LIMNOLOGY and OCEANOGRAPHY

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Limnol. Oceanogr. 70, 2025, S432–S447
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doi: 10.1002/lno.70156

RESEARCH ARTICLE

Varying vulnerabilities: Seagrass species under threat from prolonged ocean warming

Marnie L. Campbell [1*], **Chi T. U. Le** [1,2]

[1]School of Science, Edith Cowan University, Joondalup, Australia; [2]School of Life and Environmental Science, Deakin University, Waurn Ponds, Australia

Abstract

Understanding the response of various seagrass species to prolonged elevated water temperatures is crucial for effective management and seagrass species restoration amid increasing climate change-induced ocean warming and marine heat waves. This is especially important in intertidal seagrass meadows, where heat can penetrate substrate depths of up to 50 cm. We assessed and contrasted the responses of five intertidal species—*Zostera muelleri* Irmisch ex Asch, *Halophila ovalis* (R.Br.) Hook f., *Halodule uninervis* (Forssk.) Asch, *Halophila decipiens* Ostenf., and *Halophila spinulosa* (R.Br.) Asch—over a month of elevated temperatures by examining rhizome growth, number of living shoots, root development, and sprig survival. While all the species appeared to negatively respond to elevated water temperatures, our results indicate notable interspecific variations in their reactions to prolonged warming stress. Two *Halophila* species, including *H. ovalis* and *H. spinulosa*, are sensitive to prolonged heat stress exceeding 10°C above ambient. *Halodule uninervis* is the most tolerant of elevated water temperature, followed by *Zostera muelleri,* although the latter is still negatively affected. Intertidal *H. decipiens* appears to be highly vulnerable to disturbance and performs poorly in mesocosm settings. This study offers an initial understanding of how climate change might impact these seagrass species, whose ecological functions are not easily replaceable once lost.

Climate change has contributed to the alarming decline of seagrass globally (Orth et al. 2006; Short and Neckles 1999; Thomson et al. 2015). Future projections indicate severe seagrass habitat loss in certain regions of the world (Chefaoui et al. 2018; Chefaoui et al. 2021). There are multiple climate change-related stressors, including (but not limited to) changes in sea surface temperatures, coastal water salinity, sea level rise, ocean acidification, and extreme climatic events, which have significant implications for seagrass ecosystems and the plants themselves (Brodie and N'Yeurt 2018; Short et al. 2016; Zimmerman 2021). Among climate change-related stressors, temperature is considered the primary distribution-limiting factor, and ocean warming is deemed the most severe threat to seagrasses (Duarte et al. 2018). Therefore, understanding how different seagrass species respond to elevated water temperatures (a prominent predicted outcome of climate change) will have significant implications for seagrass management and restoration efforts.

Ocean warming, identified as a significant human-induced stressor, adversely affects seagrasses at multiple functional levels, from molecular, biochemical/physiological, morphological/population, to ecosystem/planetary levels (Nguyen et al. 2021). While ocean warming refers to the gradual rise in average water temperatures, it also includes anomalous thermal events such as marine heatwaves (MHW). Marine heatwaves are defined as a period lasting at least five consecutive days to several months, during which sea surface temperatures exceed the 90th percentile of a three-decade historical baseline (Hobday et al. 2016).

*Correspondence: marnie.campbell@ecu.edu.au

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Associate editor: Christopher Cornwall

Special Issue: Mesocosms: Bridging the gap between in situ and laboratory studies. *Edited by: Christopher Cornwall, Christian Pansch-Hattich, Maren Striebel, Jens Nejstgaard and Deputy Editors Julia C. Mullarney, Steeve Comeau, and C.-Elisa Schaum*

Data Availability Statement: The data and R code used for the analyses in this study are publicly available at https://doi.org/10.6084/m9.figshare.28169399 [Figshare]. This information has been included in the manuscript's Acknowledgments section.

It is increasingly evident that ocean warming and MHW are associated with mass seagrass mortality, often referred to as "seagrass collapse." This phenomenon has been observed globally, including in the Western Mediterranean (Díaz-Almela et al. 2009; Marbà and Duarte 2010), Australia (Serrano et al. 2021; Strydom et al. 2020; Thomson et al. 2015), and the United States (Carlson et al. 2018; Moore and Jarvis 2008; Moore et al. 2014). Over the past century, the frequency and intensity of MHW have increased, with a 34% increase in frequency and a 17% increase in duration from 1925 to 2016, leading to a 54% increase in annual marine heatwave days (Oliver et al. 2018). This trend is expected to worsen in the future (Frölicher et al. 2018; Oliver et al. 2019), suggesting that seagrasses and other marine organisms will likely face more severe and prolonged thermal stress.

The ability of seagrasses to withstand ocean warming, especially MHW, varies across species based on their thermal tolerance (Bass and Falkenberg 2023; Marín-Guirao et al. 2016; Nguyen et al. 2020). This variation also exists among populations of the same species in different thermal regions (Bergmann et al. 2010; Marín-Guirao et al. 2019; Winters et al. 2011). In general, tropical and subtropical seagrass species have higher optimal temperatures for growth and photosynthesis compared to temperate species (Bulthuis 1987; Lee et al. 2007). Additionally, intertidal seagrass species that are restricted to tropical and subtropical regions exhibit greater tolerance to elevated water temperatures, likely as an adaptive response to frequent exposure to high temperatures during low tides and peak irradiance (Campbell et al. 2006; Serrano et al. 2021).

High water temperatures promote seagrass growth, reproduction, photosynthesis, respiration, and sucrose-P synthase activity (Greve and Binzer 2004; Lee et al. 2007; Marsh et al. 1986). However, when temperatures exceed a species' upper thermal threshold, growth and photosynthesis rates decline, and mortality increases due to metabolic imbalances, such as the increased loss of primary production to respiration (Collier and Waycott 2014; George et al. 2018; Massa et al. 2009). These issues are particularly significant in intertidal seagrass meadows, where vertical thermal transfer can reach substrate depths of up to 50 cm (Kim et al. 2007; Thomson 2010).

Inter-species differences in response to ocean warming have been increasingly documented in the scientific literature (e.g., Campbell et al. 2006; Collier et al. 2011; Marbà et al. 2022). However, there remains a significant knowledge gap regarding the effects of warming on seagrasses, with most of the world's seagrass species yet to be studied (Nguyen et al. 2021). A better understanding of how seagrasses respond to prolonged elevated water temperatures would significantly aid in predicting changes in their population distribution under warming scenarios. Additionally, insights into the varying responses of seagrass species to thermal stress could help identify the most viable species and suitable restoration sites (Campbell et al. 2018), which are crucial for the success of seagrass restoration projects (Campbell 2002; Ganassin and Gibbs 2008).

Our study aims to examine the impacts of elevated water temperatures on five intertidal species, *Zostera muelleri* Irmisch ex Asch, *Halophila ovalis* (R.Br.) Hook f., *Halodule uninervis* (Forssk.) Asch, *H. decipiens* Ostenf., and *Halophila spinulosa* (R. Br.) Asch, in an experimental setting. These five species are pioneer species characterized by small body size, rapid growth, and high turnover rates. While *H. uninervis* and *H. spinulosa* are typically associated with tropical and subtropical regions, *Z. muelleri*, *H. ovalis*, and *H. decipiens* have a broader distribution across temperate and tropical regions (Green and Short 2003; Short et al. 2011).

Previous studies show that several seagrass species possess high thermal tolerance. *H. ovalis* is considered a eurythermal species (Hillman et al. 1995). It exhibits tolerance to acute heat shock in the range of 15–30°C (Ralph 1998) and resistance to marine heatwaves (Bass and Falkenberg 2023). *H. uninervis* has a high upper thermal limit (> 33°C) (Collier et al. 2011) and demonstrates a root foraging strategy that involves deeper (and cooler) rhizome substrate depths compared to the other species studied (Campbell et al. 2018), potentially reducing its vulnerability to climate change. *Halophila spinulosa* has deep intertidal/subtidal zonation at the study site (Campbell, per. obs.). Deep-water *H. spinulosa* appears to withstand heat stress up to 30°C (Chartrand et al. 2018). We, therefore, hypothesized that *H. ovalis*, *H. uninervis*, and *H. spinulosa* would be more resistant to warming conditions than the other two investigated species.

