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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

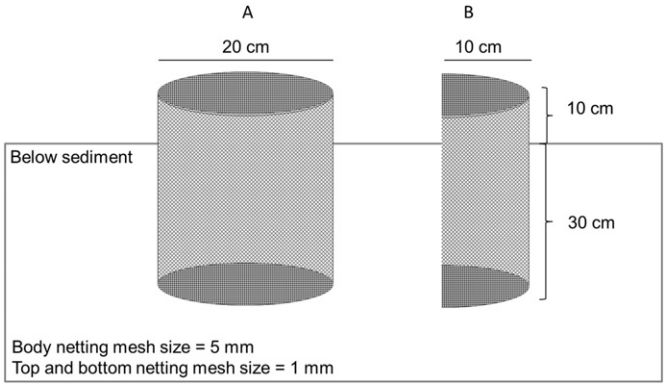

Fig. 1. Schematic diagram of (A) Complete cage and (B) Half-cage designs of the experimental cages.

of its feeding chelipeds using small scissors. Similarly, adult male fiddler crabs *U. vomeris* were treated by removing the distal segment of the minor (feeding) chela used for picking up sediment; 4) Half-cage: half-complete cage to measure any (direct or indirect) effects due to either the material or the construction on meiofaunal density. Crabs had access to the area, i.e. there is no crab exclusion effect, but any effect due to caging is expected to be discernable by comparing the results of this treatment and the Ambient; and 5) Ambient: no manipulation was made to the activity area of the crabs, i.e. crabs exerted their effect at the natural density without interference from any procedures.

The meiofaunal density in the Exclusion and Inclusion treatments was first compared to detect any significant general impact of the crab's presence, i.e. if the crab's presence might have reduced or increased meiofaunal density (Table 1). The nature of the interaction between crabs and the meiofauna were further investigated by comparing the Exclusion and Inclusion treatments to look for any significant physical effect, and the Exclusion and the Disabled treatments were compared to test any significant trophic effect.

Crabs are usually able to regenerate their feeding claws in one or two ecdyses. As the impact of the crabs on the meiofauna is expected to occur over short time scales, and to avoid repeated treatment of the crabs upon claw regeneration, the experiment was conducted over a short period. After two days of disabling the crabs, both crab species were able to survive with feeding claw segments removed and left sediment working marks on the surface and continued with burrow construction and maintenance.

Key sediment variables were measured to provide basic information on sediment condition. Sediment samples ($n = 3$) were collected from the Ambient area to describe the substrate grain size according to the Wentworth grade scale, using the dry sieving technique (Bale and Kenny, 2005). The top sediment surface (1 cm) from the Ambient and the Exclusion cages was collected ($n = 9$) to evaluate the cage design effect and the effect of the crab's presence and absence on microphytobenthos (MPB) density (measured as Chl *a* concentration) and the total organic content (measured as loss-on-ignition, LOI). Irradiance in terms of PAR photon flux density was measured using a light meter ($n = 5$). For chlorophyll a (Chl *a*) measurements, the sediment samples were sampled using a corer and put on ice during transportation to the laboratory, before immediate chlorophyll extraction using 90% aqueous acetone in the dark for 24 h. Chl *a* concentration was measured following the spectrophotometric method of Parsons et al. (1984). One core sample for measurement of the meiofauna was collected from each cage, frozen and washed through 500 μm and 63 μm meshes within 48 h, and preserved in 70% alcohol and rose bengal for later counting.

