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Effects of persistent thermal plumes on *Zostera muelleri* reproductive effort, seed bank densities and seed bank viability

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ABSTRACT

A warming climate poses significant threats to seagrass species worldwide, resulting in ecosystem impacts such as reduced foreshore stabilisation, decreased fisheries habitat, and diminished carbon sequestration. The recovery of seagrass is often inconsistent, taking weeks to years, and in severe cases, recovery may not occur. Recovery is facilitated through both asexual and sexual reproduction, with smaller or short-term disturbances typically favoring asexual reproduction, while large-scale disturbances rely on a persistent seed bank. This study investigated reproductive metrics of *Zostera muelleri* in persistent thermal plumes, measuring reproductive shoot density, spathe counts, and seed bank density and viability. An estuary affected by thermal effluent, Lake Macquarie, NSW, Australia, was used as a proxy for future climate scenarios and compared with two other east coast Australian estuaries. Seed banks in all three systems were relatively small (averaging 16 seeds m^{-2}), suggesting that these populations may not rely strongly on seed banks for recovery. Mean reproductive shoot densities ranged from 4 to 8 shoots m^{-2}, while spathe counts averaged between 10 and 20 per reproductive shoot, with peak reproductive metrics observed in November and January. Importantly, no significant differences in reproductive shoot densities, spathe counts, or seed bank viability were found between thermally affected (mean maximum temperatures ~2 °C higher) and ambient conditions, indicating that *Zostera muelleri* reproduction on the east coast of Australia may have the capacity to acclimate to temperatures expected by the end of the 21st century.

1. Introduction

Seagrasses are a critical coastal habitat that facilitates important ecosystem function in the form of fisheries habitat, shoreline stabilisation, nutrient cycling and carbon storage (Heck Jr et al., 2003; Christianen et al., 2013; Macreadie et al., 2014a, 2014b). A warming climate combined with other stressors such as urbanisation, increased nutrient inputs and increased frequencies of severe weather events, has resulted in global seagrass decline of approximately 7 % yr^{-1} since 1990 (Waycott et al., 2009; Turschwell et al., 2021). In estuarine environments, the multitude of stressors associated with potentially high rates of urbanisation, can have unpredictable interactions with changing climates, resulting in a demand for a greater understanding of the ecological implications of these stressors on seagrass ecosystems (Dafforn et al., 2012). The persistence of seagrass ecosystems and their myriad of benefits relies on successful recovery strategies, employed through a mix of both asexual and sexual reproduction, however, the in situ impacts of warming waters on reproduction still requires further research (Rasheed et al., 2014; Smith et al., 2016a, 2016b; Soerensen, 2020).

Seagrasses can reproduce through rhizome elongation or fragmentation (asexually) or through the production of flowering shoots and seeds (sexually), both of which are a key mechanism for resilience that allows for population persistence if one method were to fail (Smith et al., 2016a, 2016b). The reproduction method favored is often energy dependent and varies by species, however, resource allocation towards reproduction is a major life history event in most clonal plants and a combination of both sexual and asexual reproduction is the optimal strategy (Eckert, 2002; Kendrick et al., 2012; Macreadie et al., 2014a, 2014b; Stafford-Bell et al., 2016). As such, seagrass recovery is highly variable, ranging from weeks to years and recovery strategies vary depending on the stressor (Nowicki et al., 2017). For small scale disturbances, such as those experienced by anchors, propellor scars, or grazing, asexual reproduction from neighbouring beds is typically the

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main method of recovery (Macreadie et al., 2014a, 2014b; Smith et al., 2016a, 2016b; Nowicki et al., 2017). However, for large scale disturbances such as severe storm events, which are increasing in both frequency and intensity due to climate change, populations rely on a persistent and viable seed bank (Jarvis et al., 2014; Jarvis et al., 2021; Johnson et al., 2021).

Zostera muelleri is a dominant seagrass on the east coast of Australia which has a similar perennial life cycle to that of its North American counterpart and the more heavily studied *Zostera marina* (Jacobs et al., 2006; Jarvis et al., 2014). Peak flowering for *Zostera muelleri* ranges from October through to January depending on local temperature, with warmer locations reaching peak reproductive effort earlier than cooler locations (Smith et al., 2016a, 2016b; Lekammudiyanse et al., 2024). Originally, *Z. muelleri* was thought to flower very little although this perception has now changed, and large flowering events have been observed frequently in Australian and New Zealand populations (Smith et al., 2016a, 2016b; Zabarte-Maeztu et al., 2021). Sexual reproduction is driven by a variety of factors such as temperature, light availability, tidal exposure, nutrient availability and grazing pressures, however, is most accurately predicted by temperature (Lekammudiyanse et al., 2024).

However, successful sexual reproduction does not necessarily mean that seeds will contribute to the population as a variety of factors may affect whether germination occurs or not (Conacher et al., 1994; Stafford-Bell et al., 2016; Tarquinio et al., 2019). Laboratory-based germination experiments have shown low germination rates (<15 %), with most germination occurring at salinities around 8 psu and temperatures below 16 °C (Conacher et al., 1994; Stafford-Bell et al., 2016). These conditions are much lower than those typically experienced in estuarine systems, where salinities on the east coast of Australia generally range between 25 and 35 ppt. However, it is possible for estuarine salinity to fluctuate more widely, from near freshwater (0 ppt) up to marine conditions (35 ppt), particularly during large rainfall events near river entrances, albeit usually for short durations (Eyre and Ferguson, 2006; Stafford-Bell et al., 2016). This means that successful germination likely requires these events to induce low salinity and temperature, however, additional factors such as sediment microbes and burial depth can also influence germination outcomes (Conacher et al., 1994; Stafford-Bell et al., 2016; Cumming et al., 2017; Tarquinio et al., 2019). Sediment grain size also influences the density and viability of seed banks within seagrass ecosystems, not only through the ability to trap or retain seeds (Orth et al., 1994), but sediment grain size can also affect the likelihood of successful germination, with finer sediments increasing germination and coarser sediments decreasing germination (Tanner and Parham, 2010; Kenworthy and Fonseca, 1977). Regardless, successful sexual reproduction is important, as it allows greater genetic variability enabling adaption of the species to new, extended stressors such as climate change and thus is important in overall resilience of the species (Smith et al., 2016a, 2016b).

Zostera muelleri seeds are negatively buoyant which means seeds mainly contribute to local patch persistence through the development of a localised seed bank (Furman et al., 2015). Seed banks for *Z. muelleri,* and other species such as *Z. nigricaulis,* are highly variable within estuaries (Smith et al., 2016a, 2016b; Dos Santos and Matheson, 2017). However, like many seagrass species in the southern hemisphere, there is little information on *Z. muelleri* seed banks or reproductive variation (Smith et al., 2016a, 2016b), and no information on how *Z. muelleri* seed banks perform under elevated temperatures despite temperature being a significant driver in reproduction (Potouroglou et al., 2014; Lekammudiyanse et al., 2024) and germination (Conacher et al., 1994).