Materials and methods

Seagrass collection

Vegetative propagules of these species were collected from intertidal mud banks on Pelican Banks in Gladstone Harbour, Queensland, Australia (Fig. 1). Gladstone, a sub-tropical location, experiences two climatic seasons: the dry season (May to October) and the wet season (November to April). The local sea surface temperature ranges from 19.4°C to 29.5°C (https://www.seatemperature.org/australia-pacific/australia/gladstone.html). Pelican Banks is covered in an intertidal mixed-species seagrass meadow spanning approximately 600 ha.

Seagrass vegetative propagules (sprigs) were hand-collected from the growing edges of the meadow during low tide to minimize impacts on the meadows. Each sprig included a rhizome with the apical meristem and at least six shoots, which were carefully extracted from the sediment and immediately placed into sample containers filled with water from the surrounding site. Sampling occurred within an hour, and the plants were transported to the Central Queensland University (CQU) Gladstone campus laboratory, a 15-min boat journey. Rhizomes were processed the same day to minimize handling, following recommendations by Campbell (2002) and Paling (2000). All sprigs were washed in a disinfectant solution (1 : 80 chlorox : seawater) to reduce potential infection and placed into seawater mesocosms, as

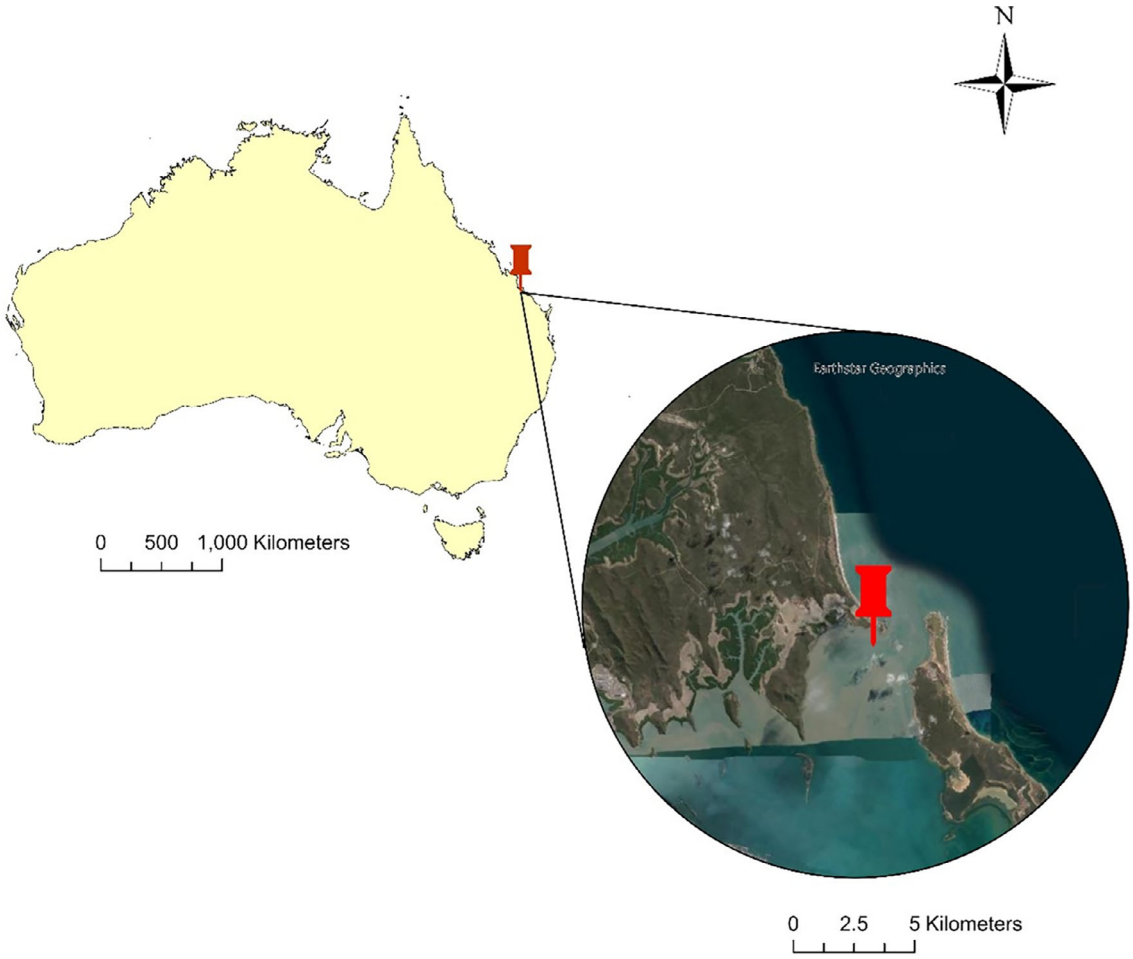


Fig. 1. Sampling site—Pelican Banks, Gladstone Harbour, Queensland, Australia, marked by a red pin.

described by (Campbell 2016). Based on our pilot experiment, where daily monitoring showed that rhizome mortality stabilized by day 14, a 14-day acclimation period was deemed sufficient for the sprigs to adapt to the experimental conditions. After the acclimation period, healthy rhizomes were randomly selected, measured (in centimeters), and randomly allocated to experimental mesocosms.

Mesocosm laboratory

All experiments were conducted in a controlled mesocosm laboratory at the CQU Gladstone campus. Isolated mesocosms were used, with each unit containing an air stone to provide minimal water movement. The light environment in the mesocosms was maintained at an average of 8.1 ± 0.2 mol^{-2} d^{-1}. A diurnal photoperiod of 14 h of light and 10 h of dark (14 L : 10 D) was used to represent natural conditions during spring and summer to support seagrass growth. Artificial seawater was used in the experiments. The average water temperature in the controls ranged from 21.8°C in September to 23.1°C in October, with an average salinity of 37.8 ± 0.6 ppt to match the natural salinity level at the sample site. During the experiments, water was topped up as needed to counter evaporation, ensuring stable water and salinity levels in the mesocosms. Tap water, left to stand for 24 h to enable chlorine to dissipate, was used for the top-ups.

Due to the limited capacity of the mesocosm facilities, two separate experiments were conducted to investigate the impacts of persistent heat stress on multiple seagrass species. The first experiment, referred to as Experiment 1, tested *Z. muelleri*, *H. ovalis*, and *H. uninervis* from 30th August to 1st October 2013. The second experiment, referred to as Experiment 2, involved *Z. muelleri*, *H. spinulosa*, and *H. decipiens* from 5th October to 6th November 2013. Experiment 1 took place during the seasonal transition from dry to wet, colloquially referred to as "the build," while Experiment 2 occurred in the early wet season. Seagrass sprigs were collected and processed separately for each experiment.

Since the experiments were conducted at different times, statistical comparisons and regressions were performed independently for each experiment, with *Z. muelleri* serving as the reference species for both. Consequently, the results are presented and discussed separately for each experiment.

Experimental design

The duration of both experiments was intended to simulate a warming event over a month (28 d). However, due to wet season flooding, the experiment period was extended slightly to 32 d, as laboratory access was not possible from days 28 to 31. Marine heatwave conditions affecting seagrass ecosystems typically last from several days to a month (Marín-Guirao et al. 2018; Oliver et al. 2021; Oliver et al. 2019). We chose a month-long exposure to encompass the cyclical variation in tidal range caused by the spring–neap tidal cycle.

Each experiment utilized nine mesocosms (100-L aquaria), with nine trays of substrate in each mesocosm, where sprigs of the three species were planted. To accommodate the space constraint within the mesocosms, the sprigs were standardized to have four shoots and an apical meristem, with no roots at this stage. Rhizomes were placed on the substrate, and sand was gently fanned onto individual sprigs to a substrate depth range of 1–4 cm, matching the natural rhizome depth profile of each species (Campbell et al. 2018).

Three mesocosms were maintained at ambient water temperature, representing the average field water temperature (September: 21.8°C [20.1–23.5°C] and October: 23.1°C [20.8–25.5°C], the National Oceanic and Atmospheric Administration (NOAA)—https://www.seatemperature.org/australia-pacific/australia/gladstone.htm) and served as a control group. Another three mesocosms were at 5°C above ambient water temperature, and the other three mesocosms were maintained at 10°C above ambient water temperature. These water temperature treatments were designed to ensure that they exceeded the monthly and seasonal 90th percentile marine heatwave thresholds for the Great Barrier Reef region (see Kajtar et al. 2021), where the study site is located. Submersible aquarium heaters with thermostats were used to maintain constant temperatures in the mesocosms. HOBO temperature loggers (three loggers per temperature treatment) monitored water temperature.

