



Indirect effects of non-lethal predation on bivalve activity and sediment reworking

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ARTICLE INFO

Article history:

Received 22 March 2010

Received in revised form 30 July 2010

Accepted 2 August 2010

Keywords:

Bioturbation
Chemical cues
Crangon crangon
Feeding activity
Macoma balthica
Predation
Predator avoidance
Sediment reworking

ABSTRACT

Deposit-feeders are the dominant bioturbators of aquatic sediments, where they profoundly impact biogeochemical processes, but they are also vulnerable to both lethal and non-lethal predation by a large variety of predators. In this study, we performed a series of experiments to test the effects of predation avoidance on the feeding activity and sediment reworking intensity of the deposit-feeding bivalve *Macoma balthica*. Feeding activity at the sediment–water interface and sediment reworking intensity (vertical displacements of inert particle tracers) were monitored using image analysis techniques for treatments including and excluding the predatory shrimp, *Crangon crangon*. Detection of *C. crangon* by *M. balthica* resulted in an immediate retraction of the feeding siphon and a reduction in feeding activity. *M. balthica* also buried deeper into the sediment in the presence of *C. crangon*. This predator avoidance behaviour indirectly affected sediment reworking modes and rates, increasing the thickness of the bioturbated sediment layer as well as the non-local transport of sediment particles at depth. Conversely, feeding activity and sediment reworking processes remained unaffected when *C. crangon* was present, but isolated from the sediment, suggesting that predator perception in *M. balthica* is tactile (i.e. induced by direct encounter) rather than being chemosensory. Collectively, these results demonstrate that predatory avoidance behaviour by benthic infauna can significantly impact benthic bioturbation and the incorporation of organic matter into the benthic food web.

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1. Introduction

Many benthic invertebrates deposit-feed at the sediment–water interface where recently settled organic material accumulates and thereby significantly increase particle redistribution and porewater irrigation within the upper sediment layers. Both biogenic sediment mixing and irrigation, collectively referred to as bioturbation (*sensu* Richter, 1952), strongly influence organic matter degradation rates, the repartition of chemical species within the sediment column and modify geochemical fluxes across the sediment–water interface (Aller, 1982; Lohrer et al., 2004). Deposit-feeders are often considered the main sediment engineers, dominating bioturbation processes in nearly all sedimentary environments (Aller, 1982).

Feeding above the sediment–water interface, however, makes individuals particularly vulnerable to both lethal and non-lethal predation by epibenthic species (e.g. nipping of bivalve siphons, Sasaki et al., 2002; ‘arm’ loss in echinoderms, PapeLindstrom et al., 1997; or antennae and feeding palp loss in polychaete worms, Zajac, 1995; Berke et al., 2009). Tissue loss from infaunal invertebrates

through such sublethal predation events can provide significant energy input to higher trophic levels (e.g. O'Connor et al., 1986), but can have negative impacts on individuals of the prey species by causing behavioural changes (Yamada et al., 1998; de Goeij et al., 2001) or by affecting reproductive success, energy budgets or post-predation survival (Meyer and Byers, 2005). At the scale of the population, however, predation is generally heterogeneously distributed in time and/or space (Berke et al., 2009; Hines et al., 2009) and has long been recognized as being influential in determining localised benthic community structure and other population characteristics (Sih, 1987; van Gils et al., 2009). Nevertheless, although the direct effects of predation on benthic invertebrate community dynamics has been studied extensively, relatively little is known about the indirect effects of sublethal predation on sedimentary processes. Classical effects of predation on the abundance, distribution, and size structure of prey populations (Sih et al., 1985) predict that the presence of predation will indirectly reduce sediment reworking intensity and thus negatively impact the kinetics of biogeochemical processes (e.g. Lindsay and Woodin, 1996; Lindsay et al., 1996) which may, in turn, effect other parts of natural systems (e.g. Cloern et al., 2007). Indeed, predation can indirectly influence biogeochemical sediment processes in unexpected ways through predator-induced modifications of prey activity (Kamermans and Huitema, 1994; de Goeij et al., 2001; Tallqvist, 2001; Stief and Holker, 2006). The mechanistic explanation is that the detection of predators by benthic invertebrates is rapidly

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translated into a change in deposit-feeding activity and burrowing depth, indirectly altering the downward transport of particles from the sediment surface to deeper anaerobic sediment layers and thus enhancing the aerobic microbial remineralization of the pool of labile organic matter. Given the high densities of predators in many benthic systems, predator-mediated changes in infaunal behaviour must have significant effects on the level of ecosystem functioning.

Assuming deposit-feeding bivalves are continuously subject to intense predation pressures (from birds, crabs, fishes and shrimps) it follows that their feeding behaviour will result from a trade-off between foraging for food and predator avoidance. In burrowing bivalves, feeding efficiency is directly proportional to the depth horizon they occupy within the sediment profile (de Goeij and Luttikhuisen, 1998); the shallower the depth the bivalves are situated when feeding, the more they can extend their inhalant siphons above the sediment–water interface and maximise the area prospected (Zwarts et al., 1994), but the greater the risk of exposure to both sublethal and lethal predation. Whilst burying deeper into the sediment appears to be a universally adopted means for bivalves to escape such predation (e.g. de Goeij et al., 2001; Persson and Svensson, 2006; Flynn and Smee, 2010), the effects of predation-induced behaviour on sediment reworking are, however, poorly documented. Moreover, predator avoidance behaviours may have different impacts on sediment reworking processes depending on whether they only affect the intensity of prey activity (as shown in Stief and Holker, 2006) or whether they also alter the characteristics of their activity (e.g. a switch between deposit and suspension feeding, Peterson and Skilleter, 1994).