Using thermal plumes in Lake Macquarie, Australia as a proxy for climate change, this study aims to determine if there are differences in seed bank development, quantity or viability under a warming climate regime relative to nearby non-thermally affected estuaries. Thermal plumes have been studied globally as a proxy for climate change and have indicated changes in fish, algal and seagrass communities (Steinbeck et al., 2005; Keser et al., 2005; Gillanders et al., 2022), however, there is no literature examining seed bank densities or viabilities in a warming climate. In Lake Macquarie, effects of elevated temperatures have caused a community restructuring in Vales Point from a *Zostera* dominated to a *Halophila* dominated ecosystem (Robinson, 1987). However, in lesser affected areas of the system, changes in seagrass biological characteristics (growth rates or carbon sequestering) have not been observed (Garthwin et al., 2014; Macreadie and Hardy, 2018). Temperatures within thermally affected areas of the system can range from ~1-7 °C above ambient depending on month, or approximately ~2 °C on average (Ingleton and McMinn, 2012; Suzzi et al., 2023; Moir et al., 2024). This range falls between predicted 2030 high emissions scenario of 1 °C SST temperature increase and the 2090 high emissions scenario of 3.1 °C SST temperature increase projected for Sydney, Australia (Dowdy et al., 2015). These temperature increases will expose thermally affected populations to significantly more common and intense heatwaves, particularly during summer months. These increases mean that thermally affected populations will commonly experience temperatures which exceed the long term exposure thermal limit of 32 °C for the species (York et al., 2013). As such, thermally affected populations here offer a unique opportunity to examine the effect of short and repeated exposure above these temperatures on the species. Due to the strong influence of temperature on seagrass phenology and reproduction, thermally affected *Z. muelleri* populations in Lake Macquarie may exhibit several key differences. If temperatures are favorable, this may include earlier onset of flowering and increased reproductive shoot and spathe count (Lekammudiyanse et al., 2024), or, if the populations are thermally stressed, differences in resource allocation could result in decreases in reproductive shoot and spathe count (Qin et al., 2020a, 2020b). If there are differences in reproductive shoot counts or spathe counts, we would expect for these to be represented as a decrease or increase in seed bank density. However, the effect on seed viabilities may be negative regardless, as *Z. muelleri* seeds show optimal germination at cooler temperatures below 16 °C (Conacher et al., 1994; Stafford-Bell et al., 2016). These temperature-driven changes may ultimately affect both the production of reproductive structures and the viability of seeds in thermally impacted areas.

2. Methods

2.1. Study site

This study was conducted in three estuaries on the east coast of Australia: Lake Macquarie (*33.050° S, 5 sites*), Tuggerah Lakes (*33.250° S, 3 sites*) and Brisbane Water (*33.475° S, 3 sites;* Fig. 1). Close proximity of each estuary provides similar ambient water temperature, however, Lake Macquarie has two coal-fired power stations which continually discharge thermally-affected water into the system and warm the receiving areas at Myuna Bay and Mannering Park by approximately 2.0–7.4 °C depending on month, with greatest temperature differentials occurring during the cooler months (Moir, 2020; Suzzi et al., 2023). This heating has occurred in the system for approximately 45 years, with Eraring power station (which outflows into Myuna Bay) being commissioned in 1984, and Vales Point power station (which outflows into Mannering Park) being commissioned in 1978. These thermally affected areas comprise 2 of the 5 sites sampled within Lake Macquarie, with the others (Yarrawonga Park, Gwandalan and Murrays Beach) located in the southern part of the lake to avoid urbanisation and metal contamination in the north (Roach, 2005). This allows a unique opportunity to examine a snapshot of a future ecosystem under an RCP 8.5 scenario in which south-east coast Australian waters are projected to warm by 2.8–5.7 °C by 2090 (Dowdy et al., 2015; Scanes et al., 2020. Two additional estuaries which are approximately 70 km to the south of Lake Macquarie were incorporated as ambient sites which do not experience any heating; Brisbane Water and Tuggerah Lakes. These are both barrier estuaries with similar stressors, estuary morphologies and

