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Meiofauna and crabs in mangroves and adjoining sandflats: Is the interaction physical or trophic?

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ABSTRACT

Meiofauna distribute widely in most soft substrates in the marine and freshwater realms. Given their small body size (63 to 500 μm) and high density, meiofauna are potential food items for predators such as deposit-feeding brachyuran crabs. Crab bioturbation may also affect meiofaunal assemblages through effects such as translocation to unsuitable microhabitats. This study aimed to investigate the significance and nature of top-down control on the density of meiofauna based on their interactions with deposit-feeding crabs in a mangrove and adjoining sandflat; specifically, whether the interaction is primarily physical or trophic. Field manipulative experiments were conducted within the aggregation zones of soldier crabs (*Mictyris longicarpus*) and fiddler crabs (*Uca vomeris*) in a mangrove-lined creek in Southeast Queensland, Australia. Meiofaunal density in five experimental cage treatments (Exclusion, Inclusion with complete crab ('Inclusion'), Inclusion with 'disabled' crab (feeding claw removed, 'Disabled'), Half-cage, and Ambient) was compared. Removal of soldier crabs from the cages (Exclusion) increased meiofaunal density (426 ± 46 ind./10 cm^2; mean ± SE) by 50% over that in the Inclusion treatment (283 ± 22). The nature of the interactions was further investigated by comparing meiofaunal density in the Inclusion treatment (with both physical and trophic effects present) with that in the Disabled treatment (with physical but no trophic effect present). Removal of trophic effect by 'disabling' the crab increased meiofaunal density by 30% compared to that in the Inclusion treatment, but at a similar density to the Exclusion treatment. This pattern suggests that the top-down control by soldier crabs on the meiofauna is fundamentally trophic, i.e. predation. In the experiment with fiddler crabs, meiofaunal densities in the inclusion treatments (Inclusion and Disabled) were not significantly different from each other, but density was reduced by more than 50% in the Exclusion treatment. Fiddler crabs significantly impact the meiofauna through their bioturbation activities such as sediment turnover and burrowing, but their trophic activities did not significantly reduce meiofaunal density. Different crab species at different habitats, therefore, may influence meiofaunal density through different processes on sub-tropical soft shores.

1. Introduction

Due to their numerical and functional dominance (Koch and Wolff, 2002), crabs are one of the most ecologically important components of the mangrove macrofauna, and may therefore exert a large influence on the distribution and density of other animals (Lee, 2015), including the meiofauna. However, species' interaction among the mangrove macrofauna and its role in shaping faunal community structure has received little attention (Lee, 1998). Despite that brachyuran crabs are dominant deposit-feeders in mangroves and the high density of meiofauna within the same habitat (Wołowicz et al., 2011), little is known about the nature of their interactions. The role of meiofauna in mangrove food chains is obscure and represents a missing link in the trophodynamics of tropical and sub-tropical soft shores. Among the crabs inhabiting mangrove and intertidal flats are members of the deposit-feeding guild, e.g. soldier crabs *Mictyris longicarpus* (Mictyridae) and fiddler crabs *Uca* spp. (Ocypodidae), which are commonly found in most tropical and sub-tropical estuaries including those in Australia and Asia (Dittmann, 1998; Rossi and Chapman, 2003).

The major activities of these crabs that may affect the meiofauna are their bioturbation (physical activities) and foraging behaviors (physical as well as trophic activities) on the surface sediment (Reinsel, 2004). *M. longicarpus* does not maintain permanent burrows (Dittmann, 1998; Rossi and Chapman, 2003) but buries and re-emerges in response to threats. This burrowing activity involves constructing an air pocket by scooping the sand in a corkscrew motion down into the sediment (Maitland and Maitland, 1992). Unlike the soldier crab, *Uca* spp., e.g. *Uca vomeris*, build permanent burrows and normally wander no more than one meter away from it such that a quick retreat is possible

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when threatened (Zeil, 1998). Fiddler crab burrows are usually simple and consist of a vertical shaft extending 10 to 40 cm into the sediment. Burrows are continuously constructed, maintained and later on abandoned (Kristensen, 2008). During the burrow construction and maintenance activities by crabs, a considerable amount of sediment is excavated and mixed, altering the quality of the organic matter on the sediment surface (Gutiérrez et al., 2006; McCraith et al., 2003).

During the low tide, *M. longicarpus* emerges to feed either on or just under the surface, creating hummocks prior to their emergence (Cameron, 1966). This species uses branchial water to separate lighter organic material from the heavier inorganic material (Quinn, 1980). Fiddler crabs feed on fine particles by picking sediment from the surface using the minor chela and placing it in the mouth cavity, but its diet varies (Kristensen, 2008). Generally, as deposit-feeders, these crabs derive nutrition from a variety of foods such as fine organic detritus, the microphytobenthos, bacteria and small metazoans, e.g. the meiofauna (Dye and Lasiak, 1986; Nagelkerken et al., 2008). However, the contribution of meiofauna to the diet of these crabs is unknown. Several lines of evidence suggest a significant impact of the crab's presence on the meiofauna, especially for the fiddler crabs (Dye and Lasiak, 1986; Hoffman and Katz, 1984; Olafsson and Ndaro, 1997; Reinsel, 2004). Few studies have reported the interaction between soldier crabs and the meiofauna, but Warwick (1990) found a significant reduction in the species' richness, species diversity and evenness of meiofaunal nematodes in sandflat areas within the aggregation zones of soldier crabs.

