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Impact of foraging soldiercrabs (Decapoda: Mictyridae) on meiofauna in a tropical tidal flat

Sabine Dittmann
Zentrum für Marine Tropenökologie, Universitätsallee GW1/A, 28359 Bremen 33, Germany.

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Abstract: In intertidal areas of the Indo-West-Pacific, foraging soldiercrabs create a disturbed sediment surface covered with pseudofaecal pellets discarded during the feeding process. To investigate the impact of feeding activities of the soldiercrab *Mictyris longicarpus* (Latreille, 1806) on small infauna, field experiments were carried out in a tropical tidal flat of Northeast Australia. A comparison of meiofaunal abundances in undisturbed sediment and sediment deposited by soldiercrabs after flotation feeding indicated an uptake of certain meiofauna taxa. Significantly reduced numbers of nematodes, copepods and plathelminthes were found both in the pseudofaecal pellets discarded by crabs foraging on the surface, and in the sediment deposited as hummocks by subsurface feeding crabs. Ostracods and newly settled bivalve larvae were not separated during flotation feeding, but discarded with the pellets. This indicated a sorting of food items by their specific density during the flotation feeding process. A caging experiment showed significant increases in the abundance of all meiobenthic taxa when soldiercrabs were excluded. Mechanical disturbance of the sediment to simulate sediment scraping by the crabs had no impact on the meiobenthos. Foraging soldiercrabs are important predators on meiofauna and significantly modify the meiofaunal community in tropical tidal flats.

Key words: Crab, benthos community, disturbance, predation, field experiment, tropical tidal flat.

Interactions between macroepifauna and meiofauna have often been shown to be repressive. Macroepifauna, mainly fish and crabs, can prey on small infauna (Reise 1979, Hoffmann *et al.* 1984, Palmer 1988, Gee 1989, Ellis & Coull 1989, Coull 1990, Olafsson & Moore 1990) or reduce their numbers by sediment disturbance (Palmer 1988). Such small scale disturbances can subsequently alter the resource spectrum (Reise 1984). It is often difficult to specify the most important process by which an organism affects infaunal community structure. Only few soft-bottom investigations address the complex or even contradictory effects of macrofauna on meiofauna abundance.

Little is known of ecological processes in tropical tidal flats (Vargas 1988, Alongi 1990 a), which are characterized by a high diversity of decapod crustaceans (Reise 1985). Among these, crabs of the family Mictyridae occur throughout the Indo-Pacific (McNeill 1926). Mictyrid crabs remain in burrows during high tide and emerge with the receding tide. During low tide they often aggregate in herds ("armies") to forage on the sandflats (McNeill 1926, pers. obs.). They are specially adapted to long air-exposure by having gill chambers divided into a gill and a lung compartment (Maitland 1987). The feeding mode of mictyrid and ocypodid crabs is described as "flotation feeding" (Altevogt 1957, Miller 1961, Cameron 1966, Quinn 1986). Sediment is scooped with the chelae into the buccal cavity where it is suspended with water to separate lighter food items. Indigestable heavy sand grains sink to the bottom of the cavity and are discarded as pseudofaecal pellets. At a low tide with intense soldiercrab activity, a large proportion of the sediment surface is turned over and pelletized. Prior to the emergence of crabs, but not implying their appearance, subsurface flotation feeding can take place (McNeill 1926; Cameron 1966). During this feeding process just below the sediment surface the crabs lift the discarded pellets with the chelae above their body, thus forming "hummocks" on the surface marking the feeding tunnel (Quinn 1983). Water for flotation feeding is taken up with the moist sediment, directly scooped with the chelae from standing water (pers. obs.) or used from branchial water which is replenished by sucking up interstitial water with specialized setae at the end of the thorax (Altevogt 1957, Quinn 1980).

At the study site, the activity pattern of *M. longicarpus* was intermittent and could not be related to environmental factors (Dittmann unpubl.). The soldiercrabs had no permanent burrowing site, but emerged from high intertidal muddy sandflats to begin foraging treks to the lower lying areas. Average size of *M. longicarpus* at the study site was 1.5 cm carapace length for males and 1.1 cm for females (Dittmann unpubl.).

