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Sediment Properties and Seagrass Density Influence the Morphological Plasticity of Seagrass *Zostera muelleri* More Than Elevated Temperatures

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Abstract
Understanding the long-term effects of elevated temperatures on foundational species like seagrasses is critical for predicting and managing the impacts of warming coastal ecosystems worldwide. Seagrasses exhibit plasticity in response to a range of environmental stressors, so the effects of climate change are likely to be context dependent. This study investigated differences in the growth and morphology of *Zostera muelleri* inside versus outside a warm water plume generated by a power station operating for ~ 26 years in Lake Macquarie, New South Wales, Australia. The effects of other factors, including sediment organic matter, season and seagrass density were also examined to ascertain their importance relative to elevated temperatures. Despite water temperatures in the thermal plume being equivalent to conditions predicted by 2090 under future climate scenarios (1.5–2.7 °C above ambient), there were no consistent effects of these elevated temperatures on *Z. muelleri* growth and morphology. Instead, growth at all sites (ambient and warm water) was greater by 40.3% in spring and 74.3% in summer when compared to winter. Increasing organic matter content in sediments was associated with a 69.8% rise in below-ground biomass and a subsequent 73.8% reduction in the ratio of above- to below-ground biomass. There was also evidence for seagrass density effects, with denser meadows having shorter leaves and reduced growth rates, likely due to self-shading. Overall, these findings demonstrate that *Z. muelleri* in the centre of its distribution in eastern Australia can tolerate moderate temperature increases over decadal scales.

Keywords Climate change · Seagrass · Sediment properties · Self-shading · Thermal effluent · *Zostera*

Introduction

Climate change is associated with a range of environmental stressors including more frequent extreme weather events, altered freshwater flows, ocean acidification, and elevated atmospheric and sea surface temperatures (Doney et al., 2012; Easterling et al., 2000; Gillanders et al., 2011; Harley et al., 2006; Hobday & Lough, 2011). Marine and estuarine environments are warming worldwide, causing shifts in community compositions and the distribution, growth and phenology of species (Champion et al., 2021; Gervais et al., 2021; Hastings et al., 2020; Jordà et al., 2012; Poloczanska et al., 2013; Short et al., 2016; Wernberg et al., 2024). Warming waters pose a significant threat to global biodiversity given that temperature influences a variety of physiological and ecological processes (Bellard et al., 2012; Maclean & Wilson, 2011; Nagelkerken et al., 2023; Wernberg et al., 2024). Estimates suggest that global sea surface temperature is increasing at a rate of 0.062 ± 0.013 °C per decade over a 120-year period (1900–2019), and this rate accelerated to 0.280 ± 0.068 °C per decade between 2010 and 2019 (Garcia-Soto et al., 2021). In contrast, the warming of shallow estuaries in eastern Australia has been estimated at ~ 0.2 °C year^{-1} over 12 years (2007–2019; Scanes et al., 2020). Assessing the effects of warming on nearshore ecosystems is essential to predict the impacts of climate change, particularly for foundation species like seagrasses (Jordà et al.,

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2012; Short & Neckles, 1999; Trisos et al., 2020; Wernberg et al., 2024).

The survival and productivity of seagrasses are strongly linked to a range of abiotic factors including temperature (Bulthuis, 1987; Burkholder et al., 2007; Collier et al., 2017; Lee et al., 2007). Optimal temperatures for the growth of temperate seagrass species typically range between 12 and 26 °C, while thermal optima for subtropical and tropical species occur between 23 and 32 °C (Lee et al., 2007). Within these temperature ranges, mild warming increases respiration, photosynthesis and growth, but once a threshold is reached, rising temperatures have a strong negative effect on seagrass health as respiration increases relative to photosynthesis (Anton et al., 2020; Bulthuis, 1987; Campbell et al., 2006; Collier et al., 2011; Olsen et al., 2012). Optimal temperatures for seagrass growth can be lower than for photosynthesis (Lee et al., 2007), although growth rates are also highly dependent on other factors, especially light (Bulthuis, 1987; Olsen et al., 2018). The effects of warming on seagrasses are likely to be variable for species with distributions extending across large gradients in temperature or light regimes. For instance, negative effects are likely at low latitudes where species are close to their upper thermal limits, whereas increased temperatures at higher latitudes may enhance growth rates (Anton et al., 2020; Clausen et al., 2014; Koch et al., 2007; Marbà et al., 2022).

Seagrasses can acclimate to a range of environmental conditions due in part to their considerable morphological plasticity (Clausen et al., 2014; Collier et al., 2007; Ferguson et al., 2016; Maxwell et al., 2014; Zimmerman et al., 1989). Morphological plasticity in seagrasses is not only driven by climate and temperature, but also other factors such as nutrients, sediment properties and light availability (Cabaço et al., 2009; de Boer, 2007; Ferguson et al., 2016; Maxwell et al., 2014; Zabarte-Maeztu et al., 2021). For example, seagrasses may upregulate root biomass to expedite nutrient uptake and promote productivity in oligotrophic systems (Ferguson et al., 2016; Lee & Dunton, 2000). In comparison, high concentrations of organic matter and fine sediments (i.e. clay/silt) cause anaerobic conditions and sulphide toxicity in seagrasses, which reduce shoot density, growth, and belowground biomass (de Boer, 2007; Holmer & Hasler-Sheet al., 2014; Pérez et al., 2007; Zabarte-Maeztu et al., 2021). Light availability is another key determinant of seagrass morphology (Bulthuis, 1983; Collier et al., 2007; Ralph et al., 2007). In response to low-light conditions (e.g. deep water, turbidity or dense meadows that cause self-shading), seagrasses may decrease their shoot density and leaf length (Bulthuis, 1983; Collier et al., 2007; Longstaff & Dennison, 1999; Olesen & Sand-Jensen, 1994a) or alter photosynthetic activity (Sharon & Beer, 2008; Sharon et al., 2009). The interdependence between density, biomass and shoot length is an established concept for marine and terrestrial plants, with populations self-thinning and plant growth slowing when intraspecific competition is high (Creed et al., 1998; Enriquez et al., 2019; Norberg, 1988; Rattanachot et al., 2016; Reed, 1990; Yoda et al., 1963).

