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The impact of burial on the survival and recovery of the subtidal seagrass *Zostera nigricaulis*

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ABSTRACT

Many seagrass beds are exposed to environmental stresses from waves, dune migration, bioturbation and storms that lead to burial events. The impact of burial on the subtidal seagrass *Zostera nigricaulis* growing in Port Phillip Bay, south-eastern Australia, was examined through experimental manipulation of sediment burial height (6.25, 12.5, 25, 50 and 100% of canopy height) in the field over 14 days. The seagrass *Z. nigricaulis* withstood burial up to a depth of 12.5% canopy height (2 cm burial), but suffered significant reduction in seagrass biomass between 41 and 68% when buried at 25–50% canopy height (4–8 cm burial). We attributed this pattern to the presence of a modified vertical, wiry stem that allows *Z. nigricaulis* to tolerate low levels of burial. However, above 25% canopy height, sediment increasingly covers areas of photosynthetic leaf tissue resulting in increasing and significant levels of mortality. In a separate experiment, recovery following burial at 100% canopy height was assessed by analyzing changes in seagrass cover, maximum leaf length and canopy height during high and low growth periods. Seagrass failed to recover fully following burial after 30 weeks during winter/spring and showed no sign of recovery 6–8 weeks after burial during summer/autumn (after which the loss of the seagrass bed made interpretation difficult). The results indicate that the tolerance of *Z. nigricaulis* to burial is greater than other *Zostera* species, most likely because the vertical rhizome (wiry stem) characteristic of this species offers a degree of resilience to burial.

1. Introduction

The burial of seagrass by sediment is a major cause of seagrass decline, potentially resulting in the patchiness and fragmentation of seagrass meadows (Duarte, 2002). The recovery following these events has a major influence on the structure of seagrass landscapes (Duarte, 2002). Seagrasses experience regular burial and erosion events and are constantly exposed to environmental stresses from waves (Paling et al., 2003), dune migration (Marba and Duarte, 1995), bioturbation (Fonseca et al., 2008) and storms (Fourqurean and Rutten, 2004). Burial events can occur rapidly, for example during storms, or over longer periods of months in the case of sub-aqueous dune migration (Marba et al., 1994). The impact of regular burial events can cause significant loss and fragmentation of seagrass meadows, but the capacity of seagrasses to tolerate and recover from these events is essential to their longevity. The level of resilience and tolerance to burial is often highly species-specific and burial thresholds vary significantly between seagrass species (Cruz-Palacios and Van Tussenbroek, 2005; Cabaço et al., 2008).

Burial is a natural phenomenon, particularly in wave and current exposed environments that ranges in intensity, scale and magnitude from small-scale depositional events to large-scale storms and cyclones. Many human activities including dredging, beach replenishment and coastal development also result in burial of seagrass beds or changes to natural burial regimes within coastal environments (Duarte, 2002). The capacity of seagrasses to recover from burial is dependent not only upon the scale of the event, but also upon the resilience of particular species. Burial has been shown to negatively affect the survivorship of many seagrass species (Cabaço et al., 2008) as it reduces the capacity of photosynthetic tissue to function by blocking light, reducing gas exchange and results in the reduction of the available photosynthetic biomass, which may negatively affect the growth and survival of plants. Burial may also increase the probability of exposure of the leaf meristems, which may be buried in the sediments, to anoxic conditions, which has been shown to lead to seagrass mortality (Cabaço et al., 2008). Meristematic tissues are especially vulnerable to low oxygen supply and exposure to anaerobic metabolites due to their high metabolic activity and continuous oxygen requirements (Borum et al., 2006). In the absence oxygen, sulfides may also increase in concentration in seagrass tissues reducing plant survival (Borum et al.,

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2005).

The capacity of seagrasses to tolerate and recover from burial is determined by a range of factors including size, growth rate and morphology. Larger, deep-rooted seagrasses such as *Posidonia* are capable of withstanding high levels of burial, but recover more slowly than other seagrass species (Badalamenti et al., 2006; Cabaço et al., 2008). By comparison, faster growing species such as *Halophila* and *Cymodocea* are highly susceptible to burial events, but recover quickly due to their capacity to colonize rapidly (Duarte et al., 1997; Cabaço et al., 2008). Hence resilience to burial is both a function of tolerance to burial impacts and the capacity and rate at which seagrass species can recover from these burial events (Cruz-Palacios and Van Tussenbroek, 2005).

Morphological traits may enhance the capacity of seagrasses to tolerate higher levels of burial. For example, species that possess vertical rhizomes are thought to tolerate higher levels of burial than species that do not possess these structures because they allow growth towards the sediment surface after burial (Cabaço et al., 2008). Vertical stems (vertical rhizomes that are emergent from the sediment) are another morphological trait that may make seagrasses more resilient to burial because the leaves are raised above the sediment surface, allowing some protection from burial of meristematic tissue (Duarte et al., 1997; Vermaat et al., 1997). In addition, vertical stems may allow seagrasses to respond to burial with vertical elongation (Vermaat et al., 1997). In contrast, species that lack vertical rhizomes or stems can only cope with burial by attaining a larger size, or, by rearranging the position of the horizontal rhizome (Vermaat et al., 1997).

