



Marine heatwaves disrupt germination and seedling physiology in *Zostera marina*

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ABSTRACT

Marine heatwaves (MHWs) are intensifying with climate change, posing a growing threat to the resilience of coastal marine ecosystems, such as seagrasses. While MHW impacts on adult seagrasses are increasingly studied, their effects on early developmental stages remain unexplored. This represents a critical knowledge gap, as recruitment success is essential for long-term population persistence, particularly in degraded or restored meadows.

Here, we exposed *Zostera marina* seeds to three realistic MHW categories (moderate, strong, and severe) during the natural spring germination period. We assessed how thermal stress influences germination dynamics, seedling morphology, and physiological performance.

Germination exhibited a non-linear response to MHW intensity. Moderate MHW (Category I) significantly delayed germination and reduced emergence, while strong MHW (Category II) unexpectedly enhanced germination but induced a shoot–root growth imbalance, with greater shoot than root development. Severe MHW (Category III) suppressed pigment concentrations and electron transport rates, suggesting reduced photo-protection and probable PSII damage.

These carry-over effects reveal a narrow thermal window for successful seedling development, where temperatures only slightly above the baseline affect germination, early growth stages and pigment composition, making early life stages a physiological bottleneck under climate extremes. By identifying critical thresholds and associated developmental trade-offs, our study advances understanding of how early-stage sensitivity can constrain population recovery and facilitates integration of seed-based responses into predictive frameworks of seagrass resilience and coastal habitat stability in a warming ocean.

1. Introduction

Climate change is driving an upsurge in extreme climate events (ECEs) (Cinto Mejía and Wetzel, 2023; Diffenbaugh et al., 2017; Turner et al., 2020), which increasingly affect both terrestrial and marine ecosystems (Handmer et al., 2012; Ummenhofer and Meehl, 2017).

ECEs such as marine heatwaves (MHWs; periods of anomalously elevated sea surface temperatures relative to long-term climatological baselines; Hobday et al., 2016) have increased in frequency, intensity, and duration, with near-annual recurrence (Garrabou et al., 2022; Marcos et al., 2025; Oliver et al., 2021; Pastor and Khodayar, 2023). MHWs severely impact coastal marine ecosystems such as corals,

macroalgae, kelp, and seagrass meadows, altering associated biodiversity, ecological function, and ecosystem service provision (Holbrook et al., 2019; Smale et al., 2019). In seagrasses, MHWs have driven important changes in cover, abundance, and carbon stocks (Marbà et al., 2022; Arias-Ortiz et al., 2018; Smith et al., 2021); however, their effects on seed germination and seedling physiology remain largely unexplored. Understanding how thermal stress affects recruitment success underpins long-term population stability, hence it is crucial for anticipating population responses in a warming ocean.

Temperate seagrass meadows, such as those formed by *Zostera marina*, play an important role in coastal ecosystems (Boström et al., 2014; McDevitt-Irwin et al., 2016). They support high biodiversity,

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contribute to carbon sequestration, and buffer shorelines against erosion (Röhr et al., 2018; Unsworth and Cullen-Unsworth, 2014). However, many seagrass species already grow near their upper thermal limits (Kim et al., 2020). While seagrasses show physiological plasticity, they remain vulnerable to abrupt or prolonged periods of warm ocean temperature anomalies (Deguette et al., 2022; Marbà et al., 2022; Rinaldi et al., 2023), particularly when compounded by other environmental pressures such as nutrient loading, turbidity, and coastal development (Babcock et al., 2019; Guild et al., 2025; Smith et al., 2021).

Emerging evidence suggests that MHWs are not only intensifying but are also shifting seasonally, with increasing occurrence during the spring growing season (Gregory et al., 2024; Li and Donner, 2022; Marcos et al., 2025). This shift is particularly concerning for seagrass populations relying on seed-based recruitment processes, as it coincides with germination and early seedling development, stages that are highly sensitive to temperature stress (Nguyen et al., 2021a; Orsenigo et al., 2015; Reusch, 2014). Unlike established plants, early life stages have limited capacity to buffer against physiological disruptions, and even brief heat stress can impair cell function (Rinaldi et al., 2023), alter hormonal signaling (Marín-Guirao et al., 2019; Nguyen et al., 2021b; Pieraccini et al., 2025a), reduce photosynthetic efficiency (Gao et al., 2019), and reallocate energy towards stress responses at the expense of growth and developmental processes (Hansen et al., 2022; Marín-Guirao et al., 2016; Sawall et al., 2021). While recent studies on different seagrass species have shown that thermal stress can increase seedling mortality and limit growth (Deguette et al., 2022; Pazzaglia et al., 2022), the specific impacts of short-term, early-season MHWs on germination dynamics and seedling physiology have not been investigated. This represents a critical knowledge gap, as successful seedling establishment underpins population persistence, particularly in degraded or restored meadows.

In this study, we simulate realistic MHW intensities, based on long-term temperature data, in a controlled experiment that matches the natural spring germination period at our field collection site, of the most widespread seagrass species, *Z. marina*. We assess whether exposure to three MHW intensities disrupts early development by delaying germination, altering seedling morphology and photosynthetic performance, or fundamentally compromises seed viability. By measuring germination dynamics, seedling growth, pigment composition, and chlorophyll fluorescence, we identify the physiological thresholds beyond which early developmental success is impaired.

2. Material & methods

2.1. Seed collection and storage

Approximately 200 reproductive shoots bearing seeds were collected from a single intertidal *Zostera marina* meadow at Hamburger hallig, Germany (54°35'49.6"N, 8°48'43.8"E) during low tide in early September 2023, under permit from the Landesbetrieb für Küstenschutz, Nationalpark und Meeresschutz Schleswig-Holstein. Shoots were transported to Ghent University (Belgium) at a controlled temperature (10 ± 1 °C) and stored under near-natural conditions, based on *in-situ* salinity and temperature data from the Federal Maritime and Hydrographic Agency (BSH, 2024). Storage conditions included full darkness and continuous seawater agitation to mimic natural hydrodynamic conditions and facilitate seed release from the reproductive shoots.

After 45 days, seeds were manually collected, rinsed in sterile seawater, and transferred to cold stratification to simulate winter dormancy. Stratification was carried out at 4 ± 0.5 °C in darkness for 130 days. The *Z. marina* ecotype used in our experiments is known to exhibit seed dormancy. Therefore, stratification was used to mimic natural winter conditions required to break the dormancy (Pieraccini et al., 2025a). The seawater solution was aerated and supplemented with 0.2 mg L⁻¹ copper sulfate (CuSO₄) to suppress infection by *Phytophthora* and *Halophytophthora* spp. (Govers et al., 2017). Throughout

cold storage, seeds were maintained in sterile seawater (30 PSU) to prevent anoxia, fungal contamination, and premature germination.

