



Low light exacerbates effects of marine heatwaves on seaweeds

Thomas Wernberg^{1,2,3,*}, Sandra C. Straub¹

¹UWA Oceans Institute and School of Biological Sciences, The University of Western Australia, Crawley, Western Australia 6009, Australia

²Institute of Marine Research, Flødevigen Research Station, 4817 His, Norway

³Department of Science and Environment, Roskilde University, 4000 Roskilde, Denmark

ABSTRACT: Marine heatwaves (MHWs) are becoming more frequent and intense. At the same time, diverse human activities are causing coastal darkening: increased turbidity and reduced light at the seafloor. Since both temperature and light are critical to the physiological and ecological performance of seaweeds — important habitat-formers and primary producers — these co-occurring stressors could have knock-on effects in coastal ecosystems. We tested the effects of MHWs under different irradiance levels on 3 brown seaweeds: the kelp *Ecklonia radiata* and 2 common understory species, *Zonaria turneriana* and *Lobophora variegata*. The seaweeds were subjected to 15 d MHWs of different maximum intensities (25° and 28°C) at 2 reduced light levels (~40 and ~10 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Effects on cover of bleached tissue, biomass, maximum quantum yield and pigment concentrations were assessed. Temperature was the main cause of observed changes in seaweed condition, with strong negative effects of the most intense MHW (28°C) especially for tissue bleaching and maximum quantum yield. Low light had a minor effect at 19°C (background temperature) and in the moderate MHW treatment (25°C). However, at extreme temperatures (28°C), low light enhanced the negative effects on virtually all seaweed condition metrics. For all species, the negative effects of the most severe MHW persisted during the recovery period, during which temperatures were returned to background conditions. The compounding effect of high temperature and reduced light highlights the need to assess the interactive nature of multiple stressors with respect to the emerging threat of MHWs to reef ecosystems.

KEY WORDS: Kelp forests · Coastal darkening · Macroalgae · *Ecklonia radiata* · *Zonaria turneriana* · *Lobophora variegata* · Extreme temperature events · Anthropocene

1. INTRODUCTION

Seaweed-dominated ecosystems, such as kelp forests, are among the most extensive, productive and diverse coastal habitats globally (Teagle et al. 2017, Wernberg & Filbee-Dexter 2019, Duarte et al. 2022, Pessarrodona et al. 2022). The biogeographic distribution of seaweeds is primarily driven by temperature (van den Hoek 1982, Lüning 1990, Martínez et al. 2018), although many other factors including irradiance and photoperiod, nutrients, wave exposure, cur-

rents, salinity and herbivores can also be important, especially at regional to local spatial scales (e.g. Hurd 2000, Wernberg et al. 2013b, Vergés et al. 2014).

Climatic conditions over long time scales have led to the evolution of species-specific thermal ranges, within which the growth, reproduction and survival of seaweeds is optimal (van den Hoek 1982, Lüning 1990). Warming affects most aspects of the biology of seaweeds (Davison 1991, Kordas et al. 2011, Eggert 2012, de Bettignies et al. 2018), and ocean warming driven by climate change has been linked to changes

*Corresponding author: thomas.wernberg@uwa.edu.au

in seaweed genetics, physiology, ecology and biogeography (Harley et al. 2012, Wernberg et al. 2019b, Coleman et al. 2020, Smale 2020, Wernberg et al. 2024). Concurrent with long-term ocean warming, marine heatwaves (MHWs), discrete warm-water events (Hobday et al. 2016), have increased in frequency and duration (Oliver et al. 2018), and these extreme events have been linked to a plethora of climate-mediated impacts on seaweeds, ranging from bleaching and reduced growth to changes in abundance and local extinctions (Straub et al. 2019).

The coastal zone is a focal point for human activities where warming and MHWs are superimposed onto other stressors such as pollution, coastal development, fisheries, invasive species and aquaculture (Wernberg et al. 2011, Halpern et al. 2015). Through effects on physiological performance and population survival, warming and MHWs have the potential to affect responses to other stressors (e.g. Wernberg et al. 2010). That is, while the direct effects can be easily observable when temperatures are extreme enough to exceed the physiological thresholds of marine organisms (e.g. Wernberg et al. 2016), warming and MHWs can have insidious indirect effects through complex interactions with other stressors (e.g. Strain et al. 2014). Conversely, local conditions can also mediate responses to high temperatures (Helmuth et al. 2006, Starko et al. 2024) and, given that seaweeds respond to numerous and complex environmental changes at local to global scales, it is important to understand their sensitivity and responses to multiple stressors (e.g. Edwards & Hernández-Carmona 2005, Ling et al. 2009, Rogers-Bennett & Catton 2019, Tait et al. 2021).

A major pressure on seaweeds and coastal ecosystems, in addition to warming and MHWs, is coastal darkening (UNEP 2023): reduced light availability caused by run-off, eutrophication and blooms of phytoplankton and turf algae (e.g. Seers & Shears 2015, Blain et al. 2021, Frigstad et al. 2023). Light availability combined with temperature drives photosynthesis and primary production (Singh & Singh 2015, Pessarrodona et al. 2022), and the combined effects of high temperature and low light on seaweeds are often synergistically negative (e.g. Tait & Schiel 2013, Strain et al. 2014, Blain & Shears 2019, Tait et al. 2021). Changes to the light and temperature environment, therefore, have major implications for primary producers (Pehlke & Bartsch 2008, Bartsch et al. 2016) and can alter the structure of coastal ecosystems (Strain et al. 2014, Filbee-Dexter & Wernberg 2018) and the productivity of coastal food webs (Singh & Singh 2015).