Are soldiercrabs taking up meiofauna during flotation feeding and if so, is it affecting the meiofaunal community structure? Reports on the diet of soldiercrabs are contradictory and range from unspecified organic matter, bacteria and diatoms to records of a nematode and gastropod eggs in their gut (Altevogt 1957, Cameron 1966, Quinn 1986). To investigate the impact of feeding, meiofauna abundances were analysed and compared between original sediment and pellets. The effect on the benthos community was studied by longterm exclusion of soldiercrabs.

Are soldiercrabs effecting meiofauna abundances by their sediment disturbance? Disturbance is caused by the foraging crabs scraping up sediment with their chelae. Warwick *et al.* (1990) have attributed an effect on meiofauna to the disturbance by *Mictyris platycheles* in Tasmania. To study the effect of sediment scraping on meiofauna, this disturbance was simulated in the field.

The goal of this study was to investigate whether the foraging behavior of Mictyrid crabs has a direct impact on meiofauna and if so, whether this is due to uptake or sediment disturbance.

MATERIAL AND METHODS

Study site: The Haughton River flows into Bowling Green Bay (19°25'68" S, 147°5'29" E) in the tropical northeast coast of Australia (Fig.1). The estuary extends over 13 km² and is fringed by mangrove forests. Tidal flats cover 5.4 km². Tides are semidiurnal with mean tidal heights of 2.4 m. Sediment temperatures range from 20°C in winter to 35°C in summer. Salinities are marine over most of the year, despite heavy freshwater input in the wet season from December to April. The sediment at the study site was fine to very fine sand (mean particle size: 100-200 µm) and well sorted (S = 1.11-1.52).

Meiofauna abundance in pellets and hummocks: To evaluate meiofauna abundance in undisturbed sediment and sediment sorted by soldiercrabs for food, sets of samples were taken from sediment, pseudofaecal pellets and hummocks. In an area where the soldiercrabs had fed less than two hours before, pellets were collected and sediment samples were taken from undisturbed patches between pellets (site 1). At site 2, samples of undisturbed sediment were taken in the vicinity (<10m) to an approaching trek of feeding soldiercrabs. Here, the pellets were collected immediately behind the crabs passing through. Both sites were sampled during the same low tide in April 1991. Ten replicate samples each of sediment and pellets were collected within a few m^2 at both sites. The sites were located in a *Callianassa*-community and the sediment was muddy sand.

Hummocks and adjacent sediment were sampled (ten replicate samples each) in May 1991 on a sandy site near the high tide line and near an *Avicennia* grove. The hummocks originated from subsurface feeding which commenced less than two hours before sample collection.

All sediment samples were taken using a syringe as a corer (3.14 cm^2 surface area) to a