2.4. Soldier crabs: experimental design

Sediment on the sandflat was dug out to make a depression, and the cage was deployed to get the required height inside and outside of the sediment. The sand was put back into the cage through a 5 mm mesh to remove existing macrofauna. The sediments were added to create the natural effect of humps (the raised area) and depressions (water puddles) that do not dry out during the low tide, and, therefore, providing a suitable feeding area for the crabs. Soldier crabs were observed to avoid the water puddle areas but feed only at the humps between the puddles. The cages were located within 1.5 to 2 m from each other and the experimental area located 5 m from the extreme low tide level. The top of each cage was covered with mosquito netting, and the cages left for one week to allow recovery of the disturbed sediment and the meiofauna. Adult soldier crabs of about the same size (1.5 ± 0.05 cm, carapace width and 2.2 ± 0.02 cm carapace length, mean ± SE) were collected from the site. One individual was put into each of the inclusion or disabling treatment cages ($n = 18$), and the treatments were left for two days. There were three low tide occasions within the experimental period; at 00:02 am, 13:13 pm and 12:53 pm. Sediment cores for meiofauna samples were collected on February 18, 2015.

2.5. Fiddler crabs: experimental design

The experimental cages were positioned randomly on the sandflat during low tide, a week before the experiment began. A shovel was used to dig out the sediment and were checked for crab presence and then removed. Similar to the experiment on soldier crabs, the experimental cages were put into the holes, and the cages were filled with the original sediment. The top of each cage was covered with mosquito netting, and the cages were left for one week to allow recovery of the disturbed sediment and the meiofauna. *U. vomeris* is sensitive to disturbance, and would retreat into any burrows when threatened. Therefore, it is difficult to remove fiddler crabs without disturbing the sediments (Hoffman and Katz, 1984). Adult male fiddler crabs of about the same size (1.5 ± 0.1 cm, carapace width) were collected from the site, and one individual was put into each of the inclusion or disabling treatment cages ($n = 18$). The cages were left for two days. There were three low tide occasions within the period; at 00:41 am, 13:10 pm and 01:18 am. Sediment cores for meiofauna samples were collected on March 4, 2015.

3. Data analysis

Distributions of the substrate particle sizes from the ambient of sandflat and mangrove sites were compared using the Kolmogorov–Smirnov two-sample test (K–S *D*), and the t-tests were used to compare the mean grain size and the sorting coefficient between the two sites. A one-sample Kolmogorov–Smirnov test was used to check normality of the data, and homogeneity of variance was evaluated using Levene's test. Data for the Chl *a*, LOI and Irradiance were log-transformed to satisfy the assumptions when required, and the meiofaunal density data were square-root transformed. Two-way ANOVA was used to determine the effect of crab species and cage treatment on the level of Chl *a*, LOI and Irradiance and the meiofaunal density. Post-hoc pairwise comparisons were applied to the significant main treatment effects to determine the pattern of difference.

4. Results

4.1. Crab density and sediment conditions

The density of soldier crabs in the swarming formation ranged from 589 to1360 individuals per swarming group. The density of the fiddler crabs was between 8 and 13 individuals per m^2 respectively of male and female crabs in the study area. Distributions of the substrate particle size for the two study sites were not significantly different (K–S $D = 1.000$, $p = 0.270$). Medium and fine sands dominated the sediment

Table 1
Summary of the type of effects expected to be present for each experimental treatment, namely "Physical" "Trophic" or "Cage" effect ($n = 9$). Symbols signify the presence (+) or absence (−) of each effect.

Treatment/effects	Exclusion	Inclusion/complete crab	Disabled/starving crab	Half-cage	Ambient
Physical	−	+	+	+	+
Trophic	−	+	−	+	+
Cage	+	+	+	+	−

substrate at both sites. However, the mean grain size (phi) and sorting coefficients for the two sites were significantly different (Table 2).