The effects of elevated temperatures were measured by assessing rhizome growth (change in total rhizome length over the experiment duration), the number of living shoots, root development (presence of roots at the end of the experiments), and sprig survival at the end of the experiments.

For *H. ovalis* only, we also observed the number of shoot clusters (i.e., ramets growing at the nodes), representing the ability to create vegetative fragments/propagules. This observation is included in our results below.

Data analysis

Response of individual seagrass species to elevated temperature

We examined and compared the responses of various seagrass species to different water temperatures, focusing on changes in rhizome length and the number of surviving shoots. Due to non-normal data distribution (Shapiro–Wilk $p < 0.05$), Kruskal–Wallis' tests were applied for multiple comparisons, followed by post hoc Dunn's tests with Benjamini–Hochberg correction for multiple comparisons (Benjamini and Hochberg 1995). The relationships between water temperatures and root development or sprig survival were investigated using Fisher's exact test. Fisher's exact test was chosen over the chi-squared test due to the low expected frequencies (less than 5) in our contingency tables. Significant results were further examined using pairwise Fisher's exact tests. The number of shoot clusters present in *H. ovalis* was also reported.

Quantifying the impacts of elevated water temperature on multiple seagrass species

The effects of elevated water temperature on rhizome length, number of living shoots, root presence, and survival were parameterized and compared among species. All the analyses were conducted in the R environment (version 4.3.3; R Core Team 2024). Preliminary analyses checked whether the initial rhizome lengths influenced the measurements.

The results of the two experiments are presented side by side, with *Z. muelleri* serving as the reference group for both experiments.

Rhizome growth

Linear mixed models were fitted to rhizome growth as a function of temperature, species, and their interaction, including mesocosm variation as random intercepts. The "lmer" function of the "lme4" R package (Bates et al. 2015) was used for the models.

Number of living shoots

The number of living shoots at the end of the two experiments was predicted as a function of temperature, species, and their interaction using a generalized additive mixed model with a Poisson distribution and a log link function for each experiment. Mesocosm ID was included as a random intercept. We used the thin plate spline function for smoothing, with smoothing parameters estimated using restricted maximum likelihood. The "gam" function of the "mgcv" R package (Wood and Wood 2015) was used for the analysis. The percentage of deviance explained and adjusted R^2 of the generalized additive mixed models were calculated for goodness-of-fit assessment, and the functional shapes of the partial effects were plotted.

Root presence and sprig survival

The probability of root presence at the end of the experiments and sprig survival was predicted using mixed-effect binary logistic models, with temperature, species, and their interaction as fixed effects, and mesocosm ID as random intercepts. The "glmer" function with a logit link and binomial distribution from the "lme4" R package was used for the analysis.

Goodness of fit of the models was evaluated based on pseudo R^2 (Nakagawa et al. 2017) calculated using "r2" and "performance" functions of the "performance" R package (Lüdecke et al. 2021).

Multivariate response

The impacts of elevated temperature on morphological characteristics and survivorship of the three seagrass species (i.e., rhizome growth, number of living shoots, probability of root presence, and survival probability) were simultaneously compared in each experiment. Probabilities of root growth and survival were predicted using the binary logistic models (see section root presence and sprig survival). We employed permutational multivariate ANOVA using Euclidean distance matrices, with explanatory variables including water temperature, species, and their interaction, and permutation restricted within mesocosms to account for their nested structure. The "adonis2" function of the "vegan" R package (Oksanen et al. 2022) was used for the analysis. Post hoc tests were conducted using the "pairwise.adonis2" function of the "pairwiseAdonis" package (Arbizu 2019). The result was visualized using the "vegan" and "ggplot2" (Wickham et al. 2016) R packages.

Results

Response of individual seagrass species to elevated water temperature

Experiment 1

Zostera muelleri exhibited no significant changes in rhizome length ($\chi^2 = 2.96$, df = 2, $p = 0.23$) and root development ($p = 0.115$), and a marginally nonsignificant difference in survivorship ($p = 0.068$) across temperature treatments (Fig. 2). The number of living shoots at + 10°C was significantly lower than that at ambient ($p = 0.02$) and + 5°C ($p = 0.028$) (Fig. 2b). It was noted that the mean and median living shoot counts of this species remained below the initial number (four) in all treatments, indicating that shoots were dying in the mesocosm experiment, regardless of water temperature.

Halodule uninervis showed no significant differences in all response measurements across temperature treatments. Similar to *Z. muelleri*, its shoot count was below four at the end of the experiment across all treatments (Fig. 2b).

H. ovalis exhibited a significant response to different water temperatures in rhizome growth, shoot counts, root development, and survival (Fig. 2). Specifically, rhizome growth was significantly lower at + 10°C compared to ambient ($p = 0.006$) and + 5°C ($p = 0.009$). A similar trend was observed in the number of living shoots. Root development also varied significantly (Fisher's exact $p = 0.002$), with fewer roots at + 10°C than ambient temperature ($p = 0.007$). While the survival of *H. ovalis* sprigs was associated with water temperatures (omnibus Fisher's exact $p = 0.004$), the post hoc test could not pinpoint specific differences, possibly due to a more stringent significance level (i.e., corrected p value) and smaller partitioned samples. The number of shoot clusters