Although seagrasses display morphological plasticity in response to multiple stressors, this can vary among and within species (Anton et al., 2020; Collier et al., 2017; Ferguson et al., 2016; Pazzaglia et al., 2021; Viana et al., 2020; York et al., 2013). Information on these relationships is vital for predicting how seagrasses will respond to environmental variation and future climate change. Furthermore, understanding the relative importance of other factors compared to elevated temperatures in driving seagrass morphological variation is necessary for predicting how species might respond to future climates and help avoid erroneous conclusions being drawn from field studies examining the impact of climate change (Pazzaglia et al., 2021). In this study, we investigate the influence of elevated temperatures on the seagrass *Zostera muelleri* subsp. *capricorni* (Asch.) S.W.L. Jacobs (hereafter *Z. muelleri*) by comparing differences in growth and morphology inside and outside of a warm estuarine-water thermal plume generated by a power station in New South Wales (NSW), Australia. This system enables the effects of prolonged exposure to elevated temperatures on seagrasses to be examined (e.g. Garthwin et al., 2014; Moir et al., 2024; Walker et al., 2024), with the power station being active for ~ 26 years prior to the time of the current study. Such a system offers some advantages over experiments in mesocosms, which examine the response of seagrasses to increased temperatures over the short term and potentially before plants have acclimated. We predicted that warmer water would enhance seagrass growth and size and that effects would be greatest when the temperature differential between sites inside and outside the thermal plume was largest. Given that the warm water treatment was not replicated at different sites, it was important to examine sediment properties that are known to impact seagrass growth and morphology and test whether these influenced our results or were more influential than temperature.

Methods

Study Area

The Eraring Power Station is Australia's largest coal-fired power station which accounts for 25% of NSW power requirements and was fully commissioned in 1984. It is situated on Lake Macquarie, which is a large wave-dominated barrier estuary connected to the Pacific Ocean via a narrow entrance. The main body of the lake has a small tidal range (< 0.1 m), an average depth of 5.7 m, and its catchment is dominated by residential and industrial

developments. The salinity in the lake is typically close to seawater, except after heavy rainfall when it can briefly fall to < 20 ppt (Ferguson et al., 2017; Suzzi et al., 2022, 2023). The power station has a generating capacity of 2880 MW and uses estuarine water supplied through an inlet canal for cooling, and warm water effluent is discharged into the southern section of Myuna Bay at temperatures typically ≤ 35 °C (Fig. 1). After the commissioning of the power station, there were trends for declining cover of *Z. muelleri* in Myuna Bay, although results were inconclusive (King & Hodgson, 1986). For several decades, *Z. muelleri* has not grown where the warmest water exits the outlet canal (NSW DPI, 2021). Seagrasses in large sections of Myuna Bay are exposed to water that is 1–3 °C above ambient temperatures, with variations depending on discharge temperature, season, depth and proximity to the outlet (Garthwin et al., 2014; Ingleton & McMinn, 2012; King & Hodgson, 1986; Walker et al., 2024). The warm water effluent exposes *Z. muelleri* meadows in Myuna Bay to warming comparable to conditions predicted in eastern Australia by 2090 (CSIRO and BOM 2015).

Field sampling of *Z. muelleri* was completed at five locations in Lake Macquarie, NSW, Australia (Fig. 1). Two locations with elevated temperatures ('warm locations') were situated in Myuna Bay (Myuna West and Myuna East; Fig. 1) adjacent to the warm-water outlet and three controls ('ambient locations') at Wangi Wangi, Sunshine Park and Mannering Park (Fig. 1). Sampling occurred in October (spring) 2010, January (summer) 2011 and August (winter) of 2011, which coincided with periods of minimum (winter), maximum (summer) and intermediate

