Bottom–up and top–down mechanisms indirectly mediate interactions between benthic biotic ecosystem components

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ABSTRACT

The loss or decline in population size of key species can instigate a cascade of effects that have implications for interacting species, therewith impacting biodiversity and ecosystem functioning. We examined how top–down and bottom–up interactions may mediate knock-on effects of a coastal deposit-feeding clam, *Macomona liliana* (hereafter *Macomona*), on sandflat meiobenthos densities. Therefore we manipulated densities of *Macomona* in combination with predator exclusion and experimental shading that was expected to alter microphytobenthos biomass. We show that *Macomona* regulated densities of meiobenthic (38–500 μm) nematodes, copepods, polychaetes, turbellarians, and ostracodes during the three months of incubation via indirect mechanisms. Predator pressure on *Macomona* by eagle rays (*Myliobatis tenuicaudatus*) was found to have a negative effect on densities of some meiobenthic taxa. Furthermore, experimental shading resulted in the loss of a positive relation between *Macomona* and microphytobenthos biomass, while concurrently increasing the density of some meiobenthic taxa. We suggest that this observation can be explained by the release from bioturbation interference effects of the cockle *Austrovenus stutchburyi* that was found to thrive in the presence of *Macomona* under non-shaded conditions. Our results highlight the importance of interactions between macrofaunal bioturbation, microphyte biomass, sediment stability, and predation pressure for the structuring of benthic communities. This experiment illustrates that manipulative field experiments may be particularly suitable to study such multiple indirect mechanisms that regulate ecosystem diversity and related functioning because such approaches may best capture the complex feedbacks and processes that determine ecosystem dynamics.

1. Introduction

The biodiversity found in coastal habitats is on the frontline of current environmental change resulting from anthropogenic activities related to the expanding exploitation of coastal areas (Airoldi and Beck, 2007; Lotze et al., 2006). The loss or decline in density of particular species populations can instigate a cascade of effects that have implications for interacting species (biodiversity) and associated ecosystem functioning (Daborn et al., 1993; Dunne et al., 2002). Consequently, the increased awareness of potential threats related to biodiversity loss for the delivery of goods and services provided by these ecosystems (e.g. Barbier et al., 2011) has stimulated research of biodiversity–ecosystem functioning relationships (BEF) over the last 10–15 years (e.g. Bolam et al., 2002; Emmerson et al., 2001; Solan et al., 2008; Van Colen et al., 2012). While these studies revealed distinct relations

between different diversity measurements (e.g. species richness, species identity and functional traits) and the variability in ecosystem processes, or vice versa, consensus exists that the magnitude, type, and direction of response strongly vary across temporal and spatial gradients (Godbold and Solan, 2009; Pratt et al., 2014a; Van Colen et al., 2013). This context-dependency highlights the potential of stressors to interact and change the outcome of BEF relationships, but the understanding of how stressors change these relationships remains little studied and poorly understood. A particular stressor for many shallow coastal habitats is the change in suspended sediment load resulting from changes in geomorphology, hydrodynamics and sediment input related to altered land use and the development of coastal regions (Thrush et al., 2004). Such increased concentrations of suspended sediments may alter the outcome of interactions between benthic invertebrates and their biotic and abiotic environment both directly and indirectly. For example, light-limited benthic primary production may be directly inhibited in high turbid waters therewith changing food supply to benthic grazers (Pratt et al., 2014b) and alter the interactions

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between microphytobenthos growth and sediment accretion that determine sediment stability (Van De Koppel et al., 2001).

Macrobenthic organisms play a pivotal role in the functioning of coastal soft-sediment ecosystems through a variety of behavioral activities. For example, these organisms bioturbate and bio-irrigate the sediment therewith facilitating the (re)mineralization of organic matter and nutrient release (Lohrer et al., 2004; Needham et al., 2011). Such interactions are often density-dependent and relate to specific functional traits of the organisms, e.g. their sediment reworking mode, size, and mobility (Queiros et al., 2013; Van Colen et al., 2012). For example, macrobenthos-mediated mineralization of organic matter may outpace consumption effects on microphytobenthos biomass at high densities (Sandwell et al., 2009; Thrush et al., 2006). This microphytobenthos biomass is a preferred high-quality food source for many soft-sediment benthic invertebrates which in turn represent a favorable food source for many intertidal predators, e.g. shorebirds and epibenthic fish. Consequently, changes in predation pressure and prey resources that alter population size and/or behavior of macrobenthic species may indirectly control the interactions mediated by these organisms. For example, macrobenthos is known to affect smaller-sized meiobenthos (32–500 µm) species populations through direct consumption (Coull, 1999) and indirect mechanisms that include mainly facilitation and competition interactions related to macrobenthos behavior that e.g. alter the distribution of food resources in the sediment (Braeckman et al., 2011), and species morphological traits such as the construction of physical structures that provide shelter from predation (Zühlke, 1998).

In this study, we aimed to investigate how decreases in incident sunlight at the sediment bed (to mimic changes in light levels due to elevated turbidity) mediate the outcome of biotic interactions between benthic invertebrates in a sandflat ecosystem. Specifically, we manipulated densities of a grazing macrobenthic bivalve (*Macomona liliana*) in situ under different light conditions, and documented the responses of the meiobenthic taxa to these experimentally manipulated conditions.

