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## Response of temperate intertidal benthic assemblages to mangrove detrital inputs



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#### ABSTRACT

Inputs of macrophyte detritus to soft-sediment habitats can be an important energy source regulating benthic community structure. In the tropics, mangrove detritus forms an essential food source for benthic invertebrates; however, it is unknown whether the same dependence occurs in temperate systems where mangrove detrital inputs to estuaries can be considerable. We investigated whether mangrove detrital deposition to temperate intertidal flats represents a cross-boundary subsidy of organic matter by structuring benthic macro-invertebrate communities on adjacent intertidal flats. To determine whether community responses to detrital deposition were spatially consistent, mangrove detritus was added ( $260 \text{ g m}^{-2}$ , equivalent to summer litter production) to two intertidal sites (with differing background sediment properties and macrofaunal community structure). Subsequent changes to the benthic macrofaunal community and sediment properties were monitored for 6 months following the addition. Benthic community responses to the detrital enrichment were similar at both sites; responses were subtle and involved only small changes in the relative abundances of a few dominant taxa (primarily a reduction in the numerically dominant spionids), rather than major shifts in community composition. The subtle response to such a relatively large detrital input suggests that mangrove detritus in temperate estuaries plays a minor role in shaping the communities on intertidal flats. We suggest that the slow decay (low bioavailability) and relatively low productivity of temperate mangroves result in communities that are less reliant on mangrove detritus, compared to those in the tropics where rapidly decaying mangrove detritus comprises the base of many food webs.

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#### 1. Introduction

Macrophyte detritus (dead, decaying organic matter) is a key source of energy input to many estuarine systems (Findlay and Tenore, 1982; Moore et al., 2004; Odum and Heald, 1975). Deposited detritus can be utilised directly by benthic detritivores (Findlay and Tenore, 1982; McClelland and Valiela, 1998; Moore et al., 2004), as well as fuel the growth of sediment microorganisms (e.g. Bishop and Kelaher, 2007; Levinton, 1985; Rublee, 1982). In addition, numerous studies in temperate estuaries have demonstrated that benthic macrofaunal community structure is modified by macrophyte detrital enrichment (see Bishop and Kelaher, 2008; Bishop et al., 2010; Kelaher and Levinton, 2003; O'Brien et al., 2010; Rossi and Underwood, 2002; Taylor et al., 2010). Accordingly, detrital deposition and distribution can be a key factor regulating small-scale variability and patchiness in soft-sediment community structure and function (Kelaher and Levinton, 2003; Kelaher et al., 2003, 2013; Rossi and Underwood, 2002).

Macrofaunal responses to detrital addition should vary with resident community structure due to species-specific responses. It is well established that macrofaunal community structure varies with sediment properties (e.g. grain size and organic content; Pratt et al., 2013; Thrush et al., 2005: van der Wal et al., 2008), and since these properties can also influence detrital decay rates (Holmer and Olsen, 2002) community response to detrital addition can be expected to vary across sedimentary gradients. However, few field-based studies have investigated the site-specific impacts of detrital deposition on estuarine benthic community structure (these are: Bishop and Kelaher, 2013b; O'Brien et al., 2010; Olabarria et al., 2010; Rossi, 2006; Rossi and Underwood, 2002), and just two of these studies have incorporated differences in sediment properties and associated differences in benthic communities among sites (O'Brien et al., 2010; Rossi and Underwood, 2002). Both of these studies explored community responses to the burial of whole algal wrack, and found that different species responded at mud compared to sand sites (Rossi and Underwood, 2002), and between sites with different organic enrichment levels (O'Brien et al., 2010).

Mangrove detritus has been shown to be an important source of energy in tropical coastal ecosystems (Doi et al., 2009; Granek et al., 2009; Odum and Heald, 1975). In temperate New Zealand estuaries, recent

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changes to catchment land use have altered mangrove distributions, which are likely to continue because of climate change and mangrove management strategies (e.g. forest clearances) (Morrisey et al., 2010). As a result, the magnitude of mangrove detrital inputs into temperate coastal systems is changing. Many tropical coastal systems rely on mangrove detritus as a subsidy of organic matter that supports the base of marine food webs (e.g. coral reefs and estuaries, Granek et al., 2009; Sheaves and Molony, 2000; Werry and Lee, 2005); however, the lack of ecological knowledge gathered in temperate mangrove systems offers little guidance to the impacts of changing detrital inputs on recipient coastal ecosystems. Whilst temperate mangroves can be substantially less productive than their tropical counterparts, detrital inputs are comparable to seagrass production in some estuaries (Gladstone-Gallagher et al., 2014), a detrital source known to be important for benthic invertebrates (Doi et al., 2009).

Mangrove leaf litter decay is slow in temperate regions compared to other detrital sources (Enríquez et al., 1993) and involves a two part process, where initial decay is rapid, followed by the gradual decay of the recalcitrant portion of the leaf. Initial decay is likely through bacterial colonisation and breakdown of the leaf, which results in nitrogen enrichment (Gladstone-Gallagher et al., 2014) and increasing palatability to organisms (Nordhaus et al., 2011). The slow, secondary decay is most likely through physical fragmentation of the recalcitrant fractions of the leaf, which is controlled by climatic variables, tidal submergence, and the presence of fauna (e.g. Dick and Osunkoya, 2000; Oñate-Pacalioga, 2005; Proffitt and Devlin, 2005). Differences between physical, chemical and biological properties of different sediment types could therefore influence detrital breakdown rates associated with both stages of decomposition. Previous studies have linked sediment properties with differences in the decay rates of both macroalgae and mangrove litter (Hansen and Kristensen, 1998; Holmer and Olsen, 2002; but see Gladstone-Gallagher et al., 2014).

