



# Experimental test of N-limitation for *Zostera nigricaulis* seagrass at three sites reliant upon very different sources of N



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## ABSTRACT

The hypothesis that seagrasses may be nitrogen-limited has been examined in a number of studies, particularly in oligotrophic waters where nutrients are typically scarce. Here we examined nitrogen-limitation for the temperate seagrass, *Zostera nigricaulis*, at three sites where seagrasses use very different sources of nitrogen (N) based on stable isotopes of N: Swan Bay - fixed and recycled N, Kirk Point - N from treated sewage, and Blairgowrie - N from catchment. Dramatic changes to source inputs during a recent prolonged drought were linked to seagrass loss in parts of the bay dependent on catchment inputs. Here we test to what extent seagrasses dependent on different sources of N are N-limited, by enriching sediment pore water levels. Sediment pore water nutrient levels varied naturally between the sites by a factor of 14, from Swan Bay (highest) to Blairgowrie (lowest), and were much higher than water column levels. There was a detectable enrichment effect for pore water nutrient concentrations within the treatment plots after one month, although the effect was greatest for the Blairgowrie site, and was most pronounced for  $\text{NH}_4$  levels. There was a significant enrichment effect for seagrass growth after 5 months, but only at a single site, Blairgowrie. Seagrass cover, above-ground biomass and mean leaf length were substantially higher in the treatment than control plots at the Blairgowrie site, but not at the other two sites. Higher %N content and lower  $\delta^{15}\text{N}$  in the leaf tissues at Blairgowrie and Kirk Point indicated that N released from the fertilizer had been assimilated by the seagrass at both these sites, but in the case of Kirk Point this did not translate into greater seagrass growth. The results suggest that seagrasses at Blairgowrie, in the southern part of the bay, are highly N-limited. This is a region that is isolated from the major source of N (the catchment) utilised by seagrass in this part of the bay. The pattern of N-limitation in this and a previous study is consistent with regions that displayed major fluctuations in seagrass cover during the 'Millennium' drought from 1997 to 2009. Consequently, predicted decreases in long-term rainfall in south-eastern Australia could have negative consequences for seagrass extent in areas that are N-limited.

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## 1. Introduction

Seagrass habitats are in decline globally and nutrients are considered to be a key factor (Waycott et al., 2009; Short et al., 2011). The loss of seagrass has typically been linked to elevated inputs of nutrients in coastal systems (i.e. eutrophication, Cloern, 2001; Ralph et al., 2006). However, where nutrients are scarce, seagrass growth may be limited by the availability of essential nutrients (Short, 1987; Fourqurean et al., 1992a; Fourqurean and Zieman, 2002; Udy et al., 1999). In coastal areas where seagrasses are dependent on nutrients derived from terrestrial catchments, seagrass area may be affected by long-term changes to river flows (Rasheed and Unsworth 2011; Hirst et al., 2016), particularly during drought and especially in parts of the world where climate change is predicted to result in reduced rainfall and lower run-off

(Chew et al., 2011; Hobday and Lough, 2011; Christensen and Kanikicharla, 2013).

The hypothesis that seagrasses may be nutrient-limited has been examined in a number of studies, particularly in oligotrophic waters where nutrients are likely to be scarce (Fourqurean et al., 1992b; Alcoverro et al., 1997; Udy and Dennison, 1997; Udy et al., 1999; Armitage et al., 2011). In general, these studies indicate that nutrient limitation in seagrasses is strongly dependent on specific plant characteristics and local conditions, particularly sediment type (Short, 1987) and proximity to source of nutrients (Ferdie and Fourqurean, 2004), and is heavily mediated by local physiological responses (Romero et al., 2006; Leoni et al., 2008; Cabaço et al., 2013). Nutrient limitation in seagrasses has been examined using two broad approaches that canvas very different spatial scales. Experimental manipulation of nutrient levels is considered the more rigorous approach (Short, 1987), but is weakened by its limited spatial and temporal scope. Alternatively, correlation of the status of seagrass tissues (using elemental ratios of Carbon, Nitrogen and Phosphorus) along gradients of nutrient availability

