



Benthic primary production in emerged intertidal habitats provides resilience to high water column turbidity



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ARTICLE INFO

Keywords:

Seagrass
Microphytobenthos
New Zealand
Estuaries

ABSTRACT

Increasing inputs of terrigenous sediments from anthropic land use change elevates water column turbidity, reducing light availability to benthic primary producers that sustain estuarine food webs. For intertidal habitats, photosynthesis during low tide periods of emergence may provide resilience against this temporally displaced stressor, yet the significance of low tide production (PP) has largely been overlooked. Emerged and submerged benthic PP was measured in adjacent seagrass (*Zostera muelleri*) and microphytobenthos-dominated (sandflat) soft-sediment habitats at three locations encompassing a turbidity gradient. Light and dark benthic incubation chambers were used to measure the flux of CO₂ across emerged sediments, and dissolved oxygen across submerged sediments to derive net (NPP) and gross (GPP) PP. Seagrass NPP and GPP exceeded sandflat habitats (by 3–8 times) at low turbidity sites during submergence and at all sites during emergence ($p < 0.01$), whereas habitat differences were absent ($p > 0.1$) in turbid locations. Emerged NPP and GPP were higher (2–16 times) than submerged in all habitats and locations ($p < 0.01$). When standardised by mean incident photosynthetically active radiation (PAR), the difference between emerged and submerged seagrass PP increased with site turbidity, from 2 to 26 times greater. In a global context of increasing inputs of terrigenous sediment to estuaries, emerged PP may be crucial for providing resilience against benthic productivity losses in highly turbid environments.

1. Introduction

Estuarine ecosystems are highly dynamic and experience natural fluctuations in water clarity due to changes in suspended particle concentrations. Riverine inputs of sediment following rainfall events, wind and wave driven resuspension, and tidal transport of sediments from one location to another can all alter suspended sediment concentrations (SSC) over short time scales (Green and Coco, 2007; Talke and Stacey, 2008; Seers and Shears, 2015). Anthropogenic catchment development has however led to elevated inputs of fine terrigenous sediments into waterways (Thrush et al., 2004; Seers and Shears, 2015), resulting in consistently high levels of turbidity in some estuaries. Elevated turbidity can significantly reduce light penetration through the water column thus limiting benthic primary productivity (Gameiro et al., 2011). In New Zealand, and many temperate estuaries, the dominant benthic primary producers are MPB and seagrass meadows (e.g. Jones et al. (2016) and Turner and Schwarz (2006a)). Significant decreases in primary production (PP) in sandflat habitats (Pratt et al.,

2014b) and biomass losses in seagrass habitats (Longstaff and Dennison, 1999) have been associated with elevated turbidity, which has negative implications for the benthic food webs they underpin. Nevertheless, films of microphytobenthos (MPB) and seagrass meadows continue to inhabit persistently turbid intertidal environments, emphasising the potential role of PP during periods of tidal exposure (emergence) in sustaining these habitats (Schwarz, 2004).

MPB communities reside in the upper millimetres of sediments and often dominate intertidal sandflats (MacIntyre et al., 1996). Where present, they can contribute up to 80% of total benthic PP (Underwood and Krompkamp, 1999; Jones et al., 2016) and play important biological and physical roles through oxygenating surface sediments (e.g. Baillie (1986) and Larson and Sundback (2008)), retaining nutrients within the benthos (e.g. Bautista and Paerl (1985) and Sundback et al. (2000)) and stabilising sediments (e.g. Yallop et al. (1994) and Lelieveld et al. (2003)). Additionally, benthic consumers exhibit a strong preference for MPB as a food source over macrophyte detritus (originating from seagrass, mangrove or saltmarsh), owing to a higher

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<https://doi.org/10.1016/j.seares.2018.09.015>

Received 19 April 2018; Received in revised form 13 August 2018; Accepted 23 September 2018

Available online 25 September 2018

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quality of organic material and greater palatability (Miller et al., 1996), such that benthic secondary production can be largely supported by MPB (Cahoon and Safi, 2002; Evrard et al., 2012; Jones et al., 2016).

Seagrass meadows may also thrive in temperate estuarine environments, providing high rates of carbon storage and habitat for fish, bird and invertebrate species via their structural characteristics (Heck et al., 2003; Fourqurean et al., 2012; Parsons et al., 2013). Seagrass habitats are recognised as one of the most ecologically and economically valuable marine ecosystems (Costanza et al., 2014), however anthropogenic pressures such as eutrophication, sedimentation and climate change continue to drive a worldwide decline in meadow area of approximately 7% yr⁻¹ (Waycott et al., 2009). In intertidal regions, seagrass beds often exhibit higher PP than MPB due to a greater biomass of photosynthesising tissues, in addition to associated epiphytes and benthic MPB within seagrass habitats (Moncreiff et al., 1992). *Zostera muelleri* is the only species of seagrass found in New Zealand and is most abundant in estuarine intertidal regions following large declines of subtidal populations between 1959 and 1996, likely in response to reductions in water clarity (Park, 1999; Turner and Schwarz, 2006b).

The distribution of marine autotrophs is influenced by light availability, depending specifically on whether photosynthesising tissues consistently receive light intensities allowing for photosynthetic gains in excess of metabolic costs. The minimum light requirements of intertidal MPB and *Z. muelleri* as reported in the literature are highly variable (Gattuso et al., 2006; Lee et al., 2007), possibly because of site-specific adaptations to varying light regimes (via physiological (Kromkamp et al., 1998; Kohlmeier et al., 2014), morphological (Park et al., 2016) and/or behavioural (Mitbavkar and Anil, 2004) adaptations). Despite this potential for adaptation, short-term increases in water column turbidity caused MPB net primary productivity (NPP) during submergence to decrease three-fold in field experiments, with even greater reductions when photosynthetic efficiency (NPP $\mu\text{g Chl } a^{-1}$) was considered (Pratt et al., 2014b). Similarly, losses in seagrass biomass have frequently been associated with reductions in light availability (Longstaff and Dennison, 1999; Ruiz and Romero, 2001).