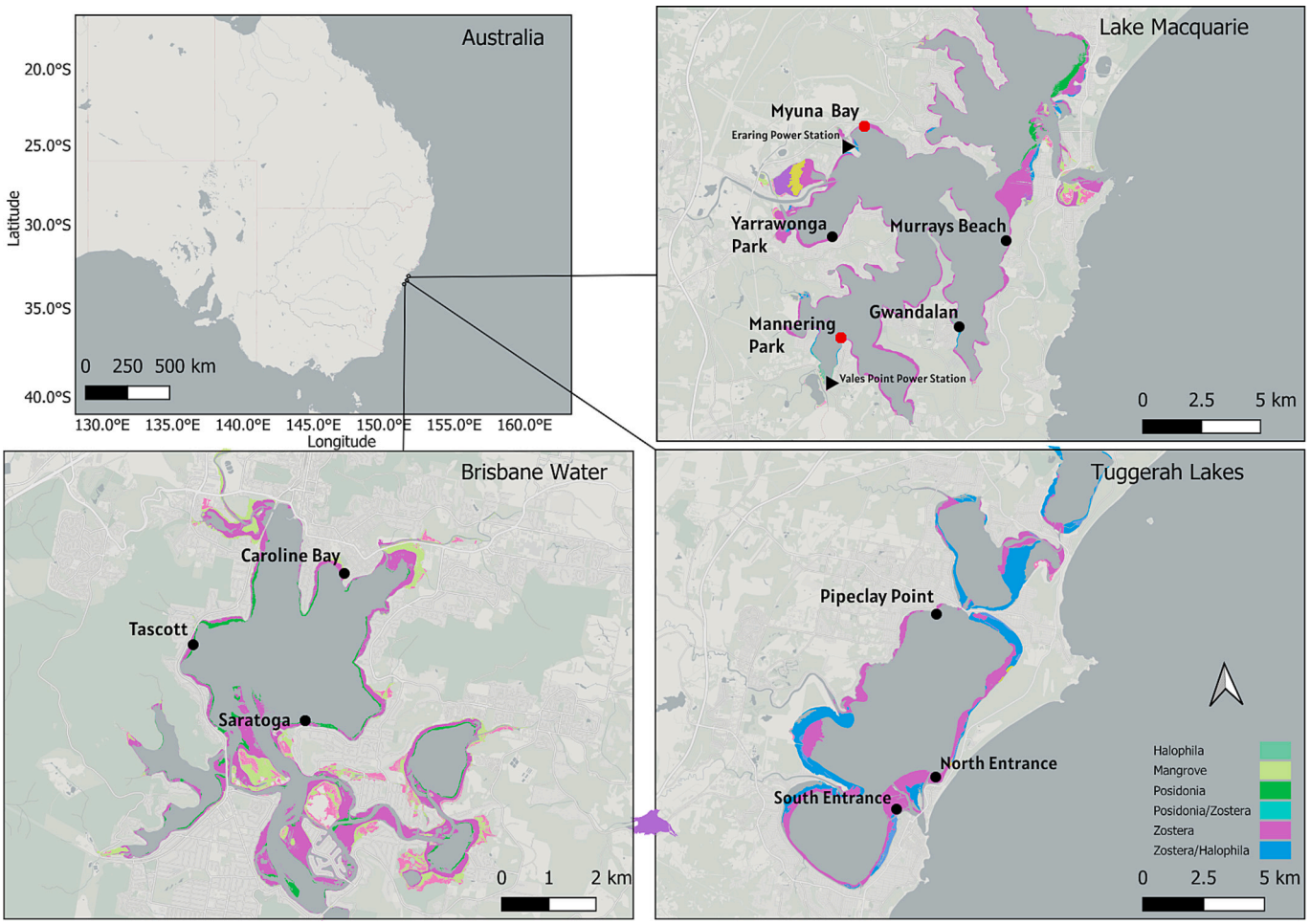

Fig. 1. Location of sampling sites on the east coast of Australia in a) Lake Macquarie (thermally affected sites in red), b) Brisbane Water and c) Tuggerah Lakes. Seagrass habitat data sourced from the NSW Fisheries Spatial Data Portal. Power station locations indicated in Lake Macquarie by the triangle symbol. Image adapted from Moir et al., 2024. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

temperature and salinity profiles (Scanes et al., 2020). Salinity values in estuaries can fluctuate, particularly in, or near mouths of tributaries where freshwater inflows are high after rainfall, however, all systems have comparable salinities and generally sit at oceanic values except for after heavy rainfall events (Mackenzie, 2010; Brennan et al., 2010; Scanes et al., 2020). At Brisbane Water, average salinities range between 20 and 33 psu (Mackenzie, 2010), in Tuggerah Lakes average salinities range between 22 and 30.5 psu (Brennan et al., 2010), and in Lake Macquarie average salinities range between 24 and 35 psu (Lake Macquarie City Council, unpublished data).

Sites with monospecific *Zostera muelleri* densities (>95 %) were chosen to ensure best chances at finding seeds, and all sampling typically occurred at depths of ~1 m. For Tuggerah Lakes, two sites were clustered near the entrance of the estuary where seagrass could be found, and in Brisbane Water, sites were evenly spaced throughout the system to encompass a variety of stressors which the system may experience from sources like tributaries or urbanisation (Fig. 1). Fieldwork was targeted to sample peak reproductive effort while maximizing the chance of finding early development of seed banks in thermally affected areas.

2.2. Temperature recording and sediment composition

Due to equipment vandalism being prevalent in these systems, temperature profiles were also established from pre-existing data from different studies (2020–2023) which were sourced using HOBO Pendant® UA-002-64 - Temperature/Light Data Loggers (64 K) (Fig. 3) which were deployed in approximately 1 m of water and logging every 15 min. This dataset encompasses multiple years of data between the months of September – April and was chosen to most accurately establish temperature profiles, however, it is not a complete continuous three year dataset and some sites may have more or fewer temperature readings than others. Additional temperature data for Tuggerah Lakes and Brisbane Water was provided by Central Coast Council and readings were not recorded from the exact location of the sites in this study. Sediment composition was determined by collecting ~50 g of surface sediment, drying at 65 °C for 24 h and then processed using a sediment shaker (Retsch AS200) with the retained sediment on each sieve (4, 2, 1, 0.5, 0.25, 0.125, 0.063 mm and pan) weighed and the total percentage of each sediment type calculated.

2.3. Seed collection

To determine the density and viability of seed banks at each site, samples were collected monthly starting in late November 2022 continuing through until the end of April 2023. Typically, mature spathes would not have dropped seeds this early on the south-east coast of Australia. Reproductive effort in this area peaks between November – December (Lekammudiyanse et al., 2024), however, previous sampling (Smith et al., n.d.) has shown that spathes in thermally affected sites develop faster than those in ambient locations and early sampling of this peak period tried to accommodate for this. For each monthly sampling

event, three sediment cores (10 cm × 10 cm diameter) (Smith et al., 2016a, 2016b) were randomly taken from the center of seagrass meadows at each site in each estuary, placed into a labelled individual zip lock bags and immediately transferred into a portable fridge at 4 °C. Samples were then returned to the laboratory where they were refrigerated for a maximum of two weeks before being sieved sequentially through a 1000 μm and 710 μm sieve to separate seeds.

2.4. Seed viability

To determine viability of seeds, a 'cut test' was used which has shown results comparable to tetrazolium staining, with no significant differences between the two (Smith et al., 2016a, 2016b). The cut test is a time and cost-efficient method to assess seed viability, where seeds are sliced in half and considered viable if the flesh is firm with a blue tinge (Borza et al., 2007; Smith et al., 2016a, 2016b).

2.5. Quantifying spathe counts and reproductive shoot density

Reproductive shoot count and spathe counts were collected monthly coinciding with the collection of seed cores from November 2022 to April 2023. For each site during each sampling event, three 0.5 × 0.5 m quadrats were haphazardly thrown into seagrass meadows. In each quadrat, total reproductive shoot count was recorded for density, and three shoots were randomly selected with spathes counted on each to estimate average spathe count.

2.6. Statistical analysis

2.6.1. Environmental parameters

Differences in temperatures between thermally affected and ambient locations were verified using a one-way ANOVA. To assess spatial differences in sediment grain size composition, we performed a Permutational Multivariate Analysis of Variance (PERMANOVA) using Bray-Curtis dissimilarity on percentage composition data across grain size classes (from 4.0 mm to <0.063 mm). The model tested for differences between sites using 999 permutations using the "*vegan*" package in R (Oksanen et al., 2025). Prior to analysis, rows with missing values were excluded. Pairwise comparisons were limited by the small number of replicates per site ($n = 3$). Consequently, the resulting p-values lacked resolution and could not reliably indicate statistical significance and thus pairwise comparisons were excluded.

2.6.2. Assessing the impact of temperature and treatment on reproductive metrics

To evaluate temporal and treatment-driven variation in reproductive metrics and seed bank properties, we used linear mixed effects models fitted with the "*lmer*" package in R (Bates et al., 2015). Models were constructed for four response variables: reproductive shoot density, spathe count per shoot, seed count, and the proportion of viable seeds. Each model included fixed effects for 'Treatment' (ambient or thermally affected), 'Month' (November to April), and their interaction. Site was included as a random intercept to account for repeated sampling across months. Location was excluded from the model as it did not improve model fit. All response variables were log-transformed to meet model assumptions of normality and homoscedasticity. Type III ANOVA tables were generated to test the significance of each fixed effect using Satterthwaite's approximation for denominator degrees of freedom. Where significant effects of 'Month' were detected, post-hoc pairwise comparisons were conducted using Tukey-adjusted estimated marginal means (via the '*emmeans*' package; Lenth et al., 2025).

To evaluate the influence of temperature on seed production metrics, and of reproductive shoot density on seed bank density, we fitted another series of models. 'Site' was included as a random intercept to account for repeated measures and spatial clustering. Due to strong collinearity between treatment and average temperature, and given that temperature was the presumed ecological driver, models were constructed using continuous temperature as the sole predictor and were not separated into individual treatments. The response variables included seed bank density, reproductive shoot density, and mean spathe count per quadrat. Predictor variables included average monthly temperature (°C) and reproductive shoot density for the seed bank density model. All analyses were conducted in R version 4.1.2 (R Core Team, 2021).