2.2. Baseline and marine heatwave calculations

Daily sea surface temperature (SST) data for the German Wadden Sea over the past 30 years (1993–2023) were obtained from the Federal Maritime and Hydrographic Agency (BSH, 2024; sea-surface temperature analysis, Wadden Sea; data provided on January 19, 2024: BSH SST Portal) and NOAA's Optimum Interpolation Sea Surface Temperature portals (NOAA OISST).

We used 30 years of daily SST observations (1993–2023), covering the region between 54.5°N and 55.0°N latitude, and 8.5°E to 9.0°E longitude, corresponding to the seed collection site.

To establish the SST baseline, we extracted SST values from this time series for the spring germination period (1 March to 30 April), which aligns with natural *Z. marina* germination phenology in the Wadden Sea (Pieraccini et al., 2025a). The baseline temperature was defined as the 30-year climatological mean for this window, calculated from daily SSTs across all years. This yielded a spring baseline of 10 °C, consistent with *in situ* temperature records from the BSH Wadden Sea platform.

Marine heatwave (MHW) events were detected using the R package *heatwaveR* (Schlegel and Smit, 2018), following the definition from Hobday et al. (2016) and classification scheme from Hobday et al. (2018) (Fig. S1): a MHW is defined as a period of at least five consecutive days with SST exceeding the 90th percentile of the historical climatology for that day of year, based on a 30-year baseline.

The MHW categories used in this experiment correspond to the classification scheme from Hobday et al. (2018), which defines Category I (moderate) as SST anomalies exceeding the climatological threshold, Category II (strong) as two times the threshold exceedance, and Category III (severe) as three times.

Based on observed SST anomalies during historical spring MHWs in the Wadden Sea, we defined the following experimental treatments relative to the 10 °C baseline:

- Category I (moderate): +1.8 °C
- Category II (strong): +3.0 °C
- Category III (severe): +5.6 °C

These values reflect the mean maximum anomaly observed during the five most intense spring MHWs in the BSH dataset over the 30-year period. While the seeds were collected from an intertidal meadow, the experimental design simplified *in situ* variability by isolating the temperature variable under constant salinity and light conditions, allowing controlled assessment of thermal stress effects.

2.3. Experimental design and conditions

During the pre-experimental phase, seeds were gradually acclimated to experimental conditions by increasing the temperature to 10 ± 0.5 °C over a two-week period (~0.43 °C increase/day). After this acclimation period, 10 °C represented the control temperature. To minimize thermally or light-induced germination cues, all handling was conducted at the control temperature and under low-light conditions (<10 μmol photons m⁻² s⁻¹).

Based on the temperature anomalies described above, we implemented four experimental temperature treatments simulating marine heatwaves (MHWs): (i) a control treatment maintained at 10 °C throughout; (ii) a moderate MHW treatment (Category I) at 11.8 °C; (iii) a strong MHW treatment (Category II) at 13.0 °C; and (iv) a severe MHW treatment (Category III) at 15.6 °C. For all treatments except the control, seeds were initially held at the 10 °C baseline during an acclimation period. Temperature was then increased over 7 days to the target MHW, maintained for 7 days, decreased back to 10 °C over 7 days, and subsequently kept at the baseline temperature for an additional 7 days

(Fig. S1). A total of 1152 seeds were hand-sorted, retaining only non-germinated seeds with intact seed coats and no visible damage. Seeds were randomly assigned to one of four MHW treatments, including the control, with 288 seeds per treatment (96 seeds \times 3 replicates \times 4 treatments). To account for potential well-plate effects, seeds were distributed across three 96-well plates per treatment. Each well received one seed to ensure spatial consistency and replication.

Prior to placement, seeds were surface-sterilized under axenic conditions in a laminar flow hood. The sterilization protocol included rinsing in sterile seawater (SSW) to remove residual CuSO_4 , immersion in 70 % ethanol for 5 min, and three final rinses in SSW.

Four TECO TK-2000 H cooler-heater units maintained water temperatures at 10 ± 0.5 °C until the onset of the simulated marine heatwaves. Seeds were exposed to LED lights (T8 2FT, BL-D60A, Wolezek) emitting a full visible spectrum (380–700 nm) at an irradiance of ~ 146 $\mu\text{mol m}^{-2} \text{s}^{-1}$ under a fixed 12:12 h light:dark photoperiod. This photoperiod was selected to ensure that temperature remained the primary experimental driver; at the reference field site (Hamburger Hallig), day length increases from ~ 11.3 h to 14.2 h during March.

2.4. Germination monitoring and data collection

Germination was monitored daily from the start of the experiment (day 0, at 10 °C baseline after the acclimation period) and defined as cotyledon emergence extending beyond seed coat rupture, based on criteria from previous studies (Brenchley and Probert, 1998; Pieraccini et al., 2025b; Sousa et al., 2017). Each well plate was inspected daily, and germinated seeds were immediately removed from the heatwave treatment and transferred to a separate growth experiment. Seeds showing signs of contamination or mold were discarded under sterile conditions.

Immediately after germination, germinated seeds were transferred to sterile 6-well plates, each containing 9 mL of SSW. Each well contained one seedling. Post-germination development was monitored under identical light and temperature conditions (10 ± 0.5 °C, $146 \mu\text{mol m}^{-2} \text{s}^{-1}$, 12:12 h light:dark cycle) for a 45-day period.

2.5. Seedling growth, photosynthetic activity, and pigment analysis

Seedling development was monitored using digital photogrammetry. High-resolution images were captured with a Canon 600D camera mounted on a Leica MZ16 stereomicroscope under uniform lighting, with seedlings placed against a black background. A 1 mm graticule (No. SC1539, PYSER-SGI) was included for calibration in each imaging session. Cotyledon, leaf, and root lengths were measured using ImageJ (NIH), and seedlings were randomly repositioned between measurements to minimize positional bias. Total seedling elongation was calculated as the sum of cotyledon, leaf, and root lengths.

After 45 days, leaf tissue was harvested from the well plates, centrifuged at $2000 \times g$ for 10 min at 12 °C, and stored at -20 °C. Pigments were extracted according to Van Heukelem and Thomas (2001), with an added disruption step: frozen tissue was bead-beaten for 30 s using 0.25–0.5 mm beads (Carl Roth), followed by sonication. Nine pigments were quantified via high-performance liquid chromatography (HPLC), including chlorophylls (a, b) and carotenoids (violaxanthin, antheraxanthin, zeaxanthin, lutein, β -carotene and neoxanthin). Pigment concentrations were expressed as μg pigment per mg dry weight of leaf tissue. All HPLC analyses were performed at the Marine Biology Laboratory, Ghent University (Belgium).