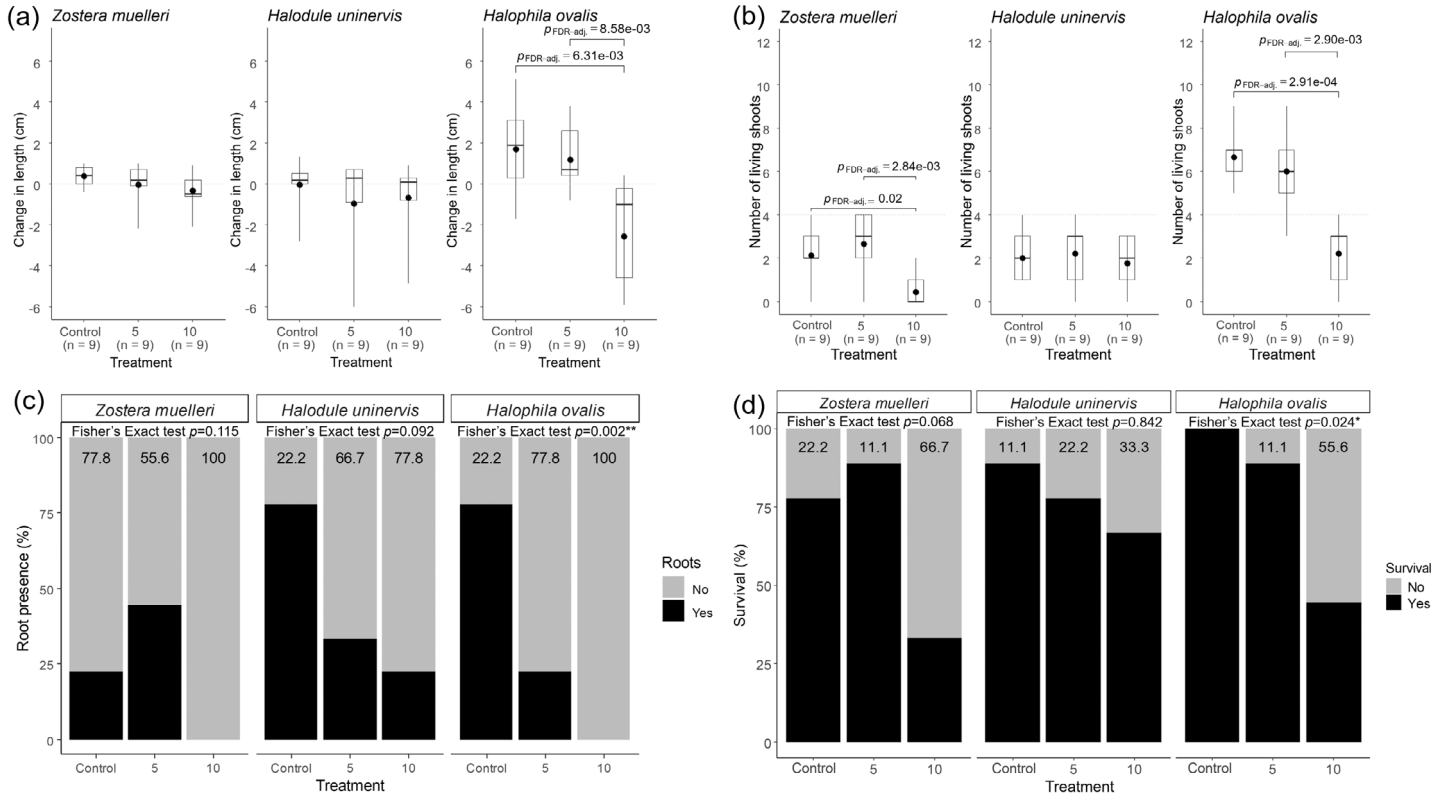


Fig. 2. Responses of the seagrass species in Experiment 1 in terms of (**a**) change in rhizome length, (**b**) number of living shoots, (**c**) root development/presence, and (**d**) survival. Only statistically significant pairwise comparisons were presented in (**a**) and (**b**) using brackets and false discovery rate (FDR)-corrected p values.

developed on *H. ovalis* showed a significant decline, with the median number of shoot clusters dropping from two at ambient temperature to one at + 5°C and zero at + 10°C (Fig. 3).

Experiment 2

Due to slightly warmer ambient conditions, all temperature treatments in Experiment 2 were about 1.3°C higher than in Experiment 1. *Zostera muelleri* exhibited clearer morphological and survival responses in Experiment 2. Rhizome growth was significantly reduced at + 10°C, compared to ambient and + 5°C ($p = 0.02$) (Fig. 4a). Similarly, the number of living shoots was lower at + 10°C than at ambient ($p = 0.005$) and + 5°C ($p = 0.001$) (Fig. 4b). Root presence was significantly lower at + 10°C compared to ambient ($p = 0.044$) and + 5°C ($p = 0.027$) (Fig. 4c). Survivorship followed a similar pattern, with significantly lower survival at + 10°C compared to both ambient and + 5°C ($p < 0.001$) (Fig. 4d).

Significant differences in rhizome growth, number of living shoots, root development, and survival of *H. spinulosa* were found only between ambient temperature and + 10°C ($p = 0.01$, 0.003, 0.007, and 0.007, respectively). In contrast, *H. decipiens* showed no significant responses to elevated water temperatures and appeared to establish unsuccessfully in the mesocosms.

Quantifying the impacts of elevated water temperature on multiple seagrass species

Rhizome length response

In Experiment 1, rhizome growth showed a statistically significant interaction between temperature and species ($\chi^2 = 12.75$, df = 2, $p = 0.002$), indicating species-specific response to warming. At ambient temperature, *H. ovalis* had significantly higher rhizome growth rates ($p = 0.015$) compared to *Z. muelleri* and *H. uninervis*. However, *H. ovalis* was also more responsive to increased temperature, with a 0.36-unit greater decline in rhizome growth per 1°C, compared to *Z. muelleri* (SE = 0.117, $t = -3.097$, $p = 0.003$). In contrast, *H. uninervis* showed no significant differences from *Z. muelleri* ($p = 0.977$). The random effect of mesocosms explained a small proportion of the variation in rhizome growth ($\sigma^2 = 0.247$, SD = 0.497, ICC [Intraclass correlation coefficient] = 0.074).

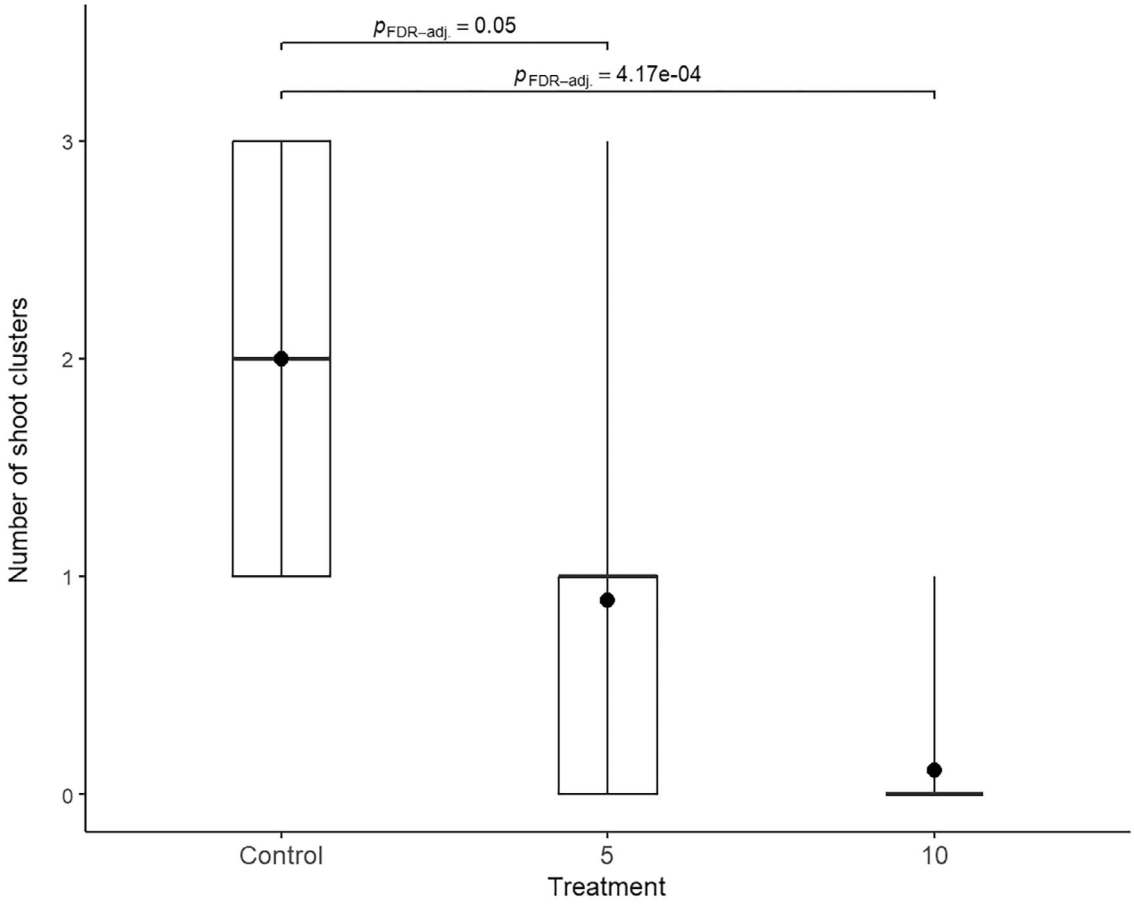


Fig. 3. Number of shoot clusters developed in *Halophila ovalis* at different conditions of water temperatures. Brackets represent statistically significant pairwise comparisons with false discovery rate (FDR) corrected *p* values.