4.2. Chl a, LOI and irradiance

The interaction between crab species and caging was significant (Fig. 2) in determining sediment Chl *a* ($F_{1,32} = 35.521$, $p < 0.001$) and LOI ($F_{1,32} = 4.528$, $p < 0.05$) but not for Irradiance ($F_{1,16} = 0.315$, $p > 0.05$). The significant interactions indicate that the effects of crab exclusion (Exclusion cage) on Chl *a* and LOI were different for *M. longicarpus* and *U. vomeris*. Chl a concentration (mg g^{-1} sediment) in the Ambient within the aggregation zone of *M. longicarpus* was significantly lower ($F_{1,32} = 13.243$, $p < 0.01$) compared to those in the Exclusion cages (1.44 ± 0.10 and 2.22 ± 0.24, respectively, mean ± SE). In contrast, *Chl a* concentration in the Exclusion cages from the *U. vomeris* experiments was significantly lower ($F_{1,32} = 22.941$, $p < 0.001$) than that in the Ambient (0.75 ± 0.13 and 1.78 ± 0.08, respectively).

The organic content of sediments as measured by LOI in the Ambient and Exclusion cages were not significantly different ($F_{1,32} = 0.588$, $p > 0.05$) for *M. longicarpus* but different for *U. vomeris* ($F_{1,32} = 5.029$, $p < 0.05$). LOI in the Ambient and Exclusion treatments for *M. longicarpus* was 0.663 ± 0.07% and 0.75 ± 0.07%, respectively. In the experiment with *U. vomeris*, the LOI was 1.524 ± 0.09% and 1.202 ± 0.15%, respectively, for the Ambient and Exclusion treatments.

There was no species effect on Irradiance ($F_{1,16} = 0.13$, $p > 0.05$), but treatment effect was significant ($F_{1,16} = 997.241$, $p < 0.001$). Irradiance inside the cages was significantly reduced ($F_{1,16} = 481.07$, $p < 0.001$), at 473.2 ± 11.12 μmol m^{-2} s^{-1} (soldier crab) and 466.12 ± 14.68 μmol m^{-2} s^{-1} (fiddler crab), compared to the mean of the Ambient treatment ($F_{1,16} = 516.49$, $p < 0.001$) at 965.36 ± 123.57 μmol m^{-2} s^{-1} and 976.08 ± 52.71 μmol m^{-2} s^{-1} for the soldier and fiddler crabs, respectively.

4.3. Meiofaunal density

The meiofaunal community on the Tallebudgera sandflat within the *M. longicarpus* aggregation zone was overwhelmingly numerically dominated (>99%) by nematodes, with <1% being harpacticoid copepods (Table 3). At the mangrove site within the aggregation area of *U. vomeris*, the meiofaunal community was also dominated by nematodes (>97%), with minor contributions from harpacticoids, oligochaetes and soft-bodied meiofauna. There was a significant interaction between crab species and the experimental treatments ($F_{4,80} = 14.624$, $p < 0.001$).

There were three homogeneous sub-groups in the experimental cage treatments for *M. longicarpus* ($F_{4,80} = 13.497$, $p < 0.001$) (Fig. 3). Meiofaunal density in the Exclusion (426 ± 46 ind. 10 cm^{-2}; mean ± SE) was not significantly different from that in the Disabled treatment (420 ± 47). Meiofaunal density in the Inclusion (283 ± 22 ind. 10 cm^{-2}) was not significantly different from the Half-cage treatment (264 ± 27 ind. 10 cm^{-2}). The third group is represented by the Ambient treatment, where the meiofaunal density was significantly lower than those in all the other treatments (130 ± 14 ind. 10 cm^{-2}).

There was a significant treatment effect on meiofaunal density in the *U. vomeris* experiment ($F_{4,80} = 11.225$, $p < 0.001$). Post-hoc tests separated the treatments into two groups. The Exclusion and Ambient treatments had meiofaunal densities of 368 ± 58 and 323 ± 52 ind. 10 cm^{-2}, respectively. In the second group, meiofaunal density was lower, with Inclusion (139 ± 25 ind. 10 cm^{-2}) grouped together with the Disabled and Half-cage treatments (145 ± 15 and 164 ± 23 ind. 10 cm^{-2}), respectively.

Table 2
Description of the substrate particle sizes at the two habitats based on the Wenworth classification. Values are mean ± SE (n = 3).