To date, no study has investigated the impact of burial and subsequent recovery on one of the most abundant seagrass species found along the southern coast of Australia, *Zostera nigricaulis* (Womersley, 1984). *Z. nigricaulis* occurs in southern Australian waters from Dongara, Western Australia, to the central New South Wales coast, including the north and east coasts of Tasmania growing at depths of 0–15 m (Womersley, 1984). *Z. nigricaulis* has a vertical wiry stem from which leaf bundles arise and this distinguishes it from most other *Zostera* species (Bulthuis et al., 1983; Hemminga and Duarte, 2000; Kuo, 2005) (Fig. 1). The morphology and reproductive features of *Z. nigricaulis* can vary in space and time (Bulthuis, 1983; Smith et al., 2016a), which may reflect differences in environmental gradients and responses to unique localized sedimentary dynamics (Campbell and Miller, 2002). Seasonality has been shown to influence growth of temperate seagrass, including *Z. nigricaulis* where higher water temperatures in warmer months is a major abiotic determinant for increases in shoot density, leaf growth rate and standing crop (Bulthuis and Woelkerling, 1983; Williams, 1988). These seasonal changes in growth rates may be expected to have a significant effect on the ability of a seagrass species to recover from sedimentation and burial. Smith et al. (2016a,b) found that *Z. nigricaulis* plants took from 2 to 8 months to recover following the removal of above-ground biomass and therefore recovery needs to be investigated over more than one season.

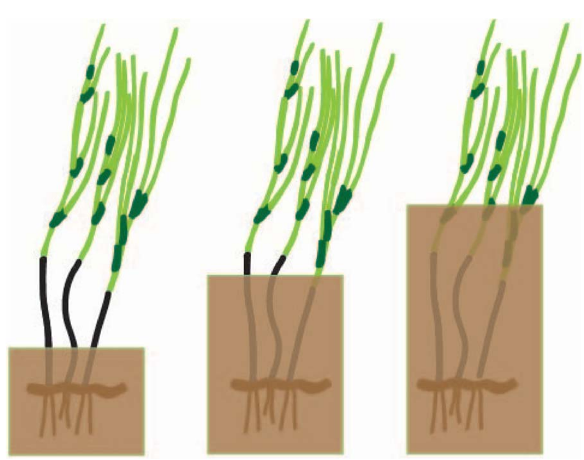

Fig. 1. Schematic diagram of *Zostera nigricaulis* plants subject to three burial treatments. Left panel, control (no burial); center panel, 4 cm (~25%) burial; right panel, 8 cm (~50%) burial.

Zostera nigricaulis is the most abundant seagrass species in Port Phillip Bay, south-east Australia (Blake and Ball, 2001) occurring in sub-tidal habitats from 0 to 8 m depth (Hirst et al. in press). *Z. nigricaulis* meadows predominantly occur in the western and southern regions of the bay, in regions protected from high wave energy (Hirst et al., 2017). In some areas of the bay, *Z. nigricaulis* grows in environments subject to moderate wave energy and subaqueous dune migration, and the risk of burial in some regions is high (Jenkins et al., 2015). Consistent with this, the effects of burial have been observed for *Z. nigricaulis* seagrass beds in field surveys of this area (Hirst et al., 2012).

Analysis of coastal aerial photography for Port Phillip Bay, south-east Australia, revealed that *Zostera nigricaulis* cover in some areas of the bay had declined by up to 90% between 2000 and 2011 (Ball et al., 2014; Hirst et al., 2016). These changes coincided with the longest drought on record for southern Australia and are hypothesised to be related to either changes in nutrient availability (Hirst et al., 2016) and/or wind patterns that influence wave strength and direction, and therefore patterns of sedimentation within the bay (Jenkins et al., 2015). In particular, the Bellarine Bank (located in the western arm of Port Phillip Bay) is associated with a combination of shallow water and wind fetch resulting in considerable sediment movement which is thought to be a major driver of seagrass distribution (Jenkins et al., 2015).

This study specifically examined: (1) the impact of burial on *Zostera nigricaulis* seagrass using experimental manipulations of varying depths; and (2) recovery following burial using experiments that controlled for re-colonisation via rhizome elongation to investigate the capacity of buried rhizomes to recover from (high-mortality) burial events during high (summer/autumn) and low growth (winter/spring) seasons. Overall, the study examined whether the morphology of *Z. nigricaulis* with its distinct vertical stem, influenced resilience to burial and the rate of subsequent recovery compared with other seagrasses, including other *Zostera* species that have been examined.

2. Methods

2.1. Study site

Burial experiments on *Zostera nigicaulis* (formerly *Heterozostera tasmanica*) were conducted at Point Richards (S38° 07′ E144°37′) at the eastern end of the Bellarine Bank, Port Phillip Bay. Bellarine Bank is located in the southwest arm of Port Phillip Bay and is subject to high sediment deposition and exposure to waves (principally from north and west) (Ball et al., 2014; Smith et al., 2016b). At low tide, shallow seagrasses become partially exposed and are susceptible to desiccation during summer. The site is characterized by sandy-sediments. Details on seagrass morphology in the area are given by Smith et al., 2016a. Average plant height in the study area ranged from 15 to 20 cm (mean = 16 cm) throughout the duration of the experiments.

The Bellarine Bank is an area characterized by dynamic sediment movement and also highly variable seagrass growth and coverage, and as such was considered an ideal site to study effects of sediment movement on seagrass. Model results focussing on the Bellarine Bank suggest an eastward flux of fine sand (Jenkins et al., 2015). The modelling estimated an eastward flow of material of ~0.1 ms^{-1} and concentrations of suspended fine sand near the seabed of ~0.075 gm^{-3}. For the ~500 m wide bank this would mean approximately 650 kg of sand would move through the area over a day (Jenkins et al., 2015).

2.2. Burial impacts

Seagrass was buried *in situ* using PVC cylinders (25 cm diameter) anchored to the bottom using screw pegs and secured using cable ties at