While these data clearly indicate that the presence of deposit-feeding crabs depresses meiofaunal density, the actual mechanism, i.e. whether the reduction is due to the physical disturbance effect or crab consumption of meiofauna, is not known. Assertions on the trophic interaction between crabs and the meiofauna are made solely based on the reduction in meiofaunal density in the presence of the crabs. This top-down reduction, however, may be achieved through physical and/or trophic effects. Different crab species may bioturbate soft sediments differently, e.g. permanent versus temporary burrows, and thus may affect meiofaunal density differently. In addition, the differences of sediment characteristics may as well contribute or influence the physical interaction between the crabs and the meiofauna.

This study aimed to investigate the significance and the nature of top-down control on the density of mangrove meiofauna based on their interactions with deposit-feeding crabs; specifically, whether the interaction is mainly physical or trophic. The research questions asked in this study were 1) Does the presence of the soldier crab *M. longicarpus* on the sandflat and the fiddler crab *U. vomeris* in the mangrove, affect meiofaunal density? and 2) Is the effect of crabs due to physical or trophic interactions? To achieve this, we conducted a manipulative experiment involving Exclusion/Inclusion cages, with additional manipulation of the feeding appendage of the crabs to ascertain the nature of the interactions. Our hypotheses were 1) Meiofaunal density is affected by the presence of the crabs in their natural habitat; 2) Physical activities of the crabs may increase or reduce meiofaunal density, but trophic interaction will reduce meiofaunal density.

2. Materials and methods

2.1. Study area

Manipulative field experiments were conducted from December 2014 until February 2015 within the aggregation zones of soldier crabs (*M. longicarpus*) on the intertidal sandflat, and within the aggregation area of fiddler crabs (*U. vomeris*) in an open area on the mangrove forest fringe at the mouth of Tallebudgera Creek, Southeast Queensland, Australia (28° 6′18.62″S 153°26′47.80″E). Tallebudgera Creek is connected directly to the Coral Sea, and the mixed but predominantly semi-diurnal tidal regime has a range of about 2.5 m. The mangrove fringe (*U. vomeris* site) was dominated by the mangroves *Avicennia marina* and *Rhizophora stylosa*. Significant gaps comprising clear and open areas with pneumatophores 1–2 cm tall occur on the sandy sediment. The aggregation area of *U. vomeris* starts at ~5 m from the lower tidal limit of the creek. Tides ranged from 0 to 1.8 m during the study period. During the experimental period, the study area received a daily average of 11.6 mm of rain (total = 1047.8 mm for the three months), with a temperature range of 16 to 37.1 °C.

2.2. Quantification of natural crab density

The emergence and activity patterns of soldier crabs are known to vary with life stages and gender (Cameron, 1966; Unno, 2008), which may have been the main reason for the lack of a convincing method to quantify the density of this crab to date. Soldier crabs are active during the low tide when they emerge from their burrow, but the proportion of time being emergent varies between days (Cameron, 1966). Once emerged, adult soldier crabs move quickly in coordinated fast feeding movements, usually wandering around the foraging area in large groups. Soldier crabs do not maintain permanent burrows but respond to the threat by rapidly burying in the sediment. Therefore, the burrow-counting method is misleading for determining the density of soldier crabs. On the Tallebudgera sandflat, soldier crabs are abundant and live within the same microhabitat of the callianassid *Trypea australiensis*. *T. australiensis* lives in deep burrows with openings often exposed even during high tide, and might be misidentified as soldier crab burrows. Therefore, the density of the soldier crabs in this study was estimated by using the photographic counting method (Vermeiren and Sheaves, 2014) during their emergence in swarming formation. The density of fiddler crabs was quantified using the visual count method (Nobbs, 1999), where 12 of 1.5 m × 1.5 m quadrats were marked on the sediment surface, and the number of crabs counted using a pair of binoculars during the active period at low tide.

2.3. General experimental design

The nature of the interactions between the meiofauna and the soldier crabs and fiddler crabs and their effects on meiofaunal density was investigated using field Exclusion and Inclusion cages. The experimental cages were 40 cm × 20 cm internal diameter cylinders made of 5 mm plastic mesh, with the bottom 30 cm embedded in the sediment (Fig. 1). The top and bottom of the cages were covered with mosquito netting to prevent crab movement into or out of the cages. There were five manipulative cage treatments, each with nine replicates, namely: 1) Exclusion: complete cages without crab inside to remove crab physical or trophic effects; 2) Inclusion: complete cages with one adult crab per cage, with all effects present; 3) Inclusion with 'disabled' crabs (hereafter known as Disabled): complete cages but with one 'disabled' crab to remove the trophic effect, but keeping the physical effect. Soldier crabs were disabled by removing the distal segment from both

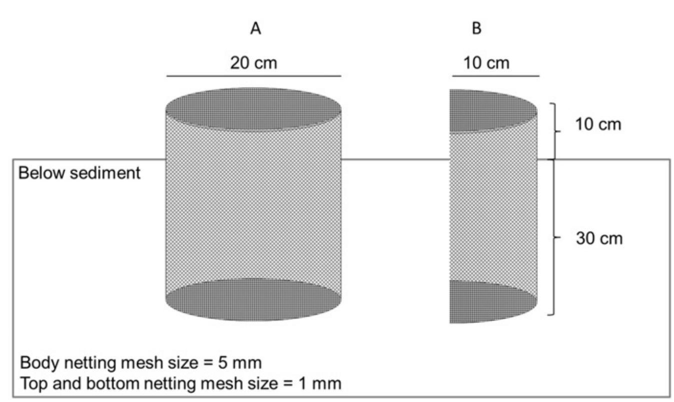

Fig. 1. Schematic diagram of (A) Complete cage and (B) Half-cage designs of the experimental cages.