10.1038/s41467-018-03732-9.

O'Sullivan, O.S., Heskel, M.A., Reich, P.B., Tjoelker, M.G., Weerasinghe, L.K., Penillard, A., Zhu, L., Egerton, J.J.G., Bloomfield, K.J., Creek, D., Bahar, N.H.A., Griffin, K.L., Hurry, V., Meir, P., Turnbull, M.H., Atkin, O.K., 2017. Thermal limits of leaf metabolism across biomes. Glob. Chang. Biol. 23, 209–223. https://doi.org/10.1111/gcb.13477.

Padilla-Gamiño, J.L., Carpenter, R.C., 2007. Seasonal acclimatization of *Asparagopsis taxiformis* (Rhodophyta) from different biogeographic regions. Limnol. Oceanogr. 52, 833–842. https://doi.org/10.4319/lo.2007.52.2.0833.

Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T.C., Chen, I.-C., Clark, T. D., Colwell, R.K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R.A., Griffis, R.B., Hobday, A.J., Janion-Scheepers, C., Jarzyna, M.A., Jennings, S., Lenoir, J., Linnetved, H.I., Martin, V.Y., McCormack, P.C., McDonald, J., Mitchell, N.J., Mustonen, T., Pandolfi, J.M., Pettorelli, N., Popova, E., Robinson, S.A., Scheffers, B.R., Shaw, J.D., Sorte, C.J.B., Strugnell, J.M., Sunday, J. M., Tuanmu, M.-N., Vergés, A., Villanueva, C., Wernberg, T., Wapstra, E., Williams, S.E., 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. Science 355, eaai9214. https://doi.org/10.1126/science.aai9214.

Perez, T.M., Andino, J.E.G., Rivas-Torres, G., Feeley, K.J., 2023. Climate constrains photosynthetic strategies in Darwin's daisies: a test of the climatic variability and Jack-of-all-trades hypotheses. Am. Nat. 201, 78–90. https://doi.org/10.1086/721957.

Pessarrodona, A., Assis, J., Filbee-Dexter, K., Burrows, M.T., Gattuso, J.-P., Duarte, C.M., Krause-Jensen, D., Moore, P.J., Smale, D.A., Wernberg, T., 2022. Global seaweed productivity. Sci. Adv. 8, eabn2465. https://doi.org/10.1126/sciadv.abn2465.

Pfister, C.A., Berry, H.D., Mumford, T., 2018. The dynamics of kelp forests in the Northeast Pacific Ocean and the relationship with environmental drivers. J. Ecol. 106, 1520–1533. https://doi.org/10.1111/1365-2745.12908.

Posch, B.C., Kariyawasam, B.C., Bramley, H., Coast, O., Richards, R.A., Reynolds, M.P., Trethowan, R., Atkin, O.K., 2019. Exploring high temperature responses of photosynthesis and respiration to improve heat tolerance in wheat. J. Exp. Bot. 70, 5051–5069. https://doi.org/10.1093/jxb/erz257.

Posch, B.C., Hammer, J., Atkin, O.K., Bramley, H., Ruan, Y.-L., Trethowan, R., Coast, O., 2022. Wheat photosystem II heat tolerance responds dynamically to short- and long-term warming. J. Exp. Bot. 73, 3268–3282. https://doi.org/10.1093/jxb/erac039.

R Core Team, 2018. R: A Language and Environment for Statistical Computing, p. 12.

Ruban, A.V., 2016. Nonphotochemical chlorophyll fluorescence quenching: mechanism and effectiveness in protecting plants from Photodamage. Plant Physiol. 170, 1903–1916. https://doi.org/10.1104/pp.15.01935.

Scafaro, A.P., Negrini, A.C.A., O'Leary, B., Rashid, F.A.A., Hayes, L., Fan, Y., Zhang, Y., Chochois, V., Badger, M.R., Millar, A.H., Atkin, O.K., 2017. The combination of gas-phase fluorophore technology and automation to enable high-throughput analysis of plant respiration. Plant Methods 13, 16. https://doi.org/10.1186/s13007-017-0169-3.

Scafaro, A.P., Fan, Y., Posch, B.C., Garcia, A., Coast, O., Atkin, O.K., 2021. Responses of leaf respiration to heatwaves. Plant Cell Environ. 44, 2090–2101. https://doi.org/10.1111/pce.14018.