Specifically, seaweeds tend to have a shallower and narrower depth range in areas with increased turbidity and lower light levels (Pedersén & Snoeijs 2001, Pehlke & Bartsch 2008, Bartsch et al. 2016) and their physiological light demand to maintain metabolic functions is higher in a warmer ocean (Stæhr & Wernberg 2009, Tait & Schiel 2013). Therefore, we tested the hypothesis that reduced light levels will interact with extreme temperatures during MHWs to compound negative effects on the performance of 3 co-occurring brown seaweeds with contrasting ecological functions and thermal affinities: *Ecklonia radiata*, *Zonaria turneriana* and *Lobophora variegata*.

2. MATERIALS AND METHODS

2.1. Study site and specimen collections

Individual thalli of juvenile kelp (stage 1 to small stage 2) *Ecklonia radiata* (C. Agardh) J. Agardh, and 2 smaller foliose seaweeds, *Zonaria turneriana* J. Agardh and *Lobophora variegata* (Lamouroux) C. Agardh, were collected at Horseshoe Reef (31° 50' 18" S, 115° 42' 60" E), approximately 25 km north of Perth (Western Australia) in November 2016 (late Austral spring). *E. radiata* is a temperate canopy-forming kelp that dominates Australia's Great Southern Reef (Wernberg et al. 2019a). *Z. turneriana* is a temperate seaweed common from Kalbarri, in Western Australia, along the southern coastline and Tasmania to Port Phillips Heads in Victoria. *L. variegata* is a tropical to warm-temperate distributed seaweed which can be abundant in tropical lagoons, on degraded coral reefs and tropicalised temperate reefs (e.g. Diaz-Pulido et al. 2009, Fulton et al. 2014, Wernberg et al. 2016). These species maximised the range and diversity of potential responses that could be expected. Around 50 individuals of each species were collected haphazardly from the reef between 7 and 10 m depth by SCUBA divers. The seaweeds were collected with intact holdfasts, placed in calico bags and transported in a dark, chilled cooler to the laboratory. Within 4 h of collection, all individuals were placed in a holding tank with flowing, temperature-controlled seawater and aeration. Individual seaweeds were then weighted by attaching holdfasts to small pebbles with rubber bands to ensure a natural upright position, transferred to the experimental aquaria and acclimated at 19°C (ambient temperature at time of collection) for 7 d prior to commencement of the experiment.

2.2. Experimental setup

The experimental setup consisted of 18×45 l indoor aquaria and two 1000 l sumps filled with recirculating filtered seawater. Both sumps fed water to and from all aquaria, and water temperatures were regulated by controlling the flow rate to each aquarium, with one 'hot' sump heated to 29°C and one 'cold' sump chilled to 18°C (Hailea 2HP Chiller/Heater units). Pre-filtered (Odyssea CFS-1200), UV-sterilized (SunSun CUV-155) hot and cold seawater was supplied to each aquarium, and experimental temperatures were achieved by direct mixing from the 2 sumps into each aquarium (combined flow rate: ~ 100 l h^{-1}) to experimental temperatures. Temperature was monitored continuously using Aquatronica temperature sensors and maintained at $\pm 0.5^\circ\text{C}$ of the assigned temperature. Aeration and additional water motion was achieved using air curtains. Fluorescent lights (GM Powerchrome T5) were placed above the aquaria on an 8 h light:16 h dark cycle. Light levels were adjusted by dimming and were ascertained in each aquarium using a hand-help PAR logger (Apogee MQ-510) prior to the experiment. Salinity was monitored twice per week using a hand-held refractometer but did not vary over the experiment.

Six different treatments were applied, combining 2 levels of light and 3 levels of temperature. Each treatment was replicated 3 times. Half of the aquaria received moderate light (ML: $\sim 40 \mu\text{mol m}^{-2} \text{s}^{-1}$; $\sim 115 \text{ mol d}^{-1}$) and the other half received low light (LL: $\sim 10 \mu\text{mol m}^{-2} \text{s}^{-1}$; $\sim 0.29 \text{ mol d}^{-1}$). These light levels were under or just over the critical compensation point for *E. radiata* (Stæhr & Wernberg 2009) and therefore likely stressful. Importantly, they mimicked summer conditions at the reef surface of the collection site under a canopy of 2–4 kelp sporophytes per 0.25 m^2 (Wernberg et al. 2005) and they represent a >75% reduction in available light, as is commonly seen as a consequence of darkening from increased dissolved matter in the coastal zone (e.g. Mustafa et al. 2020, Blain et al. 2021).

Within the 2 light levels, aquaria were randomly assigned a temperature treatment of either background/control (19°C), moderate (25°C) or extreme (28°C) MHW conditions, where the moderate and extreme MHW conditions were within the range of temperatures recorded during previous events in the region (cf. Smale & Wernberg 2009, Wernberg et al. 2018). Seaweeds were acclimated at 19°C for 1 wk, with ~ 25 specimens per species acclimated at ML levels and ~ 25 specimens per species acclimated at LL levels. At the end of the acclimation period, 3 healthy-looking

specimens of each seaweed species were haphazardly assigned to each aquarium. Temperature increases were applied at a rate of 1°C h^{-1} until experimental conditions were reached and then maintained for 15 d before returning to control temperature conditions at a rate of 1°C h^{-1} , where they were kept for a 1 wk period of recovery.

2.3. Measurements

Tissue bleaching, biomass and maximum quantum yield (F_v/F_m) were measured periodically over the experimental period ($n = 6$ measurements per species per treatment). Pigment composition and concentration were assessed on Day 15 after termination of treatments ($n = 3$ per species per treatment).