2.6. Seed viability

Prior to experimentation, all seeds were visually inspected and those that were unripe, already germinated, broken, or buoyant in natural seawater were discarded (Xu et al., 2019). After 45 days from the start of the germination experiment, all seeds that had not germinated were

subjected to viability testing using a 2,3,5-triphenyl-tetrazolium chloride (TTC) assay (Lakon, 1949). Each seed coat was punctured with a fine syringe needle and immersed in 100 μL of 1 % TTC solution for 48 h in the dark. Stained seeds were considered viable, and viability was expressed as the percentage of viable seeds per marine heatwave treatment and replicate (Table S1). Seed germination (%) was then calculated as the proportion of germinated seeds relative to the total number of viable seeds. This approach ensures that differences among MHW treatments reflect variation in germination performance rather than underlying variation in seed viability. By quantifying viability post-experiment, germination and growth analyses could be interpreted relative to the pool of truly viable seeds, reducing potential bias from latent mortality or handling damage.

2.7. Statistical analyses

All analyses were performed in the R software environment (v4.0.2; R Core Team, 2020). Final seed germination (%) was compared among treatments using a penalized logistic regression (Firth correction (Firth, 1993), LogistF package). Germination timing was evaluated by fitting a Cox proportional-hazards model (coxph, survival package), with likelihood-ratio tests for treatment effects and hazard ratios (HR) reported; proportional-hazards assumptions were checked via cox.zph. Seedling growth (cotyledon, leaf, root elongation) was analyzed using linear mixed-effects models (package lme4), with fixed effects of heatwave Category, time (days) and their interaction, and a random intercept per seedling ID. Fixed-effect significance was assessed by Type III ANOVA (package car) and pairwise contrasts using the emmeans package (Tukey adjustment). Pigment concentrations were compared across treatments by one-way ANOVA (lm package). Prior to analysis, homogeneity of variance was tested using Levene's test (car package). Where variance heterogeneity was detected (e.g., chlorophyll-a), log-transformations were applied. Post-hoc comparisons for pigments were performed using Dunnett's test to compare each treatment against the control (package emmeans). We used Tukey's HSD for seedling growth and Dunnett's test for pigment analyses based on different hypotheses: Tukey's test allows pairwise comparison across all groups (appropriate for multi-treatment growth response), whereas Dunnett's test focuses on comparisons against a common control (appropriate for pigment response relative to baseline conditions).

Where statistical assumptions were marginally violated (e.g., normality or homoscedasticity at the 0.5 % threshold), results were interpreted as non-significant trends.

3. Results

3.1. Marine heatwaves alter germination success and timing in *Zostera marina*

Germination success in *Zostera marina* varied non-linearly across marine heatwave (MHW) categories (Fig. 1). Under control (no MHW) conditions, seeds achieved 5.6 % germination (95 % CI: 0.86 %–4.26 %). Category I MHW (+1.8 °C, moderate – 11.8 °C) reduced final germination to 1.7 % (95 % CI: 0.15 %–2.37 %), whereas seeds exposed to Category II MHW (+3.0 °C, strong – 13 °C) boosted final germination to 10.1 % (95 % CI: 1.91 %–6.30 %). Under Category III MHW (+5.6 °C, severe – 15.6 °C), germination fell to 4.6 % (95 % CI: 0.66 %–3.83 %).

Penalized logistic regression confirmed a significant overall effect of MHW on germination outcome (likelihood-ratio $\chi^2_3 = 8.72$, $p = 0.033$). Relative to control, Category I seeds had significantly lower odds of germination (log-odds = -1.13 ± 0.52 ; $z = -2.16$, $p = 0.031$; OR = 0.32), while Category II exhibited significantly higher odds (log-odds = 0.63 ± 0.29 ; $z = 2.01$, $p = 0.044$; OR = 1.88). Category III did not differ statistically from control ($p = 0.72$).

Over time (Fig. 2) control seeds showed steady germination over 45 days. In contrast, seeds exposed to Category I MHW showed a marked

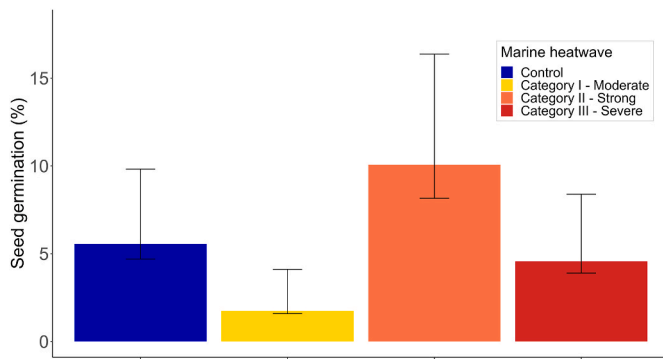


Fig. 1. Seed germination (%) ± binomial confidence interval in *Zostera marina* under control conditions (10 °C) and three simulated marine heatwave categories: Category I (+1.8 °C = moderate heatwave), Category II (+3.0 °C = strong heatwave), and Category III (+5.6 °C = severe heatwave). Colors represent the marine heatwave category. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

delay in germination, while categories II and III followed intermediate trajectories. A Cox proportional hazards model confirmed a significant MHW effect on time to germination (LRT $\chi^2_3 = 10.43$, $p = 0.02$; concordance = 0.647). Compared to control, seeds exposed to Category I MHW were over seven times less likely to germinate at any time point (HR = 0.13; $p = 0.0018$). Categories II (HR = 0.77; $p = 0.52$) and III (HR = 1.46; $p = 0.42$) did not differ significantly from control.

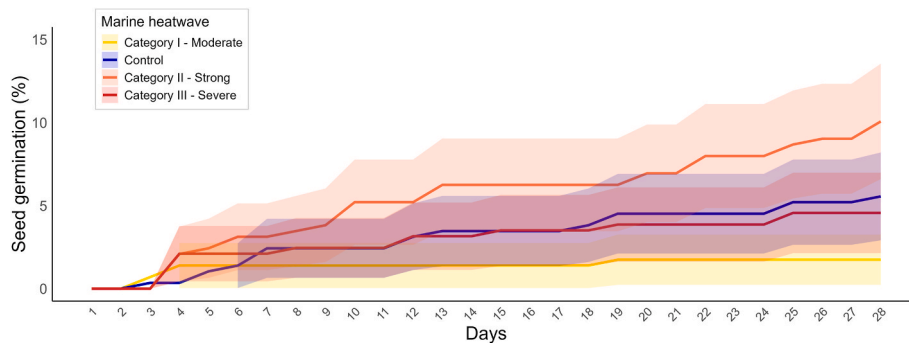


Fig. 2. Cumulative seed germination (%) over time (±95 % confidence intervals) for *Zostera marina* under control (10 °C) and three marine heatwave treatments: moderate (+1.8 °C), strong (+3.0 °C), and severe (+5.6 °C). Lines represent the proportion of seeds germinated across the 40-day experimental period. The +1.8 °C treatment showed delayed and reduced germination, while the +3.0 °C treatment closely matched the control, suggesting a potential hormetic response to intermediate heat exposure. The +5.6 °C treatment exhibited intermediate dynamics with variable germination timing.