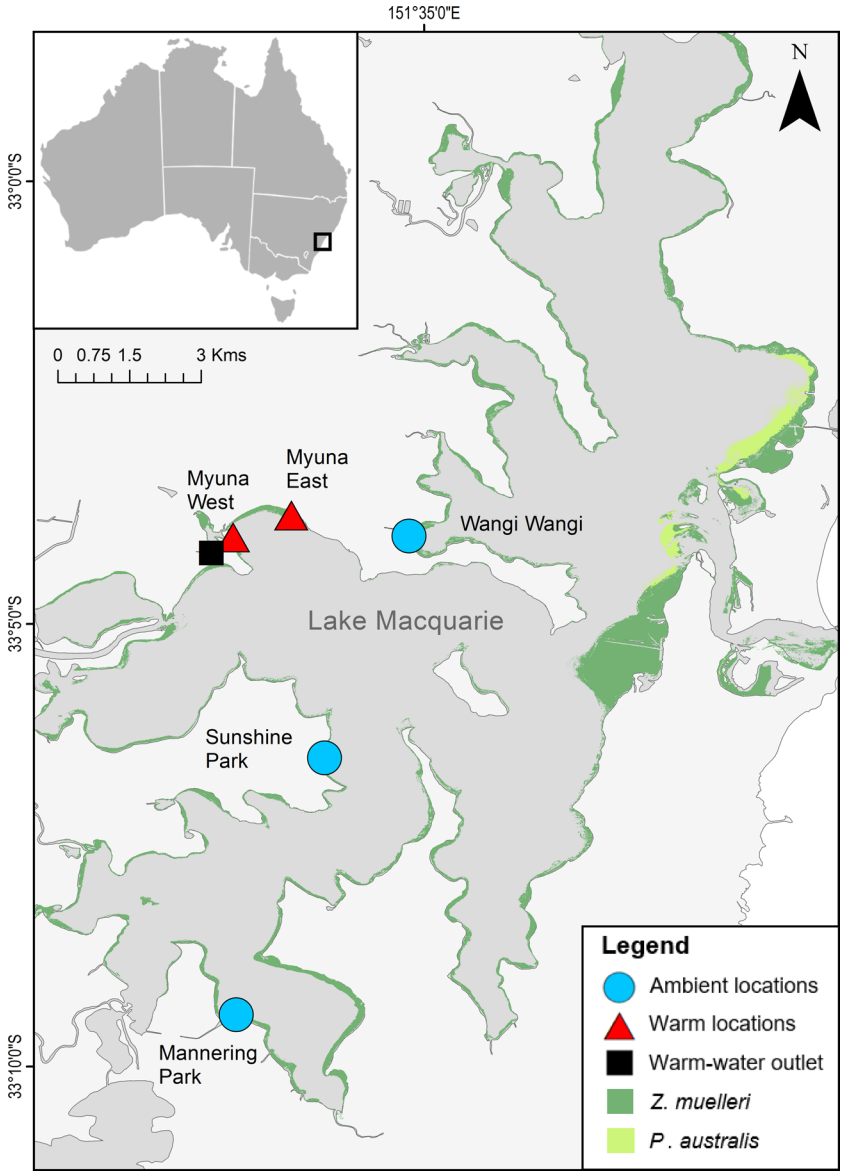

Fig. 1 Location of the Eraring Power Station warm-water outlet, the warm and ambient locations, and the distribution of the two dominant seagrass species *Zostera muelleri* and *Posidonia australis* in Lake Macquarie. Two sites approximately 50 m apart (not shown) were sampled at each location

(spring) growth for *Z. muelleri* in south-eastern Australia (Kerr & Strother, 1989, 1990).

Seagrass Sampling

At each location, two sites were established 50 m apart at a low-tide depth of ~ 0.5 m. Four fixed quadrats (30 × 30 cm) separated by a minimum distance of 2 m were permanently fixed at each site in each sampling period, and the areas within these quadrats were divided into 10 × 10 cm grids, with the central grid used for seagrass measurements. All *Z. muelleri* shoots within the central 10 × 10 cm grid were marked using the 'hole-punch' (or leaf marking; West & Larkum, 1983; Zieman, 1974) technique, using a needle to create two parallel holes in the sheath region just below the ligule. The quadrats were resampled 9 to 20 days after marking the shoots, with the duration varying due to logistical constraints. The central grid, where the shoots were marked, was then extracted using a 10-cm-deep corer. The samples were cleaned of epiphytes and washed in freshwater over a 5-mm sieve to remove the sand, shell grit, gravel and detritus. Samples were then refrigerated and examined the next day, recording the number of shoots, leaf length, leaf extension (mm of growth per day) and dried above- and below-ground biomass.

Five shoots from each core sample were randomly selected for measuring the longest leaf and leaf extension. Leaf extension represented the greatest length of displacement and was measured as the longest distance between the reference scar and the corresponding leaf scar, or in the case of new leaves, the tip of the new leaf. Next, all shoots were cut at the point where they intersected the rhizome to separate above from below-ground material, which was oven dried at 60 °C for 72 h and weighed.

Sediment Properties and Water Temperature

Water temperature loggers (Odyssey, Dataflow Systems Pty Ltd, New Zealand) were deployed at each site and recorded temperature every 15 min from the date quadrats were established until the cores were removed for each sampling period (between 9 and 20 days). Typically, there was one logger deployed at each site, except in October 2010 when there were two at each site for Wangi Wangi and Sunshine Park, and one logger at Mannering Park was lost. Sediment sampling was done during spring 2010 in triplicate at each site. Sediments were only sampled once as their properties were not expected to change substantially over the study period. At each site selected for seagrass sampling, sediment properties (grain size and organic matter content) were collected haphazardly by removing the top layer (1 cm) of sediment from a 7-cm diameter core, as per Ferguson et al. (2016). Collected samples were then transported to the lab and refrigerated at 4 °C until processing. The fraction of silt/clay in the sediments (< 63 µm grain size; hereafter referred to as 'fine grains') was calculated using wet sieving followed by oven-drying (60 °C for 2 days or until completely dry) and weighing. Percent organic matter content was determined gravimetrically by re-weighing following ashing (550 °C for 4 h).

Statistical Analyses

Differences in temperature between warm and ambient locations during each sampling period were statistically tested using a Mann–Whitney *U* test, while differences in sediment properties among locations were tested using a Kruskal–Wallis test, as the data were not normally distributed. Generalised additive mixed models (GAMM) were used to test relationships between seagrass metrics and temperature (i.e. 'ambient' or 'warm' sites nested within locations), sampling month and sediment properties. Shoot density was hypothesised to be an important determinant of seagrass growth due to self-shading effects, so it was included as a predictor in all models except where shoot density was the response variable. Preliminary data exploration identified potential extreme outliers, homogeneity and collinearity between predictor variables. Outliers determined through visual inspection occurred for the below-ground biomass ($n = 2$) and the above- to below-ground biomass ratio (AGB:BGB; $n = 1$) and were excluded from subsequent analyses. Sediment properties included in the analyses were averaged across the triplicate samples at the two sites. Strong collinearity was present between the percent of fine grains and organic matter content within the sediment (Pearson's correlation $\rho = 0.78$), with sediments containing a high proportion of fine grains also having high organic matter. We therefore only included organic matter into the model as high levels of organics are known to cause anaerobic conditions and sulphide toxicity in seagrasses (de Boer, 2007; Govers et al., 2014; Holmer & Kendrick, 2012; Koch, 2001) while noting these areas had a large proportion of fine grains. In all GAMM models, a Gamma distribution with a log link function was specified and a random effect of site nested within location. The smoothing terms of organic matter content and shoot density were fitted using a cubic regression spline with the number of knots set to 3 to avoid over-fitting. To test whether thermal effluent effects varied among sampling periods (in different seasons), an interaction between the fixed effects of temperature (warm versus ambient locations) and sampling period was included. R^2 values were used to indicate the predictive power of the model, and model diagnostics were checked using the '*gam.check*' function. The '*anova.gam*' function was used for approximate hypothesis testing of smooth and parametric terms (see Table S1 for a summary of model parameters, including *t*-values, estimates

and 95% confidence intervals for parametric terms). All analyses were completed in the statistical software 'R' (R Core Team, 2023) using the packages '*dplyr*' (Wickham et al. 2022), '*mgcv*' (Wood, 2011) and '*ggplot2*' (Wickham, 2016).