As a first step in determining the indirect impact of predation on sediment ecosystem functioning, here we experimentally investigate the effects of trophic interactions between the deposit-feeding bivalve *Macoma balthica* and the predatory shrimp *Crangon crangon* on (1) bivalve feeding activity and (2) sediment reworking. Additionally, since benthic invertebrates are capable of anticipating predatory threats (e.g. through the detection of chemical cues released by the predator; Griffiths and Richardson, 2006; Smee and Weissburg, 2006), we used predator-enclosure and enclosure experiments to test whether the mechanistic basis for any observed predator avoidance behaviour in *M. balthica* is predominantly governed by physical contact with the predator or by the detection of chemical signals.

2. Materials and methods

2.1. Fauna and sediment collection

The bivalve *M. balthica* inhabits temperate intertidal mudflats and shallow subtidal areas, where it can be found at high densities ($\geq 15,000 \text{ ind. m}^{-2}$) (Richards et al., 1999) and it deposit-feeds at the sediment–water interface from depth (typically <6 cm) using its inhalant siphon (Zwarts et al., 1994; Kamermans and Huitema, 1994; de Goeij and Luttikhuisen, 1998). Specimens of *M. balthica* were collected in October 2007, at low tide, from an intertidal mudflat in the Ythan estuary (Aberdeenshire, Scotland), by sieving the surficial sediment layer (ca. 5 cm). Individual *M. balthica* valve length (longest axis) ranged from 10 to 14 mm.

The brown shrimp *C. crangon* is an abundant species of estuarine systems and coastal shallow waters (Pihl and Rosenberg, 1982, 1984) and feeds on various benthic invertebrates, including bivalve siphons (Kamermans and Huitema, 1994; Norkko, 1998). Specimens of *C. crangon* (rostrum–telson length, ~20–35 mm) were collected with a push-net from the study site. Estuarine water temperature was 11.5 °C and salinity was 33 at the time of sampling. Individual *C. crangon* were fed every second day with freshly minced cockles (*Cerastoderma edule*) collected from the sample site.

2.2. Activity monitoring

M. balthica is capable of suspension feeding but is primarily a surface deposit-feeder (Olafsson, 1986; Kamermans and Huitema, 1994). Accordingly, the feeding activity of *M. balthica* can be quantified through measurements of the movements of the inhalant siphon above the sediment surface. A similar approach has already been used to assess feeding activity in two other closely-related deposit-feeding bivalves, *Abra ovata* and *Abra nitida* (Grémare et al., 2004; Maire et al., 2007).

Activity experiments were carried out, at field temperature (11.5 °C), in large aquaria (45 × 30 cm) filled with 15 cm of natural sediment overlain with 10 cm of aerated seawater (UV sterilised, 10 µm filtered, salinity 33). Prior to the experiments, the sediment was sieved through a 1 mm mesh to remove all macrofauna and left to settle for 48 h in the aquaria. Three individuals *M. balthica* (10–14 mm in length) were introduced 24 h prior to the experimental period in order to acclimate and establish burrows. We established three replicated (n = 5) treatments: *C. crangon* present and unrestricted, *C. crangon* present but restricted to the water column at an elevation 4 cm above the sediment–water interface, and *C. crangon* absent. Feeding activity (i.e. siphon motion above the sediment surface) was monitored under infra-red lighting using an automated image analysis system (for further detail, see Maire et al., 2007). A video sensor (VC51, fitted with a 25 mm objective) connected to a microcomputer was fixed directly above the aquaria. The frequency of image acquisition was 10 s. Behaviour was observed for 24 h for the restricted *C. crangon* treatment and for 48 h for the remaining two treatments. All individuals of *M. balthica* and *C. crangon* remained in the field of view for the duration of each observation period. Custom made image analysis procedures (Grémare et al., 2004; Maire et al., 2007), based on differences in grey scale values between the inhalant siphons of *M. balthica*, the body of *C. crangon* and the sediment surface, were used to extract specific activity measurements, i.e. the total amount of *M. balthica* siphon motion. These data were used to calculate two activity indices: (1) the percentage of time active (PTA) corresponding to the amount of time devoted to deposit-feeding at the sediment surface and (2) the mean activity per time active (MATA) corresponding to the average feeding activity per unit of time during bouts of active feeding (=feeding intensity). MATA was defined as the net surface area modified between two consecutive images. For convenience all MATA values were scaled to 1 h. Both PTA and MATA were based on the whole activity record. They correspond to the average values recorded for the three individuals of *M. balthica* in each aquarium. The effects of the *C. crangon* on *M. balthica* feeding activity indices were assessed using the Wilcoxon signed rank test for paired samples.

2.3. Sediment reworking

Sediment reworking experiments were conducted in thin aquaria (L = 20 × W = 5 × H = 30 cm) filled to a depth of 12 cm with pre-sieved (1 mm) sediment from the study site overlain with 15 cm of aerated seawater (UV sterilised, 10 µm filtered, salinity 33). All aquaria were maintained in a constant temperature room (11.5 °C) for two days prior to the introduction of the fauna to allow for the physical and chemical stabilization of the sediment matrix. The body size (10–11 mm) of individual *M. balthica* was held constant across all treatments. We established five unreplicated treatments: (1) *M. balthica* (3 individuals, = 300 ind. m⁻²), (2) *C. crangon* (1 individual, unrestricted), (3) *M. balthica* (3 individuals) + *C. Crangon* (1 individual), (4) *M. balthica* (3 individuals) + *C. crangon* (1 individual restricted to the water column at an elevation 4 cm above the sediment–water interface), and (5) no macrofauna. These treatments allow the behaviour of *M. balthica* in the presence or absence of *C. crangon* to be distinguished, as well as the mechanistic basis for any

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