

# Ocean warming, but not acidification, accelerates seagrass decomposition under near-future climate scenarios

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**ABSTRACT:** The majority of marine macrophyte production is not consumed by herbivores but instead is channeled into detrital pathways where it supports biodiversity and drives coastal productivity, nutrient cycling and blue carbon sequestration. While it is clear that detrital pathways will be affected by ocean climate change, the relative importance of changing temperature or pH, or their interactions, has not been assessed. We used outdoor mesocosm experiments to assess the relative importance of ocean warming, acidification and latitude of litter origin on the decomposition and biomechanical properties of seagrass *Zostera muelleri*. Seagrass, collected from 2 sites at each of 2 latitudes (29° and 35° S), was subjected to an orthogonal combination of current and predicted future ocean warming (+3°C) and acidification (−0.3 pH unit). Elevated temperatures resulted in a 15% greater loss of seagrass detrital mass. Mass loss of seagrass detritus was also greater in seagrass from higher than from lower latitudes. The stiffness (Young's modulus) of decomposing seagrass was greater at 22°C than at 25°C. Elevated sea temperatures also weakened decomposing seagrass, but the magnitude of these effects was greater for *Z. muelleri* originating from higher than from lower latitudes. Overall, ocean warming is likely to have a much larger influence on seagrass decomposition than ocean acidification. As climate changes, however, if seagrass from higher latitudes takes on similar characteristics to seagrass currently growing at lower latitudes, there may be a negative feedback against the impacts of ocean warming on decomposition, moderating changes in associated primary and secondary productivity that supports coastal fisheries and ecosystem processes.

**KEY WORDS:** Ocean climate change · Ocean warming · Acidification · Seagrass · Decomposition · Eelgrass · *Zostera*

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## INTRODUCTION

Anthropogenic climate change, and the associated CO<sub>2</sub> enrichment of oceans, is impacting marine ecosystems (Hoegh-Guldberg & Bruno 2010, Doney et al. 2012). Ocean warming and acidification (hereafter collectively referred to as ocean climate change) can affect the performance of individual species (Kordas et al. 2011, Koch et al. 2013), their ecological inter-

actions (Provost et al. 2017) and the structure of the communities in which they reside (Wernberg et al. 2016). Additionally, ocean climate change may impact ecosystem processes, such as nutrient cycling and the decomposition of detritus (i.e. non-living organic matter) (Kelaher et al. 2013). Changes in detrital dynamics are of particular interest because detritus underpins diverse food webs through its provision of food and habitat (Moore et al. 2004), en-

hances fisheries production (Connolly & Waltham 2015), influences greenhouse gas dynamics (Pendleton et al. 2012) by determining whether carbon is sequestered or remineralized (Duarte et al. 2013) and drives nutrient cycling (Mann 1988, Eyre et al. 2011).

Ocean climate change may change marine detrital dynamics by altering the traits, productivity and species composition of primary producers, which supply the bulk of detritus to ecosystems (Cebrian 1999, Bishop & Kelaher 2013). Ocean warming is already changing the composition of aquatic macrophyte communities (e.g. loss of kelp beds, Wernberg et al. 2016), which in turn influences the physical and chemical traits of detritus entering ecosystems (Arnold et al. 2012, Duarte et al. 2013). Within species, leaf traits such as carbon to nitrogen ratios and concentrations of phenolics, which are important determinants of decomposition rates, vary across climatic gradients (Ainley et al. 2016). Ocean acidification could also affect detrital decomposition through increasing carbon availability to living macrophytes, which in turn results in elevated lignin content in tissues, slowing decomposition rate and the overall mineralization of organic matter (Mann 2000). Similarly, when ocean warming and acidification affect living macrophyte growth rates, surface area to volume ratio, structural complexity, carbon, nutrients and secondary metabolites (e.g. Short & Neckles 1999), there will be flow-on effects to detrital processes when they die or shed material (e.g. Mann 1988, Holmer & Bachmann Olsen 2002, Moore et al. 2004). Furthermore, ocean climate change may affect the magnitude and frequency of detrital enrichment events through increased storm intensity (Bishop & Kelaher 2007) and production of opportunistic marine algae (e.g. Davis et al. 2017, Provost et al. 2017). This may result in more labile detritus entering benthic systems, which would initially increase production and organic matter mineralization (Kelaher & Levinton 2003, Kelaher et al. 2013), but could also lead to anoxia, decreased denitrification efficiency and enhanced benthic ammonium fluxes (Lavery & McComb 1991).

