

PERSISTENCE OF SEAWEED FORESTS IN THE ANTHROPOCENE WILL DEPEND ON WARMING AND MARINE HEATWAVE PROFILES¹

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Marine heatwaves (MHWs), discrete periods of extreme warm water temperatures superimposed onto persistent ocean warming, have increased in frequency and significantly disrupted marine ecosystems. While field observations on the ecological consequences of MHWs are growing, a mechanistic understanding of their direct effects is rare. We conducted an outdoor tank experiment testing how different thermal stressor profiles impacted the ecophysiological performance of three dominant forest-forming seaweeds. Four thermal scenarios were tested: contemporary summer temperature (22°C), low persistent warming (24°C), a discrete MHW (22–27°C), and temperature variability followed by a MHW (22–24°C, 22–27°C). The physiological performance of seaweeds was strongly related to thermal profile and varied among species, with the highest temperature not always having the strongest effect. MHWs were highly

detrimental for the furoid *Phyllospora comosa*, whereas the laminarian kelp *Ecklonia radiata* showed sensitivity to extended thermal stress and demonstrated a cumulative temperature threshold. The furoid *Sargassum linearifolium* showed resilience, albeit with signs of decline with bleached and degraded fronds, under all conditions, with stronger decline under stable control and warming conditions. The varying responses of these three co-occurring forest-forming seaweeds under different temperature scenarios suggests that the impact of ocean warming on near shore ecosystems may be complex and will depend on the specific thermal profile of rising water temperatures relative to the vulnerability of different species.

Key index words: climate change; *Ecklonia radiata*; Great Southern Reef; kelp; macroalgae; *Phyllospora comosa*; *Sargassum linearifolium*; temperate reefs; temperature anomalies

Abbreviations: MHW, Marine heatwave; PAM, Pulse amplitude modulated; PERMANOVA, Multivariate analysis of variance by permutation; RCP,

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Representative concentration pathway; RGR, Relative growth rate; WW, Wet weight

The biosphere has warmed at an accelerating rate over the past century, with the ocean functioning as the primary heat reservoir of the global climate system (Durack et al. 2018). In particular, around 70% of the world's coastlines have warmed over the past four decades (Lima and Wethey 2012). Natural variability has been superimposed onto these long-term persistent increases in mean temperature, increasingly causing extreme, often unprecedented conditions (Coumou and Rahmstorf 2012, Oliver et al. 2018). In particular, marine heatwaves (MHWs), defined as discrete periods of extreme ocean warming (Hobday et al. 2016), have increased by 34% in frequency and 17% in duration from 1925 to 2016 (Oliver et al. 2018). These MHWs have arisen from interactions among a broad range of atmospheric and oceanographic processes causing fluctuations in ocean temperature (Holbrook et al. 2018), and projections indicate that they will continue to become more frequent, intense, and prolonged throughout the next century (Frölicher et al. 2018, Oliver et al. 2019).

Globally, organisms are affected by long-term increasing temperatures, precipitating shifts in species distributions, and the reorganization of ecosystems (Sorte et al. 2010, Wernberg et al. 2011b, Raybaud et al. 2013, Bates et al. 2014, Burrows et al. 2014, Vergés et al. 2014a, Sunday et al. 2015, Straub et al. 2016, Pecl et al. 2017). This extensive reshuffling of species with novel distributions and species interactions often comes with widespread ecological and socio-economic consequences and affects the global ocean from the tropics to the poles (Molinos et al. 2017, Pecl et al. 2017, Vergés et al. 2019, Smith et al. 2021). Although considerable attention has been directed to understand the consequences and impacts of long-term gradual warming (Parmesan and Yohe 2003, Poloczanska et al. 2013, Pecl et al. 2017), mounting evidence highlights that MHWs can also significantly affect species and ecosystems, driving major ecological (Wernberg et al. 2016a, Arafeh-Dalmau et al. 2019, Oliver et al. 2019, Smale et al. 2019) and genetic (Coleman et al. 2020a, Gurgel et al. 2020) change. A variety of impacts have been associated with these anomalous events (Smale et al. 2019, Straub et al. 2019), including shifts in species ranges and local extinctions (Wernberg et al. 2016a, Thomsen et al. 2019), range expansions, and tropicalization from the level of genes to ecosystems (Tuckett et al. 2017, Zarco-Perello et al. 2017, Coleman et al. 2020a), with flow-on effects to economic values (Caputi et al. 2016, 2019, Oliver et al. 2017, Smith et al. 2021).

The sudden changes in environmental conditions during MHWs may affect organisms more strongly than elevated mean temperatures resulting from

gradual warming (Gaines and Denny 1993), with substantial and wide-ranging effects of MHWs on species' physiological performance (Garrabou et al. 2009, Hawkins et al. 2009, Hughes et al. 2017, Mamo et al. 2019, Straub et al. 2019). Small variations in temperature can result in mortality and local extinctions, if the upper thermal threshold and acclimation capability of a species is exceeded (Bennett et al. 2015a, Hampe and Petit 2005, Wernberg et al. 2018b). Recognizing the risks of losing valuable ecosystem services, experimental studies testing the potential effect of gradual ocean warming on marine organisms have gained momentum in recent years (Cheung et al. 2009, Gruber 2011, Hughes et al. 2017, Phelps et al. 2017). However, while increasingly in focus, the effects of discrete short-term changes experienced during heatwaves (HWs) have been considerably less studied (Wernberg et al. 2012, Bass et al. 2021).

The wide range of responses to warming (Straub et al. 2016, Wernberg and Straub 2016) and MHWs (Smale et al. 2019, Straub et al. 2019) challenges accurate prediction of climate-induced responses in marine forests. In particular, the response of species to different profiles of temperature change and variability (varying maximum intensities, durations, shapes, and spatial extends) that reflect natural MHW events, is poorly understood (Hobday et al. 2016, Bass et al. 2021). This is likely because the complexity of effects due to changing temperatures goes beyond simple responses to averaged environmental factors such as mean summer temperature (which are often what is manipulated in experiments).

Temperate rocky reefs globally are dominated by seaweed forests, that create habitats and supply food for associated species (Coleman and Wernberg 2017, Teagle et al. 2017, Wernberg and Filbee-Dexter 2019), as well as support immense value in ecosystem services (Bertocci et al. 2015, Bennett et al. 2016). Over the past half century, threats to seaweed forests have increased (Krumhansl et al. 2016, Filbee-Dexter and Wernberg 2018, Vergés et al. 2019, Wernberg et al. 2019). In particular, temperature-mediated declines in abundance and shifts in the distribution of seaweeds have been observed in many regions globally (Wernberg et al. 2011b, Moy and Christie 2012, Smale and Wernberg 2013, Filbee-Dexter et al. 2016, Krumhansl et al. 2016, Straub et al. 2016, Arafeh-Dalmau et al. 2019, Thomsen et al. 2019). In temperate Australia, marine forests stretch over 8000 km along the southern coastline, and are a global biodiversity hotspot with a high degree of endemism (Bennett et al. 2016, Coleman et al. 2017, Wernberg et al. 2019a). Ongoing rapid warming over the past five decades resulted in a poleward retraction of temperate seaweeds and a poleward expansion of tropical species (Wernberg et al. 2011b, 2016a). For example, along the east coast of Tasmania, a discrete warming event in 2000/01 resulted in performance reduction and

mortality of *Phyllospora comosa* and *Ecklonia radiata* (Valentine and Johnson 2004). More dramatically, a major MHW in 2010/11 along the south-western Australian coastline (Pearce and Feng 2013) resulted in local extinction and range contraction of *E. radiata* and the furoid *Scytothalia dorycarpa* at their northern distribution limits, and a concurrent expansion of *Sargassum* ssp. (Gurgel et al. 2020, Smale and Wernberg 2016, Wernberg et al. 2016a). These changes precipitated significant population level genetic change in seaweeds, compromising overall adaptive capacity (Wernberg et al. 2018a, Coleman et al. 2020a, Gurgel et al. 2020) but potentially increasing future thermal performance via selection (Coleman and Wernberg 2020b).