3. Results

3.1. Environmental conditions

3.1.1. Temperature profiles

Temperature regimes differed significantly between treatments and among estuaries (Fig. 2). Mean temperatures at thermally affected sites (25.0 °C ± 3.6) were notably higher than at ambient sites (21.9 °C ± 3.5), with minimum and maximum recorded temperatures of 14.1 °C and 40.5 °C, respectively, compared to 12.8 °C and 36.0 °C at ambient sites. An ANOVA confirmed that temperatures at thermally affected sites were significantly greater than ambient sites across all estuaries ($p < 0.001$). Consistent with these differences, thermally affected sites accounted for 36 of the 50 hottest recorded days, with peak temperatures reaching 40.5 °C.

3.1.2. Sediment composition

Sediment composition data were compared between sites using PERMANOVA which identified significant differences in sediment composition ($F = 21.96$, $R^2 = 0.913$, $p = 0.001$). Due to low replication, pairwise comparisons could not be conducted to determine which sites differed in their overall sediment compositions. Sediment grain size distributions were broadly similar among most sites, being dominated by medium (0.25 mm) and fine (0.125 mm) sands. In Brisbane Water, these two fractions together accounted for 60–80 % of the matrix, with coarser particles (> 1 mm) and the finest silt clay fraction (< 0.063 mm) each contributing less than 5 %. A comparable pattern was observed at Myuna Bay and Yarrawonga Park in Lake Macquarie and at all three sites in Tuggerah Lakes. By contrast, Mannering Park contained a markedly higher proportion of coarse material: pebbles, granules and very coarse sand (> 1 mm) comprised approximately 35–40 % of the sample.

3.1.3. Reproductive shoot densities and spathe counts

Reproductive effort varied significantly across months for both shoot density and spathe production (Table 1, Fig. 3). There was no significant effect of treatment or the treatment × month interaction for either metric. Mean reproductive shoot density (Fig. 3b) was highest during November and January across all estuaries, and significantly lower from February onward ($F = 31.32$, $p < 0.001$). Post-hoc comparisons confirmed that shoot densities in November and January were significantly higher than in March and April ($p < 0.001$), with the strongest seasonal decrease observed in Lake Macquarie.

Spathe production followed a similar temporal trend (Fig. 3a), with peak values observed in November and January ($F = 31.3$, $p < 0.001$). Mean spathe counts declined significantly by March across most sites. While visually higher spathe counts were evident in thermally affected locations during peak months in Lake Macquarie, these differences were not statistically significant and no treatment × month interaction was detected.

3.1.4. Seed bank densities

Seed banks across all estuaries were relatively sparse, averaging only 16 seeds m^{-2} (Fig. 4). Seed count varied between months and sites, but there were no significant differences between treatments or treatment-by-month interactions. While Lake Macquarie and Brisbane Water showed general increases in seed counts over time, Tuggerah Lake

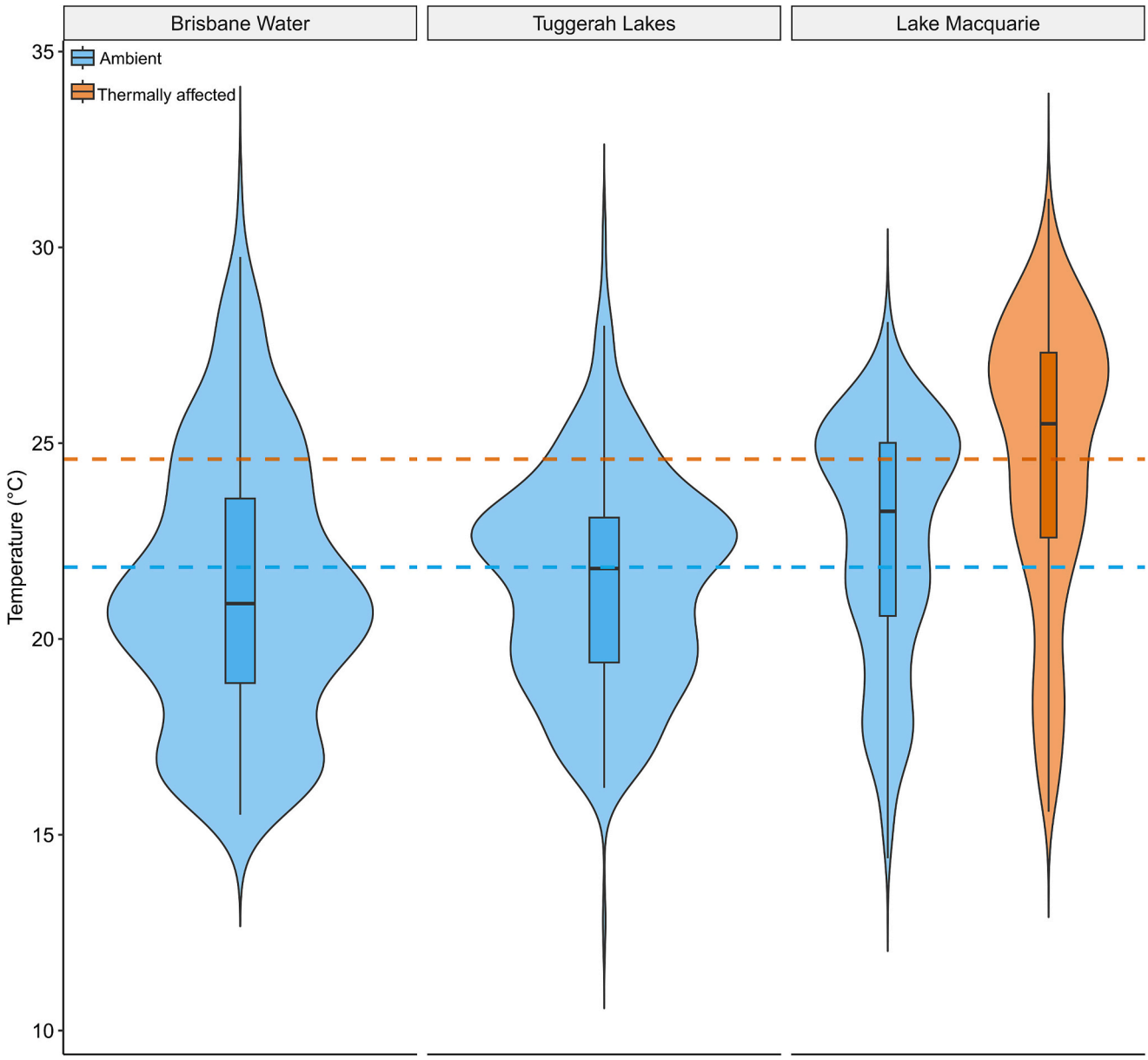

Fig. 2. Box and violin plot temperature distributions of ambient and thermally affected treatments across the three estuaries sampled. Treatments are distinguished by colour, with blue representing ambient conditions and orange representing thermally affected conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

exhibited a decline. The highest densities were recorded in Lake Macquarie during January, primarily due to a single site (Murrays Beach), while most seeds in Tuggerah Lakes (70 %) were sourced from Pipeclay Point. Despite the temporal mismatch between seed counts and reproductive shoot peaks, with reproductive effort highest in November and January, seed densities often continued to rise into later months, suggesting seed deposition lagged behind reproductive output.