Ocean climate change will also alter the abiotic conditions that regulate detrital decomposition (Ainley & Bishop 2015). Elevated ocean temperatures, for example, increase the rate of breakdown of detritus by accelerating leaching, altering metabolic processes in microbes (Pedersen et al. 2011) and influencing detritivore assemblages (Kristensen et al. 1992). Although elevated ocean temperatures usually result in greater rates of organic matter mineralization, there are thresholds beyond which

microbial processes break down (Weston & Joye 2005). As oceans become more acidic, we could also expect increased detrital decomposition and dissolution, particularly for calcified macrophytes, such as coralline algae. However, the role that ocean acidification may play in macrophyte decomposition has yet to be addressed. Filling this knowledge gap will improve predictions of ecosystem responses to future ocean climate change (Wernberg et al. 2012), providing insight into what this could mean for nearshore fisheries, nutrient dynamics and blue carbon sequestration.

Here, we investigate how the effects of ocean warming and acidification interact to influence biomass loss, biomechanical integrity and changes in carbon and nitrogen composition of decomposing seagrass. To increase the generality of our results, and to assess how indirect effects of climate on intraspecific variation in leaf traits interact with its direct effects on the physical environment, we included seagrass from 2 different latitudes that are ~650 km apart and have a difference in mean water temperature of ~2°C (Table S1 in the Supplement at [www.int-res.com/articles/suppl/m605p103\\_supp.pdf](http://www.int-res.com/articles/suppl/m605p103_supp.pdf)). We also assess how the biomechanical properties of decomposing seagrass, which in turn may influence the susceptibility of litter to fragmentation by shredders and physical processes, may be impacted by ocean climate change. We focused on detritus from seagrass *Zostera muelleri* (Jacobs et al. 2006), which has a broad distribution around much of Australia, southern Papua New Guinea and New Zealand and is a structural analogue to other *Zostera* spp. distributed globally. Specifically, we tested the hypotheses that (1) the loss of biomass and biomechanical integrity of decomposing seagrass *Z. muelleri* will increase with ocean temperature and acidification and will be influenced by the latitude where the seagrass was grown and (2) ocean temperature and acidification will influence changes in the elemental composition of decomposing seagrass.

## MATERIALS AND METHODS

### Seagrass collection and preparation

Entire blades of seagrass *Zostera muelleri* were collected from 4 estuarine sites situated at each of 2 latitudes (~29° and ~35° S) along the east coast of Australia. Two estuaries were located on the north coast (Sandon River [29° 40' 26.94" S, 153° 19' 27.53" E] and Wooli River [29° 52' 53.98" S, 153° 15' 54.11" E])

and 2 on the south coast of New South Wales (NSW) (Callalla Bay [35° 00' 32.03" S, 150° 43' 2.30" E] and Sussex Inlet [35° 09' 54.72" S, 150° 08' 36.73" E]) about 650 km south of the northern sites (Table S1 in the Supplement). Each estuary was classified as an intermediate to mature, wave-dominated estuary or embayment (Roy et al. 2001, Roper et al. 2011), with an average tidal range of 1.5 m. The latitudinal difference between the northern and southern sites created a temperature difference of  $\sim 2^\circ\text{C}$  (Table S1; Ainley & Bishop 2015). To characterize the %C, %N and C:N ratio of seagrass used in the experiment, three  $\sim 20$  g samples of seagrass from each site were dried at  $60^\circ\text{C}$  to a constant weight and the percentage of elemental carbon and nitrogen determined using a Thermo Finnigan Flash 1112EA interfaced via a Thermo ConFlo III with a Thermo Delta IV Plus isotope ratio mass spectrometer (IRMS) (see 'Experimental design and sampling' for detailed methods and Table S1 for results). By chance, there was a site that had seagrass with a relatively high ( $\sim 30$ ) and low ( $\sim 18$ ) C:N ratio at both northern and southern latitudes (Table S1).