Here, we conducted an outdoor tank experiment exposing three dominant, co-occurring forest-forming seaweeds to different warming profiles: constant contemporary summer temperature (22°C), low sustained warming (24°C) reflecting a 2°C increase under an RCP 4.5 (emission stabilization) scenario, a MHW (22–27°C), and a MHW with prior temperature variability (22–24°C; fig. 1). Specifically, we predicted that there would be (1) differences in thermal tolerance, with the temperate-tropical *Sargassum* (Martinez et al. 2018) being more resilient and the temperate *Phyllospora* (Coleman and Wernberg 2017) being vulnerable to especially MHWs, and (2) species-specific responses depending on the physical attributes of the applied temperature stress (warming vs. HW vs. HW with prior variability). We provide evidence that responses to temperature are

not solely determined by a fixed thermal threshold and that co-occurring species can have different responses to a range of ocean warming scenarios.

MATERIAL AND METHODS

Study site and species description. Individual whole plants of three co-existing dominant canopy-forming seaweeds, *Ecklonia radiata*, *Phyllospora comosa*, and *Sargassum linearifolium* (hereafter referred to as “*Ecklonia*,” “*Phyllospora*,” and “*Sargassum*”), were collected on 1 March 2017 (late austral summer) by SCUBA off Sydney, Australia (34°03'59.0" S 151°09'44.3" E). *Ecklonia* is a laminarian kelp found throughout Australia's temperate subtidal reefs (Wernberg et al. 2019a). *Phyllospora* is a temperate furoid distributed along the south-eastern coastline of Australia (Coleman and Wernberg 2017), and *Sargassum* is a temperate-tropical furoid (Steinberg et al. 1991, Martinez et al. 2018), and the most widely distributed southern Australian species of *Sargassum*. Around 150 juveniles (< 30 cm total length) per species were collected haphazardly, with their holdfasts intact, from a shallow subtidal rocky reef between 3 to 6 m depth. The collected specimens were transferred into calico bags and transported (by air) in chilled, dark styrofoam boxes to the National Marine Science Centre in Coffs Harbour, Australia. Specimens were weighed down by the holdfast and placed in tanks with flowing seawater within 4 h of collection. Seaweeds for the ambient, HW and variability treatments were acclimated at ambient temperature 22°C (~120 individuals per species), and seaweeds for the warming treatment were acclimated at 24°C (~40 individuals per species).

Experimental setup. Four different treatments were applied over 48 days to test for the effects of different profiled temperature exposures (Fig. 1). Treatments were established at (i) ambient temperature at 22°C (ambient), (ii) persistent warming at 24°C (warming), (iii) a MHW moving from 22 to

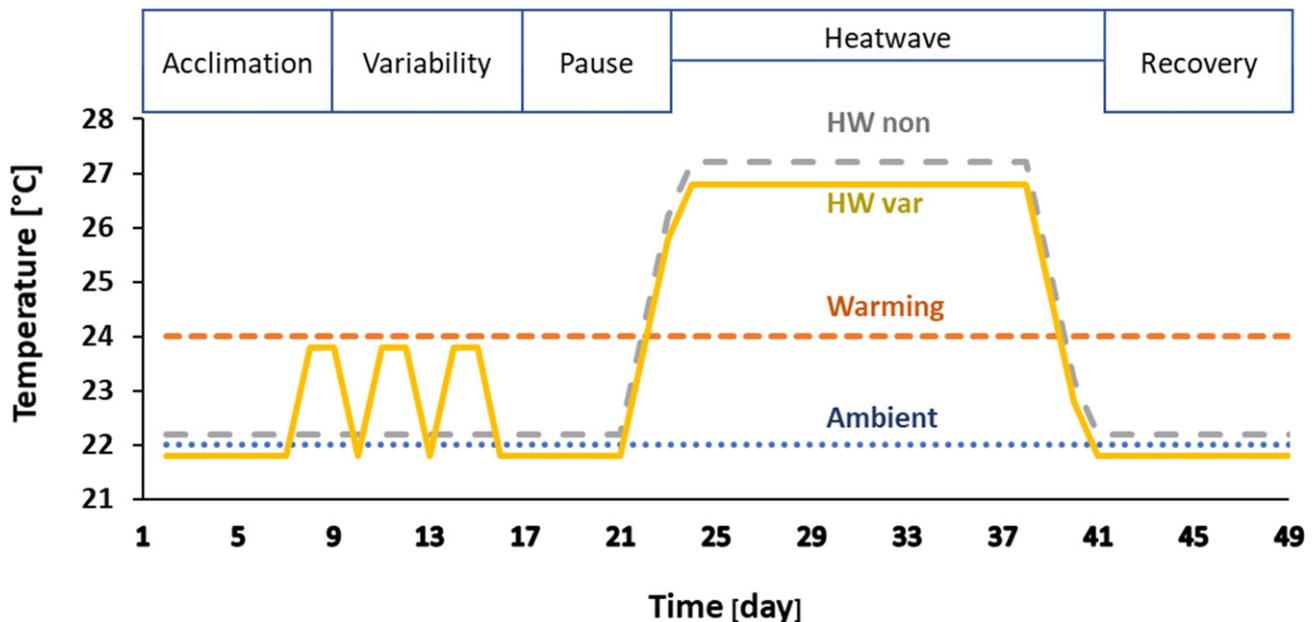


FIG. 1. Schematic visualization of treatments: ambient conditions at 22°C, warming conditions at 24°C, HWnon from 22 to 27°C, and HWvar with temperature variability between 22 and 24°C, followed by a MHW to 27°C. HWnon and HWvar treatments were offset by $\pm 0.2^\circ\text{C}$ to avoid stacking of lines. Lines are smoothed for illustration purposes, small variability occurred but on the same magnitude for all treatments and tanks. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/jpy.13222)]

27°C and back to 22°C after 3 weeks (HWnon), and (iv) a MHW with prior temperature variability, which included rapid fluctuations between 22 and 24°C for 8 days, remaining at 22°C for 6 days followed by a HW moving from 22 to 27°C and back to 22°C after 3 weeks (HWvar). The ambient control treatment of 22°C mimicked the typical contemporary summer water temperature experienced at the collection site (Schaeffer and Roughan 2017) and the persistent warming treatment of 24°C represented a 2°C increase as projected under the RCP 4.5 (emission stabilization) scenario (IPCC 2013). MHW temperature profiles were chosen to mimic a recent MHW in Western Australia, with the smaller heat spikes in the HWvar treatment representing temperature fluctuations that occur during MHW events (Hobday et al. 2016).