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can allow researchers to examine the incidence of nutrient limitation at larger spatial scales. However, interpretation may be confounded by a range of factors including variation in depth, levels of disturbance, and the presence of multiple nutrient sources (Fourqurean et al., 1997). The absence of a response to nutrient addition has been frequently documented and sometimes misinterpreted as an experimental failure (Romero et al., 2006). However, if sufficient nutrients are added, a negative result indicates that nutrient availability is in excess of seagrass nutrient demands.

Nutrients enter seagrass ecosystems via a range of pathways, but principally as dissolved inorganic nutrients or via sedimentation of seston that contains variable amounts of organic N and P (Hemminga et al., 1991). Seston is likely to be an important source of nutrients in seagrass ecosystems, in part because seagrass canopies act as particle traps, facilitating sedimentation (Koch et al., 2006). A third source, nitrogen-fixation, may also be an important N source in some seagrass ecosystems (Welsh, 2000). A significant proportion of nutrients entering seagrass ecosystems are subsequently recycled via decomposition of leaf material which regenerates nutrients, returning them to a soluble form (Mateo and Romero, 1997). Nutrients released in dissolved forms can be re-used by seagrasses or other primary producers; incorporated by bacteria and then re-mineralized following ingestion by detritivores; and bound to refractory compounds in detritus that can be either exported or stored as organic nutrients in the sediments (Romero et al., 1992). Finally, seagrasses may suffer substantial nutrient losses through the export of leaf detritus, transported by waves and currents away from the seagrass bed. This net loss of N may also lead to seagrass beds becoming nutrient limited during some periods (Hemminga et al., 1991).

Seagrasses take up nutrients through both root and leaf tissue (Touchette and Burkholder, 2000), although in general, root tissues are exposed to sediment pore waters that have much higher nutrient concentrations than the water column (sometimes by orders of magnitude) and this has led to a belief that sediment nutrient concentrations are more important in determining whether seagrass growth is nutrient limited (Bulthuis et al., 1992). However, leaf tissues have much higher nutrient uptake affinities than root tissues, particularly at lower nutrient concentrations (Pedersen et al., 1997; Lee and Dunton, 1999). Hence, nutrient uptake by leaf tissues may contribute significantly to the nutrient acquisition of seagrasses (Lepoint et al., 2002).

Hirst et al. (2016) hypothesized that patterns of seagrass expansion and decline in Port Phillip Bay (PPB) were linked to nutrient availability mediated by the way in which seagrasses in different regions utilised N from different sources. Previous work has indicated that *Z. nigricaulis* growing on sandy sediments in PPB are nitrogen, but not phosphorus, limited (Bulthuis et al., 1992). Hirst et al. (2016) argued that seagrasses growing in regions dependent on N from the catchment may be more N-limited than seagrasses growing in regions reliant upon less variable sources of N (e.g. fixed and regenerated N or N from treated sewage) and indeed regions where seagrass area declined between 2000 and 2010 utilised a greater proportion of N from the catchment. Catchment derived N is inherently more variable than other sources of N within the bay because catchment inputs are directly linked river flows, which in turn are driven by climatic variability (rainfall and run-off). Here we test the hypothesis that seagrass at sites dependent on N from catchment inputs are more N-limited than seagrasses growing at sites largely dependent on fixed and regenerated N or N from treated sewage. Few enrichment studies have considered N-limitation at broader spatial scales and none, that we are aware of, have considered the importance of the identity of N source utilised in determining patterns of N-limitation.

