



# Influence of New Zealand cockles (*Austrovenus stutchburyi*) on primary productivity in sandflat-seagrass (*Zostera muelleri*) ecotones

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## ABSTRACT

New Zealand cockles (*Austrovenus stutchburyi*) are ecologically important, intertidal bivalves that have been shown to influence nutrient cycles and the productivity of microphytobenthos on sandflats. Here, we investigated the potential for cockles to impact the productivity of seagrass, *Zostera muelleri*, and examined interactions between these habitat-defining species where they co-occur. We sampled bivalve densities and sizes, sediment properties, and seagrass shoot densities across the boundaries of two seagrass patches on an intertidal sandflat in northern New Zealand, and measured dissolved oxygen and nutrient fluxes in light and dark benthic incubation chambers in conjunction with a 0–97% gradient in seagrass cover. Although gross primary production (GPP,  $\mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$ ) increased predictably with the cover of live seagrass, the density of cockles and sediment properties also contributed directly and indirectly. Seagrass cover was positively correlated with cockle density (ranging from 225 to 1350 individuals per  $\text{m}^2$ ), sediment mud percentage (0.5–9.5%), and organic matter content (0.5–2.2%), all of which can affect the efflux of ammonium (readily utilisable inorganic nitrogen) from sediments. Moreover, the cover of green seagrass blades plateaued (never exceeded 70%) in the areas of highest total seagrass cover, adding complexity to cockle-seagrass interactions and contributing to a unimodal cockle-GPP relationship.

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## 1. Introduction

Seagrass beds are viewed worldwide as valuable habitats linked to the delivery of ecosystem services (Costanza et al., 1997; Orth et al., 2006; Waycott et al., 2009). There are a variety of different seagrass species, representing differing thallus types and depth distributions in both temperate and tropical areas, and the ecosystem services they deliver vary accordingly. Nevertheless, seagrass beds have been shown to be hotspots for primary productivity (Duarte and Chiscano, 1999) that can sequester atmospheric carbon (Duarte et al., 2005; Fourqurean et al., 2012) and export carbon-rich substrates to adjacent habitats (Suchanek et al., 1985; Savage et al., 2012). They have also been shown to support an array of harvested fish and shellfish species (Heck Jr. et al., 2003;

Parsons et al., 2015), bolster macroinvertebrate diversity (Battley et al., 2011), and feed organisms like manatees, dugongs and sea turtles (Orth et al., 2006). Seagrass beds can also stabilise bed sediments (Heiss et al., 2000; Tuya et al., 2014), and are major contributors to nutrient cycling (Touchette and Burkholder, 2000; Gras et al., 2003). Therefore, understanding the factors affecting seagrass productivity and health is an important conservation objective in many coastal marine systems worldwide (Short and Wyllie-Echeverria, 1996; Duarte, 2002; Orth et al., 2006; Waycott et al., 2009).

In New Zealand, the seagrass flora is represented by a single species, *Zostera muelleri* (Waycott, 2004; Jones et al., 2008). This species is most widespread on estuarine intertidal flats, though it has been reported on rocky intertidal platforms where sediments are present (Woods and Schiel, 1997), and can extend to several metres depth in the sub-littoral zone in sufficiently clear waters (Schwartz et al., 2006). The beds on intertidal flats can be thick, with seagrass blades covering 100% of the sediment surface area;

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and extensive, covering tens of km<sup>2</sup> in some of the larger harbours (van Houte-Howes et al., 2004). However, there can be a high degree of variation in seagrass shoot density within patches and considerable patchiness at the landscape scale (Mills and Berkenbusch, 2009). The unvegetated areas between patches of seagrass often contain other types of structure-forming, habitat-defining species such as cockles, wedge shells and tube-building polychaetes (de Juan and Hewitt, 2011), and seagrass in New Zealand does not necessarily elevate macrofaunal diversity relative to adjacent habitat types (Turner et al., 1999; van Houte-Howes et al., 2004; de Juan and Hewitt, 2011). The heterogeneous mosaic of habitat types on New Zealand's intertidal flats has important implications for overall biodiversity (Ellingsen, 2002; Thrush et al., 2006a) and key ecosystem functions such as primary production and nutrient regeneration (Thrush et al., 2006b; Lohrer et al., 2010; Pratt et al., 2015a,b).

The mosaic of habitat types present on New Zealand intertidal flats also results in the presence of ecotones, which are transitional zones between adjacent ecological communities. An ecotone often has characteristics in common with the two bordering ecological communities, but unique properties can emerge in the transitional zones as well (Cadenasso et al., 2003a, 2003b; Yarrow and Marín, 2007). Although the biodiversity of adjacent habitat types has been compared in New Zealand intertidal flats (van Houte-Howes et al., 2004; de Juan and Hewitt, 2011), interactions between different habitat-defining species in ecotonal areas and how transitional zones contribute to ecosystem functioning remain poorly understood.