Treatments were designed with comparable magnitude of cumulative warming intensity, which represents the integral of intensity (i.e., area under the temperature curve in Fig. 1) over the duration of the event (Hobday et al. 2016; Warming = 96 degree-days, HWnon = 85 degree-days, and HWvar = 97 degree-days cumulative warming intensity above the ambient control treatment; Fig. 1).

The experimental system consisted of 3 header tanks using heater/chillers (Aquahort Ltd.) regulating temperatures to 22, 24, and 27°C, respectively. Tanks (N = 20) were round outdoor tanks (80 cm diameter × 45 cm high, 230 L water volume) which received constant inflow (flow rate ≈ 2 L · min⁻¹) from the appropriate header tank for their respective temperature treatment and were continuously aerated. Filtered seawater (50 µm) was sourced from Charlesworth Bay (30°16'3.78" S, 153° 8'25.60" E) and supplied to the header tanks. The use of a common water supply created an unaccounted link between the treatments, however, this is a standard solution for experimental setups and generally has no effect on the outcome (Wernberg et al. 2012).

Seaweeds were acclimated for 6 d to allow them to adjust to their new environment. The timeframe was chosen after a series of pilot experiments and prior studies showed that short acclimation periods are suitable for seaweeds (Wilson et al. 2015, Xiao et al. 2015, McCoy and Widdicombe 2019). Seaweeds at 22°C were randomly assigned to one of three treatments starting at 22°C (ambient, HWnon, HWvar). Seaweeds acclimated at 24°C were part of the warming treatment and got randomly assigned a replicate number and tank. Five tanks were randomly assigned per treatment, and within each tank, $n = 7$ individuals of *Ecklonia*, *Phyllospora*, and *Sargassum* were placed (total $n = 21$ seaweeds per tank).

Survival and tissue bleaching. The health status of the seaweeds was assessed twice per week as tissue bleaching ($n = 3$ per tank per species; $n = 15$ per species per treatment) and survival ($n = 7$ per tank per species; $n = 35$ per species per treatment). Tissue bleaching is a primary indicator of visible temperature stress in seaweeds (Xiao et al. 2015). Bleaching was defined as visible discoloration (whitening or turning faded green) of the blade tissue due to loss of surface integrity within alga (adopted from Marzinelli et al. 2015). Tissue bleaching was examined using six broad categories, ranking from 1 (less than 1% of surface area showing signs of bleaching) to 6 (full blade showing signs of bleaching). Survival was assessed as a binary variable (dead or alive) and percent survival for each treatment and species was calculated. Seaweeds were characterized as dead when the specimen lost its structural integrity or was fully degraded.

Relative growth rate. Relative growth rates (RGR) were calculated based on measurements of wet weights (WW; $n = 3$ per tank per species; $n = 15$ per treatment per species) taken on day 6 (end of acclimation phase), day 20 (start of MHW treatments), days 26, 33, and 37 during the MHWs, day 40 (return to ambient

conditions after the MHW), and day 48 (end of experiment). RGR were calculated using the following equation:

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

where W_i = initial WW, W_t = WW at respective day, and t = days passed in treatment.

Maximum quantum yield of photosystem II. Photosynthetic quantum yield (F_v/F_m) of photosystem II was assessed between 10 a.m. and 2 p.m. twice weekly by pulse amplitude-modulated (PAM) fluorometry (Diving-PAM, Walz, Effeltrich, Germany). Dark-leaf clips were positioned midpoint on the thallus and closed for dark-acclimation (15 min) prior to reading ($n = 3$ per tank per species; $n = 15$ per species per treatment). Quantum yield measurements were taken for *Ecklonia* and *Phyllospora*, but not for *Sargassum* as the blades were too narrow to fit the dark-leaf clips from the PAM apparatus.

Statistical Analysis. Data were analyzed separately per species and measurement using permutational multivariate analysis of variance (PERMANOVA) in PRIMER v.6 (Euclidian Distance dissimilarity, 9999 permutations; Clark and Gorley 2006). Where appropriate, PERMANOVA main tests were followed by pair-wise comparisons. PERMANOVA was used as it is a robust method of calculating probabilities especially where data possibly not follow a normal distribution. Treatment (Tr) and Time (Da) were fixed factors, and individual replicates (ID) were treated as a random factor nested in Tank (Tank), and Tank was nested in Treatment to account for repeated measures of the same individuals and test if tank location affected the outcome. Analyses were conducted for treatment [Tr], Time [Da], Tank (Tr), ID [ID(Tank(Tr))], and their interaction (Tr × Da) for each species and variable separately. ID was statistically significant for all measurements and species, highlighting the variability between individuals. Tank within treatment was not significant and following the procedure of pooling nonsignificant treatments (Underwood 1997) were combined to test for overall treatment effects.

Due to severe bleaching, disintegration, and mortality, several seaweeds could not be assessed for the full duration of the experiment. Missing values in the maximum quantum yield measurements were mostly due to mortality, blade degradation, or bleaching. For the biomass dataset, various outliers due to loss of attachment weights ($n < 10$) were removed from the dataset as well as dead individuals after 100% biomass loss was recorded.

RESULTS

Survival. Survival was strongly species- and treatment-dependent (Fig. 2, Table S1 in the Supporting Information). All individuals of *Sargassum* survived (albeit with significant loss of foliose parts of the thallus; Fig. 2c), whereas the survival of *Ecklonia* and *Phyllospora* was significantly different between treatments (PERMANOVA, pseudo- $F_{3,120} > 2.46$, $P \leq 0.022$) and over time (PERMANOVA, pseudo- $F_{11,1320} > 48.57$, $P \leq 0.001$) as well as treatment over time (PERMANOVA, pseudo- $F_{33,1320} > 2.04$, $P \leq 0.001$) Warming had a strong effect on survival of *Ecklonia* in the middle of the experiment (days 16–30) with a drop to 60% after 20 days that was significantly lower than all other treatments (Fig. 2a, Table S2 in the Supporting Information). *Phyllospora* survival showed greatest