Description	Particle size range (mm)	Frequency, wt% (mean ± SE)		T-test
		Sandflat	Mangrove	
Coarse sand	0.710–1.0	0.33 ± 0.03	0.00	
	0.50–0.710	1.95 ± 0.07	1.37 ± 0.28	
Medium sand	0.25–0.50	58.20 ± 1.15	35.55 ± 2.04	
Fine sand	0.125–0.25	38.00 ± 1.09	46.88 ± 0.90	
Very fine sand	0.0625–0.125	1.12 ± 0.12	9.71 ± 0.80	
Silt/clay	<0.625	0.40 ± 0.06	6.45 ± 0.35	
Mean grain size (phi)		2.11 ± 0.02	2.29 ± 0.04	$t_4 = -6.76$, $p < 0.01$
Sorting		0.56 ± 0.1	0.86 ± 0.14	$t_4 = -19.33$, $p < 0.001$
Sorting classification		Moderately well-sorted	Moderately sorted	

5. Discussion

5.1. Physical vs. trophic interactions

In general, the presence of either crab species at the respective habitats has a significant negative impact on meiofaunal density (Exclusion vs. Inclusion). The meiofaunal density in the Exclusion and Disabled treatments were not significantly different, suggesting that there was no significant physical effect of the soldier crabs. However, a significant trophic impact of soldier crabs occurred on the meiofauna, where the presence of the complete crab (Inclusion treatment) significantly reduced meiofaunal density compared to crabs that were not able to feed (Disabled treatment). For the fiddler crabs, meiofaunal density in the Disabled treatment was significantly reduced compared to that in the Exclusion treatment, but not the Inclusion treatment. This pattern suggests that the effect of the fiddler crabs on meiofaunal density was mainly due to their physical but not trophic activities.

This study, which is the first to manipulate crab's feeding ability to elucidate the nature of their interaction with the meiofauna, clearly shows that soldier and fiddler crabs imposed a different type of top-down control on the meiofauna at the respective habitats. Despite being exposed to the massive physical activities of the soldier crabs, the meiofauna on the sandflat seem to be able to cope with the physical disturbance. In contrast, physical disturbance by the fiddler crabs in the mangrove habitat significantly reduced the meiofaunal density. While significant negative response by meiofauna to physical disturbances including bioturbation is common, it is not universal (Austen and Widdicombe, 2006). Several factors may account for this observation. First, the different impact of the crabs' physical activities on the meiofauna may be due to the different physical activities (e.g. temporary vs. permanent burrows, burrow maintenance) of the soldier and fiddler crabs in their natural habitats. While the difference is apparent, a fair comparison of the magnitude of the disturbances caused by the two crab species in their habitats could not be made in this study.

Second, the response of the meiofauna towards the physical disturbance suggests that the capability of the meiofauna to recover from the crab's physical disturbance is different between the two habitats. It has been shown by a previous study that the meiofauna were able to recover sooner in sandier substrates compared to muddier sediments (Dernie et al., 2003). To test this hypothesis, we compared the capability of the meiofauna to recover their density after being excluded from the Ambient (Exclusion vs. Ambient) in the two habitats. After the crab's removal, meiofauna on the sandflat were able to recover quickly by tripling their density from that in the Ambient. However, the meiofauna from the mangrove habitat did not show such a significant recovery following the exclusion of the fiddler crabs.

However, lack of change in the overall density of the meiofauna does not necessarily show that there is no physical impact by the crab at all. This is because physical disturbance may not affect total density but the structure of the meiofauna assemblage at the lower taxonomic levels (Warwick, 1990). Future examination of the nature of the interaction between crabs and the meiofauna should preferably be conducted