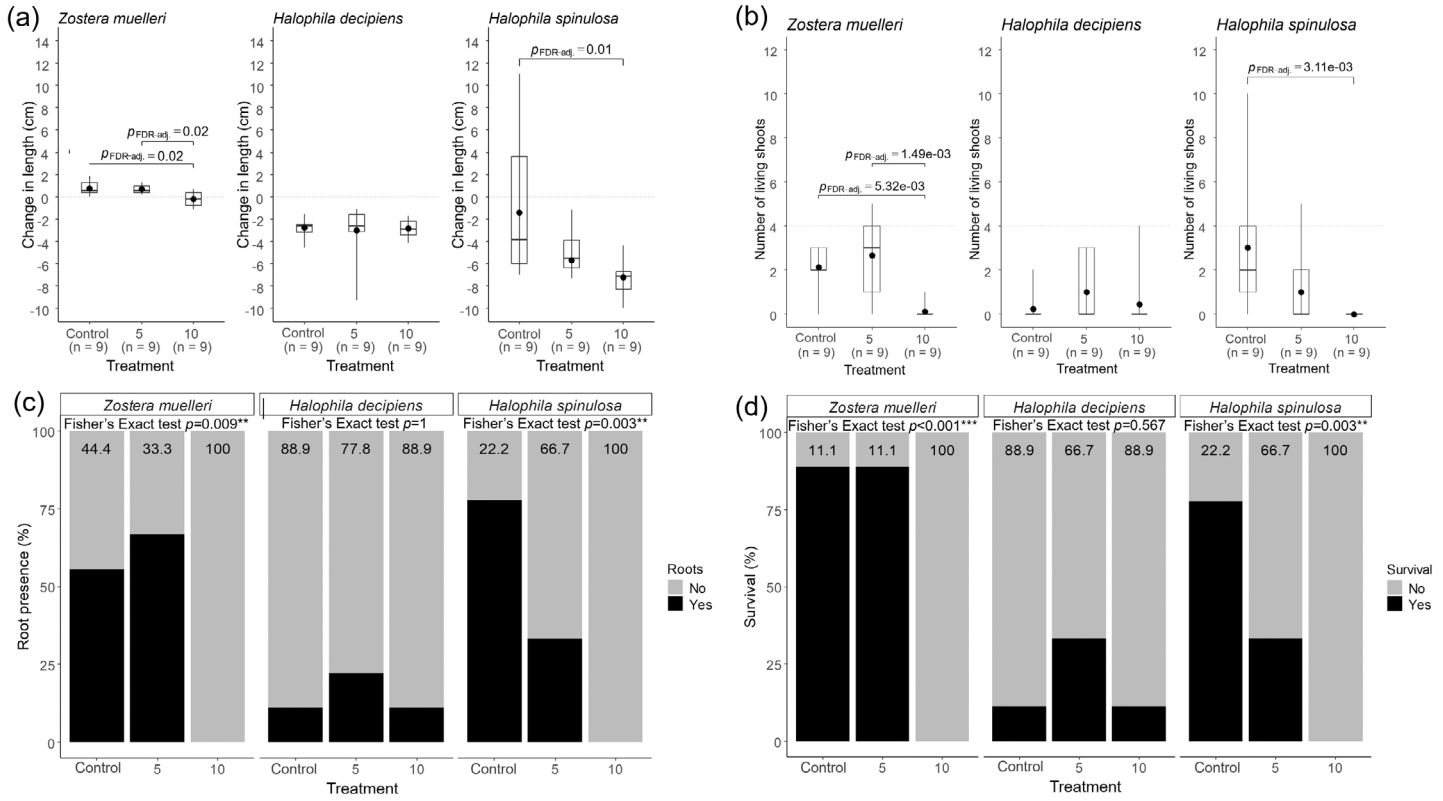


Fig. 4. Responses of the seagrass species in Experiment 2 in terms of (**a**) change in rhizome length, (**b**) number of living shoots, (**c**) root development/presence, and (**d**) survival. Only statistically significant pairwise comparisons were presented in (**a**) and (**b**) using brackets and false discovery rate (FDR)-corrected *p* values.

In Experiment 2, both *H. decipiens* and *H. spinulosa* experienced a decline in rhizome length over 1 month (i.e., negative rhizome growth), regardless of water temperature (Fig. 5b). All else being equal, *H. spinulosa* showed a significantly greater decline in rhizome growth per 1°C than that of *Z. muelleri* (coefficient = − 0.524, SE = 0.186, $t = -4.461$, $p < 0.001$). Rhizome growth responses of *H. decipiens* and *Z. muelleri* were not significantly different ($p = 0.754$). Mesocosm variation was negligible ($\sigma^2 = 0$).

The model results are illustrated in Fig. 5 (fitted lines without observed data), Supporting Information Fig. S1 (fitted lines with observed data), and Supporting Information Table S1.

Number of living shoots

The effect of increased water temperature on living shoot counts was statistically significant and nonlinear for *Z. muelleri* (estimated degree of freedom = 1.90–1.92, $p < 0.01$), *H. ovalis* (estimated degree of freedom = 1.89, $p < 0.001$), and *H. spinulosa* (estimated degree of freedom = 1.81, $p = 0.009$). The partial effects (i.e., isolated effects when holding other variables constant) of temperature on the number of living shoots by species are demonstrated in Fig. 6a–c for Experiment 1 and Fig. 6d–f for Experiment 2. For *Z. muelleri*, ambient temperature and + 5°C treatment had a positive effect on the number of living shoots in Experiment 1, while + 10°C had a negative effect in both experiments (Fig. 6a, d). Elevated temperature had a negative effect on the number of living shoots for *H. ovalis* (Fig. 6c), while the metric was significantly higher in ambient temperature than in elevated temperature for *H. spinulosa* (Fig. 6f). The effects of temperature on *H. uninervis* and *H. decipiens* were not statistically significant ($p > 0.05$). The mesocosm random effects were nonsignificant in both experiments. The approximate significance of the smooth terms is illustrated in Supporting Information Table S2.

Root presence

The interaction term between temperature and species was nonsignificant in both experiments, indicating consistent effects of temperature on root development across species. Therefore, it was removed from the final regression. The summary of the mixed-effect logistic regressions is presented in Supporting Information Table S3, with predicted probabilities of root development illustrated in Fig. 5c, d. At equal water temperatures, the odds of developing roots were 4.56 times higher for *H. uninervis* compared to *Z. muelleri* ($p = 0.046$; 95% confidence interval [CI]: 1.10–22.55) in Experiment 1. Conversely, *Z. muelleri* had five times the odds of growing

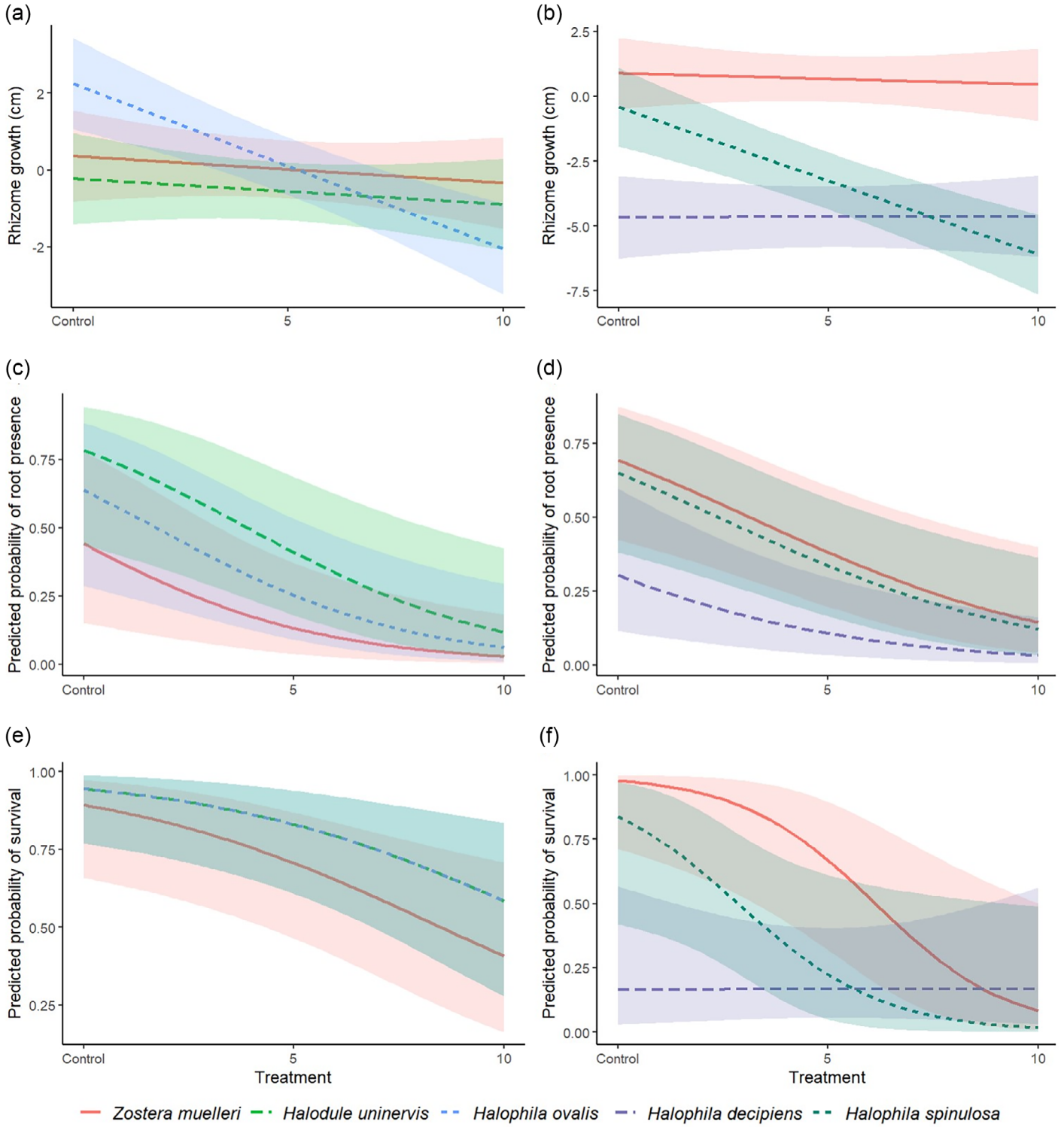


Fig. 5. Impact of elevated temperature on rhizome growth (i.e., rhizome length), root presence probability, and survival probability (from top to bottom). The left plots (**a**, **c**, **e**) represent Experiment 1, and the right plots (**b**, **d**, **f**) represent Experiment 2.