Tissue bleaching (% cover of thallus) was visually assessed every second day as visible discolouration of the thallus tissue (Xiao et al. 2015). Biomass (in g wet weight [WW] after gentle removal of water) was measured at the start of full treatment exposure (Day 0), at the termination of MHWs (Day 15) and on the last day of the recovery period (Day 22). Relative growth rates (RGR; % day^{-1}) were calculated based on the biomass measurements for the treatment duration and the recovery period following the equation:

$$\text{RGR (\% d}^{-1}\text{)} = [(W_t / W_i)^{1/t} - 1] \times 100$$

where W_i is the initial WW, W_t is WW on the respective day and $t = 15$ d for treatment duration and 7 d for recovery phase.

F_v/F_m was determined every 2–3 d throughout the treatment exposure as well as at the end of the recovery period. F_v/F_m values were measured between 09:30 and 14:30 h (MINI-PAM II, Waltz). Prior to F_v/F_m measurements, the seaweed tissue was dark-acclimated for 15 min using dark leaf clips. Measurements were taken fully submerged within the aquaria to maintain stable treatment conditions and to minimise any stress for the seaweeds.

Tissue samples for pigment composition and concentration were taken on Day 15 ($\sim 0.2 \pm 0.4$ g WW randomly sampled from the middle of the lamina $\sim 1/3$ of the length above the meristem), placed in tin foil packages, snap-frozen in liquid nitrogen and stored at -80°C . For the extraction of chlorophylls and carotenoids, tissue samples were dipped in liquid nitrogen and ground in a cold mortar while adding high-performance liquid chromatography (HPLC)-grade acetone. After sonication in an ice bath for 3 min to further disrupt cell walls, extracts were incubated overnight in a dark refrigerator at 4°C and sonicated

the following morning. Extracts were transferred into Eppendorf tubes, centrifuged (5 min at $13000 \times g$) and then 0.8 ml of supernatant was transferred to HPLC vials and stored at -80°C until HPLC measurements. The HPLC analyses were performed according to Tamm et al. (2015) with minor modifications. Separation was achieved at a temperature of $25 \pm 1^{\circ}\text{C}$ in 50 min on a Spherisorb ODS2 (Waters) column (250 mm \times 4.6 mm i.d. with 5 μm particle), using a Waters® HPLC system (600E pump, 717+ autoinjector with carousel temperature control set at 10°C and 996 photodiode-array detector). The mobile phase consisted of 2 pre-mixed eluents: A = 80:20 methanol:0.5 M ammonium acetate (pH 7.2) and B = 80:20 methanol:acetone. Data acquisition with the photodiode array was from 350 to 750 nm at a resolution of 1.2 nm, with achieved detection and quantification of the pigments at 450 nm. All linear calibrations were calculated according to peak area, and pigment standards were run routinely to ensure the validity of pigment retention time.

2.4. Statistical analysis

Data were analysed by analysis of variance by permutation (PERMANOVA) in PRIMER v.6 (9999 permutations) (Anderson et al. 2008). Given the permutation-based approach, it was assumed that tests were robust to deviations from normal distribution. Temperature (Te), light (Li) and time as days (Da) since the start of the experiment were considered fixed factors. Species and measures were analysed separately and as such were treated as independent tests with no adjustment for multiple testing. Full statistical outputs are provided in Tables S1–S5 in the Supplement at www.int-res.com/articles/suppl/m747p049_supp.pdf.

3. RESULTS

3.1. Tissue bleaching

Tissue bleaching varied significantly with temperature, light and duration of exposure for *Ecklonia radiata*, *Zonaria turneriana* and *Lobophora variegata*

($p \leq 0.001$; Table S1). Interaction terms were significant for Da \times Te as well as Te \times Li for all 3 species, and additionally the interaction terms of Da \times Li and Da \times Te \times Li for *Z. turneriana* and *L. variegata* (Table S1). Generally, for all species, only minor bleaching was observed at 19° and 25°C (Fig. 1). For *E. radiata*, the extreme MHW (28°C) resulted in significantly increased bleaching in comparison to background conditions (ML: $p \leq 0.003$; LL: $p \leq 0.009$) and 25°C (ML: $p \leq 0.007$; LL: $p \leq 0.007$) at both light regimes (Fig. 1A). Similarly, 25°C significantly increased bleaching of *Z. turneriana* (Fig. 1B) after 15 d at ML ($p \leq 0.015$) and after 19 d at LL ($p \leq 0.036$) levels. The MHW (28°C) significantly increased bleaching at ML after 4 d (19°C : $p \leq 0.003$; 25°C : $p \leq 0.030$) and at LL after 6 d (19°C : $p \leq 0.009$; 25°C : $p \leq 0.046$). In contrast, the onset of tissue bleaching was later but more rapid

