



## Oxygen and carbon metabolism of *Zostera muelleri* across a depth gradient – Implications for resilience and blue carbon



Angus J.P. Ferguson<sup>a, \*</sup>, Renee Gruber<sup>a, b</sup>, Jaimie Potts<sup>a</sup>, Aaron Wright<sup>a</sup>, David T. Welsh<sup>c</sup>, Peter Scanes<sup>a</sup>

<sup>a</sup> NSW Office of Environment and Heritage, Sydney, Australia

<sup>b</sup> University of Western Australia, Perth, Australia

<sup>c</sup> Griffith University, Gold Coast, Australia

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### ABSTRACT

There is growing interest in the role that seagrasses play as 'blue carbon' stores or sinks, and their potential to offset rising CO<sub>2</sub> levels in the atmosphere. This study measured primary aspects of the carbon balance (biomass, community metabolism, dissolved organic carbon [DOC] fluxes, seston trapping) across the depth gradient in a *Zostera muelleri* meadow during the seasonal biomass minimum and maximum. Over the annual estimation, the meadow was neither a sink nor source of carbon, with inputs of seston (~58% of total inputs) balanced by exports of wrack and DOC. The carbon sink represented by wrack export depends on the nature of the environment where the wrack accumulates; if it reaches subtidal sediments it will largely be remineralised over the annual cycle, whereas between 14 and 26% of the wrack may be preserved if the material is exported to terrestrial environments. The fate of DOC exuded by seagrasses is unknown due to a lack of knowledge about its composition and lability; however, a number of lines of evidence suggest that a large fraction of DOC is mineralised. The net community metabolism (NCM) of the meadow was balanced, indicating that photosynthetic O<sub>2</sub> production balanced community respiration and/or the reoxidation of reduced compounds (sulphur and iron) in the rhizosphere. We suggest that a balanced NCM may be the preferred state for *Zostera* spp. and may limit their occurrence in environments where plants cannot balance the respiratory demand exerted by seston inputs. There was a close coupling between metabolism and biomass, which in turn is forced by antecedent light over the preceding 120 days (the time integration window for antecedent light that best predicted biomass). Increased metabolism with depth and seasonal variation in light is accompanied by a decrease in the above ground:below ground biomass ratio (AGB:BGB). This trend is suggested to be a morphological adaptation that balances the competing requirements of maintaining a neutral plant carbon balance across enrichment and light gradients. Our results suggest that *Zostera muelleri* may be most important as a 'blue carbon' store (i.e. carbon stored as biomass standing stock), which is therefore vulnerable to degradation if seagrasses are lost.

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### 1. Introduction

Seagrass meadows are important and iconic coastal systems that provide a range of ecosystem services including serving as a food source and habitat for other species; stabilising subtidal sediment; and constituting a store of carbon (Heck et al., 2003; Emmett Duffy, 2006; Waycott et al., 2009; Kennedy et al., 2010). Recent concern over rising atmospheric carbon dioxide levels due

to climate change has prompted greater scientific focus on the 'blue carbon' sink potential represented by seagrasses (Duarte et al., 2010) (Fourqurean et al., 2012). Seagrass meadows store carbon in living biomass ('stores') and as buried refractory seagrass detritus ('sinks'), such as rhizome mats in *Posidonia* meadows (Duarte et al., 2011). Many seagrasses exist in sediments with low organic carbon (Ferguson et al., 2016), suggesting they may store carbon primarily in living biomass, therefore the significance of their role as 'blue carbon' stores depends on their continued survival (Lavery et al., 2013a). Seagrasses are under increasing pressure globally due to multiple stressors associated with human development (Orth et al., 2006), and global declines have already

\* Corresponding author.

E-mail address: [angus.ferguson@environment.nsw.gov.au](mailto:angus.ferguson@environment.nsw.gov.au) (A.J.P. Ferguson).

resulted in substantial loss of carbon storage (McLeod et al., 2011).

Central to determining the carbon balance of seagrass meadows is a knowledge of the net community metabolism (NCM), defined as gross primary production (GPP) less community respiration (CR) over the diel period, which can also be expressed as a ratio of GPP to CR (P:R). Assessments of NCM are commonly based on the measurement of O<sub>2</sub> and/or CO<sub>2</sub> fluxes over a diel period (Duarte et al., 2010). Net autotrophic systems (P:R > 1) fix more carbon than is released by respiration and provide the conditions for a potential carbon sink, as long as that carbon is buried either within the meadow or elsewhere. Balanced NCM (NCM = 0, P:R = 1), implies that all allochthonous and autochthonous carbon inputs are balanced by microbially mediated remineralisation of the labile organic matter (OM) plus burial of refractory material. In the absence of significant burial of OM within the meadow, a balanced NCM implies that it functions primarily as a store of carbon in living biomass. Net heterotrophic metabolism (NCM < 0, P:R < 1) implies an allochthonous carbon source to the meadow. However, the net import or export of carbon from the seagrass meadow complicates this simple assessment of carbon budgets based on NCM or P:R alone. If carbon is exported as 'wrack' (dead seagrass biomass) or exuded dissolved organic carbon (DOC), its fate is crucial to determining whether the meadow is a sink of carbon (Duarte and Cebrian, 1996). The import of organic matter (e.g. via trapped seston (Gacia et al., 2002); may contribute significantly to community metabolism and further complicate the assessment of the meadow carbon balance (Barron et al., 2004). Finally, there may also be temporal lags between O<sub>2</sub> production and consumption where OM undergoes anaerobic remineralisation and O<sub>2</sub> consumption is dominated by the re-oxidation of reduced compounds (e.g. sulphur) (Jørgensen, 1982). Clearly, a comprehensive assessment of the role seagrass meadows play in the global carbon budget must consider rates of autochthonous and allochthonous inputs to the system, respiration and burial within the system, exports from the system and the fate of these exports (Macreadie et al., 2014). To date there are few examples of closed carbon budgets for seagrass meadows, with conclusions commonly being made despite the exclusion of one or more important terms.