Results

As predicted, locations exposed to thermal effluent had higher temperatures than ambient locations in all sampling months (Oct 2010 $W = 1504$, $p = < 0.0001$, $n = 81$, Jan 2011 $W = 3708$, $p = < 0.0001$, $n = 130$, Aug 2011 $W = 7423$, $p = < 0.0001$, $n = 210$; Fig. 2). On average, locations adjacent the power station were 1.9 °C warmer across the study period. Mean temperature differentials (including 95% confidence intervals) between ambient and warm locations for each sampling period were as follows: October 2010 2.7 °C (2.1–3.3 °C, 95% CI); January 2011 2.1 °C (1.7–2.4 °C, 95% CI) and August 2011 1.5 °C (1–2 °C, 95% CI). The maximum daily temperature recorded during the study was 30.2 °C in January at Myuna East, while the lowest was 12.4 °C in August 2011 at Mannering Park. When averaged over hourly intervals, temperatures exceeded 32 °C for a few hours on 3 days at Myuna East during January 2011.

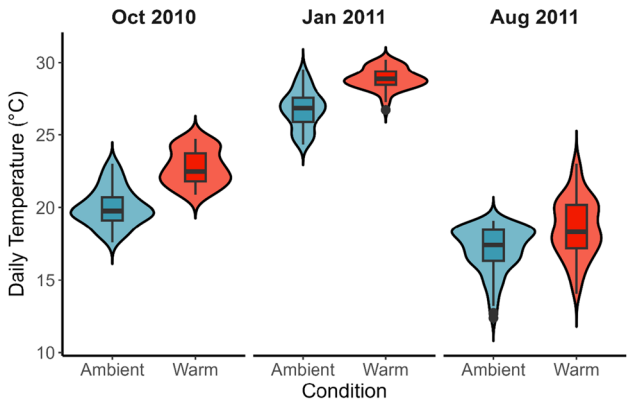

Fig. 2 Violin and box plots illustrating the distribution of the daily temperature at ambient and warm locations in each sampling period

Both the percentage of organic matter ($\chi^2_{4df} = 14.7$, $p = 0.0054$, $n = 30$) and fine grains ($\chi^2_{4df} = 16.3$, $p = 0.0026$, $n = 30$) within sediments varied between locations. Notably, sediment composition at Myuna West differed from the other locations, with organic matter content ranging from 1 to 1.7% less, and percent fine grains between 2.6 and 6.8% less than other locations (Table 1). The highest mean organic matter content and percent fine grains occurred at the ambient locations, Sunshine Park and Wangi Wangi, respectively, whereas the maximum values occurred at Myuna East (warm) and Mannering Park (ambient) (Table 1).

The GAMMs explained between 19.8 and 65.2% of the deviance for the various seagrass metrics (Table 2). The random effect of site nested within the location was correlated with all metrics except below-ground biomass, reflecting small-scale spatial variability in seagrass growth and morphology (Table 2). No explanatory variables predicted seagrass shoot density within the cores (Table 2). Below-ground biomass was predicted to increase by 69.8% from 4.3 g ± 0.7 SE to 7.3 g ± 1.3 SE, as organic matter content rose from 0.9 to 3.3% (Table 2; Fig. 3a). Similarly, below-ground biomass increased by 88.9% from 4.5 g ± 0.7 SE to 8.5 g ± 1.8 SE, as shoot density increased from 10 to 67 shoots per 0.01 m^2 (Table 2; Fig. 3a). There was also evidence for the interaction between sampling period and temperature predicting change in below-ground biomass (Table 2; Table S1; Fig. 3a). Specifically, below-ground biomass was predicted to be greatest at ambient sites in August (7.5 g ± 1 SE) when water temperatures were coolest (17.1 °C ± 0.1 SE), whereas other treatments remained lower and ranged from 4.8 g ± 0.7 SE and 5.7 g ± 0.9 SE despite temperatures varying between 18.6 °C ± 0.2 SE and 28.9 °C ± 0.1 SE.

Above-ground biomass was influenced by shoot density, with an 87.5% predicted increase from 0.8 g ± 0.2 SE to 1.5 g ± 0.4 SE (Table 2; Fig. 3b). There was no consistent association between above-ground biomass and temperature

Table 1 Mean sediment properties averaged across two sites for each location (% of dry weight), including minimum and maximum values

Location	Condition	Sediment variable	Mean (±SD)	Min	Max
Myuna West	Warm	Organic matter	1.02 (0.27)	0.69	1.31
		Fine grains	2.21 (0.79)	1.21	3.21
Myuna East	Warm	Organic matter	2.49 (1.46)	1.32	4.75
		Fine grains	6.56 (3.99)	3.56	11.96
Mannering Park	Ambient	Organic matter	2.0 (0.64)	1.16	2.9
		Fine grains	7.38 (3.83)	2.77	13.67
Sunshine Park	Ambient	Organic matter	2.68 (0.62)	2.05	3.74
		Fine grains	4.76 (1.84)	3.08	8.1
Wangi Wangi	Ambient	Organic matter	2.4 (0.83)	1.43	3.37
		Fine grains	8.98 (2.88)	4.55	12.11

Table 2 Generalised additive mixed model results for each response, including the proportion of variance explained by the model (R^2), sample size (n), degrees of freedom (df), effective degrees of freedom (edf), reference degrees of freedom (Ref.df), F-values (F), and p-values (p)

