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Indirect effects of *Atrina zelandica* on water column nitrogen and oxygen fluxes: The role of benthic macrofauna and microphytes

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Abstract

The effects of ecosystem engineers can be mediated by direct and indirect interactions. For suspension-feeding bivalves that contribute to benthic–pelagic coupling, indirect effects have been linked to hydrodynamics; however, the influence of these ecosystem engineers may also operate through interactions with surrounding sediments, microphytes and macrofauna that, in turn, affect nutrient and oxygen fluxes. This study investigated the indirect effects of an epibenthic suspension-feeding bivalve (*Atrina zelandica*) on ammonium and nitrate–nitrite effluxes from the sediment, and oxygen consumption in the overlying waters, under dark conditions, at two sites with different environmental characteristics. Location-dependent effects were observed in the relative strength of the effect of *Atrina* on microphyte and macrofaunal abundance. The difference between the strength of the effect of *Atrina* on macrofauna between sites was not driven by a single species or type of species; rather all the species decreasing in abundance away from *Atrina* were small species that utilised the sediment water interface. Location-dependent effects were also observed in the relative strength of the effect of microphyte and macrofaunal abundance on oxygen and nutrient fluxes. While microphytes were an important consumer of oxygen at one site, at the other site, small infaunal macrofauna were important. Similarly, the strength of the effect of surrounding macrofauna on ammonium efflux varied between sites. These findings demonstrate the importance of natural history and species functions for understanding complex responses. They suggest that indirect effects by key benthic macrofaunal species in marine systems can also be important to benthic–pelagic coupling. In particular, while key species are often large, excretion and respiration of smaller macrofauna can be important to the exchange of nutrients near the seafloor and oxygen consumption in the benthic boundary layer.

Keywords: Benthic–pelagic coupling; Macrofauna; Microphytes; Nutrient fluxes; Oxygen consumption; Suspension feeders

1. Introduction

Suspension-feeding bivalves can play important roles as ecosystem engineers through their influence on benthic–pelagic coupling and the use of their shells as attachment surfaces for encrusting organisms. When suspension-feeding bivalves protrude from the seafloor into the water column, the potential for both direct and indirect effects on surrounding macrofauna is frequently mediated by hydrodynamics affecting boundary flows, sedimentation and resuspension (Frechette et al., 1989; Green et al., 1998; Nikora et al., 2002). However, the potential for these ecosystem engineers to affect benthic–pelagic coupling via indirect effects on microphytes and surrounding macrofauna is relatively unexplored, even though direct effects due to respiration, excretion and increased fluxes from the water column of

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sediment and organic matter have been described (Loo and Rosenberg, 1989; Dame and Libes, 1993; Frechette and Bacher, 1998; Dame et al., 2001; Dowd, 2005; Gibbs et al., 2005 but see Newell et al., 2002).

Recent studies have demonstrated the potential for interactions and feedbacks between large bioturbators, microphytes and sediment nutrients (Hughes et al., 2000; Reise, 2002; Lohrer et al., 2004). Other studies suggest that not only bioturbators are important but that large, high density macrofauna may affect nutrient fluxes from the sediment into the water column and oxygen consumption in the overlying water (Welsh, 2003; Thrush et al., in press). A potential, usually not considered, also exists for smaller surrounding macrofauna to directly introduce nutrients into, and consume oxygen from, the water.

Atrina zelandica (Gray) is a large suspension-feeding pinnid bivalve that has been previously demonstrated to influence community structure and ecosystem function in coastal soft-sediment habitats (Warwick et al., 1997; Cummings et al., 1998; Norkko et al., 2001; Hewitt et al., 2002). *Atrina* are large (up to 30 cm long) and protrude above the sediment surface, and modify boundary flow conditions (Green et al., 1998; Nikora et al., 2002). *Atrina* can produce copious amounts of biodeposits (Hewitt and Pilditch, 2004) influencing nutrient and oxygen fluxes (Norkko et al., 2001; Gibbs et al., 2005), sediment fluxes and surrounding sediment characteristics (Norkko et al., 2001). Previous work suggests effects are location-dependent, with strongest effects on surrounding macrofauna and oxygen and nutrient fluxes at low turbidity (Gibbs et al., 2005; Norkko et al., in press). While Gibbs et al. (2005) provide an estimate of the separate effect of direct *Atrina* excretion and respiration on their measurements of nutrient and oxygen fluxes between the seafloor and the water column, they were not able to determine whether fluxes were affected by indirect interactions with microphytes or surrounding macrofauna. Some indications of a microphyte interaction were suggested by an observed increase in sediment chlorophyll a away from *Atrina*.

This study was designed to understand better the direct and indirect effects of *Atrina* highlighted by previous studies. Two key questions were posed. (1) Knowing that *Atrina* can indirectly affect nutrient and oxygen content of the water, is this indirect effect associated with effects on sediment characteristics, microphytes or surrounding macrofauna? And (2) if the strength of the effect of an ecosystem engineer on surrounding macrofauna is location-dependent, is the effect on microphytes and oxygen/nutrient fluxes also location-dependent? The answers to these questions were used to build a conceptual model of the direct and indirect linkages between *Atrina*, microphytes, surrounding macrofauna, and nitrogen and oxygen fluxes. This conceptual model was used to highlight the potential for, and importance of, location-specific indirect interactions.

2. Methods

2.1. Study location and sampling design

Based on information from previous studies (Norkko et al., 2001, in press), we chose two sites differing in environmental characteristics (e.g., turbidity), microphyte and macrofaunal communities (Table 1). The first site, MI, was located off Motoroa Island, at the mouth of Kawau Bay (Fig. 1). This site had sandy sediments, low suspended sediment loads, and weak currents. The second site, TK, was located in Mahurangi Harbour, near the mouth (Fig. 1). Sediments were fine sand, suspended sediment loads were high on the outgoing tide, and currents were strong at mid-ebb and flood.

At both sites, patches of various sizes and densities of *Atrina* were observed. As the effect of *Atrina* on macrofauna has been predicted to depend on the density of *Atrina* and patch structure (see, Hewitt et al., 2002), samples were distributed along gradients in these characteristics at both sites. Seven locations of differing densities/patch size of *Atrina* were selected at each site, varying from an area with one *Atrina* per square meter area to areas of 25 *Atrina* per square meter. A benthic chamber (13.9 cm diam.; volume 0.8 l) was placed next to an *Atrina* in each location (location A). Another chamber was placed adjacent to the first (location N), but as far away from other *Atrina* in the patch as possible, such that the distance between it and any *Atrina* was greater than the distance between the first chamber and an *Atrina*. Bare areas (>50 cm diam.) were selected as

Table 1
Environmental characteristics of the two sites, MI and TK, derived from unpublished data

Location	MI	TK
	Large coastal embayment	Small harbour
Mean peak tidal current	0.5 m s^{-1}	0.57 m s^{-1}
Mean peak bed orbital velocity	2.6 cm s^{-1}	1 cm s^{-1}
Baseline suspended sediment concentration	10–20 mg l^{-1}	20–60 mg l^{-1}
Predominant sediment type by weight	Coarse, medium, fine sands	Fine sands

Tidal current and bed orbital velocity were derived from hydrodynamic models of the area. Suspended sediment concentrations were measured on three occasions over a tidal cycle at nearby sites. Sediment type was measured once on a composite core of the surface 2 cm of sediment.