2. Material and methods

2.1. Study area and experimental design

The experiment was conducted on an intertidal sand flat at Wiroa Island in the Manukau Harbor, New Zealand. Tides are semi-diurnal with mean neap and spring tidal ranges of 2 and 3.4 m, respectively. The average inundation time at the study site is 7.2 h and the sediment consists mainly of fine sand (median grain size = 201 µm, % fine sand fraction (125–250 µm) = 64%). The macrofaunal community at the study site is dominated both numerically and in terms of biomass by bivalves, in particular the tellinid *M. liliana* (~100 ind·m^{-2} for individuals >20 mm shell width), and the venerid *Austrovenus stutchburyi* (~32 ind·m^{-2} for individuals >10 mm shell width). The meiofauna community predominantly consists of nematodes (79.7%), copepods (18.6%), turbellarians (1%), ostracodes (<1%), bivalves (<1%) and oligochaetes (<1%), with nematodes being the only taxon abundantly occurring <5 cm depth (~450 ind·30 cm^{-2}). Densities of other taxa present between 5 and 10 cm depth are <10 ind·30 cm^{-2}.

Macomona densities were manipulated in 2 × 2 m (4 m^2) plots to achieve 3 densities of adults: 0–50–200 ind·m^{-2}. Therefore each plot was first excavated to 18 cm depth and the sediment sieved on 10 mm mesh to remove shell hash and large macrofauna. Subsequently, the sieved sediments were returned to the excavated plots and *Macomona* (>20 mm shell length) were added to achieve the treatment densities in the central inner 1 m^2 of the plot. Each density treatment was combined with one of three light levels: shaded sediment, non-shaded controls, and bare sediment; yielding 9 experimental treatments in total. The shade treatment consisted of a shade cloth designed to cut ~70–80% of the incident light. This cloth was supported on a 4 m^2 metal grid (mesh size = 150 × 150 mm) suspended 15–20 cm above

the sediment surface. Non-shaded controls had the same set-up but with only the metal grid covering the plots. Both shaded and non-shaded controls thus excluded large predators, like eagle rays (*Myliobatis tenuicaudatus*), that feed predominantly upon *Macomona* at the study site (Thrush et al., 1994). Hobo data loggers (Onset Corp.) and Thermochron i-buttons were used to quantify differences in light intensity and temperature between treatments. These nine experimentally manipulated plots (2 × 2 m) are a subset of treatments that formed part of a larger experiment designed to examine the interactive effects of light intensity, nutrient loading, and *Macomona* grazing pressure on sand flat community biodiversity and ecosystem functioning (Thrush et al., 2014). The full experiment consisted of 28 treatments that were randomly positioned in 7 blocks (14 × 56 m, one replicate of each treatment per block). For each block, one plot was sieved and seeded at ambient *Macomona* density to serve as a procedural control for the initial faunal manipulation. Meiofauna responses to the applied treatments were only studied in blocks 1–6. General abiotic and biotic properties for all blocks are given in Table S1. All experimental treatments were set-up on 25–29 October 2011.

2.2. Sampling

Samples for the identification of macrobenthos abundance, meiobenthos population size and abiotic sediment properties were collected from the center 1 m^2 of the plots 14 weeks after the initiation of the experiment (7–10 February 2012). Specifically, sediment granulometry and the concentration of chlorophyll *a* (as a proxy for microphytobenthos biomass) were determined from three corers (2.3 cm diameter) collected from the top 2 cm of sediment in each plot. Samples for the determination of abiotic properties were stored frozen until processing in the laboratory. Three corers for macrobenthos (10 cm diameter) and meiobenthos (3.2 cm diameter) were collected until a depth of 10 cm, and the number of *Macomona* >20 mm was determined from the inner 0.5 × 0.5 m of the plot by excavating the sediment to a depth of 15 cm. The meiofauna samples were subdivided into two depth slices, i.e. 0–5 cm and 5–10 cm. All biotic samples were stored in a 70% isopropanol.

2.3. Sample processing

The three samples for meiobenthos and abiotic properties were pooled prior to the analysis in the laboratory. Sediment for chlorophyll analysis was freeze dried and homogenized. A small quantity of sediment (~0.1 g) was soaked in 10 ml of MgCO$_3$ buffered acetone (90%) for approximately 20 h. Samples were shaken after 12 h and again prior to centrifugation. Samples were centrifuged for 10 min at 3300 rpm before fluorometric analysis. Sediments for particle size analysis were digested in 10% hydrogen peroxide, to remove organic matter until bubbling ceased before using the standard operating procedure for marine sediments on a Malvern mastersizer-S (300 FR lens) to determine grain size fractions in the range of 0.05 µm to 2000 µm. Meiofauna organisms <500 µm retained on a 38 µm sieve were extracted from the sediment by centrifugation with Ludox (Heip et al., 1985). After staining with Rose Bengal, all individuals were identified to taxon level.

2.4. Statistical analysis

Bottom–up control of *Macomona* interference effects on meiobenthos was analyzed by comparing meiofauna response to the *Macomona* densities between shaded and non-shaded controls. In addition, potentially confounding factors related to the metal grid construction in shaded and non-shaded controls (e.g. hydrodynamical change, predator exclusion) were assessed by comparing meiofauna responses to *Macomona* densities between the bare sediment and non-shaded control treatments. Due to the variability in the number of *Macomona* collected from the replicate plots after 14 weeks, these analyses were conducted using