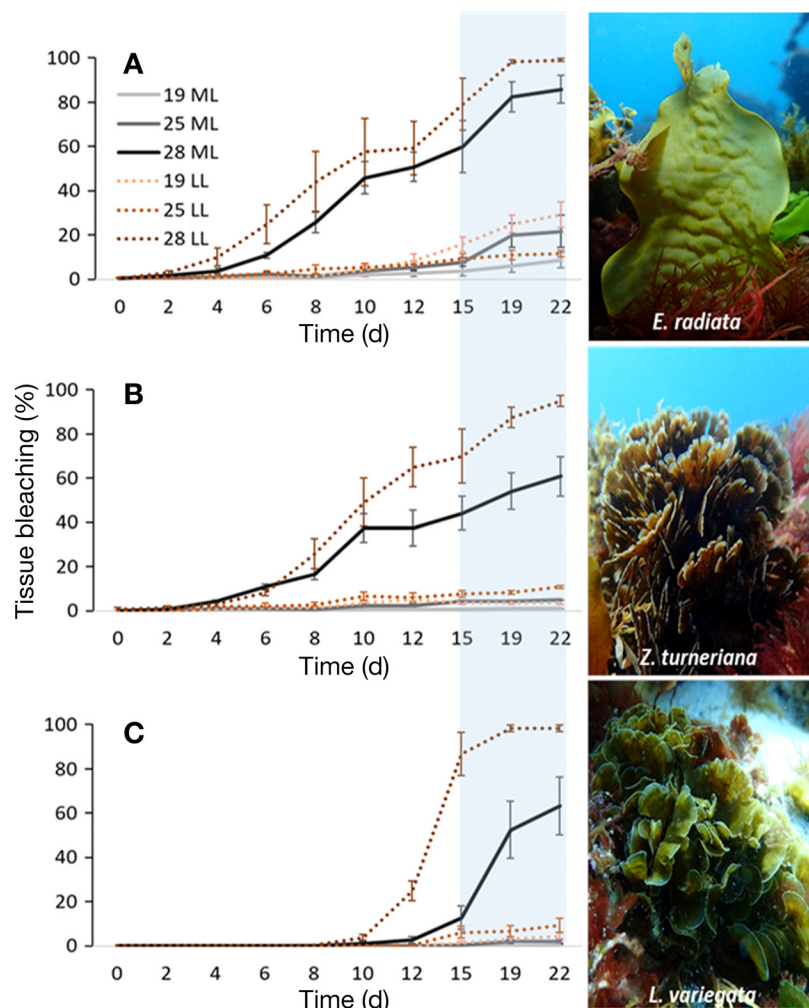


Fig. 1. Mean (\pm SE) tissue bleaching (% thallus cover) for (A) *Ecklonia radiata*, (B) *Zonaria turneriana* and (C) *Lobophora variegata* over time for different temperature (19° , 25° , 28°C) and light (ML: moderate: LL: low) levels. Shaded area: recovery period during which all treatments were returned to 19°C

in *L. variegata* (Fig. 1C), and exposure to 28°C resulted in significantly increased bleaching rates of *L. variegata* at ML after 15 d (19°C: $p \leq 0.002$; 25°C: $p \leq 0.006$), and at LL from Day 10 onwards (19°C: $p \leq 0.009$; 25°C: $p \leq 0.003$). LL levels resulted in significantly increased bleaching of *E. radiata* at 19°C after 15 d ($p \leq 0.027$) and at 28°C after 19 d ($p \leq 0.039$). LL levels significantly increased bleaching cover of *Z. turneriana* at 19°C after 10 d ($p \leq 0.033$), and at 25°C ($p \leq 0.048$) and 28°C ($p \leq 0.016$) after 19 d. For *L. variegata*, LL increased tissue bleaching in comparison to ML levels, with significantly higher bleaching at 19° and 25°C from Day 15, and at 28°C from Day 12 onwards. For all 3 species, 28°C led to the highest tissue bleaching rates, with LL levels further enhancing

tissue bleaching in contrast to ML levels. No recovery was observed in the recovery week during which seaweeds were returned to control conditions at 19°C.

3.2. Biomass and growth rates

The biomass of *E. radiata* (Fig. 2A) was significantly affected by temperature ($p \leq 0.001$; Table S2) and the interaction $Da \times Te$ ($p = 0.024$). While *E. radiata* biomass remained relatively unchanged at 19° and 25°C, it decreased over time when exposed to 28°C at both ML and LL levels by Day 15. In contrast, the biomass of *Z. turneriana* (Fig. 2B) was not significantly