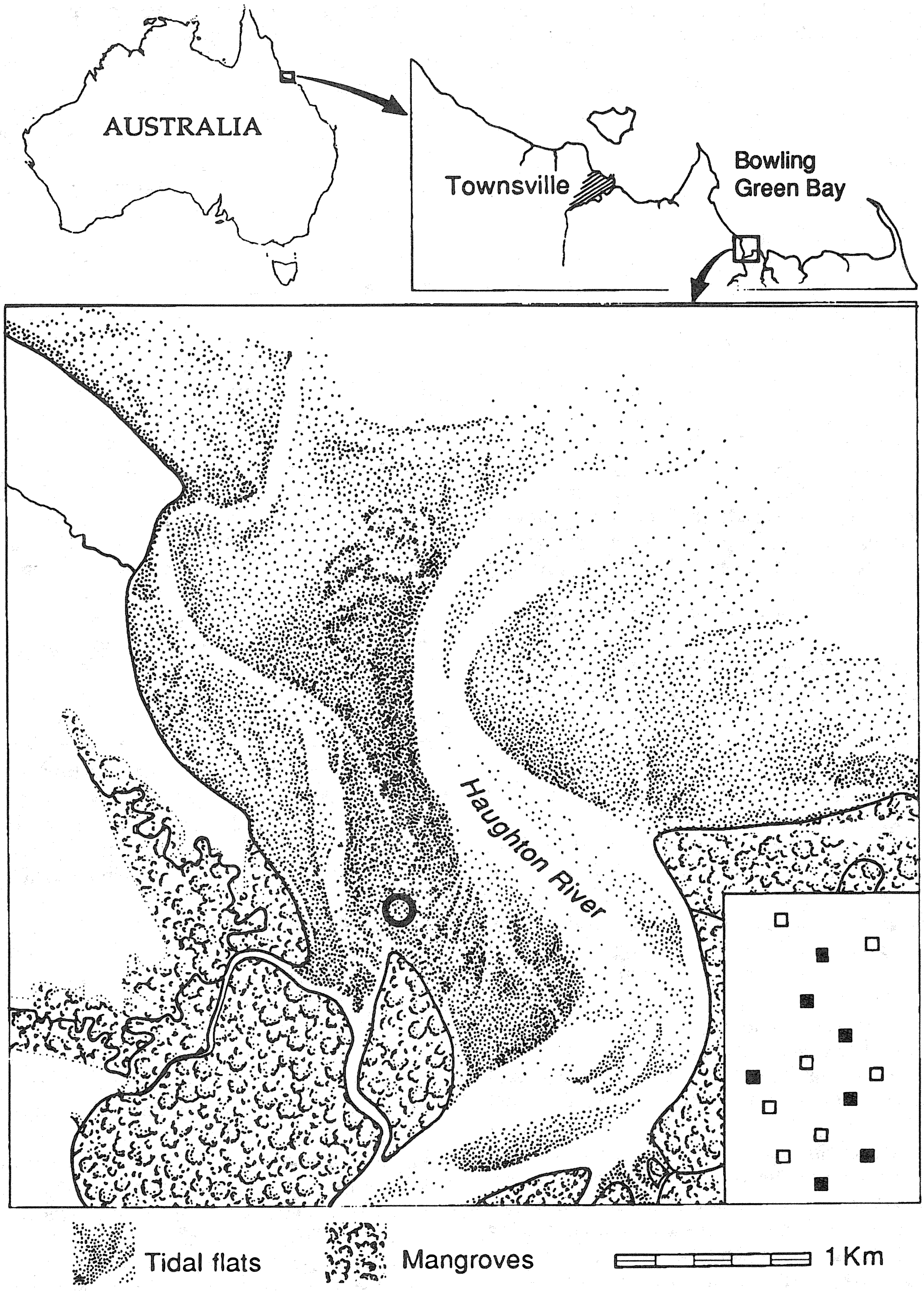

Fig. 1. Location of the study site in the Haughton estuary in Bowling Green Bay, northeast coast of Australia. The circle marks the location of the experiments and the layout of the cages is shown in the inlay, dark squares being exclusions and open squares being control cages.

depth of 1 cm. Pellets were carefully lifted from the sediment surface with a spoon and filled into the syringe to make up the same volume as sediment samples. The sediment of hummocks was lifted from the roof of the feeding tunnel with a spoon and filled into the syringe respectively.

Soldiercrab exclusion: The impact of foraging soldiercrabs on infaunal communities was studied by excluding them from sandflat sites. Since the crabs are migratory, a longterm enclosure would have been unnatural to their biology. Alterations of behaviour and unnaturally high densities in enclosure cages can cause false predation impact (Raffaelli *et al.* 1989, Webb & Parsons 1991). Thus exclusion cages had to be used, and since the direction of foraging treks was not predictable, the cages had to be closed on the four sides. A fine mesh size was attached to cages to prevent entry to soldiercrabs. A mesh size of 1.25 cm was used initially to exclude crabs, but as they were observed to pass through this mesh, fly screen (1x2mm mesh size) was laced to the exclusion cages. To control for the procedural treatment (Hurlbert 1984), the same closed cage devices had to be used, but had to permit entry to soldiercrabs, which was achieved with a meshsize of 5 cm. All cages were of 1 m^2 size and left open on top. Fourteen cages (seven of each treatment) were positioned randomly in a sheltered sandflat of the Haughton estuary within an area of 100x50 m in a *Callianassa*-community, with a distance of at least 10 m between cages (see inlay in Fig. 1). Benthic samples taken at the beginning of the experiment revealed homogeneity of the area, showing no significant differences (Mann-Whitney-U-test) for any of the meio- or macrobenthic fauna of control and exclusion sites. The cages were set up in July 1989 and three months later the flyscreen was mounted and benthos samples were taken after another two months in November 1989.