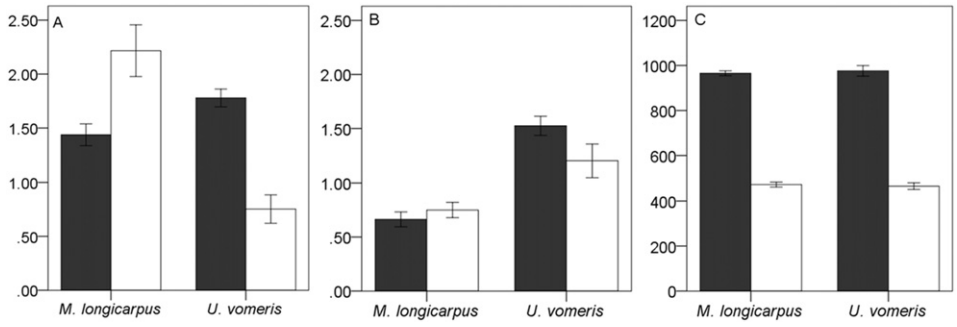

Fig. 2. A) Chl *a* concentration (mg g^{-1} sediment), B) LOI (%) and C) Irradiance (μmol m^{-2} s^{-1}) in the Ambient (black bars) samples within *U. vomeris* and *M. longicarpus* activity areas compared to the Exclusion cages (white bars). All data are mean ± SE.

with higher taxonomic resolution, e.g. genus or species level, to be able to measure any crab effect on meiofaunal assemblage structure. This requirement is, however, understandably challenging to meet in ecological studies, which usually require large sample sizes.

In this study, we found a significant trophic interaction between the soldier crabs and the meiofauna (Disabled vs. Inclusion). *M. longicarpus* is reported to use predominantly the microphytobenthos as food (Cameron, 1966; Quinn, 1986; Spilmont et al., 2009), but meiofauna are occasionally found in their diet (Cameron, 1966; Lee et al., 2011a). Meiofauna offer several advantages as potential food for the soldier crabs due to their size and nutritional value, e.g. harpacticoid copepods are high in essential fatty acids (Nanton and Castell, 1998; Coull, 1999) beneficial to the higher trophic levels. There is, however, little evidence to date supporting consumption of the meiofauna by the soldier crabs. Even though the feeding mechanisms of *M. longicarpus* have been described in detail, reports on the examination of their gut content are limited (Warwick, 1990). In addition, meiofauna such as nematodes may be digested quickly with no visual remains (Coull et al., 1995).

Further, unlike the MPB which are primary producers, assessing the trophic contribution of meiofauna using the tracer approach, such as stable isotope or fatty acid analysis is more challenging. Application of the lipid biomarker and dual stable isotope approach to identifying the food sources for *M. longicarpus* could only emphasize the consumption of the microphytobenthos and bacteria end members (Spilmont et al., 2009), but unable to confirm the contribution of the meiofauna to the diet of the crabs. However, these authors strongly suggested that meiofauna could be part of the diet of the soldier crabs, due to the distinct $\delta^{13}C$ and $\delta^{15}N$ values of the crabs compared to the shrimps that selectively fed on the microphytobenthos. Moreover, recent reports have shown a significant trophic interaction between the meiofauna and soldier crabs using the stable isotope enrichment approach (e.g. Lee et al., 2011).

In contrast, in this experiment, we could not detect a significant trophic interaction between the fiddler crabs *U. vomeris* and the meiofauna, as the meiofaunal density in the Inclusion treatment was not significantly reduced compared to that in the Disabled treatment. Commonly referred to as a detritivore, fiddler crabs have been reported to feed on MPB, bacteria and fine organic materials either through gut contents or gut ecomorphology analysis (Robertson and Newell, 1982; Dye and Lasiak, 1986; Griffen and Mosblack, 2011), fatty acid (Meziane et al., 2006) and stable isotope analysis (Abrantes and Sheaves, 2009). The limited foraging range from their burrows (Zeil, 1998) may prevent fiddler crabs to be selective in their food. The crabs may therefore make full use of the abundant fine organic detritus or microphytobenthos close to their burrows for subsistence (di Virgilio and Ribeiro, 2012). Similar manipulative experiments covering a wider range of locations and different seasons (e.g. for variations in MPB production) may help assess the generality of these findings.

