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## Seagrass tolerance to herbivory under increased ocean temperatures

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## ABSTRACT

Climate change is acknowledged as a major threat to marine ecosystems, but the effect of temperature on species interactions remains poorly understood. We quantified the effects of long-term warming on plant–herbivore interactions of a dominant seagrass, *Zostera muelleri*. Growth, herbivory and tolerance to damage were compared between a meadow warmed by the thermal plume from a power station for 30 years (2–3 °C above background temperatures) and three control locations. Leaf growth rates and tissue loss were spatially variable but unrelated to temperature regimes. Natural herbivory was generally low. Simulated herbivory experiments showed that the tolerance of *Z. muelleri* to defoliation did not differ between warm and unimpacted meadows, with damaged and undamaged plants maintaining similar growth rates irrespective of temperature. These results suggest that the ability of temperate *Z. muelleri* to tolerate herbivory is not strongly influenced by warming, and this species may be relatively resilient to future environmental change.

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## 1. Introduction

Climate change presents a major threat to biodiversity and ecosystems worldwide, and understanding how ecological processes may be impacted is essential for future management and conservation efforts. Increasing temperature is arguably one of the most significant changes occurring as a result of climate change, as temperature is one of the key determinants of biological processes, both physiological and ecological (IPCC, 2007). Global average sea surface temperatures have increased by about 0.74 °C in the last 100 years, and a further increase of 2–3 °C is predicted to occur by 2050 (IPCC, 2007). The direct effects of climate change have now been well-documented on many individual species, including changes in the physiology, distribution, and phenology of species in both terrestrial and aquatic systems (Parmesan, 2006; Hoegh-Guldberg and Bruno, 2010). Far fewer studies have addressed the effect of warming on species interactions in the ocean (Wernberg et al., 2012). However, evidence increasingly shows that changes in species interactions can be crucial in determining community responses to climate change, as effects on one trophic level trigger knock-on effects on other levels (Harley, 2011; Zarnetske et al., 2012). Such changes in predator–prey or competitive interactions may occur through population level variations to the

relative abundance of interacting species, or by causing shifts in *per capita* interaction strength (Kordas et al., 2011; Van der Putten et al., 2010).

Marine herbivores strongly control the abundance of primary producers (algae and seagrasses) in coastal habitats (Poore et al., 2012) and warming temperatures may influence the strength of this top-down control by affecting the abundance and distribution of producers or herbivores (Wernberg et al., 2011), the per-capita consumption rates (e.g., O'Connor, 2009; Yee and Murray, 2004), the rates of primary production (Raven and Geider, 1988), or the plant traits that affect their susceptibility to herbivores (e.g., C:N ratio: Staehr and Wernberg, 2009 or defensive secondary metabolites: Sudatti et al., 2011). Such alterations to plant–herbivore interactions result in temperature indirectly affecting multiple species, which can potentially reverse the direct negative effects of climate change (Suttle et al., 2007) and will complicate predictions of temperature impacts based on studies with single species (Connell et al., 2011).

In this study, we aim to examine the effect of temperature on plant–herbivore interactions in a temperate seagrass. Seagrass meadows are a highly productive habitat in near-shore systems throughout the world and support extensive food webs, aid in nutrient cycling, provide protection against erosion, and serve as nursery habitats for a variety of economically important fish and invertebrates (Orth et al., 2006). Despite their economic and ecological importance, seagrass meadows are declining at an alarming rate around the world (Duarte, 2002; Orth et al., 2006), and are now considered among the most vulnerable ecosystems

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on earth (Waycott et al., 2009). The factors causing this decline include nutrient pollution, coastal developments, and climate change (Orth et al., 2006).

The role of herbivory in seagrass population dynamics has been poorly studied compared to other communities (Valentine and Duffy, 2006). Although direct herbivory of seagrasses is relatively low in contrast to other marine primary producers (Poore et al., 2012), intense grazing, albeit temporally and spatially highly variable, has been recorded in many species (Valentine and Duffy, 2006) and there is now clear evidence of the central importance of grazing in structuring these communities (Heck and Valentine, 2006; Prado et al., 2007). Organisms that are known to feed directly on seagrasses include vertebrate herbivores (fishes, turtles and dugongs), sea urchins, and mesograzers (amphipods, isopods and small gastropods) that usually feed on epiphytes attached to the seagrass leaves (Valentine and Duffy, 2006). While the direct effects of temperature on seagrass metabolism and growth rate are relatively well known (Campbell et al., 2006), far less is known about how temperature alters the trophic interactions between seagrasses and their consumers. This interaction may be influenced by changes to the traits of seagrasses that affect their susceptibility to herbivores (Koch et al., 2013), and/or by changes to growth rates, that are likely to alter the ability of seagrasses to tolerate tissue loss to herbivores. Compensatory growth is one of the most important mechanisms of defence used by seagrasses to tolerate herbivory, whereby plants compensate for biomass loss to herbivory via regrowth (Valentine et al., 1997; Vergés et al., 2008).