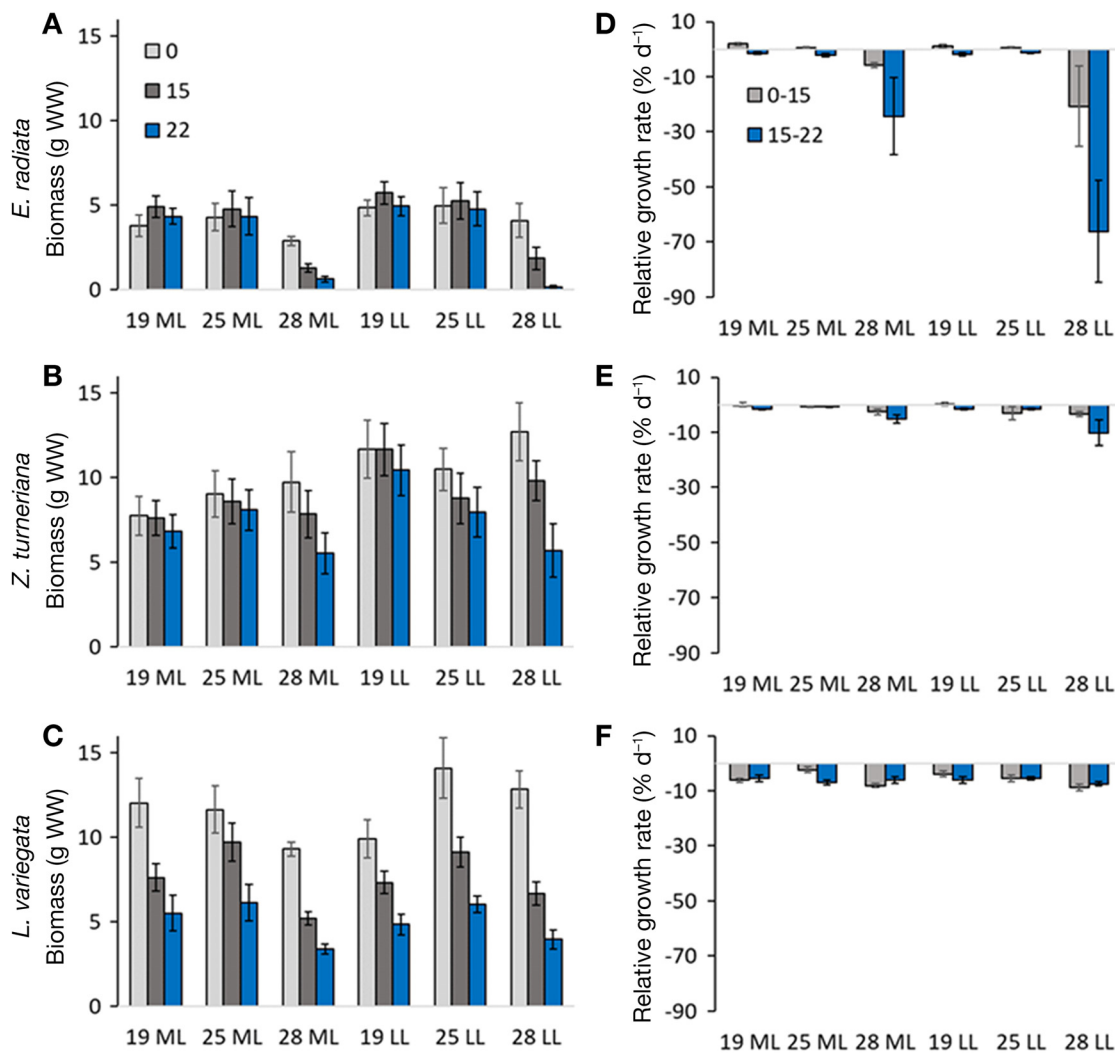


Fig. 2. Mean (\pm SE) biomass and relative growth rate (RGR) at different times after starting the experiment (exposure durations: 0, 15 and 22 d) for (A,D) *Ecklonia radiata*, (B,E) *Zonaria turneriana* and (C,F) *Lobophora variegata* for different temperature (19°, 25°, 28°C) and light (ML: moderate; LL: low) levels. Biomass was wet weight (WW) of seaweed on Days 0, 15 and 22. RGR was calculated over the heatwave (Days 0–15) and the recovery period (Days 15–22). Measurements taken at start (Day 0) and end (Day 15) of the heatwave are shown in grey; recovery measurements are shown in blue (Day 22)

affected by any of the treatments ($p > 0.262$), although it did show a decreasing trend over time in all treatments, with the most pronounced trend in the 28°C LL treatment. The biomass of *L. variegata* (Fig. 2C) was affected by exposure duration ($p \leq 0.001$) and temperature ($p = 0.002$), but light levels had no effect ($p = 0.428$).

Temperature had a negative effect on RGRs for all 3 species ($p \leq 0.002$; Table S3). The temperature effects were complex for *E. radiata* (Fig. 2D), with significant interactions for exposure duration ($Da \times Te$; $p = 0.015$) and light ($Te \times Li$; $p = 0.018$). Relative growth of *E. radiata* (Fig. 2D) remained constant over time at 19° and 25°C irrespective of light levels; however, at 28°C, RGR declined after 15 and 22 d, with LL levels clearly exacerbating the negative effects even during the recovery phase. RGR of *Z. turneriana* (Fig. 2E) was affected by temperature ($p \leq 0.001$), exhibiting a similar but much smaller drop in growth during the recovery phase at 25° and 28°C. RGR remained relatively constant for *L. variegata* (Fig. 2F), although there was a significant effect of temperature ($p = 0.002$) and $Da \times Te$ interaction ($p \leq 0.033$).

3.3. F_v/F_m

Temperature and duration of exposure were the main factors causing a change in F_v/F_m for all 3 species ($Da \times Te$, $p \leq 0.001$; Fig. 3, Table S4). For all species, yield declined slightly over the treatment duration at 19° and 25°C, with a strong reduction when exposed to 28°C. For *E. radiata* (Fig. 3A), yield values were reduced already after 5 d at 28°C under both light levels. In comparison, yield values of *Z. turneriana* (Fig. 3B) were unaffected at 25°C; however, at 28°C, yield declined at LL levels after 5 d and after 15 d at ML levels. Similarly, yield values for *L. variegata* (Fig. 3C) were negatively affected at 28°C with a reduction at both light levels after 15 d, where the greatest decline was seen at LL levels. Due to tissue deterioration and loss, no measurements were possible at 28°C and LL levels after the recovery period.

3.4. Pigments

HPLC measurements identified 10 different pigments: chlorophyll (chl) *c1*, *c2* and *a*, fucoxanthin, neoxanthin, lutein, β -carotene and the xanthophyll cycle pigments violaxanthin, antheraxanthin and zeaxanthin. From these, concentrations could be quantified for 7 pigments: fucoxanthin, chl *a*, β -carotene, lutein and the xanthophyll cycle pigments. As expected for brown seaweeds, the major pigments for all 3 species were fucoxanthin, chl *a* and chl *c*. *E. radiata* had the lowest and *Z. turneriana* the highest overall pigment concentrations of the 3 species (Fig. 4).