Intertidal soft-sediment communities are dynamic (e.g. Morrisey et al., 1992; Thrush, 1991; Thrush et al., 1994) and a temporally variable response to detrital addition could be expected as the decay process proceeds. However, only a few studies investigating macrofaunal responses to detrital deposition have incorporated temporal sampling into study designs, with most monitoring responses on only one or two sampling dates after addition (often sampling two or more months after the addition; e.g. Bishop et al., 2007, 2010; Taylor et al., 2010). The two studies that have incorporated temporal sampling have demonstrated a strong time dependent response: in one, macrofaunal abundance took 24 weeks to respond to the addition of seagrass detritus (Bishop and Kelaher, 2007); whilst in the other, annelids responded to an *Ulva* detrital addition after only four weeks (Kelaher and Levinton, 2003). These examples illustrate that macrofaunal responses may be variable through time due to differences in detrital types, quantities, decay rates, and the ambient community composition. Accordingly, studies that are restricted to a single sample date may miss some or all of the community response to detrital addition.

Here, we investigate the role of mangrove detrital inputs in structuring intertidal benthic communities in a temperate setting. Mangrove detritus was added at two adjacent sites with different background sedimentary properties and macrofauna. The benthic community response was monitored several times over a six month period. We anticipated that changes in macrofaunal community structure would vary with site and time, because detrital processing/decay would be influenced by site-specific sediment biogeochemistry and species responses to enrichment

#### 2. Material and methods

#### 2.1. Study site

The study was carried out in the northern region of Whangamata Harbour (North Island, New Zealand). The New Zealand endemic mangrove Avicennia marina subsp. australasica inhabits 101 ha of the harbour (approximately 22% of the 467 ha harbour area), which has expanded from 31 ha of mangrove forest prior to catchment urbanisation, deforestation and agriculture since the 1940s (Singleton, 2007). Such changes in catchment land use have increased the delivery of terrestrial sediments via streams and rivers into many New Zealand estuaries and mangroves have expanded in response to sedimentation (Morrisey et al., 2010). Two unvegetated mid-intertidal sites were selected: site 1 (37°10′43.0″S, 175°51′36.9″E) is characterised by fine organic-poor sands and the adjacent site 2 (37°10′38.6″S, 175°51′36.5″E) has higher mud content and relatively organic-rich sediments (see Results). The two sites are located 20-40 m down-shore of the mangrove forest edge, occupying similar tidal elevations (0.05-0.25 m above mean sea level) and are separated by an along-shore distance of approximately 50 m. The spring-neap tidal range is 1.71-1.27 m (Hume et al., 2007), and inundation periods at the sites were similar (site 1 = 5-6 h and site 2 = 6-7 h).

#### 2.2. Experimental protocol

In early February 2011 (late austral summer), 18 evenly dispersed plots (1.15 m dia., 1.04 m<sup>2</sup>) were established at each site within a 32  $m \times 14$  m area. Five metres separated each plot. In each of three rows of six plots, we randomly assigned two replicates of the following treatments: detrital addition (DA), procedural control (PC), and control (C) (n = 6 for each treatment). DA plots were enriched with mangrove detritus by finger churning 270 g of detritus ( $260 \,\mathrm{g m^{-2}}$ ) into the top 3 cm of sediment (as in Bishop and Kelaher, 2008; Bishop et al., 2010; Kelaher and Levinton, 2003). The addition equates to the total amount of leaf litter produced during the productive summer months (November-February) in New Zealand forests, with the timing of the addition coinciding with the end of this production peak (Gladstone-Gallagher et al., 2014; May, 1999; Oñate-Pacalioga, 2005; Woodroffe, 1982). PC plots were finger churned, identical to DA plots, but no detritus was added, and were included in the experimental design to delineate benthic community effects of the one off sediment mixing disturbance from detrital enrichment effects. C plots were left untouched.

The mangrove detritus used in the manipulation was prepared by firstly collecting yellow senescent (ready to abscise) mangrove leaves from trees in Whangamata Harbour (January 2011). To simulate natural incorporation of mangrove detritus into the sediments, the leaves were oven dried at 60 °C to constant weight and ground into 2 mm pieces. This drying of leaf material is thought to be comparable to the drying out that a fallen leaf would experience if it fell on a mid-afternoon summer low tide, and was necessary to standardise the amount of detritus added to each plot (Bishop and Kelaher, 2008).

Experimental plots were repeatedly sampled for macrofauna  $(1 \times 13 \text{ cm dia.}, 15 \text{ cm depth core per plot})$  and surface sediment properties (photosynthetic pigment content, organic content and grain size) at 2, 4, 8, 12 and 24 weeks following the detrital addition. This monitoring period incorporated a series of sampling dates to determine temporal variability in macrofaunal responses to detrital inputs. The sampling period encompasses that of other studies (e.g. Bishop and Kelaher, 2007, 2008; Kelaher and Levinton, 2003), and is also longer than the half-life of mangrove leaf litter in New Zealand (63-88 days; Gladstone-Gallagher et al., 2014). Sediment samples (3 pooled syringe core samples; 3 cm dia., 2 cm depth) were taken within a few centimetres of each macrofaunal core. To minimise the effect of repeated sampling on the benthic community, macrofaunal cores were taken from different positions within the plots on each sampling date and the resulting core holes in-filled with defaunated sand (Lohrer et al., 2010). Additionally, both sites were sampled for macrofauna and sediment properties on day 0 at 6 randomly chosen locations outside of the experimental plots but within the study area. Macrofaunal cores were sieved over a 500 µm mesh

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