Linear mixed-effects models indicated that temperature had no significant effect on seed bank density, reproductive shoot density, or spathe production (Fig. 5A, C, D). In contrast, seed bank density, although an almost non-existent relationship (R^2 = 0.02), increased significantly with reproductive shoot density (F = 5.4, p = 0.021; Fig. 6B, Table 2). Random site effects accounted for considerable variation in seed bank density models (site variance = 162.4 for the seed bank density ~ temperature model, and 145.1 for the seed bank density ~ shoot density model). This was reflected in higher conditional R^2 values (0.131 and 0.132, respectively) compared to the marginal R^2 (0.010 and 0.022), suggesting much of the variation was site-specific rather than temperature or shoot-driven. For models predicting shoot density and spathe production, both marginal and conditional R^2 values were notably lower (e.g., marginal R^2 = 0.015 and 0.023, conditional R^2 = 0.023 and 0.072), reinforcing that little variance in these metrics was explained by temperature.

3.1.5. *Seed bank viabilities*

Seed viability exhibited high variability across sites and sampling months (Fig. 6), with no significant differences detected by treatment or treatment-by-month interaction (Table 1). Brisbane Water and Tuggerah Lakes displayed inconsistent patterns in viability, ranging from 0 % to 100 % among replicates and several months with no viable seeds detected in January for either estuary. In contrast, Lake Macquarie showed more consistent seed presence across months, with viabilities generally ranging between 50 % and 75 % in both ambient and thermally affected sites.

Table 1
Summary of fixed effects from linear mixed-effects models evaluating the influence of treatment (ambient vs. thermally affected), month (November–April), and their interaction on reproductive shoot count, spathe count per shoot, proportion of viable seeds, and seed count. Site was included as a random effect in all models. Asterisks indicate statistically significant effects ($p < 0.05$).

Response	Predictors	DF	F-statistic	*P* value
Reproductive shoot count	Treatment	1	0.0222	0.8847
	Month	4	31.3193	< 0.001 **
	Treatment × Month	4	1.2623	0.2875
Spathe count	Treatment	1	0.9084	0.3655
	Month	4	40.5402	< 0.001 **
	Treatment × Month	4	0.9969	0.4113
Proportion of viable seeds	Treatment	1	0.7387	0.4096
	Month	4	2.6866	0.0336 *
	Treatment × Month	4	1.3027	0.2718
Seed count	Treatment	1	0.2318	0.6409
	Month	4	1.9213	0.1098
	Treatment × Month	4	1.7006	0.1529

4. Discussion

Contrary to our hypothesis that thermally affected areas may have increased reproductive shoots or spathe counts earlier than ambient locations, or greater seed densities or differences in seed viability, we found no evidence demonstrating an effect of temperature on reproductive metrics. This research highlights that reproduction within these systems will likely not be altered by warming soon, however, low seed banks in general may leave populations susceptible to a warming climate. This refutes a hypothesis that thermal discharge at thermally affected areas would alter seed bank densities by reducing overall reproductive effort or efficiency (due to thermal stress), or cause seed banks to develop earlier (more favorable temperatures earlier) or have decreased viabilities. It's worth noting that moderate thermal increases may not always be detrimental and could indicate the species exists closer to its thermal optimum, which would result in greater photosynthetic efficiency, resource generation and potentially reproductive effort (Collier et al., 2011; Lekammudiyanse et al., 2024).

The results of our mixed models indicate that temperatures are not a significant driver of reproductive effort in these systems, despite it being a key trigger to start the reproductive season (Lekammudiyanse et al., 2024). Temperature did not explain any variance in the models, which is contrary to other studies which found that increasing temperatures decreased reproductive intensity in another Zostera species (see Qin et al., 2020a, 2020b). Given the documented effects of temperature on reproduction and germination, it is entirely possible that we do not have enough temperature data to detect a relationship between temperature and reproductive metrics. Our analysis included monthly averages, but flowering in similar species such as *Zostera Noltii* can occur in as little as 43 days (Alexandre et al., 2006). This would mean that on a short time scale like we have sampled, much finer resolution temperature data may be required to detect an influence. It is also just as likely that because the study locations lie in the midpoint of the species distribution (Swadling et al., 2025), that temperature does not have an influence at all, and