Fucoxanthin, chl *a* and β -carotene concentrations of *E. radiata* were not significantly affected by treatment conditions ($p > 0.188$; Table S5); however, a trend toward reduced concentrations at 28°C was evident

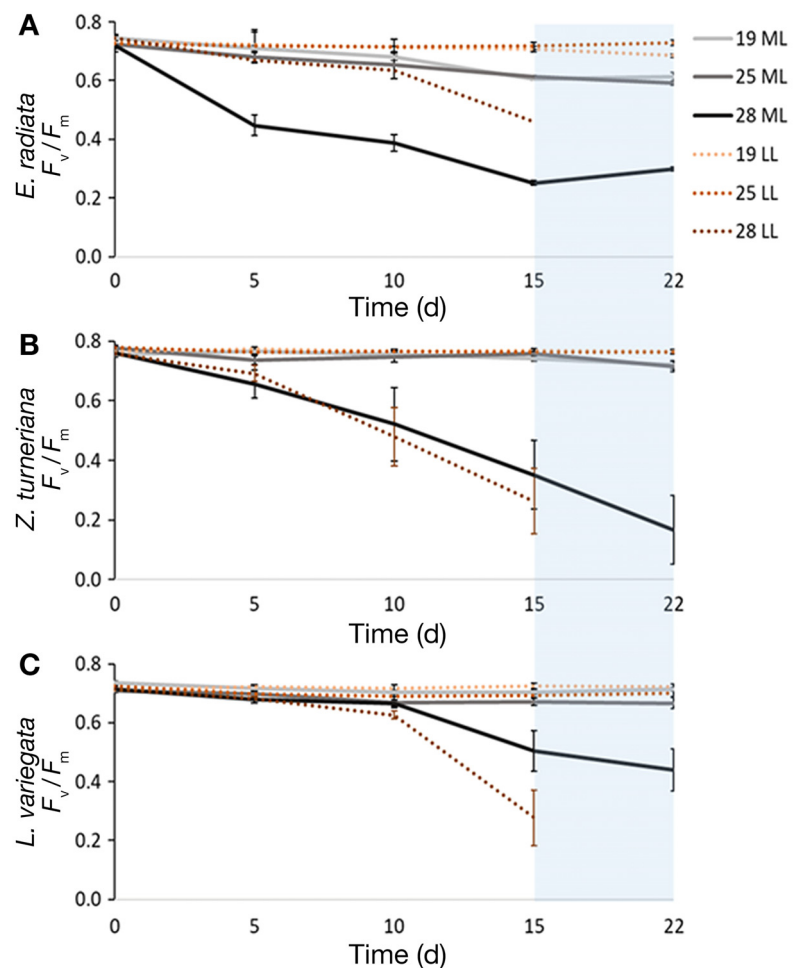


Fig. 3. Mean (\pm SE) maximum quantum yield (F_v/F_m) measured after 15 min dark acclimation for (A) *Ecklonia radiata*, (B) *Zonaria turneriana* and (C) *Lobophora variegata* over time for different temperature (19°, 25°, 28°C) and light (ML: moderate; LL: low) levels. Shaded box: recovery period during which all treatments were returned to 19°C

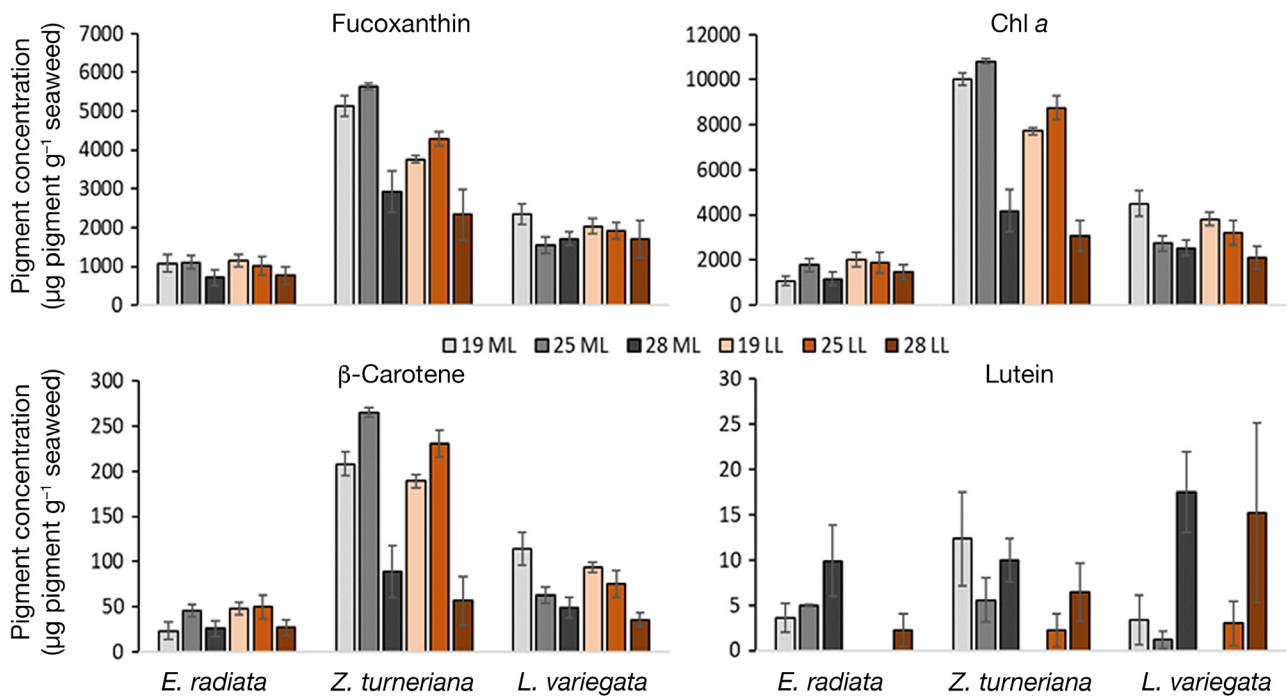


Fig. 4. Mean \pm SE pigment concentrations of fucoxanthin, chlorophyll *a* (chl *a*), β -carotene and lutein for *Ecklonia radiata*, *Zonaria turneriana* and *Lobophora variegata* at Day 15 for different temperature (19°, 25°, 28°C) and light (ML: moderate; LL: low) levels