roots compared to *H. decipiens* ($p = 0.026$; 95% CI: 1.30–25). No significant differences were found between *Z. muelleri* and *H. ovalis* or *H. spinulosa* ($p > 0.05$).

Every 1°C increase in water temperature reduced the odds of root presence in the seagrasses by 28% ($p = 0.004$, 95% CI: 10–46) in Experiment 1 and 23% ($p < 0.001$, 95% CI: 11–39)

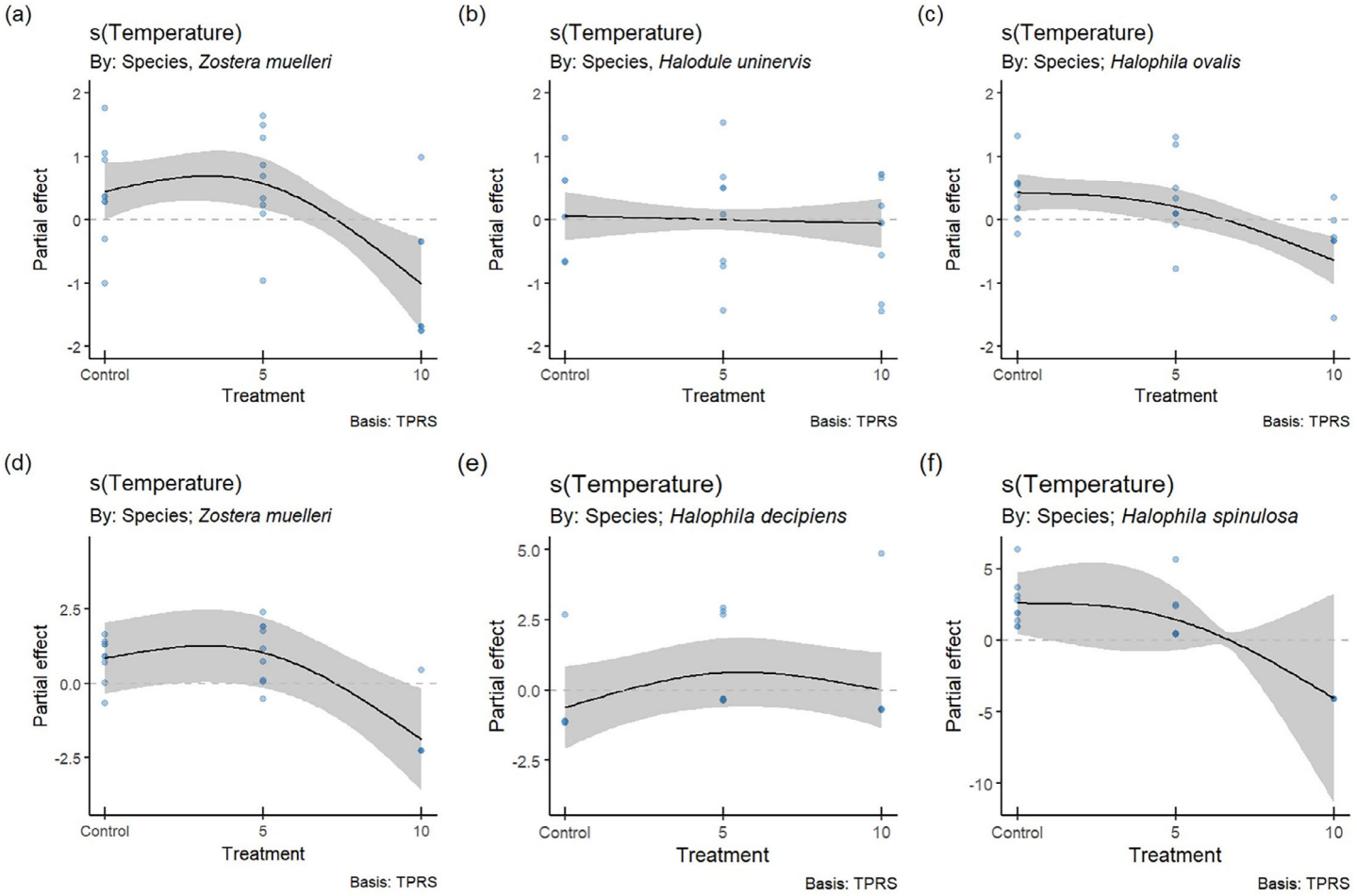


Fig. 6. Partial effects of increased temperature on the number of living shoots by species in Experiment 1 (**a**–**c**), and Experiment 2 (**d**–**f**). Shaded areas represent the 95% confidence intervals. s(Temperature) represents the smooth terms (i.e., nonlinear effects) of temperature. The blue points represent partial residuals from the generalized additive mixed models.

in Experiment 2. Mesocosm variation contributed moderately in Experiment 1 ($\sigma^2 = 0.785$, SD = 0.886, ICC = 0.193; pseudo-R^2: conditional = 0.48, marginal = 0.35). In Experiment 2, mesocosm variation was negligible ($\sigma^2 = 0.046$, SD = 0.215, ICC = 0.014) with pseudo-$R^2 \approx 0.34$.

Seagrass survival

In Experiment 1, elevated water temperature significantly reduced the survivorship of *Z. muelleri*, *H. uninervis*, and *H. ovalis*, with a 22% decrease in odds per 1°C increase ($p = 0.001$, 95% CI: 6–37; illustrated in Supporting Information Table S4 and Fig. 5e). The mixed-effect logistic regression had a pseudo-R^2 of 0.31 (conditional) and 0.24 (marginal). The variance attributed to mesocosms was 0.337 (SD = 0.580, ICC = 0.093).

In Experiment 2, temperature effects on survival varied across the three seagrass species (*Z. muelleri, H. decipiens*, and *H. spinulosa*) (Supporting Information Table S4). *Zostera muelleri* and *H. spinulosa* had a high survival at ambient temperature but dropped sharply at + 10°C, with no significant difference in decreasing rates (odds ratio = 1.045, $p = 0.214$). *H. decipiens* maintained a low survival across temperatures (Fig. 5f). The mixed effect logistic regression for seagrass survivorship yielded a pseudo-R^2 of 0.63 (conditional) and 0.58 (marginal). Mesocosm variance was 0.406 (SD = 0.637, ICC = 0.110).

Multivariate response

The permutational multivariate ANOVA results confirmed the species-specific multivariate responses to water temperatures (Supporting Information Table S5). The main effects of species were significant in both experiments, with pseudo-$F = 17.45$ and $p < 0.001$ for Experiment 1, and pseudo-$F = 22$ and $p < 0.001$ for Experiment 2. Similarly, the main effects of temperature were also significant (pseudo-$F = 22.11$ and $p < 0.001$ for Experiment 1, and pseudo-$F = 12.46$ and $p < 0.001$ for Experiment 2).

The interaction between species and temperature was significant for both experiments (Experiment 1: pseudo-$F = 7.04$, $p < 0.001$; Experiment 2: pseudo-$F = 6.34$, $p = 0.002$), explaining 10% and 9% of the variance, respectively. This indicated species-specific responses to warming, except for *Z. muelleri* and *H. uninervis*, which showed similar patterns (pairwise comparison pseudo-$F = 1.02$, p value $= 0.354$; Supporting Information Table S6). Slightly under 50% of the variance in each experiment was explained by species, water temperature, and their interaction. The multivariate responses are visualized in Fig. 7.