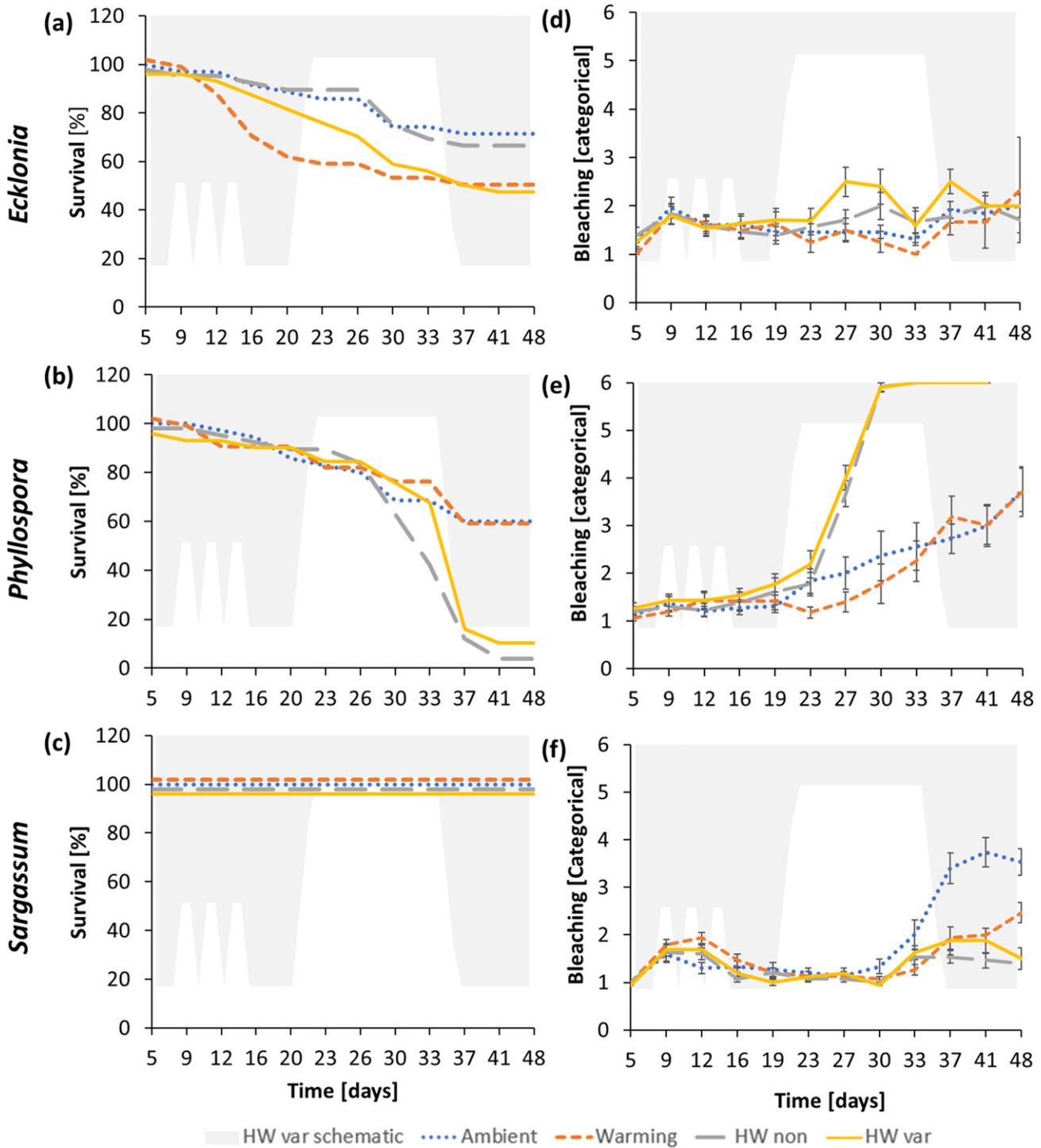


FIG. 2. Survival for (a) *Ecklonia*, (b) *Phyllospora*, and (c) *Sargassum* (treatments set slightly ajar, 100% survival in all 4 treatments) and species-specific bleaching for (d) *Ecklonia*, (e) *Phyllospora*, and (f) *Sargassum* as mean \pm SE over time. Area [MHW] shows in which stage of the climate variability and MHW treatment measurements were taken. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

vulnerability to HW conditions with only 5.7% survival under HWnon and 14.3% under HWvar conditions by the end of the recovery period (Fig. 2b). Survival values of *Phyllospora* subjected to MHW conditions were significantly lower (PERMANOVA pairwise tests, $P \leq 0.001$) than for individuals subjected

to either warming or ambient conditions, where 57.1% and 60% survived, respectively (Table S2). *Phyllospora* often showed tissue necrosis at the stipe resulting in the rapid loss of entire plants.

Tissue bleaching. Bleaching scores were low at the start of the experiment (Figs. 2, 3). For all three

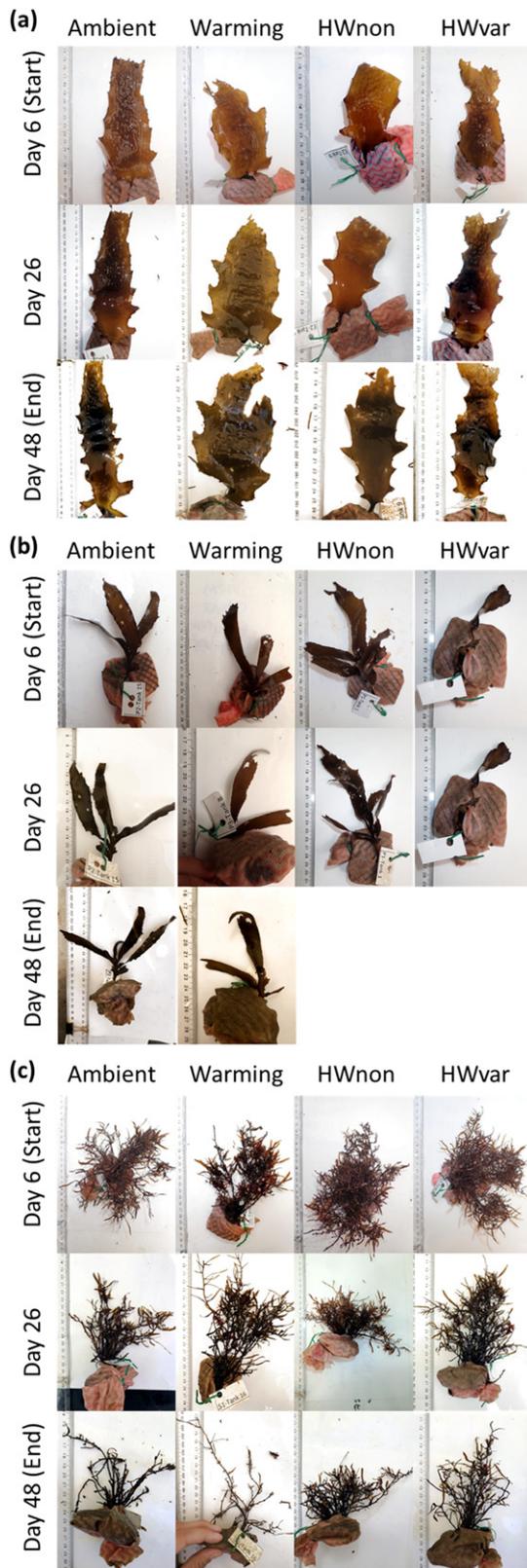


FIG. 3. Example progression of thallus health (a) *Ecklonia*, (b) *Phyllospora*, and (c) *Sargassum* within the four treatments (ambient, warming, Hwnon, HWvar) over time (Start—Day 6, Intermediate during first half of MHW—Day 26, End of Recovery/Experiment—Day 48). [Color figure can be viewed at wileyonlinelibrary.com]