Upon collection, *Z. muelleri* blades were transported to the laboratory in ice-chilled coolers and refrigerated at  $8^\circ\text{C}$ . Within 48 h of collection, seagrass blades were cleaned of epiphytes by gently scraping with a plastic ruler and towel dried. Seagrass from each site was weighed into forty-eight 10 g portions, each of which was placed into a 1 mm nylon mesh litter bag (100 mm length  $\times$  100 mm width) (N = 196 litter bags). Previous sampling of the 4 study sites across a number of seasons (Ainley et al. 2016) revealed no significant difference between latitudes or sites in specific leaf area (i.e. leaf area to dry mass ratio), one of the leaf traits that may influence decomposition rate (Cornelissen & Thompson 1997). To determine an average wet to dry weight conversion factor, five  $\sim 7$  g seagrass samples from each site were weighed following towel drying and then reweighed again after drying at  $60^\circ\text{C}$  to constant weight. Dry weights were converted to equivalent wet weights for detrital mass loss calculations.

### Experimental design and sampling

Seagrass in litter bags was exposed to ocean warming and acidification within a flow-through aquarium system at the National Marine Science Centre in Coffs Harbour (35° 00' 32.03" S, 150° 43' 2.30" E), NSW, Australia. The experiment had crossed factors of warming (2 levels: current [ $\sim 22^\circ\text{C}$ ] and future

[ $\sim 25^\circ\text{C}$ ]) and acidification (2 levels: current [ $\text{pH}_T = \sim 8.07$ ;  $\text{pCO}_2 = \sim 370 \mu\text{atm}$ ] and future [ $\text{pH}_T = \sim 7.78$ ,  $\text{pCO}_2 = \sim 800 \mu\text{atm}$ ]) (see Table S2 for details), with the ambient conditions representing approximately the average summer conditions of the NSW coast and the future conditions corresponding to RCP 8.5 model predictions for 2081 to 2100 (Collins et al. 2013). This design produced 4 ocean climate change treatments.

Sixteen litter bags (4 of each seagrass source) were deployed randomly in each of 12 large trays in an outdoor aquarium facility. Each litter bag was attached to a weighted plastic mesh to ensure it sat flat on the bottom of the tray and did not overlap with other litter bags. The trays had been randomly assigned to 1 of the 4 ocean climate change treatments, to give  $n = 3$  of each. Each tray was 860 mm long  $\times$  650 mm wide  $\times$  96 mm deep and received seawater from its own header tank at  $3 \text{ l min}^{-1}$ . Each of the 12 header circular tanks was 1100 l (1350 mm diameter  $\times$  900 mm depth) and received seawater that was pumped from the adjacent ocean and filtered by a  $50 \mu\text{m}$  filter. Water temperature was controlled using heater-chiller units (Aqua hort), and pH was manipulated by bubbling in ambient or  $\text{CO}_2$ -enriched air via a gas mixer (PEGAS 4000MF). Water temperature, conductivity and pH were measured daily in each sea tray using a Hach HQ40d multiprobe. The pH probe was calibrated using NIST buffers with readings subsequently converted to  $\text{pH}_T$  following methods outlined in SOP 6a (Dickson et al. 2007). Total alkalinity ( $A_T$ ) for the system was measured daily using Hg-fixed water samples and a potentiometric titration (888 Titrand, Metrohm). Concentrations of the  $\text{pCO}_2$ , the saturation states of calcite ( $\Omega_{\text{calc}}$ ) and aragonite ( $\Omega_{\text{arag}}$ ) and the concentrations of carbonate ( $\text{CO}_3^{2-}$ ) and bicarbonate ( $\text{HCO}_3^-$ ) were subsequently calculated from the  $A_T$ ,  $\text{pH}_T$  and temperature measurements with constants from Mehrbach et al. (1973), as adjusted by Dickson & Millero (1987).

Seagrass blades were allowed to decompose under the experimental conditions for up to 40 d. At Days 5, 10, 20 and 40 of the experiment, 1 litter bag from each site was collected. For each time of sampling, the dry weight of seagrass in each litter bag was determined after drying to constant weight at  $60^\circ\text{C}$ . From the mass loss in the litter bags, the decay constant  $k$  and half-life  $t_{1/2}$  of decomposing seagrass in the various treatments were also calculated and analyzed using methods outlined in Table S3 in the Supplement.