Discussion

Our study demonstrates the impacts of a simulated persistent heating event on five intertidal seagrass species (*Z. muelleri*, *H. uninervis*, *H. ovalis*, *H. decipiens*, and *H. spinulosa*) that commonly occur in Australia and other parts of the world. Although *Z. muelleri* appeared in both consecutive experiments, the comparisons were made independently for the two groups of seagrasses (i.e., *Z. muelleri*, *H. uninervis*, and *H. ovalis* for Experiment 1; and *Z. muelleri*, *H. decipiens*, and *H. spinulosa* for Experiment 2). Since all the investigated species co-occur in the same meadow and are exposed to the same seasonal environmental conditions, we assumed that they may exhibit synchronized seasonal growth cycles, as observed in some seagrass species (Marbà et al. 1996). It is important to note that our mesocosm setup did not replicate key aspects of the in situ intertidal environment, such as natural inundation patterns and temperature cycles. Additionally, it lacked ecological realism, including multi-species interactions and thermal ecosystem engineering, which may influence seagrass responses to thermal stress in natural settings (Buñuel et al. 2021; Gilman et al. 2010; Lurgi et al. 2012). Despite these limitations, we believe that examining single-species responses to prolonged thermal stress provides valuable insights into the potential impacts of intensifying marine heatwaves on seagrass meadows under future climate scenarios. Most of the species responded negatively to increased water temperature, except *H. decipiens*, which performed poorly in mesocosm settings regardless of water temperature. The outcomes we have demonstrated here have serious implications for how we manage seagrass ecosystems and their restoration in the context of climate change.

We acknowledge that, although the analyses demonstrated significant effects of water temperature on the response variables (both univariate or multivariate), the proportion of variance explained by the predictor variables, including species, water temperature, and their interaction, after accounting for mesocosm-level variance, was relatively low (e.g., low R^2). This suggests that unmeasured factors, potentially related to environmental disturbances associated with the mesocosm setup, might have influenced the observed patterns in the seagrass measurements, which were not accounted for in the analyses. Therefore, the interpretation of our study's results is limited to the variation explained by the analyses.

In general, *H. uninervis* exhibited a similar response pattern with *Z. muelleri*, whereas the other species showed distinct responses to prolonged warming stress. *H. ovalis* and *H. spinulosa* appeared to be more sensitive to elevated water

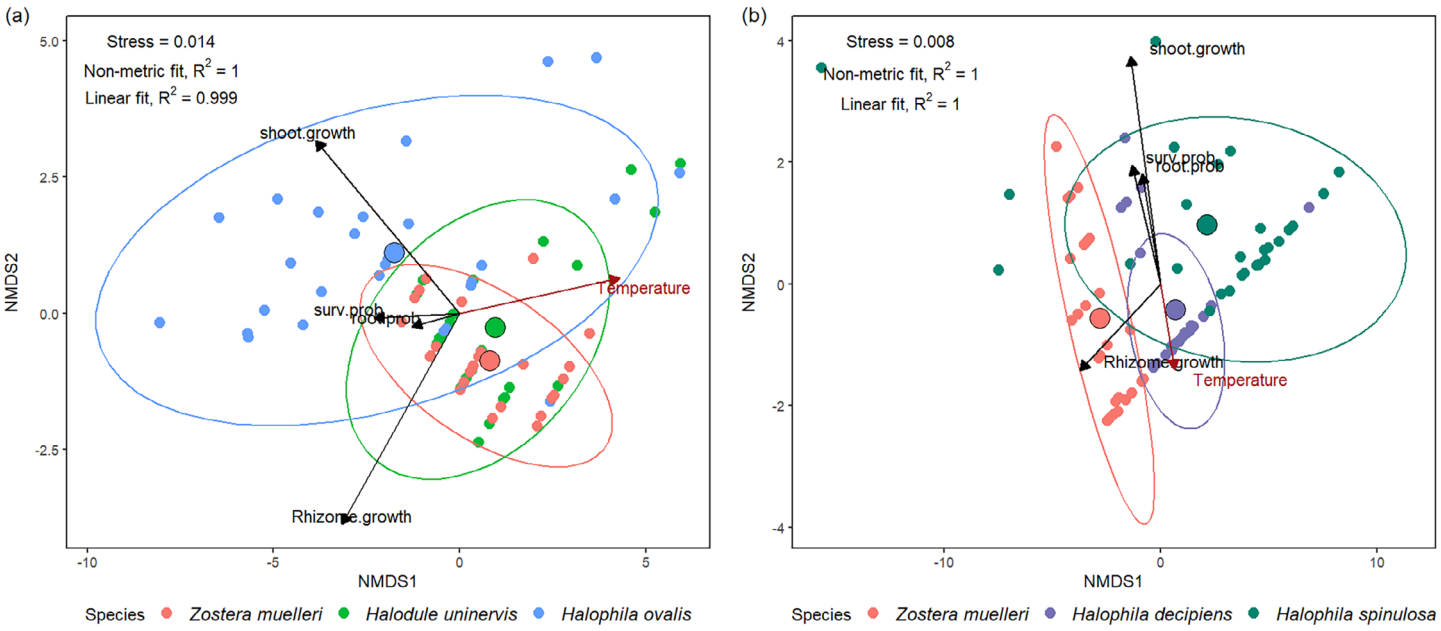


Fig. 7. Multivariate response to elevated temperature in (**a**) Experiment 1, and (**b**) Experiment 2. Larger solid circles with black borders represent the centroids of the groups. Arrows represent the directions of the variables' gradients. Shoot.growth: number of surviving shoots; Rhizome.growth: change in length of rhizome; surv.prob: probability of survival; root.prob: probability of root presence.

temperature, while *H. decipiens* performed poorly in all temperature treatments, compared to the other species in our experiments. Similarities in responses to prolonged and elevated water temperature for *H. uninervis* and *Z. muelleri* may be linked to their root foraging strategy: both species have rhizomes located at deeper substrate depths than the other species we examined and both species have similar edaphic temperature envelopes (i.e., the range of soil temperatures and related conditions that are suitable for a particular species) in the field (Campbell et al. 2018).

Our results support previous studies that show responses to warming events vary among different seagrass species, even in two seagrass species of the same genus (Bass and Falkenberg 2023; Collier et al. 2017; Marín-Guirao et al. 2016). Marbà et al. (1996) have demonstrated that seagrass growth depends on both external components (i.e., environmental forcing) and intrinsic components (species-specific capability to buffer, or amplify, the external environmental forcing). While it is unsurprising that the response of the seagrasses to water temperature was species-specific, there were some unexpected responses among the investigated seagrass species.

Water temperature in the range of ambient temperature and + 10°C treatment (i.e., approximately 21.8°C to 31.8°C) in Experiment 1 only had a significant impact on *Z. muelleri*'s number of living shoots. The number of living shoots was significantly lower at + 10°C compared to the other temperature treatments. A reduction in the number of living shoots significantly associated with water temperature could suggest that longer periods of heat exposure, such as what occurs during MHW (Oliver et al. 2021), may lead to deleterious impacts.

With an increase of about 1.3°C for each temperature treatment in Experiment 2, compared to Experiment 1, the maximum temperature treatment of Experiment 2 was over 33°C. This temperature treatment caused significant declines in all the morphological metrics of interest and complete mortality of *Z. muelleri* at the end of Experiment 2. This aligns with research by York et al. (2013), which illustrates thermal damage occurring to *Z. muelleri* at 32°C. This thermal exposure negatively impacted the species' effective quantum yield of photosystem II, resulting in complete fatality at day 42. This finding also corroborates the results of Collier et al. (2011) where water temperature at 33°C over a month severely affected this temperate seagrass species, causing critical metabolic imbalances.