(Fig. 4). Lutein concentrations in *E. radiata* increased with increasing temperatures, but the photoprotective pigment was absent at 19° and 25°C under LL conditions ($p = 0.006$). In contrast, fucoxanthin ($p = 0.003$), chl *a* ($p \leq 0.001$) and β -carotene ($p = 0.001$) concentrations of *Z. turneriana* were significantly affected by temperature, with a slight increase in pigment concentrations at 25°C and a strong reduction at 28°C. Additionally, LL levels significantly reduced concentrations of fucoxanthin ($p = 0.038$) and chl *a* ($p = 0.048$) of *Z. turneriana*. Lutein concentrations in *Z. turneriana* were not affected by temperature ($p = 0.510$) but showed a response to light levels ($p = 0.043$), with the absence of lutein at LL and 19°C and reduced levels at 25°C and ML. Fucoxanthin concentrations of *L. variegata* were not affected by treatment conditions ($p > 0.388$); however, chl *a* ($p = 0.031$), β -carotene ($p = 0.01$) and lutein ($p = 0.034$) concentrations were significantly affected by temperature. Increasing temperatures resulted in a reduction of chl *a* and β -carotene of *L. variegata* and an increase of lutein. Overall, 28°C generally reduced concentrations of fucoxanthin, chl *a* and β -

carotene, whereas lutein concentrations increased with increasing temperature.

The xanthophyll cycle pool, as the sum of the 3 pigments violaxanthin, antheraxanthin and zeaxanthin, showed strong species-specific responses (Fig. 5, Table S5). At ML levels, the xanthophyll pool size increased for *E. radiata* with increasing temperatures, with a significant reduction of violaxanthin ($p = 0.034$) and increased zeaxanthin concentrations. At ML levels, zeaxanthin ($p = 0.003$) concentrations of *E. radiata* significantly increased, whereas at LL levels,

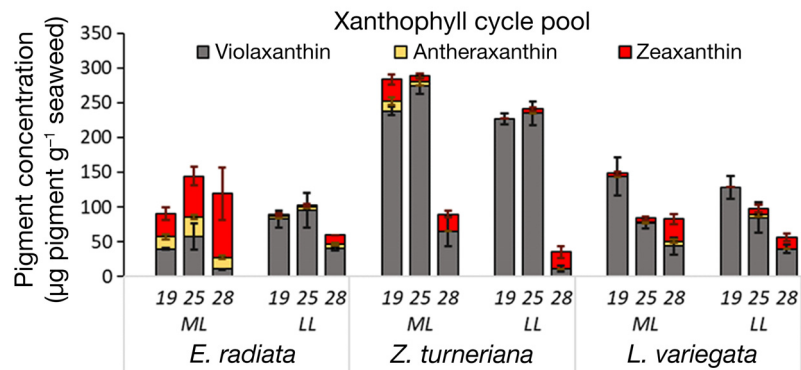


Fig. 5. Mean \pm SE pigment concentrations of the xanthophyll cycle pigments zeaxanthin, antheraxanthin and violaxanthin for *Ecklonia radiata*, *Zonaria turneriana* and *Lobophora variegata* after 15 d for different temperature (19°, 25°, 28°C) and light (ML: moderate; LL: low) levels

violaxanthin ($p = 0.027$) content was significantly higher. In contrast, the xanthophyll pool size of *Z. turneriana* was drastically reduced at 28°C due to a strong reduction of violaxanthin ($p \leq 0.001$) levels. Additionally, the zeaxanthin content of *Z. turneriana* was significantly reduced at LL levels ($p = 0.046$). Xanthophyll cycle pigment concentrations of *L. variegata* were not affected by light levels ($p > 0.309$), but violaxanthin ($p = 0.005$) concentrations decreased with increasing temperature, whereas zeaxanthin concentrations were significantly increased at 28°C ($p = 0.005$). Overall, at 28°C, zeaxanthin levels increased, whereas violaxanthin levels were reduced with increasing temperatures for all 3 species of seaweeds.

4. DISCUSSION

MHWs and coastal darkening are increasing anthropogenic stressors in many marine ecosystems globally. Our study showed that when seaweeds simultaneously experience discrete warming and low levels of light, their responses mainly depend on the magnitude of temperature increase, with irradiance levels having a lesser effect. However, under extreme temperatures, low light levels drastically compounded the negative effects on seaweed performance and there was little to no indication of short-term recovery once the temperature stress abated. These results support growing evidence that the combined effects of MHWs and coastal darkening on marine primary producers — the foundations of coastal ecosystems — could accelerate habitat loss (Strain et al. 2014, Filbee-Dexter & Wernberg 2018, Kendrick et al. 2019).