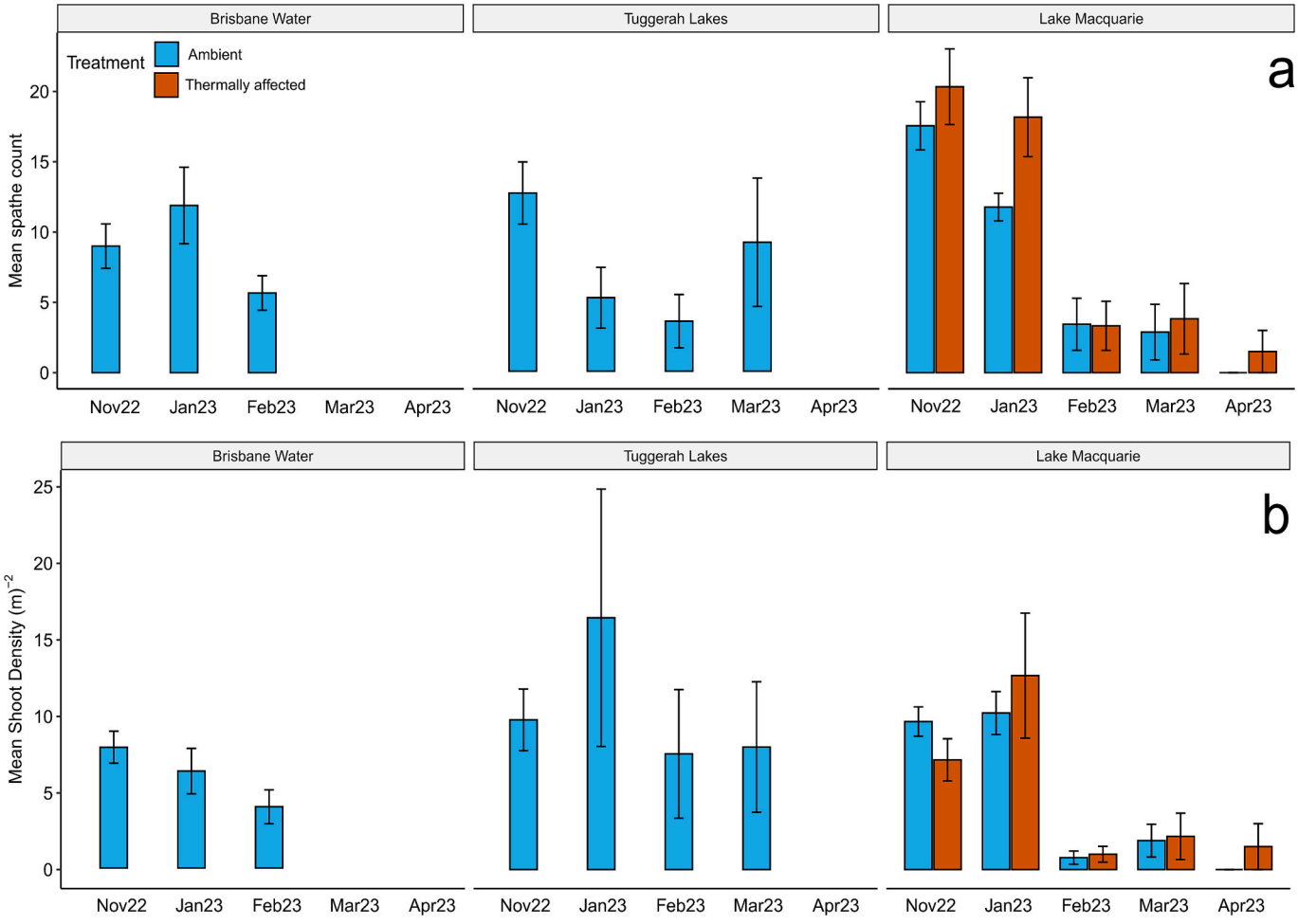

Fig. 3. Reproductive shoot metrics across all estuaries averaged by estuary per month ($n = 9$) for a) mean spathe count per shoot (±SE) and b) mean shoot density (±SE, m^{-2}). Note: Lake Macquarie had $n = 15$ because of additional thermally affected sites ($n = 3$).

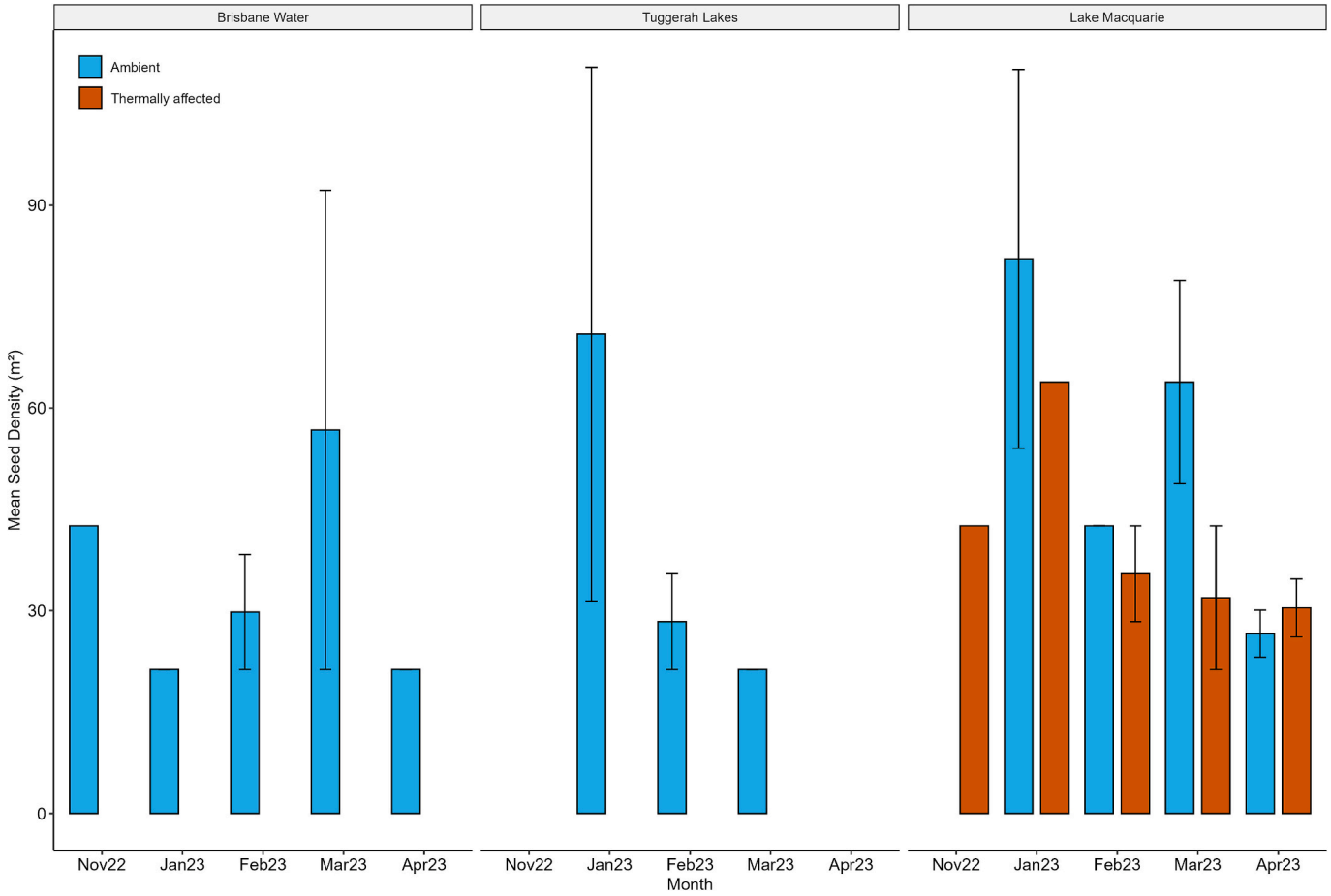

Fig. 4. Mean (±SE) seed density obtained from sediment cores by month from each estuary (Brisbane Water, Tuggerah Lakes and Lake Macquarie). Bars with missing error bars contained only one replicate during that month which had seeds.

perhaps at either end of its distribution we would see a temperature effect more prominently.

Site specific differences in reproductive shoot count (such as those in Tuggerah Lakes where one site (Pipeclay Point) contributed 70 % of values) are indicative of the variable reproductive effort of the species and seagrasses in general (Macreadie et al., 2014a, 2014b; Smith et al., 2016a, 2016b, Dos Santos and Matheson, 2017). The other two sites in Tuggerah Lakes (Entrance North and Entrance South) were in areas which experience significant recreational activity, and this is likely to be a significant factor impacting reproductive shoot counts. Before the height of the Austral summer, these sites both had healthy reproductive shoots, however, following this period none could be found. It is likely that vessels such as jetskis and boats from holiday traffic had a direct impact on the flowering of these patches due to heavy wave action or scarring caused by the vessels (Glasby and West, 2018) which could have dislodged any shoots present. Further, the monthly variation in both reproductive shoots and spathe counts is consistent with the literature, and our peak flowering times aligned with that of Lekammudiyanse et al. (2024) in the same system. Considering the importance of warmer temperatures accelerating flowering onset, with peak reproductive effort being earlier in lower latitudes and later in higher latitudes (Lekammudiyanse et al., 2024), it is interesting that thermally affected sites did not flower earlier than ambient sites.