At the final time of sampling, 5 entire and intact seagrass blades were randomly selected prior to oven

drying and their lengths, widths and thicknesses measured using precision calipers ( $\pm 0.01$  mm). These blades were subject to tensile testing using an Instron 5542 with pneumatically controlled clamps following Nicastro et al. (2012). Each blade was placed lengthways between 2 pneumatic clamps that gradually separated at a rate of  $0.17 \text{ mm s}^{-1}$ . For each blade, the force and the displacement were recorded at 0.1 s intervals until the leaf broke. The force ( $F$ ) and elongation of the leaf ( $\delta$ ) at failure, the cross-sectional area of the leaf ( $A$ ) and the starting distance between the 2 clamps ( $L_0$ ) were used to calculate the ultimate tensile stress (UTS), the maximum stress a material can withstand while being stretched or pulled before failing or breaking:

$$\text{UTS} = F/A \quad (1)$$

and Young's modulus ( $E$ ), the stiffness of decomposed blades, was used in this instance for the ultimate tensile stress:

$$E = \frac{F/A}{\delta/L_0} \quad (2)$$

Toughness (the energy that the leaf can absorb before breakage) was calculated as the area under the force by displacement curve using the trapezoidal rule (trapz function within the package pracma in R).

After tensile testing, the seagrass in each litter bag collected on Day 40 was dried at  $60^\circ\text{C}$  to a constant weight. Each sample was then ground to a homogenized powder using a ball and mill, and an  $\sim 2.3$  mg portion of each ground sample was weighed into  $8 \times 6$  mm tin capsules and sampled for %C, %N and C:N ratio using a Thermo Finnigan Flash 1112EA interfaced via a Thermo ConFlo III with a Thermo Delta IV Plus IRMS. Samples were run bracketed by working standards calibrated against relevant international standards (NBS19 and LSVEC for C, IAIA N1 and N2 for N) with 0.1 ppt precision.

### Statistical analyses

Permutational analyses of variance (PERMANOVAs using PRIMER 6.0 and PERMANOVA+ add-on) (Anderson et al. 2008) were used to evaluate the influence of ocean warming, ocean acidification and seagrass source latitude on the loss of seagrass detrital mass as well as the percentage change in %C, %N and C:N ratio and the Young's modulus ( $E$ ), ultimate tensile stress and toughness of seagrass blades. These analyses had 5 factors: temperature (2 levels, orthogonal and fixed), acidification (2 levels, orthogonal and fixed), latitude (2 levels, orthogonal and

fixed), sites (4 levels, random and nested in latitude) and tray (12 levels, random and nested in temperature and acidification). All univariate PERMANOVA analyses used Euclidean distances on untransformed data. A multivariate PERMANOVA analysis of seagrass mass loss was undertaken using detritus remaining at each time of sampling to provide replicate time series for each treatment in each tray. These multivariate analyses used Euclidean distances on  $\ln(x)$ -transformed data. Figs. 1 & 2 show only main effects because there were no significant interactions involving temperature, acidification or latitude for mass loss. Full details of analyses are reported in Tables S4–S6 in the Supplement.