To account for spatial heterogeneity in the cages and prevent pseudoreplication (Hurlbert 1984), several cores were taken from each cage to form one sample. For meiofauna, five cores of 1 cm^2 and 5 cm depth were taken from each cage and mixed into one jar. For macrofauna, three cores of 33 cm^2 and 10 cm depth were taken per cage and mixed into one sample.

The infauna of the two cage treatments was compared with the null-hypothesis being that no difference exists in the population densities of infauna in cages with coarse and cages with fine mesh size, and the alternative hypothesis being that densities of infaunal populations differ between the two treatments. Furthermore the composition of the plathelminth- and polychaete-assemblages were analysed.

Sediment disturbance: To investigate whether disturbance to sediment by foraging soldiercrabs affects infauna, experimental sediment disturbances were performed by stirring sandflat sites of 20x20 cm with a pair of small wooden sticks. This was done in a way to resemble the raking of sediment by crabs with their chelae. Pelletization as such could not be simulated. Twelve sites were marked in a sandflat in August 1989. Half of the sites were stirred every day on five consecutive days and the other half remained undisturbed. Meiofaunal samples were taken with a 1 cm^2 corer to a depth of 1 cm. In each site three cores were taken and mixed into one jar as a sample to prevent pseudoreplication.

Sample treatment: All samples were treated alive. Meiofaunal samples were sieved through a set of sieves of 125, 80 and 40 µm after repeated shaking and decantation with filtered seawater and narcotization with $MgCl_2$. Counts were made under a dissecting microscope. Macrofaunal samples were sieved through 0.5 mm mesh size and animals counted in sorting trays.

Representative of a meiofauna and a macrofauna taxon, plathelminthes and polychaetes were determined to species level in all investigations.

Data analysis: To compare faunal densities between sample sets and treatments, distribution-free statistics were applied. Outlying densitity values occured in many data sets and with the standard deviation exceeding the mean three times, transformation of data is no longer valid. As the number of replicate samples did not exceed 10, the more conservative non-parametric test was considered more efficient even for those cases where data were suitable for parametric analysis. The Mann-Whitney U-test was used throughout the study and

TABLE 1

Meiofaunal densities (x ± sd, individuals 10 cm^{-2}, n = 10) in natural sediment and pellets formed by flotation feeding of soldiercrabs. At site 1 sediment samples were taken from undisturbed patches between pellets in an area where crabs had fed recently. At site 2 sediment samples were taken from an area the crabs had not yet fed upon, but where feeding crabs were approaching. Here the pellets were collected immediately after they were dropped

	Sediment	Pellets	% reduction
Site 1			
Nematoda***	74.20 (42.68)	4.46 (5.67)	94
Copepoda***	110.51 (92.55)	9.55 (8.69)	91
Plathelminthes***	23.89 (13.79)	0	100
Ostracoda^{ns}	2.23 (2.61)	1.27 (1.66)	-
Total pm***	213.38 (110.76)	15.29 (10.92)	93
Bivalve larvae^{ns}	2.87 (4.62)	0.64 (1.34)	-
Site 2			
Nematoda***	33.44 (15.48)	2.55 (2.93)	92
Copepoda***	251.59 (46.37)	74.20 (45.67)	71
Plathelminthes**	7.01 (5.96)	0.64 (1.34)	91
Ostracoda^{ns}	3.18 (2.99)	1.59 (1.69)	-
Total pm***	295.54 (50.26)	78.98 (43.50)	73
Bivalve larvae**	3.50 (2.36)	0.64 (1.34)	82

Total pm is the sum of all permanent meiofauna. Asterisks indicate the significance value, ns = non-significant.

significance levels given are *= $0.05>P>0.01$ **= $0.01>P>0.001$ ***= $P<0.001$.