Sites with lower sexual reproductive effort are likely favoring asexual reproduction as the primary form of recovery from small scale disturbances in Lake Macquarie (Macreadie et al., 2014a, 2014b). Genotypic diversity of the population has been identified as a significant influence driving which reproductive method is favored, with seagrass meadows that exhibit high genotypic diversity continuing to favour sexual reproduction (Reusch, 2006; Macreadie et al., 2014a, 2014b). Consequently, the genotypic diversity in these populations is likely quite low which may leave these populations susceptible to large scale stress events such as marine heatwaves or storm surges (Hughes and Stachowicz, 2004, Reusch et al., 2005, Hughes and Stachowicz, 2004).

While there were no notable differences in seed bank densities between estuaries and sites, they were generally quite low. Small seed banks present in this study may represent a future threat to these populations, especially in thermally affected areas. Particularly during heatwaves, thermally affected areas will reach the upper limit of *Zostera muelleri* much sooner than ambient areas and these acute temperature spikes above thermal maxima may significantly affect seagrass populations (Collier et al., 2011, York et al., 2013). Seagrass loss resulting from a large-scale stress event, such as a heatwave, can begin a feedback loop where it is extremely difficult for the population to recover. Loss is followed by bank and sediment destabilisation, turbidity is then increased leading to an increase in light attenuation, and this makes it difficult for existing stressed plants to recover or establish (Nowicki et al., 2017). In these scenarios, it is not until conditions return to ambient or improve which allow persistent seed banks to become an important mode to recovery (Jarvis and Moore, 2010). Further, the additive interaction of multiple stressors is a key component of real-world stress events (York et al., 2013; Moreno-Marín et al., 2018). For example, already elevated temperatures coupled with other stressors such as storm surges and tidal movements likely means that surviving plants will not be able to reproduce effectively (Lekammudiyanse et al., 2023) due to altered resource allocation, and recovery will depend on the seed banks within the system. With small or no seed bank to rely on, recovery will be greatly reduced or likely not occur.

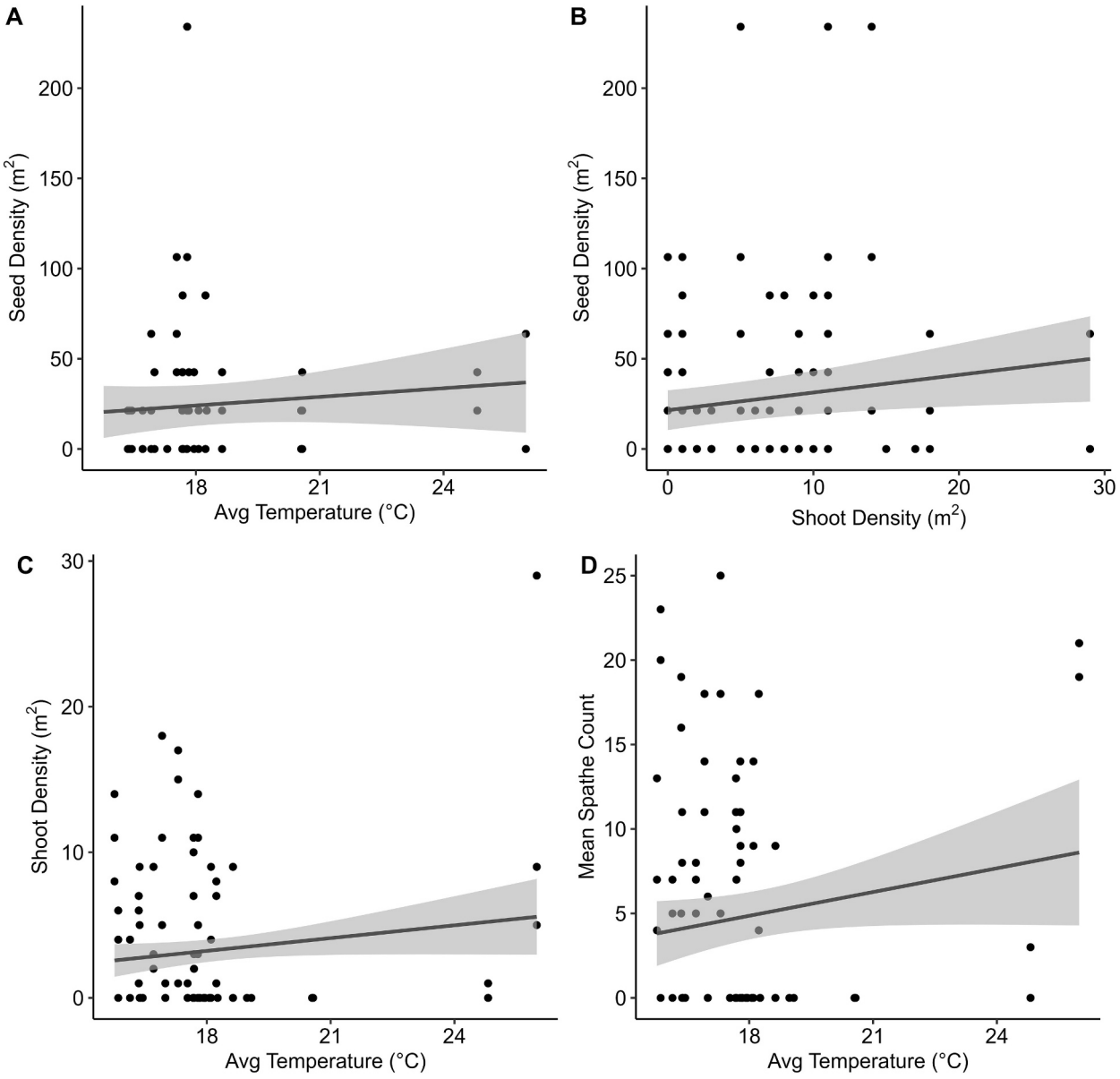

Fig. 5. Relationships between temperature and reproductive metrics in Zostera muelleri, and reproductive shoots and seed bank density: (A) Seed density (m^2) as a function of average temperature (°C); (B) Seed density (m^2) as a function of shoot density (m^2); (C) Shoot density (m^2) as a function of average temperature (°C); (D) Mean spathe count as a function of average temperature (°C). Solid lines indicate fitted linear regression models with 95 % confidence intervals (shaded area). Panel B was the only model to show a statistically significant relationship ($p < 0.05$). Conditional R^2 values shown reflect the variance explained by both fixed effects (e.g., temperature) and random effects (site-level differences).

The viability of seeds found within thermally affected sites compared to ambient locations did not differ significantly. There is little information on what may affect seed viability in situ, however, in laboratory experiments oxygenation, temperature and salinity are significant variables (Conacher et al., 1994). In these experiments, higher temperatures reduced viability of seeds (Seeds stored at 22–24 °C saw significant declines compared to those at 5–10 °C) however, this is a much more significant contrast compared to the present study. Seeds from thermally affected sites in Lake Macquarie have previously shown higher germination rates than ambient (Moir et al., 2024), however, this is not due to differing viabilities of these seeds, which when compared to ambient are all >95 %, and may be the result of better-quality seeds in thermally affected areas.