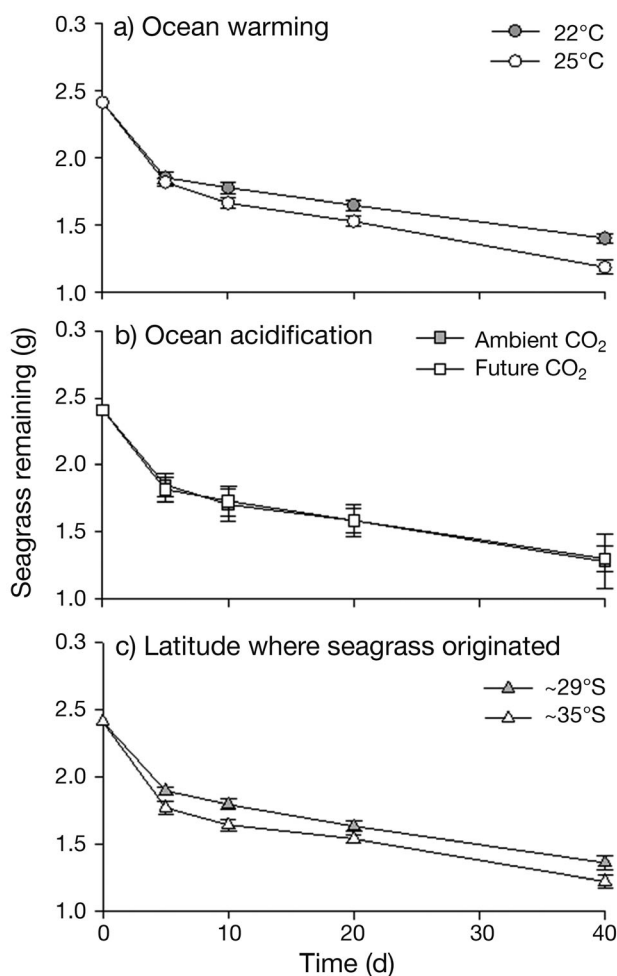


Fig. 1. Effects of (a) ocean warming (circles), (b) acidification (squares) and (c) latitude where seagrass originated (triangles) on the loss of seagrass detrital biomass. The means ( $\pm$ SE) of the main effects are shown, as there were no significant ocean warming by acidification interactions. The mass loss information in this figure was used to calculate the seagrass decay constant  $k$  and half-life using the exponential model  $x_t = x_0 e^{-kt}$  (see detailed methods and results in Table S3 in the Supplement)

## RESULTS

Loss of seagrass mass was significantly affected by ocean warming ( $p < 0.01$ ; Fig. 1, Table S2). On average, mass loss was 1.8, 6.4, 7.3 and 15.4% greater at 25°C than at 22°C after 5, 10, 20 and 40 d of decomposition, respectively. The source latitude of seagrass also influenced mass loss ( $p < 0.05$ ; Fig. 1, Table S3), with seagrass from the higher latitude (~35°S) decomposing 7.1, 9.3, 6.1 and 7.3% faster than seagrass from the lower latitude (~29°S) after 5, 10, 20 and

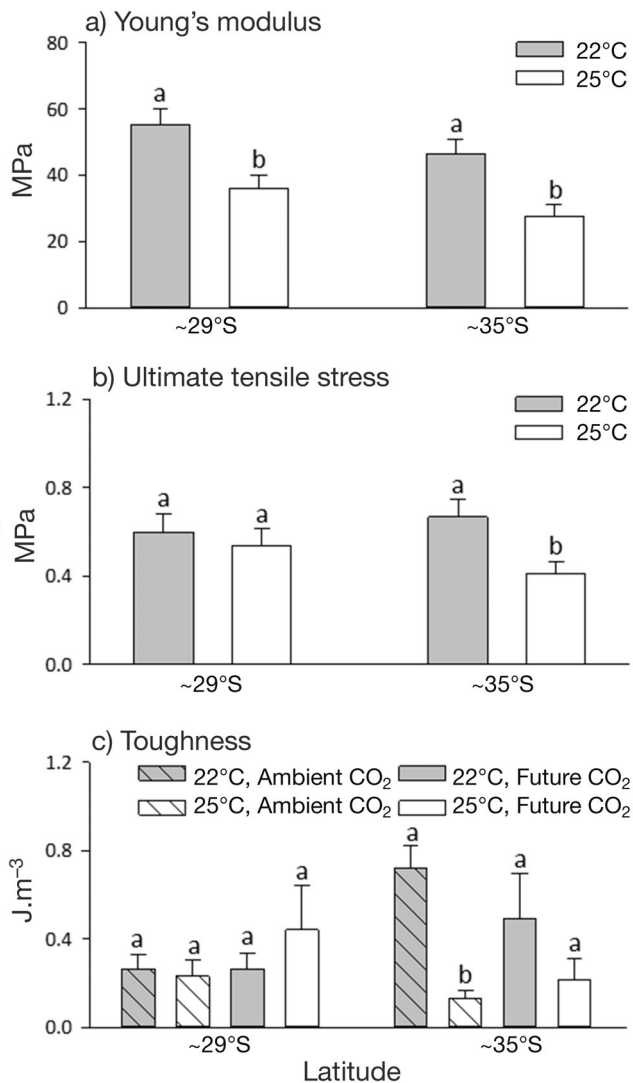


Fig. 2. Effects of ocean warming, acidification and latitude where seagrass originated on (a) Young's modulus, (b) tensile stress and (c) toughness of detrital seagrass blades. The means ( $\pm$ SE) for the relevant significant interaction terms are shown. The figure for toughness differs from the others because it needed to represent the significant  $\text{CO}_2 \times \text{temperature} \times \text{latitude}$  interaction (Table S6 in the Supplement). Different letters indicate significant difference at  $p < 0.05$

40 d, respectively. In contrast to temperature and the source latitude of seagrass, neither ocean acidification nor source site (within latitude) nor their interactions with other factors influenced mass loss ( $p > 0.05$  for all tests; Fig. 1, Table S3). Similar trends were also observed in the average decay constant  $k$  and half-life  $t_{1/2}$  of decomposing seagrass in the various treatments (Table S2).