Table 3
Meiofaunal density (n = 9) for the *M. longicarpus* and *U. vomeris* experimental treatments. All data are mean ± SE.

Site	Meiofaunal density (no. ind. 10 cm^{-2})				
	Exclusion	Inclusion	Disabled	Half-cage	Ambient
Sandflat (*M. longicarpus*)					
Nematode	426 ± 46	282 ± 22	419 ± 46	263 ± 26	127 ± 14
Harpacticoid	1 ± 0	1 ± 0	0	1 ± 1	2 ± 0
Mangrove (*U. vomeris*)					
Nematode	359 ± 57	134 ± 25	142 ± 15	157 ± 22	320 ± 52
Harpacticoid	2 ± 1	2 ± 1	1 ± 1	3 ± 1	1 ± 1
Oligochaetes	6 ± 1	4 ± 1	2 ± 1	3 ± 1	2 ± 1
Soft-bodied	2 ± 1	0	0	1 ± 0	0

5.2. Experimental design

In the Exclusion experiment with *U. vomeris*, light irradiance inside the cage was reduced by 50% (Fig. 2C), and as expected, has contributed to the reduction of Chl *a* content inside the Exclusion cage. However, the experiment with *M. longicarpus* resulted in the opposite trend, where a significant increment of 30% (over the Ambient treatment) was found inside the Exclusion cage. This demonstrates a significant impact of soldier crab activities on the density of the microphytobenthos on the sandflat habitat. Conversely, fiddler crab activities in the mangrove habitat do not have the same significant impact on Chl *a* as that inflicted by the soldier crabs on the sandflat habitat.

The mangrove site within the aggregation of *U. vomeris* had a higher mean organic content compared to the sandflat habitat, which is attributed to the high density of organic detritus, especially from mangrove litter and root materials. Our cage design has significantly reduced the organic content in the mangrove habitat, but not on the sandflat. This indicates that within a week of the experiment, soldier crab activities did not result in a significant impact on the organic content to the same level as has been imposed on the Chl *a* content. This trend also reflects the importance of MPB to the soldier crabs as compared to the sediment organic detritus, especially within the habitat where organic detritus is limited. The reduction of the organic content inside the cages at the mangrove site was probably due to the alteration of sediment structure during the cage deployment at the beginning of the experiment. In order to remove the existing crabs inside the experimental cages, the sediments were disturbed and resulting a mixing of the organic content on the surface and the sediment below.

In both of the experiments, the presence of the Half-cages has significantly affected the meiofaunal density as compared to what have been found in their natural habitat (Ambient). On the sandflat, the meiofaunal density increased, but the density reduced in the experiment with the fiddler crabs in mangrove habitat. There are several explanations that can be related to this situation. Firstly, it may be caused by the sediment disturbance at the beginning of the experiment. However, if this is true, we should have seen significant changes in the meiofaunal density in all cage treatments including the Exclusion cage

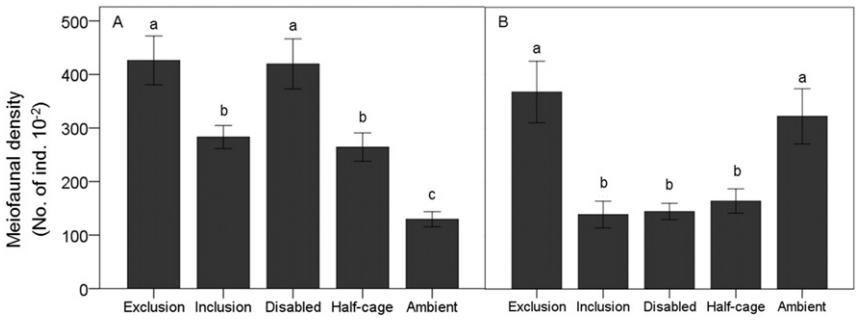

Fig. 3. Meiofaunal density (mean ± SE, n = 9) in the five experimental treatments for (A) *M. longicarpus* and (B) *U. vomeris*. Treatments with different letters are significantly different from each other ($p < 0.05$).