Infaunal communities were described with univariate measures (Shannon-Weaver diversity H', Margalef's species richness d, Hurlbert's dominance index D and Pielou's eveness e), applied on the two taxa which were treated on species level (Plathelmintha and Polychaeta). Differences in their assemblages were compared with the Sorensen-index QS for species similarity ($QS = 2c/(a+b)$, with a and b being the species numbers of the two sites or experimental treatments and c being the number of species they have in common) and the Renkonen-index R_s for abundance similarity of species common to both sites ($R_s = \Sigma p_k$, where p-values are the relative individual shares of species in each community and p_k the lower p-values of k-species occurring in both sites). The closer both indices are to 1, the more the two sites resemble each other. If the indices are 0, they have no species in common.

RESULTS

Meiofauna abundances in undisturbed sediment, pseudofaecal pellets and hummocks: The pseudofaecal pellets soldiercrabs drop after flotation feeding on the sediment surface contained significantly less meiofauna than the sediment they took up (Table 1). The mean reduction rates from site 1 and 2 were 98 % for plathelminthes, 94% for nematodes and 77 % for copepods. Although nematodes were more numerous at site 1, at both sites only 6-8% of the nematodes were left in the pellets. The copepod density was twice as high at site 2 than at site 1, but the reduction of copepods was higher at site 1. All the plathelminthes of site 1 were depleted and at site 2, where their density was lower, they were nearly all removed. Only the slightly heavier ostracods and bivalvae larvae were not as efficiently extracted. Ciliates, which were recorded qualitatively, were frequent in the sediment, but not found in pellets. Benthic microalgae (diatoms) were seen in both sediment and pellet samples.

The sediment discarded as hummocks during subsurface feeding contained significantly less meiofauna than the original substrate (Table 2), but the percentage reduction was not as high as during surface feeding. Mainly nematodes and plathelminthes were reduced, whereas Ostracoda and bivalve larvae were not selected for. Unlike during surface feeding, copepoda were not taken up during subsurface feeding. Ciliates were rare in both sample sets, whereas diatoms were recorded from sediment and hummocks.

TABLE 2

Meiofaunal densities (x ± sd, individuals 10 cm^{-2} 0-1 cm depths, n=10) in sediment and hummocks created by subsurface feeding of soldiercrabs. For further information see Table 1 and text

	Sediment	Hummocks	% reduction
Nematoda***	97.77 (31.59)	22.93 (19.39)	77
Copepoda^{ns}	33.12 (22.29)	46.82 (18.95)	-
Ostracoda^{ns}	1.91 (2.23)	1.91 (2.23)	-
Plathelminthes*	11.78 (10.29)	4.46 (3.41)	62
total pm***	144.59 (31.02)	76.11 (28.82)	47
Bivalve larvae^{ns}	0.32 (1.02)	0.64 (1.34)	-

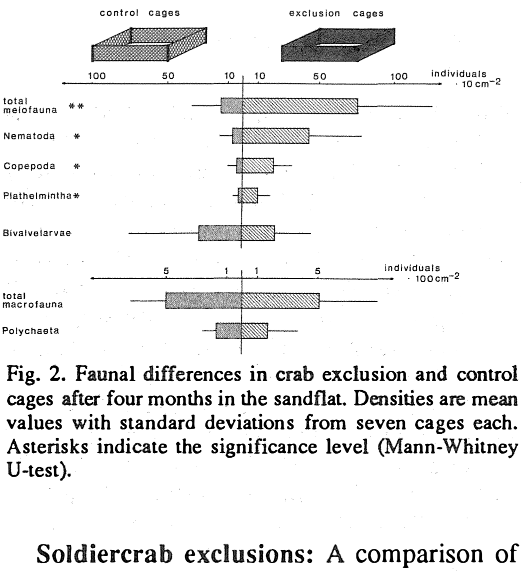

Fig. 2. Faunal differences in crab exclusion and control cages after four months in the sandflat. Densities are mean values with standard deviations from seven cages each. Asterisks indicate the significance level (Mann-Whitney U-test).