The percentage change in neither C nor N nor the C:N ratio of decomposing seagrass was significantly influenced by ocean warming, acidification, latitude of origin or interactions among these factors ( $p > 0.05$  for all tests; Fig. S1, Table S4). The percentage change in each of C, N and the C:N ratio was, instead, influenced by the site of origin ( $p < 0.01$  for all tests of sites nested in latitude, Table S4), which was likely a reflection of site-specific differences in the C:N ratio of the collected seagrass.

The Young's modulus ( $E$ ), or stiffness of decomposing seagrass blades, was significantly greater at 22°C than at 25°C ( $p < 0.01$ ; Fig. 2, Table S5 in the Supplement). However, the influence of temperature on the ultimate tensile stress of decomposing seagrass was dependent on the latitude of seagrass origin ( $T \times L$ :  $p < 0.05$ ; Table S5). Seagrass blades from the higher latitude (~35°S) were significantly weaker when exposed to 25°C compared to 22°C ( $p < 0.01$ ; Fig. 2). In contrast, decomposing seagrass blades from the lower latitude (~29°S) had an ultimate tensile stress that was not affected significantly by ocean warming ( $p < 0.01$ ; Fig. 2).

The toughness of decomposing seagrass blades depended on an interaction among ocean warming, acidification and the latitude of seagrass origin ( $C \times T \times L$ :  $p < 0.01$ ; Table S5). For the seagrass blades collected from ~35°S and exposed to ambient  $p\text{CO}_2$ , the toughness of the decomposing seagrass was significantly lower at a seawater temperature of 25°C than at 22°C ( $p < 0.01$ ; Table S5). Although there was a similar trend for seagrass blades collected from ~35°S and exposed to future  $p\text{CO}_2$ , this effect was not significant ( $p > 0.05$ ; Table S5). In contrast to seagrass from ~35°S, the toughness of decomposing seagrass blades collected from ~29°S was affected by neither ocean warming nor acidification ( $p > 0.05$ ; Table S6).

## DISCUSSION

Our study provides evidence that the pervasive influence of ocean climate change will affect detrital processing in marine systems. Warmer climates are

generally associated with greater rates of marine macrophyte decomposition (Kristensen et al. 1992, Ainley & Bishop 2015). Here, when seawater was elevated to near-future conditions (3°C), seagrass decomposition was 15% greater after 40 d. However, this temperature-dependent decomposition did not appear to be driven by loss of C or N (i.e. C:N ratio did not significantly change). Rather, higher seawater temperatures appeared to increase overall decomposition over time, increasing autolysis of dissolved organic matter and likely stimulating microbial-driven decomposition compared to the cooler temperature. In general, our results indicate that rates of carbon and nutrient liberation and loss of biomechanical integrity of decomposing seagrass will be greater under future ocean conditions. The significant influence of latitude of origin on the seagrass decomposition suggests, however, that the extent of any changes to resource liberation may be modulated by the physical and biological properties of seagrass grown in warmer waters. It should be noted that the 25°C treatments represented an ~3 and ~5°C increase above annual average water temperatures for seagrass from low and high latitudes, respectively, which may have contributed to relative decomposition rates.

As well as increasing decomposition rates, ocean warming also reduced the structural integrity of decomposing seagrass blades from higher latitudes. The reduced stiffness and tensile strength of decomposing high-latitude seagrass subject to ocean warming may increase the fragmentation of material by physical (e.g. wave action) and biological (e.g. shredders) processes (Ainley & Bishop 2015). When seagrass is broken into smaller particles, more surface area becomes available for consumption by the microbial community and faunal detritivores, which further accelerates decomposition (Harrison 1989, Moore et al. 2004). At the same time, weaker detrital material is less likely to accumulate into complex 3-dimensional deposits that provide habitat to marine and terrestrial invertebrates (Dugan et al. 2003, Moore et al. 2004), with potential ramifications to higher-order consumers (e.g. shorebirds) that prey on these organisms (Dugan et al. 2003).