Schreiber, U., Berry, J.A., 1977. Heat-induced changes of chlorophyll fluorescence in intact leaves correlated with damage of the photosynthetic apparatus. Planta 136, 233–238. https://doi.org/10.1007/BF00385990.

Sharpe, P.J.H., 1983. Responses of photosynthesis and dark respiration to temperature. Ann. Bot. 52, 325–343. https://doi.org/10.1093/oxfordjournals.aob.a086581.

Smith, K.E., Burrows, M.T., Hobday, A.J., King, N.G., Moore, P.J., Sen Gupta, A., Thomsen, M.S., Wernberg, T., Smale, D.A., 2023. Biological impacts of marine heatwaves. Annu. Rev. Mar. Sci. 15, 119–145. https://doi.org/10.1146/annurev-marine-032122-121437.

Staehr, P.A., Wernberg, T., 2009. Physiological responses of Ecklonia Radiata (laminariales) to a latitudinal gradient in ocean Temperature1. J. Phycol. 45, 91–99. https://doi.org/10.1111/j.1529-8817.2008.00635.x.

Straub, S.C., Wernberg, T., Thomsen, M.S., Moore, P.J., Burrows, M.T., Harvey, B.P., Smale, D.A., 2019. Resistance, extinction, and everything in between – the diverse responses of seaweeds to marine heatwaves. Front. Mar. Sci. 0. https://doi.org/10.3389/fmars.2019.00763.

Straub, S.C., Wernberg, T., Marzinelli, E.M., Vergés, A., Kelaher, B.P., Coleman, M.A., 2022. Persistence of seaweed forests in the anthropocene will depend on warming and marine heatwave profiles. J. Phycol. 58, 22–35. https://doi.org/10.1111/jpy.13222.

Tano, S.A., Eggertsen, M., Wikström, S.A., Berkström, C., Buriyo, A.S., Halling, C., 2017. Tropical seaweed beds as important habitats for juvenile fish. Mar. Freshw. Res. 68, 1921–1934. https://doi.org/10.1071/MF16153.

Thomsen, M.S., Mondardini, L., Alestra, T., Gerrity, S., Tait, L., South, P.M., Lilley, S.A., Schiel, D.R., 2019. Local extinction of bull kelp (Durvillaea spp.) due to a marine heatwave. Front. Mar. Sci. 6, 84. https://doi.org/10.3389/fmars.2019.00084.

Umanzor, S., Shin, S., Marty-Rivera, M., Augyte, S., Yarish, C., Kim, J.K., 2019. Preliminary assessment on the effects of the commercial seaweed extract, AMPEP, on growth and thermal tolerance of the kelp Saccharina spp. from the Northwest Atlantic. J. Appl. Phycol. 31, 3823–3829. https://doi.org/10.1007/s10811-019-01852-3.

Veenhof, R.J., Champion, C., Dworjanyn, S.A., Shalders, T.C., Coleman, M.A., 2023. Reproductive phenology of the kelp Ecklonia radiata at its Australian warm-range edge and the influence of environmental factors. Mar. Freshw. Res. 74, 928–940. https://doi.org/10.1071/MF22259.

Vergés, A., Doropoulos, C., Malcolm, H.A., Skye, M., Garcia-Pizá, M., Marzinelli, E.M., Campbell, A.H., Ballesteros, E., Hoey, A.S., Vila-Concejo, A., Bozec, Y.-M., Steinberg, P.D., 2016. Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory, and loss of kelp. Proc. Natl. Acad. Sci. 113, 13791–13796. https://doi.org/10.1073/pnas.1610725113.

Vranken, S., Wernberg, T., Scheben, A., Severn-Ellis, A.A., Batley, J., Bayer, P.E., Edwards, D., Wheeler, D., Coleman, M.A., 2021. Genotype–Environment mismatch of kelp forests under climate change. Mol. Ecol. 30, 3730–3746. https://doi.org/10.1111/mec.15993.

Way, D.A., Yamori, W., 2014. Thermal acclimation of photosynthesis: on the importance of adjusting our definitions and accounting for thermal acclimation of respiration. Photosynth. Res. 119, 89–100. https://doi.org/10.1007/s11120-013-9873-7.

Wernberg, T., Thomsen, M.S., Tuya, F., Kendrick, G.A., 2011. Biogenic habitat structure of seaweeds change along a latitudinal gradient in ocean temperature. J. Exp. Mar. Biol. Ecol. 400, 264–271. https://doi.org/10.1016/j.jembe.2011.02.017.