Response	R^2	n	Parametric terms				Smooth terms				
			Variable	df	F	p	Variable	*edf*	Ref.df	F	p
Shoot density (per 0.01 m^2)	41.8	115	Sampling period	2	1.168	0.315	Organic matter	1	1	0.528	0.469
			Temperature	1	0.794	0.375	Location, site	6.16	7	7.805	< 0.0001
			S × T	2	0.934	0.396					
Below-ground biomass (g)	38.4	113	Sampling period	2	6.527	0.002	Organic matter	1	1	7.4	0.008
			Temperature	1	0.054	0.82	Shoot density	1	1	7.53	0.007
			S × T	2	3.07	0.051	Location, site	3.405	7	0.928	0.076
Above-ground biomass (g)	19.8	115	Sampling period	2	2.661	0.075	Organic matter	1	1	0.005	0.946
			Temperature	1	1.457	0.23	Shoot density	1	1	3.83	0.053
			S × T	2	2.065	0.132	Location, site	4.655	7	1.62	0.024
Biomass ratio (AGB:BGB)	43.4	114	Sampling period	2	9.117	0.0002	Organic matter	1	1	3.03	0.085
			Temperature	1	1.155	0.285	Shoot density	1	1	0.152	0.698
			S × T	2	1.321	0.271	Location, site	5.169	7	2.358	0.004
Longest leaf (mm)	64.4	115	Sampling period	2	7.933	0.0006	Organic matter	1	1	1.24	0.268
			Temperature	1	2.678	0.105	Shoot density	1.56	1.803	8.148	0.003
			S × T	2	4.344	0.016	Location, site	6.218	7	5.513	< 0.0001
Leaf extension (mm day^{-1} $shoot^{-1}$)	65.2	115	Sampling period	2	25.59	< 0.0001	Organic matter	1	1	0.77	0.38
			Temperature	1	1.08	0.3	Shoot density	1.61	1.847	8.83	0.002
			S × T	2	1.152	0.32	Location, site	5.962	7	4.268	< 0.0001

throughout the study. It was predicted that warmer water would increase above-ground biomass and although there was a trend for this in spring (October 2010) when temperature differences were greatest (2.7 ℃), this pattern was reversed in winter (August 2011) and non-existent in summer (January 2011) despite mean temperature differentials of 2.1 ℃ (Table S1; Fig. 3b). At ambient sites, however, above-ground biomass was maximal when water temperatures were greatest (January 2011). The AGB:BGB ratio decreased linearly by 73.8% with increasing organic matter content (Table 2; Fig. 3c). The AGB:BGB was also dependent on the sampling period, with values in August being 33% and 37.9% lower than those in October and January, respectively (Fig. 3c).

Leaves were 32.1% longer at warm (153.1 mm ± 23.7 SE) compared to ambient (115.9 mm ± 15 SE) locations, but only in October 2010 (Table 2; Fig. 4a). Both the longest leaf length and leaf extension rate had strong non-linear negative associations with shoot density, with an apparent threshold at ~ 35 shoots per 0.01 m^2 (Fig. 4). Specifically, the longest leaf length declined by 33% as shoot density increased from 10 to 35 shoots per 0.01 m^2, decreasing more gradually (17.4%) as density increased further (Fig. 4a). Leaf extension rate followed a similar pattern, decreasing by 40.5% as density increased to 35 shoots per 0.01 m^2, and then by only 18% beyond this threshold. The extension rate of leaves also differed by sampling period, irrespective of whether the sites were in warm or ambient locations, with extension rates being 74.3% greater in January 2011 and 40.3% greater in October 2010 compared to August 2011. When averaged across locations, this pattern of change corresponded to a 6.4 °C decrease in temperature from January to October, and a 4.1 °C decrease from October to August.

Discussion

Unravelling the responses of various species to elevated temperatures is essential for understanding the potential implications of climate change. By utilising a power station's warm water plume that had discharged over a seagrass meadow for decades, we examined the effects of sustained elevated temperatures (up to ~ 3 °C) over ~ 26 years on the growth and morphology of *Zostera muelleri*. We found no consistent detrimental effect of these elevated temperatures on *Z. muelleri* in Lake Macquarie, which is near the centre of the species distribution in eastern Australia. Results were broadly consistent with two other studies done at the same site (Garthwin et al., 2014; Walker et al., 2024), although our greater temporal replication and inclusion of a wider range of environmental variables identified factors that are potentially more important than elevated temperature for predicting *Z. muelleri* plasticity. Our results suggested that the anticipated temperature increase of 2–3 °C by 2090 under RCP 8.5 (CSIRO and BOM 2015) would not have negative impacts on *Z. muelleri* growth in this part of its