The varying environmental, ecological and evolutionary pressures on living seagrass from different latitudes influence its physical and chemical traits (e.g. mechanical elasticity and nitrogen content, Ainley et al. 2016), which in turn can influence the rate at which seagrass detritus breaks down (Ainley & Bishop 2015). Seagrass from lower-latitude sites (~29° S) had a much slower rate of decomposition and retained its

biomechanical properties better than seagrass that originated from higher-latitude sites (~35° S). If differences in the traits of high- and low-latitude seagrass populations are at least partially climatically determined, it is possible that the effects of climate warming on decomposition arising indirectly from intraspecific changes in leaf traits may counter the direct effect of accelerated decomposition in a warmer environment (Kristensen et al. 1992, Mann 2000). Two traits that have been strongly implicated in controlling decomposition rates—the C:N ratio of leaves (which is negatively correlated with decomposition) and %N (which is positively correlated)—each display strong gradients with latitude, the former decreasing and the latter increasing with latitude, across and within seagrass species, at small and large scales (Reich & Oleksyn 2004, Ainley et al. 2016). By chance in our experiment, we had one site with a high and one site with a low C:N ratio in each latitude, which was caused by one site having a much greater %N than the other site. For our system, therefore, the lack of significant site (nested within latitude) effects or interactions involving this factor suggests that ocean temperature and latitude of origin were significantly more important drivers of decomposition rate in our system than either C:N ratio or %N.

Ocean acidification did not influence the decomposition of *Zostera muelleri*. Increasing  $p\text{CO}_2$  in seawater could potentially elevate the leaching phase of decomposition, if the acidification of seawater is large enough to impact breakdown. Acidification of freshwater has been shown to significantly increase detrital decomposition rates and affect carbon and nitrogen liberation of macrophyte detritus (Leuven & Wolfs 1988) as well as the structure of associated microbial and faunal communities (Clivot et al. 2013). However, the pH changes in these freshwater systems (>2 pH units) are much larger than the average change predicted for oceans by ~2100 (i.e. -0.3 pH unit), on which we based our experiments.

To manipulate ocean warming and acidification simultaneously, our experiment involved litter bags in outdoor mesocosms. While the litter bags provided a bulk estimate of detrital mass loss, we did not discriminate among detrital fragmentation, leaching, respiration or microbial community composition. Although the outdoor mesocosms allowed for the sunlight and microbial decomposition of seagrass, they did not accommodate other important factors that can influence decomposition in the natural systems, such as wave action, faunal interactions (e.g. shredding by amphipods or consumption by detritivores), sediment processes and variation in nutrient loading

(see reviews by Harrison 1989, Mann 2000). While each of these factors has the potential to influence seagrass decomposition, how their effects will be altered by ocean warming and acidification is not known. In some cases, physical (e.g. wave action) and biological (e.g. consumption by microbes) processes may act synergistically with climate change effects, in which case the decomposition rates will increase significantly in the future. Less likely, the opposite could occur in which ocean climate change could slow decomposition rates through interaction with local factors in some systems. To better predict how detrital-based processes will be influenced by ocean climate, future experiments are needed that test hypotheses about the influence of local and global stressor interactions on detrital decomposition.

In summary, ocean warming increased the rate of seagrass decomposition, whereas ocean acidification had much less influence. This parallels outcomes for living species subjected to stressors from ocean climate change, which also often find ocean warming to be a more pervasive stressor (e.g. Byrne et al. 2009, Paul et al. 2015, Provost et al. 2017). As seagrass from lower latitudes decomposed more slowly than *Z. muelleri* populations from more temperate areas, there is potential for a negative feedback loop resisting the impacts of ocean warming on seagrass decomposition. This requires that the leaf traits of living *Z. muelleri* at higher latitudes adapt or acclimate to higher ocean temperatures in similar ways to current populations of low-latitude seagrass, which will then flow on to detrital-based processes. Understanding how feedback loops linking living macrophytes and their decomposition may be altered will provide insight into predicting how detrital processes will affect food web dynamics, greenhouse gas production, carbon sequestration and nutrient cycling in response to ocean climate change.

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