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Prolonged buoyancy and viability of *Zostera muelleri* Irmisch ex Asch. vegetative fragments indicate a strong dispersal potential

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ABSTRACT

The establishment of clonal marine plant populations, including the seagrass *Zostera muelleri* (Zosteraceae), may be more dependent on the availability of viable vegetative fragments rather than seed. New populations may establish through long-distance dispersal of viable vegetative fragments, potentially increasing genetic diversity and resilience to anthropogenic or naturally occurring disturbance. A number of activities can dislodge vegetative fragments of *Z. muelleri* (leaves, rhizomes and roots) from the sediment. These fragments can remain positively buoyant, floating on the surface of the water. As the time since dislodgement increases, buoyancy may become reduced, causing fragments to move lower into the water column. However, what is not known is how long these fragments remain buoyant and potentially viable for recolonization. To address this knowledge gap, we collected wrack samples ($n = 125$) of *Z. muelleri* from four Victorian estuaries. Fragments were floated in outside aquaria for up to ten weeks, with subsamples tested for metabolic activity using tetrazolium violet. Porosity of seagrass rhizomes was also investigated to understand the influence of lacunae (large air filled spaces within plant tissues) on the flotation of vegetative fragments. The average proportion of potentially viable fragments collected in wrack ranged from 3.6% (SD = 2.23) to 11.2% (SD = 5.9). While there was a steady decline in the buoyancy of fragments across the ten-week period, initial buoyancy was relatively high, with approximately 50% of the fragments remaining positively buoyant for the initial five weeks. The viability of fragments following flotation was high. One hundred percent of fragments ($n = 25$ per assay) remained viable after floating for three weeks, with only a marginal decline (=96% viability) occurring after five weeks. When considered in conjunction with the highly porous nature of seagrass rhizomes (lacunae accounted for 45.2% of total volume), our findings indicate that the species may be capable of prolonged periods of transport dispersal within the marine environment.

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1. Introduction

Seagrasses, including *Zostera muelleri* Irmisch ex Asch. (Zosteraceae), flourish in near shore coastal environments in both temperate and tropical waters (Short et al. 2001; Walker et al. 1999) where they provide a multitude of benefits to coastal ecosystems, with some authors regarding them as 'ecosystem engineers' (Bos et al. 2007; Jones et al. 1994). In this role, seagrasses alter water flows and increase sedimentation, providing firm substrata for further colonisation by macroalgae and invertebrates (Bos et al. 2007). Other notable benefits include important nutrient cycling services, provision of critical nursery habitat for economically significant fish and prawn species, and protection from predators for many marine invertebrates (Waycott et al. 2009; Zhou et al. 2014). In *Z. muelleri*, anchorage to the sediment is achieved by the development of herbaceous, laterally compressed rhizomes. These structures are also important for mechanical support, storage of nutrients and vegetative propagation, which is an important process in the spread and ongoing survival of seagrass meadows (Kuo & den Hartog 2006; Tomlinson 1974). Vegetative growth, through the development and horizontal extension of rhizomatous biomass, has provided seagrasses with the ability to thrive on all continents with the exception of Antarctica (Short et al. 2001).

Once established from seed, individual genets may form large clones that rely heavily on vegetative growth for ongoing survival (Arnaud-Haond et al. 2012; Jarvis & Moore 2010; Kendrick et al. 2012). While a mix between the two main reproductive strategies, sexual and vegetative, may provide optimum growth opportunities, vegetative reproduction and rhizome encroachment increases the capacity for seagrasses to colonise bare substrates following disturbance events (Macreadie et al. 2014).

The dispersal of propagules of aquatic species within marine and freshwater environments plays a critical role in the establishment of new populations. Colonisation of new environments by seagrasses,

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including *Z. muelleri,* is important for the exchange of genetic material between populations, potentially increasing their resilience to natural and anthropogenic disturbances (Procaccini et al. 2007). While it is generally accepted that seagrass seed dispersal distance may be limited (<100 m if not contained within detached infructescences) (Ackerman 2006), if suitable conditions exist, the dispersal potential of vegetative fragments may be much greater. For example, for the seagrasses, *Zostera nigricaulis* J. Kuo and *Zostera noltii* Hornem, dispersal potential has been estimated between several hundreds and 2300 km respectively (Berković et al. 2014; Thomson et al. 2014). Similar trends have been observed in other marine and freshwater flora, including the invasive marine alga *Caulerpa taxifolia* (Vahl) C. Agardh (Smith & Walters 1999), the giant kelp *Macrocystis pyrifera* (L.) C. Agardh (Hernández-Carmona et al. (2006), the freshwater *Elodea canadensis* Michaux (Riis & Sand-Jensen 2006) and a number of species of *Ranunculus* (Johansson & Nilsson 1993).

Lacunae, or air filled spaces within plant tissues, facilitate greater oxygen transport in species growing in waterlogged and anoxic conditions and aid in the dispersal of vegetative propagules (Coutts & Philipson 1978; Justin & Armstrong 1987). Lacunae are continuous within *Z. muelleri* from the leaves to the roots and allow for the movement of gases throughout the entire plant. Of particular importance is the ability of the species to release oxygen, via lacunal spaces, directly into the sediment from the roots thereby creating an oxygen rich environment in very close proximity (<1 mm) to roots and rhizomes (Moriarty & Boon 1989). A high proportion of lacunae within leaf tissue also provides greater buoyancy to both submerged and emergent aquatic species including seagrasses (Hemminga & Duarte 2000) the water lily, *Nymphaea odorata* Ait. (Etnier & Villani 2007) and species of marine macroalgae (Stewart 2004). The increased buoyancy that lacunal spaces provide also facilitates dispersal of detached fragments via water currents. It is this dispersal potential and the ability to retain long-term viability which are critical factors in the establishment of new populations. Long term viability and effective dispersal potential of detached fragments following removal from the sediment have been reported for the seagrasses *Z. noltii,* (55 days) (Berković et al. 2014) and *Posidonia oceanica* (L.) Delile (408 days) as well as the marine alga *Hormosira banksii* (Turner) Decaisne (96 days) (McKenzie & Bellgrove 2008).