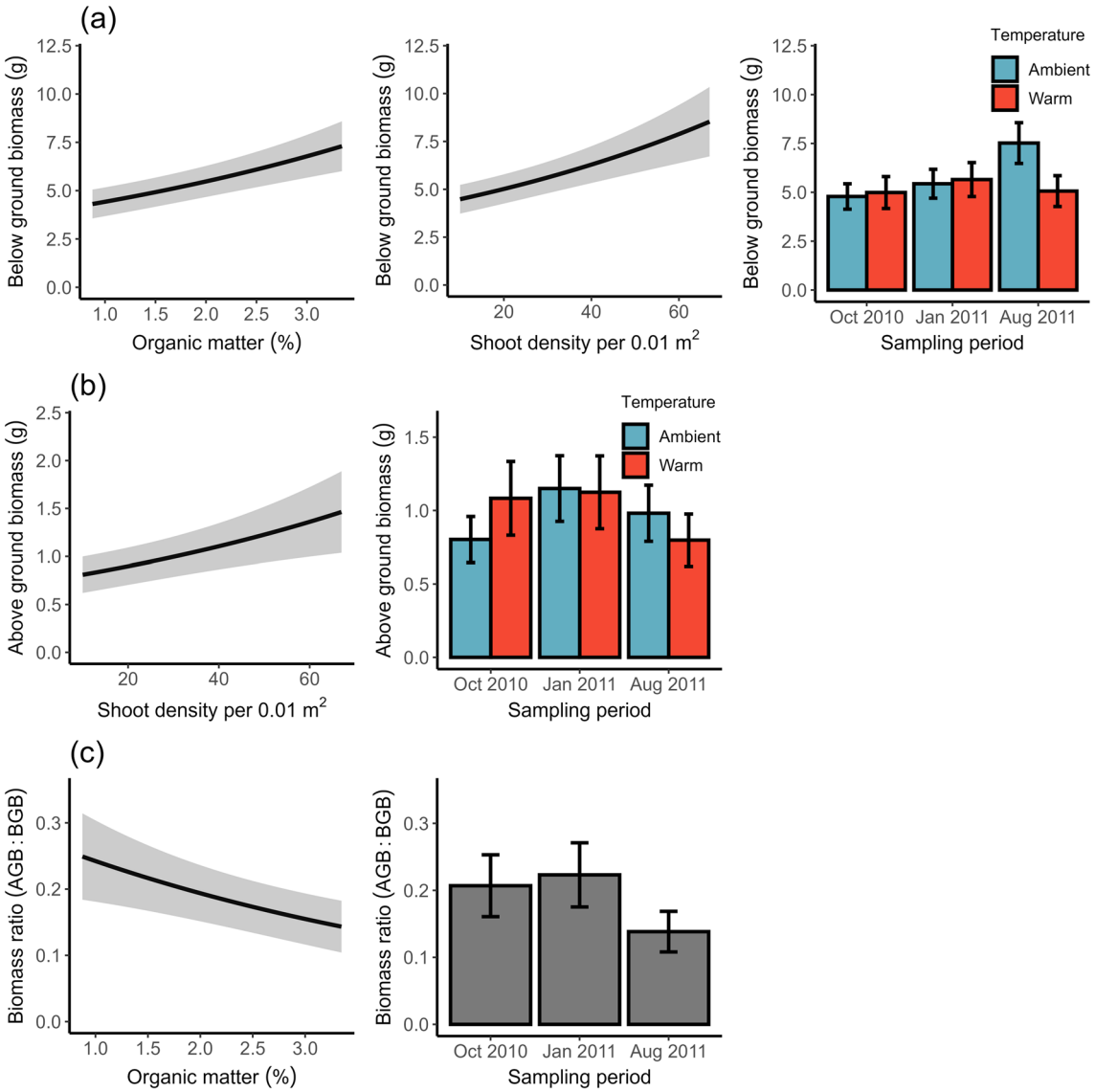

Fig. 3 Relationships from generalised additive mixed models between significant explanatory variables and **a** below-ground biomass (g), **b** above-ground biomass (g), and **c** AGB:BGB ratio. Biomass is calculated as grammes per 0.01 m^2. Fitted GAMM prediction curves (solid line) are included, and ribbons and error bars represent ± SE

distribution. This finding cannot be extrapolated to other sites where *Z. muelleri* might be near the limits of its temperature tolerance, or subjected to numerous other stressors (e.g. reduced light or extreme salinity) which may compound temperature effects and result in losses of seagrass (Kendrick et al., 2019; McMahon et al., 2022). We found differences in the species' growth and morphology were generally better related to sediment organic matter content, season and shoot density than to elevated water temperature. Such findings underscore the importance of considering these factors when investigating the response of seagrasses to climate change.

Although it is well known that extreme temperatures adversely impact seagrasses (Nguyen et al., 2021), the limited effect on the persistence and growth of *Z. muelleri* in the current study was likely attributable to temperatures not surpassing critical thresholds in terms of magnitude and duration. Research on various seagrasses has reported that high temperatures can reduce photosynthetic capacity, plant growth and cause mortality (Campbell et al., 2006; Collier & Waycott, 2014; Koch et al., 2007; Olsen et al., 2012; Ralph, 1998; Sawall et al. 2021; York et al., 2013). For *Z. muelleri*, the optimum temperature for growth is ~ 27 °C, while temperatures of 32–33 °C have been shown to generate significant shoot loss and mortality (Collier et al., 2011; York et al., 2013). However, these prior investigations reporting shoot loss and mortality involved continual exposure