species, there was a significant effect of treatment (PERMANOVA, *Ecklonia*: pseudo- $F_{3,120} = 2.27$, $P \leq 0.043$; *Phyllospora*: pseudo- $F_{3,120} = 14.90$, $P \leq 0.001$; *Sargassum*: pseudo- $F_{3,120} = 5.24$, $P \leq 0.011$) and exposure time (PERMANOVA, pseudo- $F_{11,1320} > 6.60$, $P \leq 0.001$ for all species) on the extent of bleaching (Table S3 in the Supporting Information). For all species, the effect of treatment varied with days (significant Tr x Da interaction: PERMANOVA, pseudo- $F_{33,1320} > 1.8$, $P \leq 0.007$; Table S3). Although the main tests for *Ecklonia* were significant, pair-wise multiple-comparison tests could only identify significant differences for the HWvar from the control (days 26 and 30) and warming (day 30) for a limited timeframe during the first half of the HW (Table S4 in the Supporting Information). Given that bleached tissue can erode at the fronds and be lost, it is possible that tissue erosion may have biased health status assessment, because after bleached tissue is shed, the remaining tissue may be largely healthy resulting in improved health status but shortened thalli. This made it difficult to detect changes in health status by percentage bleaching alone for *Ecklonia*.

For *Phyllospora*, individuals deteriorated more under HWnon and HWvar conditions, with HWvar showing significantly higher bleaching rates from day 23 (early HW start) in comparison to the control, and both MHW treatments were statistically significantly different from the control and warming conditions from day 26 onward (PERMANOVA pair-wise tests, $P \leq 0.047$; Table S4, Fig. 2E). In contrast, *Sargassum* was negatively affected by the stable ambient and warming conditions. After day 33 (mid-HW), bleaching under ambient conditions strongly increased in comparison to all elevated temperature treatments (PERMANOVA pair-wise tests, $P \leq 0.013$; Table S4), with warming enhancing bleaching cover in contrast to both MHW treatments during the last week (PERMANOVA pair-wise tests, $P \leq 0.040$). Overall, *Sargassum* showed decreased health status in stable conditions, with most individuals shedding the majority of their blades, but new blades continually sprouting from the healthy holdfast.

Relative growth rates. Mean relative growth rates (RGR) were significantly different over time for all three species (PERMANOVA, pseudo- $F_{11,1320} > 21.63$, $P \leq 0.001$ for all species; Table S5 in the Supporting Information). In addition, RGR of *Ecklonia* differed among treatments (PERMANOVA, pseudo- $F_{3,120} = 1.59$, $P \leq 0.019$) and the treatment effect varied with time for both *Ecklonia* and *Phyllospora* (Tr x Da interaction: PERMANOVA, *Ecklonia*, pseudo- $F_{33,1320} = 1.34$, $P \leq 0.025$; *Phyllospora*, pseudo- $F_{33,1320} = 1.09$, $P \leq 0.024$). Overall, *Ecklonia* showed mainly positive RGR throughout the experimental period (Fig. 4), whereas *Phyllospora* showed a strong downward trend in RGR after day 20 (start MHW; Fig. 4). *Sargassum* showed negligible

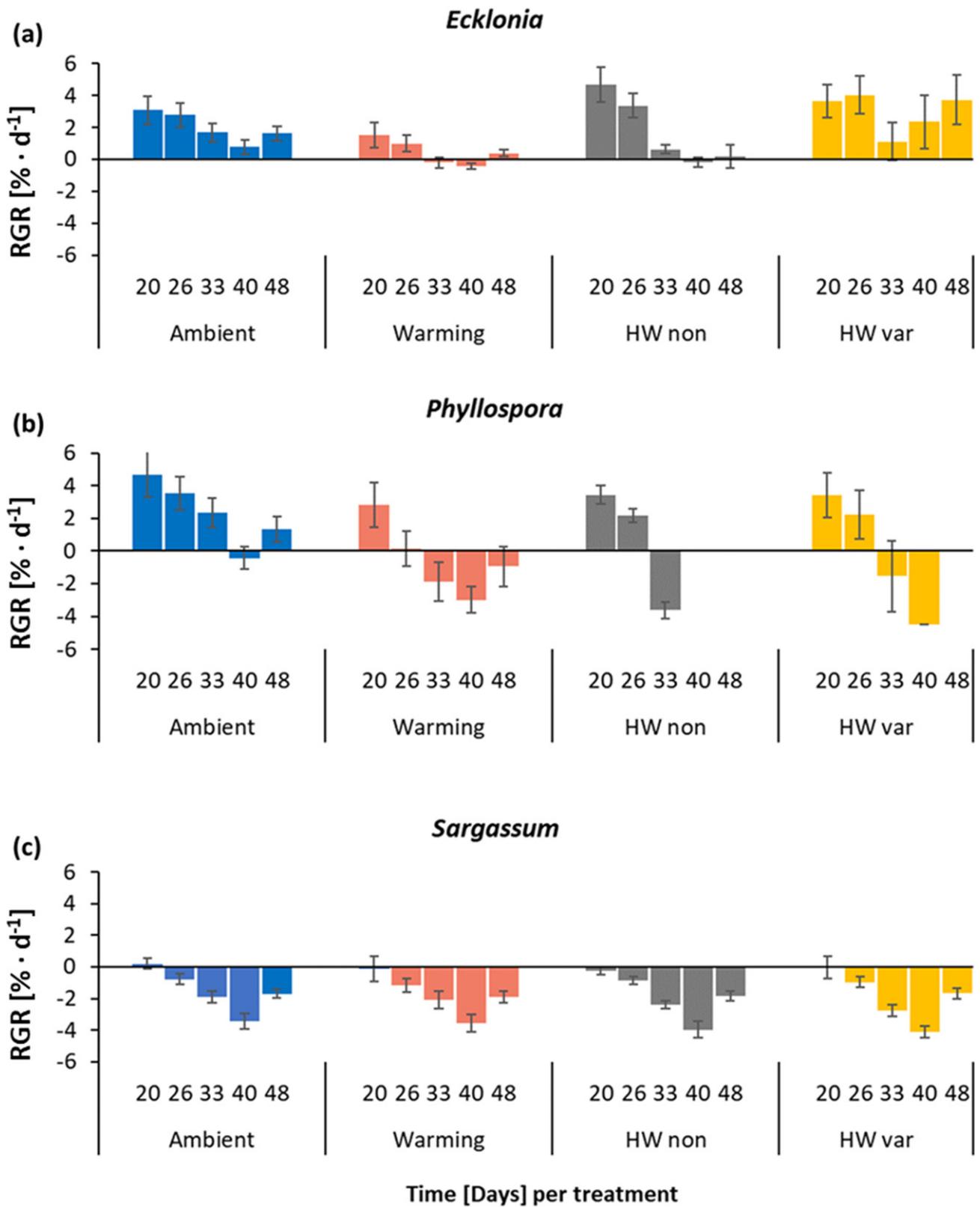


FIG. 4. Relative growth rate (RGR) as $\% \cdot d^{-1}$ over time under ambient, warming, HWnon and HWvar conditions for (a) *Ecklonia*, (b) *Phyllospora*, and (c) *Sargassum* as mean \pm SE start date to day 20 (start MHW) to 48 (end recovery phase). [Color figure can be viewed at wileyonlinelibrary.com]

RGRs until day 20, and from then onward exhibited negative growth due to loss of fronds.