Z. muelleri has come to populate much of the eastern and southern coasts of Australia and is the dominant seagrass species in New Zealand (Jones et al. 2008; Waycott et al. 2014). This wide distribution may be attributable to the species' capacity for long-distance dispersal. Fragments of *Z. muelleri* can be dislodged from the sediment through both natural (e.g. wave action, consumption by large herbivores) or anthropogenic (e.g. propeller scarring, dredging activities) processes (Erftemeijer et al. 2006; Greve & Binzer 2004; Kenworthy et al. 2002; Lanyon & Sanson 2006). Once dislodged, their fate is often varied and related to a number of species-specific traits or prevailing environmental conditions. For instance, fragments may sink out of the water column and decompose, re-establish in new environments or they can be carried ashore where they remain to decompose or are resuspended in response to local hydrological and meteorological conditions (Oldham et al. 2010; Pattiaratchi et al. 2011).

Although the movement of reproductive seagrass propagules has been well documented, what is less understood is the potential for vegetative fragments of *Z. muelleri* (leaves, rhizomes and roots) to remain viable subsequent to being dislodged from the sediment. This research was undertaken to identify the potential dispersal and viability of *Z. muelleri* vegetative fragments. This was performed by, firstly, estimating the proportion of vegetative fragments found in beach wrack that were potentially capable of regrowth. Secondly, identifying the period of time that dislodged vegetative fragments remained buoyant. Thirdly, by examining the relationship between rhizome porosity and buoyancy. And finally, by measuring the viability of vegetative fragments following extended periods of flotation.

2. Material and methods

2.1. Determining proportion of viable seagrass in wrack

Collection of fresh beach wrack that had been deposited during the previous high tide (<6 h prior) occurred in January 2014 at the following five sites within Victoria, Australia: Shallow Inlet (two sites: 38°49′8.89″S, 146°10′13.62″E and 38°50′9.99″S, 146° 9′6.76″E); Corner Inlet (two sites: 38°48′37.98″S, 146°16′7.13″E and 38°41′47.26″S, 146°14′51.46″E) and Westernport (one site: 38°31′41.21″S, 145°22′ 11.19″E). Enough beach wrack to fill a 25 cm × 35 cm sealed freezer bag was collected from the high tide mark at 20 m intervals along the beach. Twenty samples were collected from each site providing 100 samples in total.

Sealed samples were returned to the laboratory on ice within 48 h. Fragments of seagrass found in wrack were determined to be potentially capable of regrowth if: a) they contained rhizome with adventitious roots attached; b) the rhizome was fresh and turgid; and c) leaf shoots were fresh and in good condition. Seagrass leaves from fragments that were deemed potentially capable of regrowth were scraped with a razor blade to remove epiphytic algae and oven dried at 60 °C for 24 hrs. All samples were weighed to determine proportion of potentially viable seagrass within the total wrack sample.

2.2. Buoyancy of vegetative seagrass fragments

One hundred vegetative fragments of *Z. muelleri* were hand collected from Corio Bay, Victoria, Australia (38°52′30.17″S, 144°24′25.98″E). Samples were returned to the laboratory where they were sorted into fragments that were potentially capable of regrowth (refer above) and those with adventitious roots only, which were discarded. The length of the leaves, rhizomes and adventitious roots was measured in remaining samples ($n = 40$) using a tape measure and digital callipers prior to being placed into a 140 L outdoor aquarium filled with recirculated (450 L/h) artificial salt water (NeoMarine, Brightwell Aquatics). Salinity was maintained at 32 for the duration of the experiment to imitate conditions at the time of sampling and light and temperature reflected ambient conditions over the course of the experiment. As a means of minimising entanglement, the samples were agitated daily by hand. To estimate the buoyancy of fragments, a scale was placed on the outside of the tank with the uppermost 10 cm being deemed positively buoyant, 11–30 cm deemed somewhat buoyant, and the lower 10 cm negatively buoyant. Buoyancy of fragments was determined on a weekly basis by counting the number of fragments whose majority was inside each of the buoyancy levels (positively, somewhat, negatively) calculated as a percentage of the total sample size.

2.3. Longevity of vegetative seagrass fragments

A total of 100 vegetative fragments of *Z. muelleri* were collected by hand from Altona Beach, Victoria, Australia (37°52′30.17″S, 144°48′ 53.84″E). Harvesting incorporated the use of a PVC corer with an internal diameter of 100 mm placed into the sediment to a depth of 10 cm. This depth was determined to be appropriate for this location as it ensured removal of all below ground biomass with the sample. Ten core samples were placed into 1 L sealed containers and covered with seawater for transport. Samples were returned to the laboratory where they were again sorted into fragments that were potentially capable of regrowth (refer above) and those with adventitious roots only. Samples with predominantly adventitious roots were again discarded and the remainder were washed in seawater to remove sediment before being placed into a 140 L outdoor aquarium filled with recirculated (450 L/h) artificial salt water (NeoMarine, Brightwell Aquatics).

Samples were floated in aquariums for one, three and five weeks, and agitated daily. At the end of each flotation period, 25 samples

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