Seagrass meadows commonly extend across wide depth gradients, with plants acclimating their morphology and physiology in order to optimise their growth across a range of light conditions (Collier et al., 2007). Seagrass productivity is commonly estimated *ex situ* or using fluorescence methods that do not include the natural benthic community, but *in situ* measures of NCM along a depth gradient are rare (Duarte et al., 2010; Maher and Eyre, 2011). Given the likely variation in processes such as net primary production and particle trapping across the depth gradient, extrapolation of results from a single depth is unlikely to realistically represent NCM of the meadow as a whole. Furthermore, variation in plant carbon balance across the depth (light) gradient is also a key feature determining depth limits and resilience to poor sediment conditions and periods of low light (Ralph et al., 2007).

Long-term persistence of seagrass meadows is critical to any evaluation of their continuing role in large-scale carbon budgets. Persistence is the result of an interaction between disturbance regimes and meadow resilience (Kilminster et al., 2015). The maintenance of a neutral plant carbon balance over seasonal timescales is critical in determining seagrass resilience at a given location (Dennison and Alberte, 1985). Seagrasses display a high degree of morphological plasticity across light and enrichment gradients (Perez et al., 1994; Lee and Dunton, 2000; Collier et al., 2007; Ralph et al., 2007; Clores and Santos Carandang, 2013; Ferguson et al., 2016), which is thought to be a strategy to balance the respiratory demands of non-photosynthetic organs (e.g. roots and rhizomes) with the oxygen production potential of its above ground

biomass (Hemminga, 1998). The ratio of above ground:below ground biomass (AGB:BGB) therefore provides an important metric of functional morphological response to environmental drivers (Lee and Dunton, 2000). Despite the importance of this link, there have been few studies that simultaneously measure seagrass metabolism and biomass response to environmental gradients. This knowledge gap impedes the development of robust seagrass resilience models that can be confidently applied across the range of environments colonised by seagrass. This, in turn, limits assessment of the potential future role of seagrass meadows in large scale carbon budgets.

This study measured key aspects of the carbon balance across the depth gradient of a seagrass (*Zostera muelleri*) meadow during the annual biomass minimum (early spring) and maximum (late summer). The aims were 1) to provide a comprehensive carbon budget for the meadow in order to determine whether it acted as a carbon store or sink, and 2) provide insights into seagrass community metabolism with respect to environmental gradients.

## 2. Methods

### 2.1. Study site

Lake Macquarie is an estuarine lagoon located on the east coast of Australia (Fig. 1). The region experiences a warm temperate climate, with most rainfall occurring during late summer to autumn. Water temperatures within the lake basin range from ~16 °C in winter to 26 °C in the summer (Table 1). A relatively small catchment area to lake volume ratio combined with efficient tidal flushing means that salinity within the lake is generally close to seawater, though large rainfall events can cause a reduction in surface salinities to <20. Tidal range is greatly attenuated by the constrained lake entrance and the tidal range within the lake basin is < 10 cm. Generally low nutrient concentrations within the lake indicate an oligotrophic system (Ferguson et al., 2016). This study was carried out in an extensive *Zostera muelleri* meadow (Swansea shoals) located just south of the lake's entrance (Fig. 1). Data were collected at 0.75 m, 1.5 m and 3 m water depth, corresponding to the upper, middle and lower limits of seagrass depth distribution in the meadow. Water quality data for the Swansea shoals site during the sample times (early September 2012, 'early spring'; and mid February 2013, 'late summer') are presented in Table 1. The sample times were close to the seasonal extremes of temperature, with similar salinity. Water clarity (as indicated by secchi depth) was lower during the late summer sample time, most likely due to higher phytoplankton biomass (indicated by chlorophyll-a concentration) at this time (Table 1).

### 2.2. Sediment properties and seagrass biomass

Samples for seagrass biomass measurements (n = 5) were taken by SCUBA divers using 250 mm I.D. cores at each depth during each sample time. Samples were stored on ice and processed within 2 days of collection. Processing involved carefully washing sediment and dead material from the sample and separating above ground biomass (AGB = leaves and shoots), and below ground biomass (BGB = roots and rhizomes). Samples were freeze dried and weighed, with biomass normalised to g DW m<sup>-2</sup> using the surface area of the collection core. Samples for grain size and organic matter (n = 5) content were collected from each depth during summer by SCUBA divers using 90 mm I.D. cores at each depth during each season. Cores were gently extruded and the top 1 cm removed and frozen until analysis. Intact samples from 2 cores were combusted (550 °C for 4 h) to determine OM content. A pilot study conducted prior to sampling indicated that it was not

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