RGR tended to be lower for *Ecklonia* under the warming treatment, but no statistically significant differences between treatments could be resolved using pair-wise comparisons (Fig. 4, Table S6 in the Supporting Information). In contrast, warming negatively affected *Phyllospora* in comparison to ambient conditions, with a statistically significant decline between days 26 to 40 (PERMANOVA pair-wise tests, $P \leq 0.049$). Although only significantly different from the ambient treatment at days 33 (PERMANOVA pair-wise tests, HWnon, $P \leq 0.010$) and 37 (PERMANOVA pair-wise tests, HWvar, $P \leq 0.019$), MHW conditions showed a contrasting response on RGR of *Phyllospora*. Under HWnon and HWvar conditions, RGR dropped from positive (growth) to negative (loss) mean values from day 33 (mid-MHW) onward.

Maximum quantum yield. Mean maximum quantum yields varied between treatments in a time-dependent manner for both *Ecklonia* and *Phyllospora* (significant Tr \times Da interaction, PERMANOVA, pseudo- $F_{24,253} > 2.12$, $P \leq 0.005$, and $P \leq 0.001$, respectively; Table S7 in the Supporting Information). Mean maximum quantum yields were similar for *Ecklonia* and *Phyllospora* at the beginning of the experiment (0.754 ± 0.005 SE and 0.764 ± 0.007 SE respectively; Fig. 5), with significant declines with treatment (PERMANOVA, *Ecklonia*: $F_{3,40} = 1.83$, $P \leq 0.008$; *Phyllospora*: $F_{3,40} = 239.33$, $P \leq 0.001$) and time (PERMANOVA, *Ecklonia*: $F_{8,253} = 3.34$, $P \leq 0.002$; *Phyllospora*: $F_{8,253} = 184.61$, $P \leq 0.001$).

Maximum quantum yields of *Ecklonia* were similar among treatments up until day 26, when specimens subjected to warming showed higher yields than treatments subjected to MHWs (PERMANOVA pair-wise tests, $P \leq 0.005$; Table S8 in the Supporting Information). Over the following weeks, MHW treatments continued to display lower maximum quantum yields than other treatments, but by the end of the recovery phase, differences between treatments were no longer observed (Fig. 5; Table S8). However, the sampling size was greatly reduced over the duration of the experiment, especially under HWvar and warming conditions. In comparison, *Phyllospora* showed a more pronounced response to MHW conditions (Fig. 5), with seaweeds in the HWnon and HWvar treatments being significantly reduced in contrast to ambient conditions and warming treatments from day 26 (early MHW; PERMANOVA pair-wise tests, $P \leq 0.001$; Table S8) onward, with no measurements after day 30 (mid-MHW) as individuals of *Phyllospora* were either dead or in too poor health with not enough remaining healthy tissue. Yield values for *Phyllospora* between the ambient and warming treatments were significantly different on days 20, 30, 33, and 48 (PERMANOVA pair-wise tests, $P \leq 0.019$) as a slight reduction in mean yield in the warming treatment was observed.

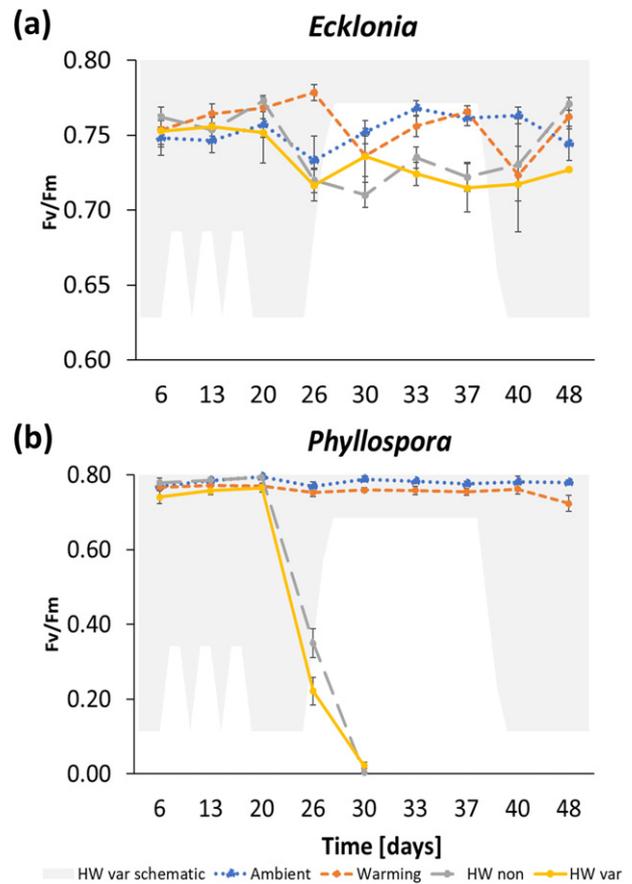


FIG. 5. Mean maximum quantum yield (F_v/F_m) \pm SE of (a) *Ecklonia* and (b) *Phyllospora* over time. [Color figure can be viewed at wileyonlinelibrary.com]

DISCUSSION

Sustained elevated temperature from gradual warming and MHWs can have strong effects on marine forest-forming seaweeds with cascading effects on entire ecosystems (Hobday and Pecl 2014, Wernberg et al. 2016a, Oliver et al. 2017, Provost et al. 2017, Smale et al. 2019). Experimental designs and modeling studies generally focus on the effect of mean and maximum temperatures, with effects of warming characterized by negative responses when the magnitude of warming surpasses the thermal threshold of a species (Smale and Wernberg 2013, Xiao et al. 2015, Filbee-Dexter et al. 2016, Gouvea et al. 2017). While such characterizations serve as a framework to understand overall ecological implications, our study found that only considering thermal thresholds as a fixed upper temperature value to assess impacts of future climate change is too simplistic. Our approach to apply different warming scenarios, that is, sustained warming and MHWs with different levels of variable temperature profiles revealed that direction and strength of responses in forest-forming seaweeds varies between warming scenarios, with the highest

temperature treatment not always triggering the strongest effect.