Soldiercrab exclusions: A comparison of the infaunal abundances between the two cage treatments showed that the surface activity of soldiercrabs had a negative effect on the composition of meiobenthic communities, but no impact on small macrofauna. Meiofaunal densities in the exclusion cages were significantly higher and exceeded those of the control cages by a factor of five (Fig. 2). Ostracod numbers were low; only four were found in the exclusions and one in the control cages. The Plathelminth assemblages in both treatments were similar in their composition and abundance of species (Table 3). The density of the most abundant plathelminth, a diatom-feeding *Macrostomum sp.*, was not significantly different between the treatments. Macrobenthic densities did not differ between treatments and their overall densities were low in November. None of the macrobenthic taxa (mainly polychaetes, oligochaetes, nemertines, amphipods, tanaids and gastropods) increased in abundance in the exclusions. No predatory polychaete occurred among the three species inhabiting exclusion cages, compared to five polychaete species in the control cages (Table 3). No difference was detected in the burrow density of callianassid shrimps between any of the cages and ambient sediment (average density 88 ±19 individuals/m^2).

Sediment disturbance: Mimicking sediment disturbance of soldiercrabs by stirring the surface had no effect on the densities of meiobenthos in a sandflat (Table 4). No meiofaunal taxa showed any significant response to the disturbance. The diatom-feeding *Macrostomum* sp. was the most abundant Plathelminth species in both sample sets. No difference was found comparing the composition of the Plathelminth assemblage of disturbed (H'=1.20; d=3.72; D=0.56; e=1.54) and undisturbed control sites (H'=1.23; d=3.32; D=0.38; e=1.76).

DISCUSSION

Soldiercrab feeding: Soldiercrabs efficiently separated meiofauna from the substrate by

TABLE 3

Composition of the plathelminth and polychaete assemblages in the cage treatments with and without exclusion of soldiercrabs for two months. Species are listed according to their rank order of abundance and rank equivalence is indicated by rank numbers

		Cage treatments	
Parameter	Control		Exclusion
Plathelminthes			
N	10		35
S	5		9
species	1. *Macrostomum* sp. 2. *Schizochilus* sp.1 2. *Duplominona* sp. 2. *Proseriata* juvenile 2. *Kalyptorhynchia* juvenile		1. *Macrostomum* sp. 2. *Proseriata* juvenile 3. *Retronectes* sp. 4. *Schizorhynchia* juvenile 4. *Cheliplana* sp. 1 4. *Kalyptorhynchia* indet. 4. *Proseriata* juvenile 4. *Duplominona* sp. 4. *Gyratrix* sp. 4. *Acoela* sp.
QS		0.71	
Rs		0.79	
H	1.23		1.38
d	4.00		5.18
D	0.60		0.58
e	1.76		1.45
Polychaeta			
N	12		12
S	5		3
species	1. *Scolelepis* sp. 2. *Heteromastus* sp. 3. *Magelona* sp. 3. *Nereis* sp. 3. *Glycera subaenea*		1. *Heteromastus* sp. 2. *Scolelepis* sp. 3. *Polydora* sp.
QS		0.50	
Rs		0.42	
H	1.42		0.72
d	3.71		1.85
D	0.72		0.40
e	2.03		1.51

N = total individual numbers, S = total species numbers, QS = Sorensen index for species similarity, R_S = Renkonen index for similarity of abundance frequency, H = Shannon-Weaver diversity, d = Margalef's species richness, D = Hurlbert's dominance and e = Pielou's eveness.

TABLE 4

*Meiofaunal densities (x ± sd, individuals $10cm^{-2}$, n = 6) after five days of experimental sediment disturbance in a sandflat compared to undisturbed control sites**

Taxa	Control	Disturbance
Nematoda	39.43 (28.10)	35.00 (6.23)
Copepoda	8.90 (11.30)	10.57 (8.27)
Plathelminthes	8.90 (5.03)	12.23 (2.73)
total pm	57.77 (9.60)	58.33 (13.80)

* All cases non-significant

flotation feeding. They reduced meiofauna numbers by direct consumption and not by disturbances caused by their feeding mode. The results of investigations and experiments of this study were coherent in showing this impact.