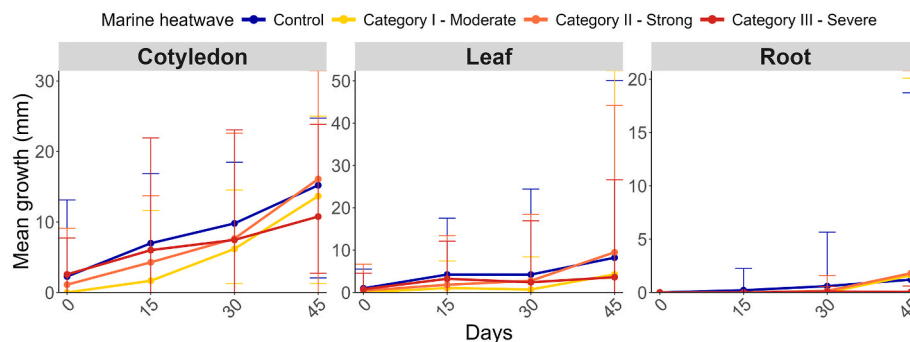


Fig. 3. Ontogenetic development (mm) ± 95 % CI across four monitoring points (after 0, 15, 30, and 45 days) of seedlings grown from seeds exposed to control conditions (10 °C) and three simulated marine heatwave scenarios: Category I (+1.8 °C = moderate heatwave), Category II (+3.0 °C = strong heatwave), and Category III (+5.6 °C = severe heatwave). Colors represent temperature treatments. Each facet shows a plant part; colors denote the marine heatwave category. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.2. Marine heatwaves drive divergent shoot and root development in early seedlings

Organ-specific growth trajectories also varied among MHW categories (Fig. 3). Cotyledon elongation increased across all treatments, peaking under Category II. Leaf growth was generally stimulated by MHW exposure but showed greater variability and less consistency after day 15. Root growth remained minimal under all categories, with categories I and III showing near-zero elongation.

Linear mixed-effects models indicated that total seedling elongation increased significantly under Category I and Category II MHWs, with model estimates of 3.82 (Category I) and 4.58 (Category II) (both $p < 0.001$). Category III also exhibited a positive effect, albeit slightly lower, with an estimate of 3.23 ($p < 0.001$). When analyzed by organ, all three MHWs significantly suppressed root elongation (Category I: -3.18 , $p = 0.0018$; Category II: -3.85 , $p = 0.005$; Category III: -3.21 , $p < 0.005$), indicating that heat stress induces divergent shoot and root growth responses.

Pigment analyses showed no statistically significant differences across MHW categories (Fig. 4). However, Category II seedlings exhibited nearly double the average chlorophyll-a content compared to control (Control: $32.7 \pm 9.6 \mu\text{g}^{-1}$; Category II: $64.9 \pm 20.2 \mu\text{g}^{-1}$), although the difference was not statistically significant ($t = 0.16$, $p = 0.87$). Similar, non-significant trends were observed for β -carotene ($4.1 \pm 3.0 \mu\text{g}^{-1}$; $t = 1.75$, $p = 0.09$) and violaxanthin ($5.2 \pm 4.3 \mu\text{g}^{-1}$; $t = 0.65$, $p = 0.52$), both of which appeared elevated under Category II. This category also showed the greatest variability in pigment concentrations, as reflected in the large standard error.

In contrast, Category III seedlings exhibited numerically lower mean

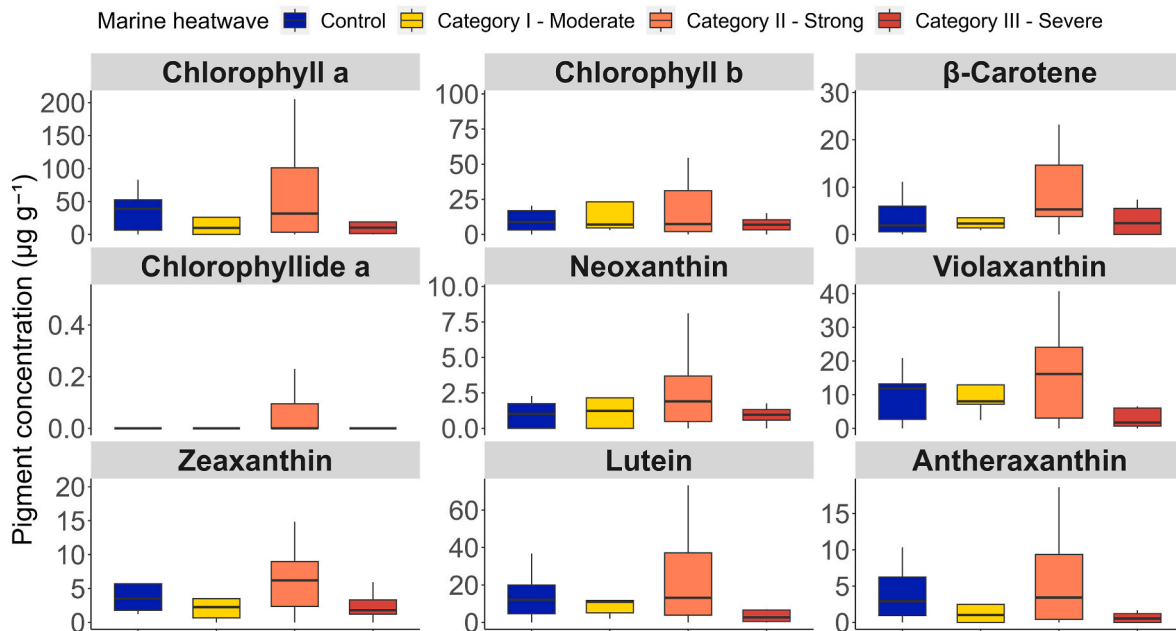


Fig. 4. Pigment concentrations ($\mu\text{g g}^{-1} \pm \text{SE}$) for nine pigments in *Zostera marina* seedlings grown from seeds exposed to control conditions (10°C) and three simulated marine heatwave categories: Category I ($+1.8^\circ\text{C}$ = moderate heatwave), Category II ($+3.0^\circ\text{C}$ = strong heatwave), and Category III ($+5.6^\circ\text{C}$ = severe heatwave). Each facet shows one pigment; colors denote the marine heatwave category. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

values for most pigments (e.g., Chl-a: $16.1 \pm 7.96 \mu\text{g g}^{-1}$, $p = 0.35$; lutein: $5.44 \pm 2.80 \mu\text{g g}^{-1}$, $p = 0.13$). Although none of the Dunnett-adjusted pairwise comparisons reached statistical significance (all $p > 0.09$), these patterns suggest differential pigment responses across MHW categories. While the observed trends are non-significant, they may reflect underlying physiological differences.