Impact of water temperature under 32°C was indiscernible for *H. uninervis*, with the sprigs persisting for 32 d. This is not surprising as *H. uninervis* is a subtropical/tropical seagrass species with its estimated thermal optima of 33°C (Adams et al. 2017; Campbell et al. 2006; Collier et al. 2017), and our temperature treatments were within its water temperature range (Collier et al. 2011; Masini et al. 2001). However, Collier et al. (2018) have suggested that prolonged exposure (e.g., 7 weeks) to temperatures that are only slightly greater than thermal optima can cause critical thermal stress for *H. uninervis*. The broad edaphic thermal envelope of *H. uninervis* rhizomes, and its rhizomes occupying deeper depths (Campbell et al. 2018), may aid in sheltering the species from thermal stress. This may provide *H. uninervis* a competitive advantage in climate conditions that are shifting toward warmer environments.

At ambient temperature (i.e., approximately 21.8°C in September for Experiment 1), *H. ovalis* exhibited better performance in terms of rhizome growth and number of living shoots, compared to *Z. muelleri* and *H. uninervis*. The rhizomes of *H. ovalis* are shallow-rooted in the sampled ecosystem, and its edaphic temperature envelop is broad, while *Z. muelleri* and *H. uninervis* rhizomes are relatively deep-rooted with smaller edaphic thermal envelopes (Campbell et al. 2018). This appears to corroborate the significant increase in leaf density after 6 d of exposure to ambient temperature (22.7°C) reported for *H. ovalis* by Collier and Waycott (2014).

We note, however, that the sharp decline in rhizome growth and number of shoot clusters with elevated temperature observed in *H. ovalis* in this present study indicates that *H. ovalis* was morphologically sensitive to persistent increased temperatures. While this species was found to be highly resistant to short-term warming events, for example, 5 d at 27°C (Bass and Falkenberg 2023), or 6 d with temperature increased to 35°C (Collier and Waycott 2014), our results suggest that *H. ovalis*' rhizome elongation would not perform well during longer-term warming events. Similarly, we postulate that carbohydrate reserves would quickly be depleted for this species (and potentially other species) under prolonged thermal stress events. *Halophila ovalis* is a small species characterized by narrow rhizomes, resulting in limited carbohydrate storage that potentially depletes more rapidly than in species with larger rhizome diameters, such as *Z. muelleri*.

We also noted that the development of shoot clusters (i.e., ramets that grow at the nodes) occurred only in *H. ovalis*, but not in the other species. This phenomenon represents a dispersal tactic in this particular species. Ramets can form at each node, which become new plants when the internodes die and ramets drift away, settle, and establish to grow in suitable areas (Campbell, pers. obs.). While the capacity for asexual reproduction through rhizome elongation or production of vegetative fragments/propagules is retained in most seagrass species in Australia (Sherman et al. 2018), we observed a higher potential for *H. ovalis* asexual propagation at ambient temperature, compared to the other species we examined. However, with increased water temperatures, the number of shoot clusters produced by *H. ovalis* declined sharply and was not present at temperatures slightly under 32°C. Our finding suggests that *H. ovalis*' asexual propagation and survival may be severely impacted by prolonged ocean warming events.

Halophila decipiens exhibited little response to increased water temperature (ranging between 23.1°C and 33.1°C). Instead, it did not perform well in mesocosm experimental settings using sprig transplantation, regardless of water

temperature. This was demonstrated by its reduced rhizome length over the experiment duration, significant loss of shoots, low probability of root development, and high probability of fatality in all temperature treatments. The impact of warming events on *H. decipiens* has been underreported, as reflected in the lack of published thermal-related studies on this seagrass species (Nguyen et al. 2021).

In Gladstone Harbour, *H. decipiens* rhizomes are present at very shallow depths (< 1 cm on average), with an extremely narrow edaphic thermal range (Campbell et al. 2018). Further research is needed to investigate the influence of increasing water temperature events on this seagrass species. This species appears to be highly vulnerable to thermal stress and disturbance, evidenced by a lack of ability to survive mesocosm experiments and transplantation efforts (e.g., Coles et al. 1990). We therefore reluctantly theorize that sprig transplantation might not be a suitable restoration method for this species. *Halophila decipiens* has rarely been a subject of seagrass transplantation in Australia (Tan et al. 2020) or globally; therefore, we assert the need for additional evidence to substantiate our theory.

Halophila spinulosa tended to be sensitive to increased water temperature, especially at 10°C above ambient temperature (i.e., approximately 33°C), demonstrated by its complete mortality. The sensitivity to elevated water temperature observed in *H. spinulosa* did not support our hypothesis that the pantropical seagrass species would be more resistant to elevated temperatures. A possible explanation may be that *H. spinulosa* has adapted to the local water temperature range, and 33°C exceeds the annual maximum sea surface temperature in Gladstone Harbour. Different water temperatures (i.e., 26°C and 30°C) over a 4-week period were found to have no discernible metabolic and physical impact on deep-water *H. spinulosa* under saturating light levels (Chartrand et al. 2018). However, to the best of our knowledge, there has not been any study on the response of *H. spinulosa*, deep-water or intertidal, to different warming conditions. *Halophila spinulosa* in the present study was collected at intertidal sites in Gladstone Harbour. We note that the species distribution in Gladstone Harbour is more subtidal than intertidal, with it being rarely exposed at low tide. Our study, therefore, provides valuable insights into the impacts of elevated water temperature on intertidal *H. spinulosa* plants.

It is anticipated that average atmospheric temperatures will increase by 3.2°C (5–95% range: 2.2–3.5°C) by the year 2100 (IPCC 2023), and an increase in average sea surface temperature by about 1–4°C in potential seagrass habitat (Marbà et al. 2022). This could see maximum monthly water temperature in Gladstone Harbour in particular, and the Great Barrier Reef, increase well over 33°C. The impact on the edaphic temperature ranges is unknown. Given the niche partitioning of intertidal seagrass species rhizomes based upon their edaphic thermal ranges (Campbell et al. 2018), further investigation of MHWs, thermal envelopes, and intertidal seagrasses is imperative.

With predictions indicating that warming oceans and MHWs will become more frequent, prolonged, and intense in the future (Frölicher et al. 2018; Oliver et al. 2019), our experiments are pertinent for forecasting the responses of the five seagrass species commonly occurring in Australia to a 1-month warming event. The ecological functions of these species are likely noninterchangeable with other seagrass species, and hence, intertidal ecosystems may be irrevocably altered (Carruthers et al. 2002; Klumpp and Kwak 2005; Tol et al. 2016). By understanding which species are affected by heat stress, we start to fill in knowledge gaps. This information enables us to develop restoration strategies that mitigate seagrass losses by taking into account a species' limits under predicted future-stress conditions.

Prolonged MHWs lasting more than 10 weeks, characterized by sea surface temperatures increasing by 2°C to 5°C above average, have been documented (Kajtar et al. 2021; Oliver et al. 2021; Strydom et al. 2020). Longer-term experiments focusing on multiple morphological, physiological, and survival metrics and spanning several seasons, while accounting for inundation and temperature patterns, are needed to truly understand the influence of thermal pressures on intertidal seagrasses.

Author Contributions

Marnie L. Campbell conceived the ideas, secured funding, designed the methodology, did field and mesocosm work, conducted initial data analysis, provided critical assessment of data outcomes, and contributed to writing, reviewing, and editing the manuscript. Chi T. U. Le performed the formal data analysis, data interpretation, and visualization/data presentation, wrote the initial draft of the manuscript, and contributed to reviewing and editing the manuscript.

Acknowledgments

We extend our heartfelt thanks to the volunteers, postdoctoral fellows, graduate students, and summer interns who assisted in collecting field data and monitoring the mesocosms. We also sincerely thank the handling editors and anonymous reviewers for their constructive and insightful feedback, which has greatly improved the quality and clarity of this manuscript. This research was funded by a Queensland Government Smart Futures mid-career Fellowship (Marnie L. Campbell). The work was conducted under the Great Barrier Reef Marine Park and the Queensland Government permit (permit no. 2013CA0845). No animal or human ethics approvals were required for this research. The data and R code used in this study are publicly available at https://doi.org/10.6084/m9.figshare.28169399 [Figshare]. Microsoft Co-pilot (AI) was used to correct grammatical and syntax errors. The draft manuscript was written and edited by the authors. Co-pilot was then used to ensure that grammar and syntax errors were fixed prior to submission. Open access publishing

facilitated by Edith Cowan University, as part of the Wiley - Edith Cowan University agreement via the Council of Australian University Librarians.

Conflicts of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Submitted 09 January 2025
Revised 26 May 2025
Accepted 20 July 2025