as well, in both of the experiments. However, the meiofauna in the Exclusion cage in the mangrove habitat were not significantly different with the Ambient. Secondly, there is also a probability that the presence of the Half-cage might have changed water flow inside the cages; but this effect would not be a primary concern in our experiment as crabs are active only during low tide. Besides, the meiofaunal assemblage was overwhelmingly dominated by the nematodes. We assumed that the meiofaunal assemblage would remain stable throughout the experimental duration due to the limited movements (Austen and Widdicombe, 2006) and burrowing habit of the nematodes.

Therefore, the best explanation for the significant impact of the Half-cage treatment to the meiofaunal density was due to the crab movement and access inside the cage. The presence of the Half-cage on the sandflat habitat within the natural aggregation of the soldier crabs has probably limiting the 'marching' crab movement around the cages and, therefore, reduced the soldier crab's access to areas inside the Half-cages. On the other hand, the fiddler crabs may have been attracted to the shading and positive thigmotactic effect provided by the Half-cages, which provide cooler environment as compared to the Ambient (Nobbs, 2003; Kon et al., 2010). As a result, more fiddler crab activities occurred inside the Half-cage thus explaining the reduction of the meiofauna as compared to the Ambient. The fact that the Half-cage treatment was not significantly different with the Inclusion treatment in both experiments has supported this hypothesis. In the first experiment, the soldier crab activities inside the Half-cages became limited to about the same degree with the inclusion of one individual crab as in the Inclusion treatment, which was not enough to depress the meiofaunal density as compared to the higher impact caused by the soldier crabs at their natural density (Half-cage/Inclusion vs. Ambient). In contrast, the magnitude of a fiddler crab activities within the Inclusion cage area is relatively higher as compared to the crabs' natural abundance in the Ambient.

6. Conclusions

Soldier crabs from the sandflat of Tallebudgera shown a significant trophic interaction with the meiofauna, but fiddler crabs from the mangrove habitat do not seem to rely on the meiofauna as food. This study suggests that the trophic interaction may be specific to the species' food preferences, the physical interaction is not solely caused by the crab's physical bioturbating activities but is also closely related to the sediment characteristics. Specifically, the sandflat site where the soldier crabs *M. longicarpus* occurred naturally has more fluid sediment due to the more frequent tidal inundation and high water content. On the other hand, the sediment of the mangrove habitat where the fiddler crab *U. vomeris* occurred was more compact due to the less frequent tidal inundation and potentially also the higher detritus content (e.g. humic substances that help bind sediment particles together), and the sediment-holding effects of the mangrove roots.

Different degrees of bioturbating activities may impact the ability of the meiofauna to recover in different habitats. In the loose sediment on the sandflat, mobility of the meiofauna would be facilitated due to the larger interstitial space among the sediment particles. However, drier and compact sediments may hinder the movement of the meiofauna between the sediment particles, resulting in slower recovery of the meiofauna after the initial disturbance in the exclusion treatment. A longer recovery period after site disturbance may be appropriate for caging experiment especially on drier and compact sediment substrates. Further, future studies may investigate the effect of different sediment substrates on the physical interaction between crabs and the meiofauna. While our inclusion and exclusion cage experiment coupled with the manipulation of the crab's feeding activities (Disabled treatment) could differentiate between physical and trophic impacts, a general conclusion on the effects of these two crab species on the meiofauna could not be made due to the lacking of temporal and spatial replicates. Considering of simple approach used in this experimental design, further replicates would be helpful to look if there are variations of the interaction between these two species and the meiofauna from different locations. In addition, modern approaches such as stable isotope analysis may help to further elucidate the nature of interactions between deposit-feeding crabs and the meiofauna on tropical soft shores.

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