4. Discussion

4.1. Early thermal stress bottlenecks recruitment

Our study reveals a non-linear germination response of *Zostera marina* seeds to short-term marine heatwaves (MHWs) experienced during the spring germination period. Exposure to moderate MHW (Category I) resulted in a more than seven-fold reduction in the likelihood of seedling emergence and significantly delayed germination onset, potentially inducing secondary seed dormancy (Finch-Savage and Leubner-Metzger, 2006). By contrast, strong (Category II) MHW significantly enhanced germination, while severe (Category III) MHW had less consistent effects on final germination success. However, both strong and severe MHW categories had greater impact on post-germination seedling development, through shoot and root growth disruption and physiological stress responses. These findings align with studies suggesting that the timing and intensity of thermal events may have greater ecological consequences than cumulative heat exposure, as even short-lived warming can delay metabolic activation and induce seed quiescence (Smith et al., 2023; Teskey et al., 2015; Yao et al., 2024). Similarly, in terrestrial plants, brief and sub-lethal heat exposure has been shown to delay or suppress germination by altering hormonal signaling and energy metabolism (Li et al., 2021; Penfield and MacGregor, 2017).

As our study focused on an intertidal annual ecotype of *Z. marina* that relies on yearly recruitment for persistence, it is possible that this population has evolved some resilience to short-term thermal shocks, given its repeated exposure to strong diel and tidal temperature fluctuations. At the same time, our results raise the question of whether subtidal meadows, which experience more thermally stable conditions, may be

more sensitive to comparable MHW regimes. In both cases, physiological disruptions at the seed and seedling stage can scale up to population-level consequences by reducing recruitment and compromising meadow recovery in the face of recurrent MHWs.

In many plant species, photoperiod is a key environmental cue regulating dormancy cycling and the timing of germination (Adams and Langton, 2005; Finch-Savage and Leubner-Metzger, 2006; Jackson, 2009). By contrast, the role of photoperiod in *Z. marina* seed germination remains largely unexplored, with only limited experimental evidence available (Phillips et al., 1983; Pieraccini et al., 2025b). In this study, a fixed 12:12 h light:dark photoperiod was chosen to isolate temperature as the primary driver of variation in germination and seedling performance. Under natural conditions, however, day length increases during the spring germination window (e.g. at our reference site, Hamburger hallig, Wadden Sea), and it is plausible that this seasonal increase in photoperiod interacts with MHWs by promoting germination and metabolic activation in a larger fraction of seeds. Thus, interactions between gradual seasonal increases in photoperiod and sudden spring MHWs could exacerbate impacts on recruitment, particularly when warming events coincide with photoperiod-driven germination.

The non-linear pattern observed in this study, where moderate MHWs strongly suppressed germination, strong MHWs enhanced it, and severe MHWs resulted in germination levels similar to the control, contrasts with many terrestrial and marine studies in which increasing thermal intensity reduces both germination and early growth (e.g. Marín-Guirao et al., 2016; Penfield and MacGregor, 2017; Li et al., 2021). A possible explanation is that *Z. marina* seedlings can briefly buffer thermal stress using embryo-derived energy reserves, allowing short-term increases in shoot elongation and maintenance of pigment pools even under warming. The positive germination response under strong MHWs may also reflect a sublethal warming threshold specific to this intertidal ecotype, which naturally experiences diel and tidal temperature fluctuations. Nevertheless, despite this apparent plasticity, severe MHWs impaired photosynthetic pigments, shoot and root development, and our experiment did not track seedling performance after 45 days of the MHW treatments. Consequently, it remains unclear

whether these short-term responses translate into long-term survival, stress memory, or enhanced tolerance. Future studies should therefore evaluate post-MHW growth, survival, and reproduction to determine whether strong MHWs act as priming stimuli or instead impose latent physiological costs.

From a population perspective, MHW-induced reductions and delays in germination and seedling emergence can directly constrain annual seed recruitment. Decreased germination probability, postponed emergence, and suppressed root development during MHWs all decrease the proportion of seeds that successfully transition into established seedlings (Alvarez et al., 2023; Orsenigo et al., 2015). Such early-life-stage bottlenecks can lead to smaller, more fragmented meadows with reduced capacity to recover from disturbance (Hyndes et al., 2016; Kendrick et al., 2019; Lefcheck et al., 2016). In annual, intertidal *Z. marina* meadows, such as the system examined in this study, populations rely entirely on yearly seed recruitment. Although these meadows may exhibit greater thermal plasticity, they may also be exposed to compounded stress from both marine and atmospheric heatwaves, potentially amplifying early-stage vulnerability. In perennial *Z. marina* meadows, clonal propagation underpins population persistence, with seed recruitment remaining important for maintaining genetic diversity and facilitating recovery after severe disturbance.

Over decadal scales, repeated exposure to springtime MHWs could therefore shift both annual and perennial populations from self-sustaining to recruitment-limited states, promoting smaller and more fragmented meadows with reduced capacity to absorb and recover from additional stressors such as storms, herbivory or eutrophication, whereas in populations with sufficient standing variation it may instead select for a reduced subset of resilient genotypes (Hyndes et al., 2016; Kendrick et al., 2019; Lefcheck et al., 2016).

Since seagrass beds form the structural foundation of coastal habitats, early-life bottlenecks that reduce seedling success may also result in lower habitat complexity and undermine associated food webs. Additionally, ENSO-driven events, such as elevated sea levels or altered tidal regimes occurring alongside MHWs, may compound physiological stress (Lin et al., 2018; Thom et al., 2014) and accelerate poleward shift of *Z. marina* populations (Wilson and Lotze, 2019; Xu et al., 2022). Finally, MHWs may also threaten seed bank size and quality, as elevated temperatures during flowering can alter seed maturation, disrupt dormancy, and reduce overall viability (Aoki et al., 2020; Strydom et al., 2020), with long-term demographic consequences.