Temperature was the main factor affecting the performance of all 3 tested species (*Ecklonia radiata*, *Zonaria turneriana* and *Lobophora variegata*). Performance (e.g. tissue bleaching, biomass, RGR, photosynthetic activity) was comparable between 19° and 25°C (representing background temperatures in spring and autumn) and warm (medium MHW) summer conditions experienced by the seaweeds at their location of collection. Currently, 25.5°C represents the upper threshold for local near-future climate predictions (Lough et al. 2012), and all 3 seaweeds withstood 25°C for 15 d with only minor effects on their performance. These projections, however, represent future mean conditions, and as the mean increases, so does the severity of MHWs (Oliver et al. 2018). Exposed to +3°C above the summer values, representing extreme MHW conditions of 28°C, the performance of all 3 seaweeds declined significantly, and these effects were compounded by LL conditions.

Intense tissue bleaching and reduced photosynthetic activity were evident for all 3 species. These negative effects of extreme temperatures are consistent with field observations from the region, where a sustained increase to similarly high temperatures during a MHW reduced the performance, productivity and survival of brown seaweeds (Bearham et al. 2013, Smale & Wernberg 2013, Andrews et al. 2014, Wernberg et al. 2016). Additionally, *E. radiata* individuals experienced a significant loss of biomass and negative RGRs at extreme temperatures. The sensitivity of *E. radiata* to 28°C is consistent with studies concerning the impacts of the 2010–2011 MHW in Western Australia, which resulted in local extinctions and reduced abundances in areas experiencing ~28°C exposure (Pearce & Feng 2013, Wernberg et al. 2016). Of the 3 species, *L. variegata* showed the highest tolerance to temperature increase for bleaching and photosynthetic activity. Still, the sensitivity of *L. variegata* to the extreme MHW was surprising, as this species is widely distributed in tropical and warm temperate seas and is known to increase in abundance on degraded coral reefs (Mumby et al. 2005, Nugues & Bak 2008) and tropicalized temperate reefs (Wernberg et al. 2016). Local adaptation might explain the temperature sensitivity and reduced performance of *L. variegata* as seen in other brown seaweeds (Bennett et al. 2015).

High temperatures can evoke photoprotection and pigmentation responses in seaweeds (Davison 1991, Kuebler et al. 1991). The carotenoid responses and other pigment concentrations were generally highest at ambient (19°C) and moderate warming (25°C), consistent with recent thermal history influencing pigment content (Davison 1991, Stengel & Dring 1998, Robledo & Freile-Pelegrín 2005). Carotenoids and xanthophyll cycle pigments are involved in photoprotection, assisting thermal dissipation of excess light energy (non-photochemical quenching), which for the xanthophyll cycle pigments involves a de-epoxidation from violaxanthin to zeaxanthin (Jahns & Holzwarth 2012). In *E. radiata*, *Z. turneriana* and *L. variegata*, photoprotective responses of the carotenoids were not evident at the extreme MHW, with reduced fucoxanthin, chl *a* and β -carotene levels and a shift within the xanthophyll cycle pool from violaxanthin to zeaxanthin. These pigment responses suggest the seaweeds were stressed beyond an ability to invest in the accumulation of photoprotective pigments (Goss & Jakob 2010, Stengel et al. 2014). The strongest overall pigment reductions were evident in *Z. turneriana*, and the strongest shift within the xanthophyll pool was present for *E. radiata*.

While the strongest effects were observed in response to temperature, light levels also had some effect on the performance of the seaweeds. At low and intermediate temperatures (19° and 25°C), light levels showed only minor effects, suggesting the seaweeds were able to respond and adjust under these conditions. However, low light combined with extreme temperatures greatly enhanced tissue bleaching, diminished photosynthetic activity and reduced pigment contents of all 3 species. *E. radiata* was the most sensitive species, experiencing strongly progressed tissue bleaching and biomass loss under the interaction between extreme warming and low light. Overall, these responses suggest that when temperatures turn extreme, low light levels compound the negative effects on seaweed performance. Similar interactions, with low light levels exacerbating the negative effects of MHWs, have been found for other kelps. In New Zealand, a broad-scale remote sensing study of *Macrocystis pyrifera* found negative effects of MHWs on kelp canopy cover everywhere but the loss was significantly greater where water clarity was low (Tait et al. 2021). In Europe, a laboratory study found a synergistic effect of low light on the effects of simulated MHWs on photosynthesis of 2 kelps, where the cool-temperate *Laminaria digitata* responded more strongly than the warm-temperate *L. ochroleuca* (Bass et al. 2023). The mechanism underpinning the interaction between MHWs and low light levels is likely the exponentially increasing respiratory demands at higher temperatures: warming and increasing turbidity have been shown to drive a non-linear increase in the light compensation point of seaweeds such as *E. radiata* (Stæhr & Wernberg 2009, Blain & Shears 2019). These findings add to a growing list of empirical studies that show how the impacts of MHWs are modulated by a range of different human activities and localised ecological and environmental conditions (Starko et al. 2024), including diseases, nutrient levels, grazers, topography and turbidity (Wernberg et al. 2013a, Rogers-Bennett & Catton 2019, Tait et al. 2021, Thomsen et al. 2021, Tolimieri et al. 2023).

In conclusion, extreme temperatures were a prominent cause of reduced performance and photoprotective response in common and ecologically significant seaweeds, and low light levels exacerbated these negative effects. MHWs and coastal darkening are key threats to marine macrophytes. These threats are almost universally projected to intensify into the Anthropocene, where increasing degradation and loss of marine foundation species are expected as a consequence (Wernberg et al. 2024). While the increasing threat from MHWs can only be confronted

through decisive global climate action, it will be disproportionately important with regional and local management of activities that reduce coastal darkening in order to curb the accelerating impacts of climate change and humans in the coastal zone.

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