A tipping point from one ecosystem state to another can occur if turbidity is frequently high and submerged benthic PP is lost, such that a shift from a clear, ecologically diverse system dominated by benthic PP towards a turbid system dominated by water column PP arises (Fisher et al., 1988). This is often characterised by a loss of submerged vegetation and benthic diversity, resulting in negative feedbacks as nutrients are not intercepted at the sediment-water interface and thus continue to fuel water column PP (Moore et al., 1996; Pratt et al., 2014b). In addition, sediment mud content (particles < 63 μm) and water column turbidity are often positively correlated, as the fine particles are easily resuspended by wind and wave action. Evidence from New Zealand suggests that high sediment mud content is associated with lower Chl *a* content (a proxy for MPB abundance) (Cahoon et al., 1999), and reduced rates of biomass-corrected gross primary productivity (GPP) in MPB-dominated sediments (Pratt et al., 2014a). To obtain meaningful data on the impact water column turbidity has on benthic PP it is therefore key that the effects of turbidity and sediment mud content are separated.

Despite the negative effects observed during submergence, turbidity in intertidal environments may be considered a temporally displaced stressor, as during periods of emergence the light attenuating effect of suspended sediments is removed. This period of emergence may therefore be critical for benthic PP should light levels during submergence consistently fall below minimum requirements for photosynthesis. It is predicted that the relative contribution of emerged PP to total benthic PP would increase in significance along a gradient of increasing water column turbidity, as contributions from submerged PP decrease. In such cases, highly turbid locations would exhibit great dependence on emerged PP to maintain function. Indeed, Vermaat and Verhagen (1996) demonstrated positive net photosynthesis occurred in seagrass habitats primarily during daylight low tides in turbid estuaries,

and predictions that emergence may provide a mechanism to avoid negative impacts of turbidity were made (Vermaat et al., 1997). More recently, Schwarz (2004) showed in a New Zealand estuary that during winter almost all seagrass PP occurred whilst plants were exposed, but concluded that emergence was not essential to the maintenance of these beds due to the presence of a subtidal fringe. However, few direct comparisons of in situ submerged and emerged seagrass community PP have been made (Ouisse et al., 2011). Moderate information does exist on PP of MPB communities during emergence, originating mainly from studies in Europe (Migné et al., 2004; Spilmont et al., 2006; Spilmont et al., 2007; Migné et al., 2009), however direct comparisons of in situ submerged and emerged community PP are again scarce (Migné et al., 2018). To our knowledge, in neither seagrass nor sandflat habitats has there been a simultaneous investigation of submerged and emerged PP in response to increasing site turbidity; such studies are crucial to understand the role of emerged sediments as potential refuges for benthic PP in light of globally increasing SSC.

In this study, the effect of increasing water column turbidity on submerged and emerged benthic PP was investigated in sandflat habitats dominated by MPB and *Z. muelleri* beds in a temperate New Zealand estuary. The PP of the whole community is considered through use of benthic incubation chambers that encompass patches of seagrass habitat (containing shoots, roots and rhizomes), and all associated organisms. The relative importance of emerged PP was determined, providing insight into whether the period of emergence can offer resilience to intertidal habitats against increases in site turbidity, and trends between PP and site turbidity were highlighted for both tidal states. If compensating for increased turbidity, we expected emerged PP to be appreciably greater in turbid locations than at clear locations.

2. Methods

The study was conducted in the southern branch of the Kaipara Harbour, New Zealand. The harbour is one of the largest estuaries in the world (947 km²) of which 43% is intertidal sand and mudflat (Heath, 1975). Water quality sampling has indicated turbidity in the harbour can range from < 5 to ~150 NTU (Cumming, 2016). Unvegetated sediments dominate the intertidal, with extensive meadows and patches of seagrass also present that at times extend into the subtidal (Hewitt and Funnell, 2005). Based on information gathered during routine monitoring of multiple mid-intertidal sites in the harbour (Hailes and Carter, 2016) and access to catchment sediment dispersion models (Lohrer, 2017), three sites were selected to span an expected gradient in turbidity. Mairetahi Creek (MAI; 36°32'51" S, 174°21'39" E) was chosen to have the highest turbidity, Kakaraia Flat (KKF; 36°25'9" S, 174°23'37" E) an intermediate level and Tapora Bank (TPB; 36°23'37.6" S, 174°17'34.5" E) being the least turbid (Fig. 1). Sites experienced a diurnal tidal cycle with similar emersion periods (4–5 h) and depths at high tide (~1.2–1.6 m), and were selected for two habitat types: unvegetated sandflat and immediately adjacent dense seagrass (*Zostera muelleri*) meadows (at least 1000 m²). Seagrass plots were chosen by eye to have similar seagrass coverage, aiming for a minimum of 80%. Both habitat types were selected to have comparable sediment properties (fine organically poor sands (1–4% organic matter content (OC)), with a low average mud (silt/clay particles < 63 μm) content (3–12%).

2.1. Field sampling

Sites were visited on two occasions to measure submerged (26th – 29th February 2016, austral summer) and emerged (13th – 15th April 2016, late austral summer) primary productivity (PP) in the two habitat types (unvegetated sediment and seagrass beds). Sites were sampled on consecutive days, with measurements occurring around midday to encompass the period when irradiance is naturally highest. This resulted in a temporal separation between the submerged (midday high tide) and emerged (midday low tide) PP measurements, which extended to

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