4.2. Organ-specific and physiological decoupling

Thermal stress during germination also induced organ-specific responses in *Z. marina* seedlings, disrupting above- and below-ground growth and affecting photo-physiological regulation. Across MHW categories, root elongation was consistently suppressed relative to the control temperature, whereas cotyledon and leaf length increased, especially under strong marine heatwaves (Category II). Because seedlings were grown in a liquid medium rather than a true sediment matrix, absolute root elongation likely underestimates root development in the field; however, all treatments, including the control, experienced the same conditions, so these relative differences still indicate that roots are particularly sensitive to MHWs. This pattern suggests a potential plastic reallocation of resources toward leaf formation and light capture, potentially at the expense of root functions such as anchorage, oxygen release and metabolite exudation, that help modulate rhizosphere redox conditions and microbial activity (Austen et al., 2019; Mishra et al., 2021; Tiwari et al., 2022), although nutrient uptake can be partly compensated via leaf nutrient acquisition (Moir et al., 2024; Plaisted et al., 2022). Persistent reductions in root functioning may increase the risk of seedling dislodgement in dynamic nearshore environments heighten vulnerability during storms or tidal fluctuations. Comparable shoot and root disruption have been reported in heat-stressed seedlings of terrestrial species such as *Oryza sativa* and *Leymus chinensis*, where

enhanced leaf growth coincides with reduced below-ground investment (Li et al., 2018; Suriyasak et al., 2020; Zafar et al., 2018).

At the physiological level, Category II MHWs were associated with higher concentrations of chlorophyll *a* and several carotenoids (including β -carotene, violaxanthin, zeaxanthin, and antheraxanthin) relative to the control. Rather than indicating the absence of stress, this pattern suggests a short-term acclimatory response in which enhanced pigment pools supports both photosynthetic capacity and photoprotection (Li et al., 2022; Simkin et al., 2022). Comparable responses have been reported during early heat exposure in adult *Z. marina* and other seagrass species (Tutar et al., 2017; York et al., 2013), as well as in terrestrial plants (Sharma et al., 2020; Zahra et al., 2023), where photosynthetic activity (e.g. ETR, Y(II)) and pigments often increase at intermediate warming before declining at higher temperatures (Evans, 1987; Haldimann, 1999; Sawall et al., 2021; Venema et al., 1999). At the molecular level, MHWs induce transcriptomic and antioxidant responses in *Z. marina*, modulating the expression of photosynthesis- and stress-related genes (Bergmann et al., 2010; Jueterbock et al., 2016; Tutar et al., 2017). In freshwater macrophytes, long and intense heatwaves can accelerate growth while reducing maximum quantum efficiency, suggesting that growth stimulation and stress-compensating photophysiological mechanisms often coexist under warming (Aker et al., 2025). We therefore interpret the Category II response as a sub-lethal warming level at which embryo-derived reserves allow seedlings to transiently up-regulate pigments and maintain photosynthetic function, a compensatory response to short-term heat exposure.

By contrast, seedlings emerging from seeds exposed to severe MHWs (Category III) exhibited lower photosynthetic pigment concentrations as compared to controls, suggesting reduced photoprotection and potential PSII damage (Cousins et al., 2002; Hawes et al., 2003). Similar thermal tipping points, characterized by abrupt declines in pigments and chlorophyll, have been reported for adult seagrasses including *Posidonia oceanica* and *Z. marina*, as well as in crop seedling (Guerrero-Meseguer et al., 2017; Marín-Guirao et al., 2016; Wahid et al., 2007; Zhou et al., 2017). In our study, the most extreme MHW treatment (Category III) reached 15.6 °C (+5.6 °C relative to the 10 °C spring baseline) and induced measurable developmental and physiological shifts in *Z. marina* seedlings, even though the stress was applied only at the seed stage, highlighting the thermal sensitivity of early life stages. Similar patterns have been observed in crop species such as tomato and rice, where high-temperature stress reduces photoprotective capacity and compromises early growth and establishment (Wahid et al., 2007; Zhou et al., 2017). In both marine and terrestrial species, the inability to maintain photoprotection under acute warming may limit recruitment success during critical developmental windows.

To our knowledge, no previous studies have examined pigment accumulation in early-stage seagrass seedlings with MHW stress applied at the seed stage and tracked for several weeks after germination (45 days). While photophysiological responses are better documented in adult *Z. marina* and other seagrasses (e.g., Sawall et al., 2021; Tutar et al., 2017), the capacity of early-stage individuals to initiate or sustain such responses under MHW conditions remains largely unexplored. This study provides the first experimental evidence characterizing photoprotective plasticity during seedling establishment in *Z. marina*.

Pigment estimates exhibited substantial within-treatment variability, likely reflecting both biological heterogeneity and technical constraints associated with studies on very small seedlings. Early-stage *Z. marina* seedlings have extremely low biomass and developing leaf tissues, limiting pigment yield and reducing the signal-to-noise ratio of both HPLC and PAM measurements. Consequently, treatment-level differences in pigments should be interpreted as indicative trends rather than definitive shifts in photoprotective capacity. Nonetheless, these data provide a valuable quantitative baseline for early-stage photophysiological responses and help constrain the plausible magnitude and direction of MHW effects.

An additional nuance is that seedlings germinating earlier in the

experiment experienced shorter MHW exposure before transfer to common post-germination conditions, whereas late-germinating individuals remained longer under the simulated MHWs. Although all seedlings were monitored over the same post-germination period, this variation in thermal history may have contributed to the observed heterogeneity in pigment and ETR responses and should be disentangled more explicitly in future work. Overall, our results delineate a narrow thermal window in which early-stage *Z. marina* can respond with compensatory mechanisms, beyond which damage increases rapidly. Moderate MHWs can prime pigment accumulation to sustain growth (Buapet and Björk, 2016), whereas severe MHWs overwhelm these defense mechanisms. Thermal tolerance thresholds are influenced by intrinsic factors such as genotype, local adaptation, and prior thermal exposure, which may affect stress memory and phenotypic plasticity (Pazzaglia et al., 2021b; Wahid, 2007). Meta-analyses confirm that early life stages generally have narrower thermal safety margins than adults (Donohue et al., 2010; Sunday et al., 2014). Disentangling germination timing from thermal exposure will therefore be important for future studies aiming to resolve the mechanistic basis of early seedling photo-physiology under MHWs.

4.3. Ontogenetic constraints on climate resilience

Our results uncover an important carry-over effect of heat stress from the seed stage into later growth stages, indicating an ontogenetic bottleneck in *Z. marina*'s climate resilience.