While there were no differences in thermally affected sites versus ambient locations, it is important to consider the limitations of the study. The unbalanced sampling design, originally designed to identify and ensure accurate representation of reproductive metrics which can be extremely variable, encompassed fewer thermally affected sites (6) compared to ambient sites (27), which may have limited our ability to detect significant differences between treatments. This reduced power means that non-significant results should be interpreted cautiously, as the absence of detected differences does not necessarily indicate equivalence between treatments (Underwood, 1997). However, the design was mostly robust, encompassing eleven sites across five months. Investigating temperature impacts in estuarine systems presents unique challenges, as these environments exhibit high variability and diverse morphologies that affect environmental parameters (Scanes et al., 2020). While our study site offers a valuable opportunity to examine temperature effects in situ, the correlation between temperature changes along with numerous unmeasured concurrent factors, complicates the interpretation of results. Due to the wide geographical range of the species, it is also possible that seagrass within the thermally affected

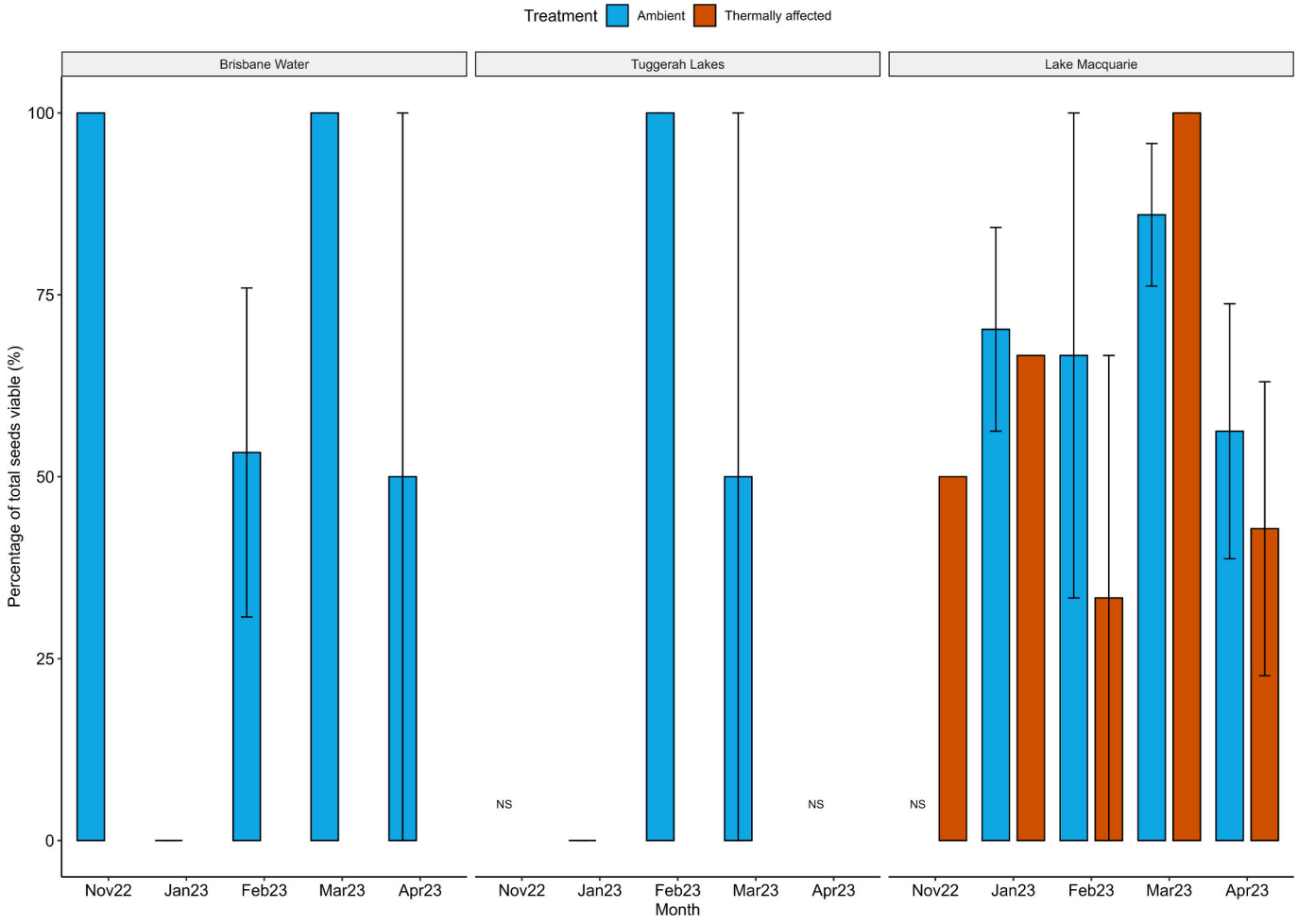

Fig. 6. Mean (± SE) percentage of viable seeds within each sediment core for each month in Brisbane water ($n = 9$), Tuggerah Lakes (n = 9) and Lake Macquarie ($n = 15$). NS represents replicates where no seeds were present and thus viability could not be tested.

Table 2
Summary of linear mixed-effects models examining the relationships between seed bank density, reproductive shoot density, spathe production, and temperature in Zostera muelleri. Models included site as a random intercept.

Model	DF	F value	p value	Site variance	R^2	Cond R^2
Seed bank Density ~ Avg Temp	27.228	0.8603	0.3618	162.4	0.010	0.131
Seed bank Density ~ Reproductive Shoot Density	210.67	5.4103	0.02097	145.1	0.022	0.132
Shoot Density ~ Avg Temp	8.7448	3.1348	0.1114	0.219	0.015	0.023
Spathe Production ~ Avg Temp	17.635	3.0271	0.0993	2.37	0.023	0.072

sites in Lake Macquarie have acclimated to the continuous temperature increases and no effect would be present regardless of a larger dataset or stronger sampling design. Perhaps it is only when these sites start to experience more common, repeated and severe heatwaves (of which frequency is increased in thermally affected areas) would we expect some differences to exhibit.

Thermally affected sites were not different from control locations in reproductive shoot counts, spathe counts or seed bank metrics, despite average temperatures being ~2 °C higher and mean maximum temperatures being 3–4 °C higher. It is evident that the three estuaries investigated had small seed banks and are likely not relying upon this method for recovery. While the sample size is quite small due to small seed banks, unaffected viabilities may suggest that temperate *Z. muelleri* seeds can acclimate to warmer conditions, which is supported by prior work of Moir et al. (2024) in this location. These findings aid in understanding the in situ effects of elevated temperatures on temperate populations of the species, which can be different to laboratory results due to the additive nature of unpredictable stressors present in estuarine environments.

CRediT authorship contribution statement

Tom Moir: Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Megan J. Huggett:** Writing – review & editing, Supervision, Conceptualization. **Timothy M. Smith:** Writing – review & editing, Methodology, Conceptualization. **Troy F. Gaston:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization.

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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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Data availability

All data used in this paper are available at the following database: https://doi.org/10.34740/KAGGLE/DSV/8901861

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