Ecklonia, the dominant kelp in Australasia along the Great Southern Reef (Wernberg et al. 2019a) performed surprisingly well when exposed to a single MHW, but sustained warming and a MHW with prior temperature fluctuations led to considerably reduced survival and physiological performance. High temperature regimes are known to negatively influence the physiological performance of *Ecklonia* species (Tanaka et al. 2012, Xiao et al. 2015, Wernberg et al. 2016b, Qiu et al. 2019), and *Ecklonia* has been declining and/or shifting southward on the east and west coasts of Australia due to warming and MHWs (Valentine and Johnson 2004, Vergés et al. 2016, Wernberg et al. 2011a, 2013, 2016a). During the extreme 2010/11 MHW in Western Australia, negatively affected reefs populated by *Ecklonia* experienced peak temperatures ranging from 26.5 to 28.3°C (Pearce and Feng 2013), comparable to the 27°C peak temperature applied in the two MHW treatments here. The absence of a strong negative effect of a single MHW, and the negative effects of prolonged warming on the survival and performance, especially growth, of *Ecklonia* suggests that this kelp may be more resilient to short-term stress than anticipated and is more susceptible to prolonged temperature stress. The 24°C in the warming treatment exceeded the physiological threshold for net growth (~23°C) for *Ecklonia* (Wernberg 2021), but is well within the kelp's thermal performance breadth of 21.2 to 26.5°C, whereas the short MHW should have exceeded the kelp's thermal breadth (Bennett et al. 2015a, Wernberg et al. 2016b, 2019a). The absence of a fixed maximum thermal threshold would explain these surprising results; hence, we suggest that *Ecklonia* either has a cumulative temperature threshold or an upper thermal limit that decreased with increasing experimental duration as previously shown for several brown seaweeds (tom Dieck et al. 1993, Graiff et al. 2015). This could mean that *Ecklonia* is more susceptible to prolonged summer warm water temperatures and protracted temperature fluctuations than to short-duration MHWs.

In contrast, *Sargassum* was expected to perform relatively well under all applied temperature conditions given its temperate-tropical distribution and broader thermal performance range than *Ecklonia* (Wernberg et al. 2016b). While *Sargassum* showed no mortality under any of the experimental treatments, we saw a significant loss of fronds and degradation down to the holdfast in most cases. The lack of treatment effect for the warming treatment compared to ambient conditions was not surprising as the temperature exposure range was less than previous studies that documented no differences in growth rates for *Sargassum* between 20.5 and 25.5° and 23 and 26°C, respectively, as well as no effects of short-term exposure up to 30°C on *Sargassum*'s

photosynthetic yield (Phelps et al. 2017, Graba-Landry et al. 2018, Campbell et al. 2020). While no significant treatment effects could be detected, the overall loss of biomass and degradation down to the holdfasts hints that *Sargassum* most likely shed its fronds due to the timing of the experiment in late austral autumn (Martin-Smith 1993). The holdfast of this species (and other *Sargassum* species) can remain and regrow fronds when conditions become favorable (Löffler and Hoey 2017, Löffler et al. 2018). Indeed, after one year, we still had the holdfasts from this experiment alive in tanks with small regenerating fronds. Interestingly, while still showing signs of bleaching and degradation, *Sargassum*'s degradation was slowed under MHW conditions compared to stable ambient and warming conditions. This suggests that increases in climate variability and MHW frequency may be either neutral or even advantageous for this species, presumably due to its potential to regenerate from holdfasts. Consequently, *Sargassum* could potentially increase in abundance on temperate reefs as other dominant species decline especially if *Sargassum* reaches its peak reproductive season shortly after localized die-offs of other canopy-formers and turf algae can utilize the opened space. This could initiate a shift to *Sargassum*-dominated reefs as an alternative to algal turfs (Filbee-Dexter et al. 2016, Vergés et al. 2019).

The temperate *Phyllospora* was the only species that followed the generalization of a fixed upper thermal threshold. Sustained warming led to reduced growth rates but no other major effects, whereas both MHW treatments resulted in drastic effects shortly after the onset of the HWs, when bleaching cover increased accompanied by great biomass loss, often from the stipe, which resulted in rapid loss of entire plants. Interestingly, the stipe degradation resembled symptoms of a microbial disease known to infect *Phyllospora*, which is more frequent when water temperatures are high, and leads to significant increases in mortality (Ferrari et al. 2021). These immediate declines in health and biomass were accompanied by a reduction of mean maximum quantum yield initially to very low values shortly after onset of MHWs, with no measurements possible from mid-MHW onward due to strong tissue degradation. A similar response to high temperatures was previously observed after above-average temperature conditions along the east coast of Tasmania during the 2000/01 austral summer/autumn period (Valentine and Johnson 2004), when *Phyllospora* first bleached and showed signs of decay, before ultimately dying off in large patches. Similarly, *Scytothalia dorycarpa*, one of the closest relatives to *Phyllospora*, was heavily impacted by the Western Australian 2011 MHW, contracting its range over a hundred kilometers (Smale and Wernberg 2013, Wernberg et al. 2016a) and losing significant genetic diversity (Gurgel et al. 2020). However, while our study and field observations reveal a

strong thermal sensitivity of *Phyllospora*, another recent study found that *Phyllospora* can resist shorter, less intense MHWs with little evidence of lasting negative effects (Britton et al. 2020). Altogether, *Phyllospora* was highly sensitive to the two applied MHW treatments, and is expected to be vulnerable to the expected increase in frequency and duration of MHWs (Oliver et al. 2018), particularly given its wide dispersal and lack of adaptive genetic structure throughout much of its range (Coleman and Kelaher 2009, Coleman et al. 2009).

Collectively, our results show different responses of key forest-forming seaweeds to different temperature scenarios with potentially far-reaching implications for ecosystem structure. Currently, many rocky reefs around Australia are dominated by these three seaweeds, with mixed patches of *Ecklonia* and *Phyllospora* (or the allopatrically distributed fucoid, *Scytothalia dorycarpa*) with interspersed *Sargassum* individuals (Underwood et al. 1991, Connell and Irving 2008, Wernberg et al. 2011a, Bennett et al. 2016, Coleman and Wernberg 2017). This current distribution could indicate dominance of *Ecklonia* and *Phyllospora* at current cooler conditions, with a subordinate role of *Sargassum*. According to Martinez et al. (2018), summer temperatures are the strongest predictor of distribution for forest-forming seaweeds around Australia, with projected major poleward shifts of dominant forest-forming seaweeds with ocean warming under the RCP 6.0 emission scenario. Specifically, *Phyllospora* may become extinct around Australia, and *Ecklonia* and *Sargassum* will retract along the east and west coast and be restricted to the southern Australian coastline by the end of the century. While this modeling study predicts distributions based on mean and peak summer temperatures, it is not taking exposure duration and sporadic extreme events into consideration. Adding the increased possibility of periodic MHWs, the ecological outcome becomes more variable and thus less predictable. Protracted peak summer temperatures and any larger temperature extremes may result in decreased physiological performance of *Ecklonia* and *Phyllospora*, accelerating poleward shifts and reductions in cover, whereas *Sargassum* might benefit from anticipated increases in MHW frequency due to release of competition, at least in the short to intermediate term. Specific effects will depend on the exact temperature profile of the occurring temperature stress. If a MHW is of shorter duration and magnitude, the demonstrated resilience of *Ecklonia* could result in its dominance upon return to favorable conditions. However, if the cumulative intensity tolerance of *Ecklonia* is exceeded, negative effects on both *Ecklonia* and *Phyllospora* can be anticipated. For example, the MHW in Western Australia in 2011 resulted in a 100 km range contraction of *S. dorycarpa* and *Ecklonia* and subsequent proliferation of *Sargassum* on the most northern reefs (Wernberg et al. 2016a). Similar

effects were observed during a clearing experiment in Western Australia where removal of *Ecklonia* with subsequent higher light levels, low abrasion levels, and release of space competition benefitted turfs as well as fucoids like *Sargassum* (Wernberg et al. 2020).