While adult mature plants possess a suite of mechanisms to withstand short-term heat stress with minimal physiological disruption (Kim et al., 2020; Lefcheck et al., 2017), early-stage seedlings showed a significant performance decline even at moderate MHW stress. Several factors likely explain this vulnerability. First, early-stage seedlings rely almost entirely on embryo reserves, which may be insufficient to support the energy-intensive repair and protection pathways activated by heat stress (Kigel, 2017; Rogo et al., 2023). Second, the protective mechanisms of seedlings, such as heat-shock proteins, antioxidant enzymes, and pigment-based protection, are both scarcer and slower to mobilize than in adult plants (Almeselmani et al., 2006; Pooja and Munjal, 2019; Yurina, 2023). Finally, newly formed tissues often lack the full regulatory networks necessary for a quick acclimation, a pattern also observed in crops, where seedlings show higher heat sensitivity than mature leaves (Jha et al., 2014; Jin et al., 2024; Ohama et al., 2017; Yao et al., 2011).

Although stage-dependent thermal thresholds have been better documented in land plants (e.g. Donohue et al., 2010; Sunday et al., 2014), they remain underexplored in seagrasses. Yet thermal stress during these early life stages, such as germination and seedling establishment, can have latent effects that undermine population resilience. This may be particularly relevant for intertidal ecotypes, which can experience combined exposure to marine and atmospheric thermal extremes during tidal cycles. These effects may not be immediately visible but can reduce the pool of recruits, only becoming apparent years later when meadow density declines. Additionally, real-world MHWs rarely occur in isolation, and their impacts likely interact synergistically with ocean acidification, increased turbidity, and other local stressors, further affecting early-stage climate resilience (Duarte et al., 2018; Waycott et al., 2009). At the same time, parental heat history can confer transgenerational plasticity (Pazzaglia et al., 2021b), potentially priming offspring for MHWs but also carrying over stress effects.

Z. marina has one of the broadest biogeographical ranges of seagrass species, spanning multiple Marine Ecoregions of the World (MEOW, Spalding et al. 2007). Thermal tolerances and germination thresholds likely vary among populations, potentially reflecting local adaptation to environmental conditions, including but not limited to temperature. While the MEOW framework is not climate-specific, patterns of divergence across ecoregions may still coincide with ecotypic variation shaped by environmental pressures that vary across regions, including both

local and broader-scale drivers. Understanding thermal responses across this broad range can help determine whether observed traits reflect species-wide patterns or are restricted to specific populations or locally adapted genotypes.

Given the foundational role of *Z. marina* in temperate coastal ecosystems, reduced seedling performance under short-term heat stress may cascade into lower meadow structural complexity, reduced carbon storage capacity, and weakened trophic support. These early-stage vulnerabilities must be incorporated into projections of ecosystem function under global change, especially in systems undergoing restoration or subject to multiple anthropogenic stressors. Understanding population-level thermal thresholds is essential for anticipating how climate extremes may reshape demographic trajectories and functional connectivity across *Z. marina*'s broad biogeographical range.

To ensure ecological relevance, the MHWs simulated in this study were derived from a 30-year time series of site-specific sea surface temperature (SST) records in the German Wadden Sea, where the seed source population was located. The 10 °C spring baseline reflects the mean SST during the natural germination window (March–May), and the MHWs applied (+1.8, +3.0, and +5.6 °C) correspond to moderate, strong, and severe marine heatwave categories, following the classification scheme of Hobday et al. (2016, 2018).

MHW exposure was initiated during early imbibition to coincide with the seasonal timing of dormancy release, germination, and early seedling growth. This timing reflects the increasing prevalence of springtime MHWs in temperate latitudes (Gregory et al., 2024; Marcos et al., 2025), and targets a developmental window known to be highly sensitive. Importantly, we applied short-term MHW profiles consisting of 7-day ramp-up, 7-day peak exposure, and 7-day cooling phases, to assess whether brief MHWs, among the shortest biologically relevant marine heatwaves, are sufficient to trigger measurable developmental and physiological responses. While laboratory conditions cannot fully replicate the complexity of field environments, isolating temperature as a single factor enables precise assessment of thermal thresholds and their consequences for seedling performance.

The non-linear pattern we observed, where moderate MHWs suppressed germination, strong MHWs enhanced it, and severe MHWs left germination largely unchanged, suggests that early developmental stages of *Z. marina* possess a degree of thermal plasticity that may allow opportunistic exploitation of short-term warming events. This divergence from terrestrial seed systems, where both moderate and severe heat typically suppress germination, indicates that *Z. marina* seeds may operate within a distinct thermal activation window shaped by marine conditions. Moreover, the decoupling between germination and morphometric development under severe MHWs, where pigments declined but germination did not, points to potential buffering mechanisms during the earliest developmental stages. Although our experiment did not track long-term performance beyond the seedling stage, such early exposure could also induce forms of thermal priming or stress memory, as observed in other marine plants (Leuendorf et al., 2020; Pazzaglia et al., 2021b). Identifying whether short-term MHWs induce beneficial priming or instead impose latent physiological costs will be essential for forecasting how *Z. marina* responds to increasingly variable temperature regimes.

Early life stages of *Z. marina* develop within highly heterogeneous natural environments, where microhabitat conditions can either buffer or amplify thermal exposure during MHWs. Such small-scale variation can strongly modulate the intensity and duration of temperatures experienced by seeds. Seeds originating from meadows regularly subjected to salinity fluctuations (driven by tidal dynamics, episodic rainfall, and freshwater inputs) may exhibit enhanced resilience to temperature variability. Similarly, microhabitat characteristics such as canopy shading, biofilm formation, and small-scale sediment topography can generate localized thermal refugia. In contrast, seeds from annual populations on unvegetated flats may experience intensified heating under calm, high-irradiance conditions (Adams et al., 2016;

Hansen et al., 2022). In these settings, seed burial depth and sediment properties can act as major determinants of the microenvironment. Sudden fluctuations in temperature can alter imbibition, osmoregulation, and metabolic activation during germination, potentially impacting early developmental responses (Nguyen et al., 2021a; York et al., 2013).

Although our simulated MHWs reflected realistic thermal anomalies, many natural MHW events persist for several weeks or recur multiple times within a single season (Oliver et al., 2021; Smith et al., 2023). Prolonged or repeated MHW events may therefore amplify the non-linear patterns observed in our study. For example, the increased germination observed under strong MHWs (Category II) could diminish or reverse as metabolic reserves become depleted with extended exposure, whereas the delayed germination and growth suppression observed under moderate (Category I) and severe (Category III) MHWs may become more pronounced. This expectation is consistent with extreme-event ecology, in which multi-week heatwaves can generate cumulative population and community-level impacts (Hyndes et al., 2016; Kendrick et al., 2019; Smith et al., 2023).