In this study, a warm-water plume created by a power station and impacting meadows of the seagrass *Zostera muelleri* in Lake Macquarie (NSW, Australia) was used to predict the effects of ocean warming on seagrass–herbivore interactions *in situ*. Thermal plumes from power stations have been used as a proxy for climate change in other parts of the world, with evidence of ecological changes to marine environments as a result of elevated water temperature (Thorhaug et al., 1978; Schiel et al., 2004; Keser et al., 2005; Steinbeck et al., 2005). Seagrass beds in Myuna Bay in Lake Macquarie have been exposed to warming from the Eraring Power Station thermal effluent since 1982, with logged temperatures being consistently 1–3 °C higher than background levels from nearby sites since the early 1980s (AWACS, 1995; Eyre, 2005). The temperature increase experienced at Myuna Bay is therefore similar to that predicted to occur globally by 2050 (IPCC, 2007). This system thus provides an opportunity to measure the effects of a prolonged, persistent increase in temperature of an ecologically relevant magnitude on the seagrass communities that have adapted to their new conditions, a more realistic representation of climate change impacts on species interactions than short-term thermal stress studies. In contrast, most studies testing the effects of warming have moved organisms from ambient conditions to elevated temperatures within short time frames, either in a laboratory (e.g. Campbell et al., 2006); or, rarely *in situ* (Morelissen and Harley, 2007; Smale et al., 2011).

The specific aims of this research are: (1) to quantify existing levels of seagrass herbivory and determine whether underlying levels of grazing are affected by thermal plume warming; (2) to determine if growth rates of *Zostera muelleri* shoots are affected by warming; and (3) to establish whether the ability of seagrasses to tolerate herbivory via re-growth is influenced by temperature using a simulated herbivory experiment.

## 2. Materials and methods

### 2.1. Study site and species

Experiments were carried out between April and June 2012 at Lake Macquarie, a coastal estuarine lake located on the temperate

southeast coast of Australia that hosts extensive seagrass meadows dominated by *Zostera muelleri* (syn. *capricorni*). *Z. muelleri* is one of the most common seagrass species found along the east coast of Australia, thriving in inshore areas such as sheltered bays and estuaries (Moore and Short, 2006). The timing of this study (Autumn) falls between the maximum (summer) and minimum (winter) periods of growth for *Z. muelleri* (Kirkman et al., 1982).

Four sampling sites were chosen within Lake Macquarie (Fig. 1). The impacted site, Myuna Bay (151°32'48.1" E, 33°03'58.6" S), is situated close to the thermal plume from the Eraring power station (0.91 km from the output) and is exposed to elevated water temperatures (AWACS, 1995; Eyre, 2005; Ingleton and McMinn, 2012). Three control sites were selected based on the presence of *Z. muelleri* meadows at 0–1 m depth, accessibility and a similar distance from Eraring power station (between 3.1 and 5.3 km away): Wangi (151°34'57.6" E, 33°03'54.2" S), Sunshine (151°33'53.5" E, 33°06'27.9" S) and Rathmines (151°35'50.13" E, 33°02'30.15" S). These sites were all similarly affected by human activities in the lake and comparably removed from known sources of industrial selenium pollution (Peters et al., 1999). Water temperature at each site was measured using a temperature logger (Onset HOB0 Pendant® Temperature/Light Data Logger 64 K, accuracy ±0.53 °C). Each logger was held approximately 3 cm over the sediment and anchored with a vertical steel peg that was pushed deep into the sediment. Temperature loggers recorded temperature continuously every 60 min for 3 months between June and September 2012.

### 2.2. Rates of growth and leaf loss

To quantify natural herbivory on *Zostera muelleri* at all four sites in Lake Macquarie, rates of absolute leaf loss in seagrass meadows were contrasted to loss within cages that excluded large herbivores. Growth rates of *Z. muelleri* were also measured at each site in both caged and uncaged plots to determine if seagrass growth was affected by thermal plume warming. These values were used to calculate the percentage of primary production lost to grazers.

Forty seagrass shoots from each site were haphazardly selected and removed from the sediment. The length, width and number of leaves were recorded on individually numbered shoots, which were tagged using the hole-punch method, whereby each shoot is marked with a needle at the basal meristem (Short and Duarte, 2001). This scars all leaves within the leaf sheath and allows measurement of growth as displacement from the meristem after a certain number of days. Shoots were haphazardly allocated one of two treatments: caged shoots were enclosed within a herbivore exclusion cage and then pegged back into the sediment, while exposed shoots were pegged without any cages and therefore were fully available to herbivores. Herbivore exclusion cages were cone shaped and had a mesh size of 1 cm<sup>2</sup>. We aimed to exclude only large herbivores such as the herbivorous leatherjackets *Meuschenia trachylepis* and *Monacanthus chinensis*, and the garfish *Hyporhamphus australis* and *Hyporhamphus regularis ardelio*, all of which have been observed to feed on *Zostera muelleri* in Lake Macquarie (Thomson, 1959; Carseldine and Tibbetts, 2005). Although cages can potentially introduce artefacts, pilot experiments with 54 independent shoots at three sites for which we did not record any leaf damage due to herbivory, showed no significant effects of cages on the parameters measured over the short duration of the experiment (leaf growth  $F_{1,2} = 0.03$ ,  $P = 0.87$ ; leaf loss  $F_{1,2} = 0.09$ ,  $P = 0.79$  in analyses of variance with caging as a fixed factor and site as a random factor). With no caging effects in this pilot study, and in other similar studies with seagrasses (McGlathery, 1995; Maciá, 2000), cage controls were therefore not used. Epiphyte cover was very low in all treatments across all sites and was therefore not quantified.

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