Kelp-dominated forests can also shift toward turf-dominated systems when dominant canopy-formers are lost due to disturbance (Russell et al. 2009, Filbee-Dexter and Wernberg 2018, Feehan et al. 2019). However, the demonstrated capacity of *Sargassum* to survive and recover might present an alternative for the expected shift to turf-dominated systems if rocky subtidal marine forests can shift toward *Sargassum*-dominated systems (Tanaka et al. 2012, Wernberg et al. 2016a, Vergés et al. 2019, Marks et al. 2015). A shift toward an alternative foundation species could retain some functions such as provision of habitat and food (Coleman and Wernberg 2017, Thomsen and South 2019) although this may not be the case for all species (e.g., abalone; Marzinelli et al. 2013). The overall ecosystem structure and services provided would likely still be substantially different (Vergés et al. 2019). Furthermore, high temperatures can reduce the tolerance of seaweeds to additional perturbations such as storms and can accelerate indirect effects of herbivory (Morelissen and Harley 2007, Vergés et al. 2014b, Bennett et al. 2015b, Miranda et al. 2019, Wernberg et al. 2010). Warmer temperatures can result in range-shifts of tropical herbivores and affect seaweed chemical defenses and nutritional quality and palatability subsequently altering grazing pressure and enhancing the likelihood of microbial diseases on seaweeds (Campbell et al. 2011, Vergés et al. 2014b, 2016, Bennett et al. 2015b, Qiu et al. 2019).

Predicting the response of biota to global warming is a fundamental challenge in the Anthropocene. Overall we have shown that the effects of gradual warming and MHWs are complex, with differential responses of smaller sporophytes of co-occurring species to different profiled thermal stressors. Although warming and MHWs are both thermal stressors driving change in marine ecosystems (Vergés et al. 2016, Wernberg and Straub 2016, Wernberg et al. 2016a, Smale et al. 2019), we provide evidence that their effects on the ecophysiological performance of species and subsequent ecological outcomes, are likely to differ. Our work also highlights the need to consider the occurrence and projected intensification of MHWs to predict and conserve the integrity of marine ecosystems.

For marine conservation and management approaches to succeed, temperature stress-specific responses of dominant species globally need to be determined through manipulative experiments over long timescales to avoid misinterpretation of resilience (tom Dieck et al. 1993, Graiff et al. 2015, Xiao et al. 2015). Additionally, interactive effects with

local and global stressors such as eutrophication (Moy and Christie 2012, Gouvea et al. 2017), ocean acidification, altered current patterns (Coleman et al. 2017, Molinos et al. 2017, Provost et al. 2017, Qiu et al. 2019), changes in herbivory (Basford et al. 2015, Zarco-Perello et al. 2017, Miranda et al. 2019), novel species introductions and interactions (Madin et al. 2012, Pecl et al. 2017, Miranda et al. 2019, Vergés et al. 2019), variability of thermal sensitivity for different ontogenetic stages (Wood 1987, Bennett et al. 2019, Wernberg et al. 2019a), and seasonal timing (Atkinson et al. 2020, Wahl et al. 2020) also need to be taken into consideration. Our experiment took place in late austral summer and autumn, meaning the seaweeds already passed their growth peak and experienced stressful summer conditions before commencement of the experiment, which could have contributed to mortality and reduced growth in all treatments. Improved understanding of the mechanisms that drive changes to our valuable reefs is essential to predict future climate change impacts and to develop and inform management strategies to “future-proof” key marine ecosystems.

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AUTHOR CONTRIBUTION

S. Straub: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Methodology (equal); Resources (supporting); Visualization (lead); Writing – original draft (lead); Writing – review & editing (lead). **T. Wernberg:** Conceptualization (equal); Funding acquisition (lead); Investigation (supporting); Methodology (equal); Project administration (equal); Resources (supporting); Supervision (equal); Writing – review & editing (lead). **E. Marzinnelli:** Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Project administration (supporting); Resources (supporting); Writing – review & editing (equal). **A. Verges:** Funding acquisition (equal); Investigation (supporting); Resources (supporting); Writing – review & editing (equal). **B. P. Kelaher:** Funding acquisition (equal); Investigation (supporting); Project administration (supporting); Resources (supporting); Writing – review & editing (equal). **M. A. Coleman:** Conceptualization (equal); Funding acquisition (equal); Investigation (lead); Methodology (equal); Project administration (equal); Resources (lead); Supervision (equal); Writing – original draft (supporting); Writing – review & editing (equal).

DATA AVAILABILITY STATEMENT

All data are available from the corresponding author on request.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. Primer PERMANOVA main test results for survival of *Ecklonia* and *Phyllospora*. Treatment (Tr) was fixed with 4 levels (ambient, warming, HWnon, HWvar), time (Da) was fixed with 12 levels. Significant results are highlighted bold with grey background. Results for *Sargassum* are not shown as all individuals survived.

Table S2. Summary of pair-wise PERMANOVA treatment effects (p values) within measurement day (day 12–48) for survival of *Ecklonia* and *Phyllospora*. Significant effects are indicated in bold with grey background. *Sargassum* was not statistically significant for any treatment at any day.

Table S3. PERMANOVA main test results for tissue bleaching of *Ecklonia*, *Phyllospora* and *Sargassum*. Treatment (tr) was fixed with 4 levels (ambient, warming, HWnon, HWvar), and time (da) was fixed with 12 levels, twice weekly measurements. Source Significant results are highlighted bold with grey background.

Table S4. Results of pair-wise PERMANOVA for treatment effects within measurement day (days 20–48) for bleaching of algal tissue of *Phyllospora* and *Sargassum*. Significant effects are indicated in bold with grey background.

Table S5. Primer PERMANOVA main test results for relative growth rate (RGR) of *Ecklonia*, *Phyllospora*, and *Sargassum*. Treatment (Tr) was fixed with 4 levels (ambient, warming, HWnon, HWvar), and time (da) was fixed with 6 levels. Significant results are highlighted bold with grey background.

Table S6. Results of pair-wise Primer PERMANOVA for treatment effects within measurement day for relative growth rate (RGR) of *Ecklonia*, *Phyllospora*, and *Sargassum*. Significant effects are indicated in bold with grey background.

Table S7. Primer PERMANOVA main test results for maximum quantum yield of *Ecklonia* and *Phyllospora*. Treatment (tr) was fixed with 4 levels (ambient, warming, HWnon, HWvar), and time (da) was fixed with 9 levels. Significant results are highlighted bold with grey background.

Table S8. Results of pair-wise Primer PERMANOVA for treatment effects within measurement day for maximum quantum yield of *Ecklonia* and *Phyllospora*. Significant effects are indicated in bold with grey background.