Consequently, the responses documented in this study likely represent conservative estimates of the impacts expected under short-term MHW scenarios. Multi-species and multifactor mesocosm experiments, including variation in sediment matrices, seed burial depth, salinity changes, and shading, would provide a more comprehensive understanding of how these interacting factors influence community-level responses.

4.4. Implications for restoration under climate change

Our findings demonstrate that early developmental stages of *Z. marina* respond non-linearly to short-term warming, with moderate MHWs suppressing germination, strong MHWs enhancing it, and severe MHWs altering photophysiology without reducing emergence. This combination of vulnerability and plasticity has direct implications for restoration practice, as seeds or newly germinated seedlings may either benefit from brief warming pulses or experience reduced establishment depending on the timing and intensity of MHW exposure. The contrasting effects across MHW categories also raise the possibility that strong, sublethal warming may act as a priming cue, a phenomenon observed in other plant systems, though its long-term consequences in seagrasses remain unknown. These experimental insights provide some initial information for climate-smart seed-based restoration strategies.

As seed-based seagrass restoration is receiving increasing attention globally, our findings carry timely relevance for restoration practitioners. Many *Z. marina* restoration projects hinge on the assumption that spring temperatures reliably support germination and early growth.

Yet even brief MHWs during this critical germination window can delay germination (Penfield and MacGregor, 2017), disrupt establishment, suppress root development (undermining anchorage and nutrient uptake), and impair photophysiological performance (Marín-Guirao et al., 2016), ultimately reducing early-stage carbon gain.

With a changing climate and more frequent MHWs, seagrass restoration practitioners will be required to adopt multi-integrated, climate-smart, and adaptive approaches to build resilient meadows. These include anticipatory actions that leverage seasonal sea-surface temperature forecasts and real-time monitoring to pinpoint seeding windows with the lowest MHW probability (Bonino et al., 2024; Gouvêa et al., 2025; Strydom et al., 2020), combined with local phenological data to maximize the likelihood that seeds encounter optimal conditions for development. Additionally, identifying genotype-specific thermal tolerances in *Z. marina* (Pazzaglia et al., 2021a), and screening populations for heat-resilient germination and seedling performance can help match seed stocks to anticipated thermal regimes (Rinaldi et al., 2023), a practice already applied in coral (van Oppen et al., 2017) and terrestrial plant restoration (Bucharova, 2017; Höfner et al., 2022). At the site scale, microhabitat heterogeneity offers further resilience: deeper seed

burial or the use of natural shading structures can create thermal refugia, though these must be balanced against light-limitation and sediment dynamics (Adams et al., 2016; Dalby et al., 2023; Pieraccini et al., 2025b). While such strategies may reduce thermal exposure during MHWs, they also entail important trade-offs. Increased burial depth can delay or entirely prevent seedling emergence if elongation capacity is insufficient, and in fine-grained or organically enriched sediments, deeper layers are more likely to be hypoxic and sulfidic (Jarvis and Moore, 2015; Jørgensen et al., 2019). Although low to moderate sulfur availability can stimulate metabolic activity and, in some cases, accelerate germination, excessively sulfidic conditions are generally detrimental, impairing root function and reducing the likelihood of seedling establishment (Rautenbach et al., 2024; Simpson et al., 2016; Zhang et al., 2025). Similarly, targeting sheltered or low-flushing sites may enhance thermal buffering but can reduce oxygen renewal and increase susceptibility to sediment instability or organic input (Jørgensen et al., 2022). Recent findings also show that seed-based restoration success in two *Zostera* species is highly site-specific, with seedling emergence depending strongly on sediment characteristics, redox depth, and local hydrodynamic conditions (Coals et al., 2025a, 2025b). Together, these findings reinforce our conclusion that early-stage responses of *Z. marina* to MHWs must be interpreted within the context of local environmental suitability.

Emerging evidence suggests that priming, via brief, sublethal heat shocks or mild osmotic stress, can precondition seeds (Srivastava et al., 2021) and seedlings (Pazzaglia et al., 2022) for thermal stress. These methods may accelerate germination, boost antioxidant and heat-shock responses, and enhance heat-stress tolerance, offering a low-cost, scalable way to “harden” young plants before seeding, outplanting, or nursery propagation. Our observation that strong MHWs can enhance germination despite subsequent physiological costs is consistent with such priming-like effects, but controlled experiments will be needed to separate beneficial priming from harmful overexposure.

Together, these strategies align with emerging frameworks for climate-resilient restoration (Mcleod et al., 2019; Ward et al., 2025) and seascape approaches (Gann et al., 2019) advocating for flexible, forward-looking planning and adaptive management towards restoring ecological functions and reconnecting fragmented seascapes.

A growing body of research is beginning to unravel the physiology of *Z. marina* seeds (Brodersen and Kühl, 2023; Brodersen and Pedersen, 2024; Dooley et al., 2013; Pieraccini et al., 2025a; Zhang et al., 2025). In seed-based studies, the harvested seed lot is often treated as a uniform starting point; yet, each seed carries a distinct history shaped by maternal environment, flowering phenology, overwintering conditions, and site-specific factors. A standardized understanding of optimal seed collection timing and maturity is still lacking, and no generalized “time zero” can be applied across populations or meadows. We argue that explicitly integrating seed phenology (i.e. when and under which conditions flowers, spathes and seeds are produced) into seagrass research will be important for understanding plant regeneration dynamics, assessing ecological responses under future climate scenarios, and improving nursery and restoration practices.

Phenological and trait-based approaches are more established in freshwater and brackish water macrophytes (Boedeltje et al., 2004; Calero et al., 2015; Catian et al., 2019; Rohal et al., 2024; Wersal and Madsen, 2018), which are phylogenetically and functionally close to seagrasses. These systems offer valuable conceptual and methodological frameworks that could be more systematically adopted in marine plant science. Building on our findings that MHWs can strongly modulate germination timing and early seedling performance, we suggest that the timing of seed production, harvesting, and planting will become an increasingly important lever for climate-smart seagrass restoration. Linking seed physiology, phenology, and restoration practice should therefore be a key priority for future work on *Z. marina* and other seagrass species.

CRediT authorship contribution statement

Riccardo Pieraccini: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation. **Ann Vanreusel:** Writing – review & editing, Writing – original draft, Validation, Supervision, Investigation, Funding acquisition. **Nico Koedam:** Writing – review & editing, Writing – original draft, Supervision, Investigation. **Chiara Marulli:** Writing – review & editing, Methodology. **Tobias Dolch:** Writing – review & editing, Resources. **Tom Van der Stocken:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2025.107789>.

Data availability

I have shared the link to the data.

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