Seagrass patches are easy to identify and map in intertidal areas, due to the green shoot biomass that is present above the sediment-water interface. The high primary producer biomass in seagrass beds translates to heightened rates of carbon fixation and oxygen evolution (Fourqurean and Zieman, 1991). In contrast, unvegetated intertidal sediments are usually characterised by macroinfauna (such as clams and worms) and microphytobenthos that are more difficult to directly observe and map. The microphytobenthos, or MPB, is positioned near to the sediment-water interface, where it is able to access stocks of inorganic nutrients present in sediment pore water as well as incident sunlight radiation (Forster and Kromkamp, 2006). Unvegetated intertidal sediments, despite oftentimes high microbial and macrofaunal oxygen demand, can be net autotrophic due to the high productivity of MPB (Sandwell et al., 2009; Rodil et al., 2011). Moreover, the productivity of MPB has been shown to be positively influenced by large burrowing fauna (Lohrer et al., 2004, 2015; Jones et al., 2011).

Bivalve beds are also important intertidal habitats in New Zealand, with both *Austrovenus stutchburyi* (cockles) and *Macomona liliana* (wedge shells) acting as bed-forming, habitat-defining species (Thrush et al., 2006b, 2012; Jones et al., 2011, 2014; Woodin et al., 2016). Cockles, suspension-feeding venerid clams, are common and widespread on intertidal flats throughout New Zealand, and can form extensive beds of remarkably high density (up to 4500 individuals per m<sup>2</sup>; Lohrer et al., 2012). Cockles have been collected by indigenous New Zealanders for centuries, and are harvested both recreationally and commercially at present (Ministry for Primary Industries, 2012). Cockles are also major ecological engineers on intertidal flats, producing copious shell material that influences sediment composition, grain size and biogeochemistry (Smith et al., 2010). The living and dead shell material in these cockle beds influences tidal flat biodiversity by attracting a number of shell-associated species (anemones, chitons, limpets, and barnacles) and increasing the heterogeneity of the habitat for other infauna (Mouritsen and Poulin, 2003; Mouritsen, 2004). Importantly, in the context of the present investigation, cockles have been shown to have positive impacts on tidal flat

primary productivity (Sandwell et al., 2009; Jones et al., 2011; Rodil et al., 2011; Pratt et al., 2015a,b). MPB appears to benefit from increased access to inorganic nutrients, ammonium in particular, which is excreted by cockles and released from sediment pore water as they move through surface sediments.

*M. liliana* adults live 2–10 cm deep in the sediment, relative to cockles that generally inhabit the upper 0–4 cm. *M. liliana* is a surface deposit-feeding tellinid bivalve species that uses long siphons to extract microphytobenthos and other organic matter from surface sediments (Pridmore et al., 1990). The exhalant siphons of *M. liliana* deliver water to sub-surface sediment layers, creating pore-water pressure gradients that are thought to influence nutrient fluxes and MPB productivity (Volkenborn et al., 2012; Woodin et al., 2016). This bivalve's size, abundance and bio-irrigation activity make it a key contributor to sandflat ecosystem functioning in New Zealand (Thrush et al., 2014; Pratt et al., 2015a,b).

The intermingling of bivalve-dominated habitats and adjacent intertidal seagrass meadows is a common feature of many New Zealand estuaries. For example, cockle densities can be very high inside seagrass meadows, particularly the smaller size classes (Alfaro, 2006). Alfaro (2006) suggests that cockles recruit to seagrass, though the mechanism of increased cockle densities may be the passive trapping of larvae and post-settled juveniles by seagrass blades that alter hydrodynamics near the bed (Lundquist et al., 2004; Bryan et al., 2007). Seagrass patch edges bordering cockle-dominated areas would be prime areas for passive propagule trapping and elevated densities of cockles. Other mechanisms for increased cockle densities inside New Zealand seagrass meadows may be reduced predation (e.g., by eagle rays; Thrush et al., 1991; Hines et al., 1997) or elevated food (Gonzalez-Ortiz et al., 2014).

In the current investigation, we examined bivalve-seagrass interactions, focusing on transitional edges between unvegetated cockle-dominated habitat and high density seagrass cover. Similar to the effects of cockles on MPB productivity, we hypothesised that cockles would have a positive influence on the productivity of seagrass. This hypothesis is consistent with Northern Hemisphere literature reporting positive effects of mussels on seagrass production (Reusch et al., 1994; Reusch and Williams, 1998; Peterson and Heck Jr., 2001a,b). The reported effects are generally related to the provisioning of inorganic nutrients to the seagrass by the mussels, though the structure provided by epibenthic mussels is also thought to influence the densities of grazers that can control the growth of epiphytes on seagrass blades (Peterson and Heck Jr., 2001a,b). Although both cockles and mussels are suspension feeding bivalves that produce organic rich faeces and pseudo-faeces (that ultimately fertilise the sediment), cockles do not attach to any substrate using byssus threads and are infaunal. The high mobility of cockles both laterally and vertically in the upper 0–4 cm of the sediment column suggests that bioturbation is a key part of their functional role in New Zealand tidal flat systems (Jones et al., 2011).

As our main questions centered on whether and how cockles influenced seagrass primary productivity, we assessed rates of seagrass primary production across a range of shoot densities *in situ* in a large New Zealand harbour, using benthic incubation chambers to measure rates of photosynthetic oxygen evolution. In conjunction, we quantified fluxes of inorganic nutrients across the sediment-water interface and several other explanatory covariables, including the densities and sizes of bivalves present in all chambers. We then used a multiple regression analytical approach to disentangle the differing influences on seagrass primary productivity and to gain insights into their relative strengths.

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