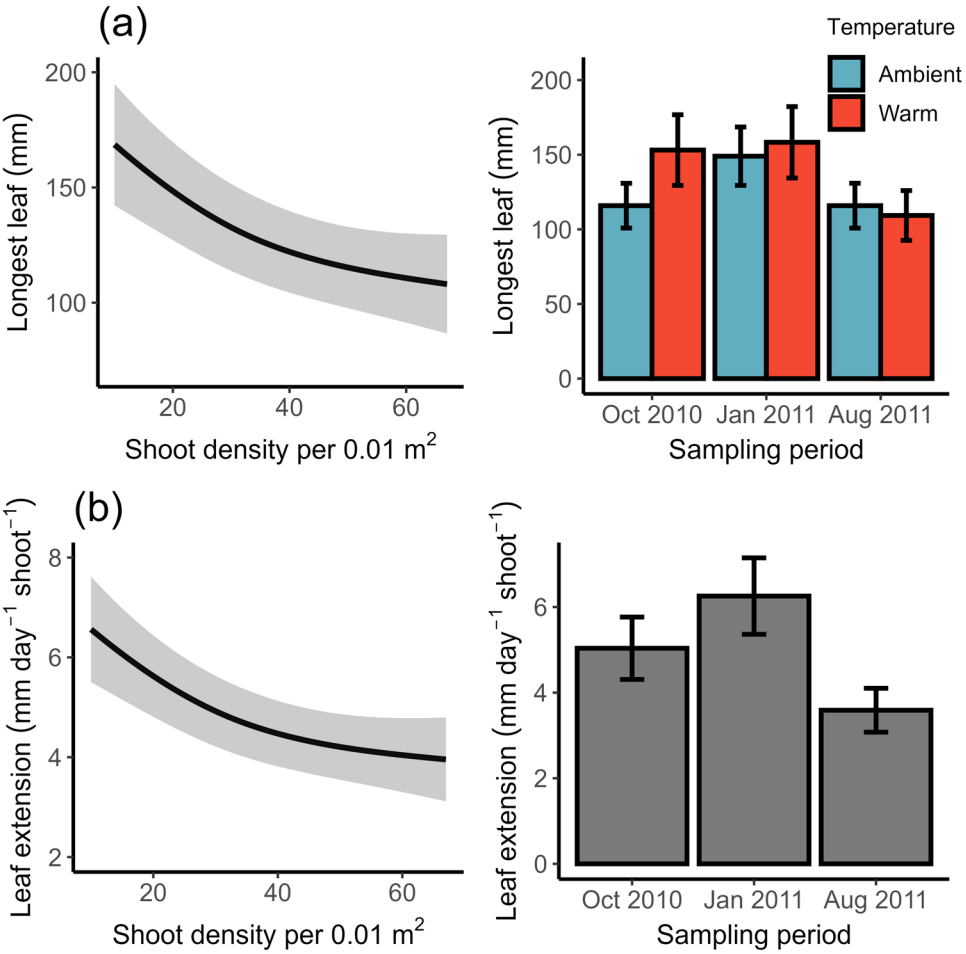

Fig. 4 Relationships from generalised additive mixed models between significant explanatory variables and **a** Longest leaf (mm), and **b** Leaf extension (mm day^{-1} shoot^{-1}). Fitted GAMM prediction curves (solid line) are included, and ribbons and error bars represent ± SE

to elevated temperatures for 35 to 42 days. In our study, maximum temperatures of 32 °C were recorded only in the warm water plume for a few hours on 3 days in January 2011 (summer). It is also possible that seagrass in our study had become adapted to the elevated temperatures given its exposure over decadal scales, whereas this would not occur in short-term experiments. Nevertheless, our results suggest that *Z. muelleri* can tolerate at least brief periods of exposure to temperatures of 32 °C, which aligns to the findings of a previous study (Campbell et al., 2006).

Zostera species are found across a diverse range of environmental settings (Short et al., 2007), so they may be more susceptible to elevated temperatures in particular conditions. For example, in eastern Australia, *Z. muelleri* is abundant throughout temperate and tropical waters and grows in a wide range of light, temperature and salinity conditions, including intertidal and brackish zones (Ferguson et al., 2018; Kilminster et al., 2015; West, 2010; West & Glasby, 2022). Indeed, *Z. muelleri* leaf growth has been shown to be more closely linked to light intensity and day length than to ambient temperature (Kerr & Strother, 1989). Considering our study was in the temperate waters of Lake Macquarie near the middle of the species' distribution, it was somewhat unsurprising that approximately 2 to 3 °C warmer water did not have a great effect. The species is likely to be more susceptible to such temperature increases in tropical locations, where long-term summer water temperatures will likely exceed 33 °C (Collier et al., 2011). Conversely, leaf growth rates and above-ground biomass may be enhanced by warmer waters in the southern parts of the species' distribution. We observed this trend in October (spring) within the warm water plume, coinciding with the largest temperature differential of any sampling period (+2.7 °C), as predicted. Similarly, previous research on *Z. marina* in mesocosms found elevated temperatures (+3.6 °C) resulted in higher growth relative to ambient temperatures in spring, whereas this pattern was reversed in summer (Sawall et al. 2021). Moreover, another study in Lake Macquarie also documented comparable patterns in the warm water plume in spring and pointed to the effects of temperature on the seagrass microbiome (Walker et al., 2024). This sort of indirect effect of climate change warrants more investigation, and future studies should aim to disentangle the roles of seagrass density, sediment conditions and season on the seagrass microbiome.

Despite no clear effect of elevated temperatures on seagrass growth and morphology, we observed patterns consistent with seasonal influences that generally followed trends reported in the literature. Numerous species of seagrass exhibit peaks in growth and biomass in summer or late spring and decreases over winter (Bulthuis & Woelkerling, 1983; Guidetti et al., 2002; Kerr & Strother, 1989, 1990; Kirkman et al., 1982; Lee et al., 2005; McKenzie, 1994; Olesen & Sand-Jensen, 1994b). In the current study, *Z. muelleri* mean daily leaf extension was lowest in winter (3.58 mm ± 0.51 SE) and greatest in summer (6.26 mm ± 0.89 SE), which aligns with previous work on the species (Kerr & Strother, 1989; Kirkman et al., 1982). Conversely, the limited seasonal effect we observed on above-ground biomass was unexpected. We did not document a large winter 'dieback' shown previously for some *Zostera* species (e.g. Lee et al., 2005; Olesen & Sand-Jensen, 1994a), including *Z. muelleri* in New South Wales (Kirkman et al., 1982), Queensland (McKenzie, 1994) and Victoria (Kerr & Strother, 1990), with one site in the latter study experiencing a 40-fold winter decline in above-ground biomass. The elevated below-ground biomass in ambient conditions during August (winter), and concomitant lower AGB:BGB ratio, was also unexpected. This pattern may reflect a strategy to store reserves to endure cooler temperatures; species of *Zostera* typically allocate biomass to below-ground structures during spring and summer periods, which are then depleted during winter (Collier et al., 2017; Lee et al., 2007). However, this general trend can be highly variable among sites. For instance, both Kerr and Strothers (1990) and Kirkman et al. (1982) reported peaks in below-ground biomass comparable to summer levels in August or September at one of their two sites. It is possible that the lack of seasonal effects at some sites may represent plasticity to other factors such as differences in exposure levels, hydrodynamics, salinity and light gradients which can affect seagrass morphology (Lirman & Cropper, 2003; Collier et al., 2007; Kohlmeier et al., 2014; Ferguson et al., 2016; Andrews et al., 2023). These results question the prevailing notion that season is the main driver for seagrass biomass and point to the need to examine seasonal differences across multiple spatial and temporal scales while accounting for important co-variables such as sediment properties and seagrass density.