Wernberg, T., Smale, D.A., Tuya, F., Thomsen, M.S., Langlois, T.J., de Bettignies, T., Bennett, S., Rousseaux, C.S., 2013. An extreme climatic event alters marine ecosystem structure in a global biodiversity hotspot. Nat. Clim. Chang. 3, 78–82. https://doi.org/10.1038/nclimate1627.

Wernberg, T., Bennett, S., Babcock, R.C., de Bettignies, T., Cure, K., Depczynski, M., Dufois, F., Fromont, J., Fulton, C.J., Hovey, R.K., Harvey, E.S., Holmes, T.H., Kendrick, G.A., Radford, B., Santana-Garcon, J., Saunders, B.J., Smale, D.A., Thomsen, M.S., Tuckett, C.A., Tuya, F., Vanderklift, M.A., Wilson, S., 2016a. Climate-driven regime shift of a temperate marine ecosystem. Science 353, 169–172. https://doi.org/10.1126/science.aad8745.

Wernberg, T., de Bettignies, T., Joy, B.A., Finnegan, P.M., 2016b. Physiological responses of habitat-forming seaweeds to increasing temperatures. Limnol. Oceanogr. 61, 2180–2190. https://doi.org/10.1002/lno.10362.

Wernberg, T., Coleman, M.A., Bennett, S., Thomsen, M.S., Tuya, F., Kelaher, B.P., 2018. Genetic diversity and kelp forest vulnerability to climatic stress. Sci. Rep. 8, 1851. https://doi.org/10.1038/s41598-018-20009-9.

Wernberg, T., Coleman, M.A., Babcock, R.C., Bell, S.Y., Bolton, J.J., Connell, S.D., Hurd, C.L., Johnson, C.R., Marzinelli, E.M., Shears, N.T., Steinberg, P.D., Thomsen, M.S., Vanderklift, M.A., Verges, A., Wright, J.T., 2019a. Chapter 6 biology and ecology of the globally significant kelp ecklonia radiata. Oceanogr. Mar. Biol. 57, 1–62.

Wernberg, T., Krumhansl, K., Filbee-Dexter, K., Pedersen, M.F., 2019b. Chapter 3 - status and trends for the world's kelp forests. In: Sheppard, C. (Ed.), World Seas: An Environmental Evaluation, Second edition. Academic Press, pp. 57–78. https://doi.org/10.1016/B978-0-12-805052-1.00003-6.

Wernberg, T., Thomsen, M.S., Baum, J.K., Bishop, M.J., Burno, J.F., Coleman, M.A., Filbee-Dexter, K., Gagnon, K., He, Q., Murdiyarso, D., Rogers, K., 2024. Impacts of climate change om marine foundation species. Annual Rev. Marine Sci. 16 (1), 247–282.

Wilson, K.L., Kay, L.M., Schmidt, A.L., Lotze, H.K., 2015. Effects of increasing water temperatures on survival and growth of ecologically and economically important seaweeds in Atlantic Canada: implications for climate change. Mar. Biol. 162, 2431–2444. https://doi.org/10.1007/s00227-015-2769-7.

Wood, G., Marzinelli, E.M., Vergés, A., Campbell, A.H., Steinberg, P.D., Coleman, M.A., 2020. Using genomics to design and evaluate the performance of underwater forest restoration. J. Appl. Ecol. 57, 1988–1998. https://doi.org/10.1111/1365-2664.13707.

Zahra, N., Shaukat, K., Hafeez, M.B., Raza, A., Hussain, S., Chaudhary, M.T., Akram, M.Z., Kakavand, S.N., Saddiq, M.S., Wahid, A., 2021. Physiological and molecular responses to high, chilling, and freezing temperature in plant growth and production: Consequences and mitigation possibilities. In: Husen, A. (Ed.), Harsh Environment and Plant Resilience: Molecular and Functional Aspects. Springer International Publishing, Cham, pp. 235–290. https://doi.org/10.1007/978-3-030-65912-7_10.

Zarco-Perello, S., Wernberg, T., Langlois, T.J., Vanderklift, M.A., 2017. Tropicalization strengthens consumer pressure on habitat-forming seaweeds. Sci. Rep. 7, 820. https://doi.org/10.1038/s41598-017-00991-2.

Zou, D., Gao, K., 2014. The photosynthetic and respiratory responses to temperature and nitrogen supply in the marine green macroalga Ulva conglobata (Chlorophyta). Phycologia 53, 86–94. https://doi.org/10.2216/13-189.1.