## 2. Materials and methods

### 2.1. Study sites

Port Phillip Bay is a large marine embayment located on the south-eastern coast of Australia (Fig. 1). The bay is dominated by a central,

deeper basin adjacent to a shallower western arm (Fig. 1). An extensive region of shallow sand banks, the 'Great Sands', stretches across the southern entrance to the bay attenuating both oceanic waves and tides. A smaller, extremely shallow (<2 m depth) bay, Swan Bay, connects to PPB in the south-west (Fig. 1). Over four million people live in the catchments that drain into PPB, most of them in the city of Melbourne which occupies the lower reaches of the Yarra River at the northern end of the bay (Fig. 1). In excess of 70% of freshwater inputs from the catchment emanate from the Yarra River which discharges into the northern part of the bay (Harris et al., 1996). The largest source of nitrogen input into PPB is the discharge of treated sewage effluent from the Western Treatment Plant (WTP) located at Werribee on the north-west coast of PPB (Fig. 1). DIN levels in the water column tend to be highest in the northern part of the bay, reflecting the influence of the WTP and catchment inputs. DIN levels tend to be low and relatively uniform in the centre of the bay, but more variable in the southern region of the bay reflecting mixing and exchange with Bass Strait oceanic waters (Harris et al., 1996). Primary production within the bay is considered to be N- rather than P-limited, because P in the water column is high relative to N (mean concentrations DIN = 1.32  $\mu\text{M}$  and DIP = 2.12  $\mu\text{M}$ , DIN:DIP ~ 0.6, EPA unpub. data).

Sediment nutrient levels were experimentally enriched in situ at three sites indicative of the importance of different sources of N for seagrass growth in PPB: Swan Bay (0‰  $\delta^{15}\text{N}$  in seagrass tissue), Blairgowrie (7‰) and Kirk Point (17‰) (Hirst et al., 2016) (Fig. 1). Hirst et al. (2016) identified four main sources of N in PPB: treated sewage derived N originating from the Western Treatment Plant (WTP), catchment derived N principally delivered by the Yarra River (accounts for 70% of freshwater inputs), seasonal influxes of N from Bass Strait and N-fixed from atmospheric N in the sediments (Cook et al., 2015). The latter was distinguished by a highly depleted  $\delta^{15}\text{N}$  characteristic of protected locations dominated by fine, organically-rich sediments (Fig. 1). Mixture model analysis of stable isotope signatures of nitrogen in seagrass tissues indicated that *Zostera nigricaulis* at the three sites were dependent upon fixed and regenerated N from the sediments (Swan Bay), catchment derived N (Blairgowrie) and treated-sewage derived N (Kirk Point) (Hirst et al., 2016).

Experiments were conducted in *Zostera nigricaulis* dominated subtidal seagrass beds in depths 1–1.5 m below mean low water spring tide (MLWS). Seagrass beds at Blairgowrie were dominated by a short (mean length = 24.5 cm), dense (mean percent cover = 80%) canopy of *Z. nigricaulis* plants growing in sandy sediments. Seagrass at Kirk Point comprised tall (mean length = 41.1 cm), sparse (mean percent cover = 25%) plants growing in a fine sand/mud substrate. Seagrass beds in Swan Bay were dominated by sparse (mean percent cover = 26%) seagrass growing in fine, organically-rich, silty sediments and supporting a naturally high macro-algal epiphyte load (mean percent epiphyte cover = 92.5%).

### 2.2. Experimental procedure

The impact of nutrient enrichment was examined by comparing seagrass growth in enriched versus control 0.25 × 0.25 m experimental plots marked with flagging tape and floats attached to screw pegs inserted into the sediment. Plots were established in homogenous patches of seagrass. Five replicate enriched and control treatment plots were allocated alternatively within a circular pattern approximately 10 m in diameter and separated by at least 2 m (i.e. total of 10 plots); well beyond the distance that nutrients diffuse in the pore water (based on the results of a pilot study conducted in 2012/13). The experiment was run simultaneously at the three sites from October 2013 to March 2014 (approx. 5 months) during the southern hemisphere spring/summer.

Sediment interstitial pore waters were enriched using slow-release fertilizer that was low in P (Osmocote® Native Gardens 18%N (w/v) and 0.8%P (w/v)) added to the sediment following the recommendations of

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