Previous research has identified negative effects of high sediment organic matter on seagrass morphometrics and growth, due to the promotion of anaerobic decomposition and production of toxic sulphides and ammonium (de Boer, 2007; Govers et al., 2014; Han et al., 2017; Holmer & Kendrick, 2012; Pérez et al., 2007). It has been suggested that the growth of aquatic macrophytes, including seagrasses, is typically limited to sediments containing less than 5% organic matter, although seagrasses with large leaves persist in sediments up to 16.4% (Barko & Smart, 1983; Kennedy et al., 2010; Koch, 2001; Wicks et al., 2009). In the current study, however, we reported increased below-ground biomass in locations with higher organic matter and a subsequent reduction in the AGB:BGB ratio. The unexpected positive relationship between organic matter and below-ground biomass may be due to the low concentrations in the sediments at the study locations, which were typically less than 3.3% when averaged at the site level. The low AGB:BGB ratios observed in this study (< 0.5) are similar to those previously reported in sediments with low organic matter in shallow meadows in Lake Macquarie (Ferguson et al., 2016) and New Zealand (Matheson & Schwarz, 2007), although the latter study reported a negative trend between organic matter and both seagrass cover and below-ground biomass. Ferguson et al. (2016) suggested that low AGB:BGB ratios represent a morph of *Z. muelleri* which allocates resources to below-ground biomass to access nutrients via the remineralisation of organic matter within the rhizosphere. Therefore, the increased below-ground biomass in relation to greater organic matter could allow nutrient uptake and seagrass growth in oligotrophic estuaries like Lake Macquarie, which are common in south-eastern Australia (Ferguson et al., 2018).

The structure and density of seagrass meadow canopies can greatly influence light attenuation and have important ramifications for seagrass morphology and growth (Bjork et al., 2021; Enriquez & Pantoja-Reyes, 2005; Enriquez et al., 2019; Hedley et al., 2014; Rattanachot et al., 2016). Seagrasses are susceptible to self-shading effects, particularly when meadows are dense, and several studies have reported negative relationships between shoot density and leaf growth, length or biomass (Bjork et al., 2021; Enriquez et al., 2019; Rattanachot et al., 2016). Our results were consistent with self-thinning effects in meadows of *Z. muelleri*, with higher shoot densities linked to lower rates of leaf growth and length. This relationship has been reported for other seagrass species (Enriquez et al., 2019), with light interception by *Z. marina* canopies ranging between 40 and 60%, and self-shading being similar among sites due to leaf length increasing where shoot density was reduced (Bjork et al., 2021).

Environmental conditions such as light availability and salinity are key determinants of seagrass growth, morphology and distribution, and these factors often interact with temperature (Bulthuis, 1983; Lee 2007; Lirman & Cropper, 2003; Ralph et al., 2007; Salo & Pedersen, 2014). For example, the optimal temperature for seagrass photosynthesis decreases under low-light conditions, meaning that while plant growth increases with rising temperatures in high-light environments, it declines when light is limited (Bulthuis, 1987; Lee et al., 2007). Consequently, as water temperatures rise due to climate change, seagrasses in low-light environments may be more vulnerable compared to those in areas

where light is saturating. In the current study, data on light and salinity differences between sites were unavailable, although we suggest that light was not limiting given that sites were shallow (~0.5 m at low tide), and *Z. muelleri* grew to ~2 m depth (unpubl. data). While previous research on *Z. muelleri* reports few interactive effects between temperature and light (York et al., 2013), future studies should consider whether the ability of seagrasses to withstand elevated temperatures may be compromised under certain light, salinity and sediment conditions.

Thermal plumes provide an opportunity to study the adaptive responses of aquatic organisms to elevated temperatures and may offer more realistic environmental conditions over extended timeframes than laboratory or manipulative experiments (e.g. Garthwin et al., 2014; Keser et al., 2005; Mulhollem et al., 2016; Walker et al., 2024). In the current study, *Z. muelleri* populations in Myuna Bay had been exposed to elevated temperatures for ~26 years. It is possible that a bottleneck event occurred when the power plant became operational, with the surviving genotypes that recolonised Myuna Bay being more tolerant to elevated temperatures than populations elsewhere. Genetic adaptation to warm temperatures has been documented for *Z. marina* (Jueterbock et al., 2016) and can involve epigenetic modification related to thermal priming as identified in laboratory studies with *Z. muelleri* (Nguyen et al., 2020). Future studies could therefore examine whether the seagrass populations inside versus outside of the thermal plume respond differently to elevated temperatures and whether this corresponds to genetic variation. However, the most parsimonious explanation for the tolerance of *Z. muelleri* to elevated temperatures in Lake Macquarie is that these temperatures are within the species' natural range.

In conclusion, this study demonstrated the tolerance of *Z. muelleri* populations to future warming of marine waters in the central part of its distribution in NSW, Australia, tolerating elevated temperatures predicted to occur by 2090 under RCP 8.5 (CSIRO and BOM 2015). The limited effects of elevated temperatures at this location are encouraging considering predicted future warming and the numerous ecosystem functions and services that *Z. muelleri* provide, such as providing essential fish habitat (Blandon & Ermgassen, 2014; Connolly, 1994; West & King, 1996). However, there may still be potential effects of warming on reproductive output or timing (Díaz-Almela et al., 2009; Sawall et al. 2011; Lekammudiyanse et al., 2024), seed germination (Moir et al., 2024), or from marine heatwaves which can have a rapid onset and are predicted to become more frequent and intense (Hobday et al., 2018; Oliver et al., 2018). Although the extent to which marine heatwaves influence estuarine waterbodies remains unclear, they have led to seagrass die-back in more oceanic environments where species were growing near their physiological limits (Moore & Jarvis, 2008; Seddon et al., 2000; Strydom et al., 2020). Our findings also do not account for how temperature influences seagrass in the presence of other impacts associated with anthropogenic processes and climate change (e.g. changes in rainfall patterns, extreme events) or the presence of interactive or cumulative effects (Moreno-Marín et al. 2018; Rasheed & Unsworth, 2011; Rees et al., 2023; York et al., 2013). Overall, our research highlighted that near the centre of its latitudinal distribution, environmental factors such as sediment organic matter content, season and shoot density are generally better predictors of *Z. muelleri* growth and morphology than moderate (+1.4–2.7 °C) elevated temperatures. Such findings reinforce the need to consider the various factors known to influence seagrass growth when testing for impacts of future climate change.

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Declarations

Conflict of Interest The authors declare no competing interests.

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