The removal of meiofauna from the sediment indicated that meiofauna is a part of the diet of *M. longicarpus*. The reduced densities in pellets and hummocks relate to an uptake by the crabs. However, some meiofauna could escape sediment handling during pelletization, but this would not account for the high percentage of reduction (73-100%). Reduction rates in pellets at site 1 and 2 were almost equivalent, rejecting the possibility that meiofauna could have left the pellets after their deposition on the sediment. At site 2 the pellets were collected immediately after deposition, whereas at site 1 they had been deposited one to two hours before. Nothing is known yet about movement and colonization times of tropical meiofauna, but from temperate tidal flats rapid recolonization of defaunated sediment by meiofauna has been reported to happen within one tidal cycle (Thistle 1980, Billheimer & Coull 1988).

Flotation feeding was selective for meiofauna light enough to float in the separation process taking place in the buccal cavity. Flotation feeding is similar to extraction methods used in meiofauna research. To extract meiofauna from a sample, the sediment is diluted with water and after shaking, the lighter meiofauna moves into suspension from where they are decanted through sieves (Uhlig *et al* 1973). This analogy may explain why heavier, more compact taxa like ostracods and bivalve larvae were discarded with the sediment.

Earlier studies concluded from the shape of setae (Cameron 1966), CN- and sediment analyses (Quinn 1986) that *M. longicarpus* feeds on organic matter and bacteria. Other flotation feeding crabs have been reported to ingest diatoms (Altevogt 1957, Cameron 1966), while some studies only state the selection of "suitable" material (Miller 1961). Diatoms were noted in both sediment, pellets and hummocks in my study and the possible uptake of diatoms should be tested by comparing the chlorophyll-a content in the sediment before and after feeding. Cameron (1966) did find a nematode and gastropod eggs in the gut content of a soldiercrab. Gut analyses alone cannot reveal the whole spectrum of diet, as meiofauna without conspicious hard structures are rarely detected in gut contents.

The uptake of meiofauna was more efficient during surface feeding than subsurface feeding. Copepoda, which were consumed from the surface, were not selected for in the latter case. This difference in feeding efficiency could be attributed to sediment properties or to a varied food spectra for male and female crabs. Subsurface feeding occurs prior to emergence or during adverse weather conditions and it is the prevailing feeding mode of females and juveniles (Quinn 1983). During subsurface feeding, pore water might become limiting for flotation feeding. While surface feeding, crabs replenish the water needed for filtering their food. Whether the food spectra varies with sex and size has not yet been addressed here, but has been shown in temperate waters for *Carcinus maenas* (Scherer & Reise 1981) and *Uca pugnax* (Weissburg 1992). Male, female and juvenile soldiercrabs spend different amounts of time on the surface at low tide and show different aggregation behaviour during their feeding and wandering phases (McNeill 1926, Cameron 1966; pers. obs.), suggesting that food selectivity might exist.

Exclusion of soldiercrabs: What effect does predation by *M. longicarpus* have on the infaunal community of the tidal flat? Released from the feeding pressure of the crabs, the meiofaunal abundances in exclusion cages increased fivefold. Consumption of meiofauna has been also reported for fiddler crabs in saltmarshes, where meiofauna abundances increased tenfold in crab exclusion cages (Hoffman *et al.* 1984). Intensive foraging on consecutive days in the same area of the tidal flat could deplete meiofaunal densities. No information is available yet on recolonization rates of meiofauna in tropical tidal flats. The wandering activities of the soldiercrabs and their intermittent occurrence could be a behavioural strategy to prevent depletion of their food source or to reduce the cost of search in relation to the food amount obtained.

Since flotation feeding is selecting prey by specific density, no species specific response of plathelminthes was found in the caging experiment and their assemblage structure was similar between treatments. Polychaetes, which were not preyed upon, showed a greater divergence in their assemblage structure. Endobenthic predatory polychaetes were absent in the exclusions inspite of the higher meiofaunal density available there. This leads to the question of whether multilevel predatory interactions, as they are known for temperate areas (Commito & Ambrose 1985), exist in tropical tidal flats.

The use of cages in field experiments has been criticized (Hulberg & Oliver 1980, Virnstein 1978), but with careful considerations they are a useful and necessary tool in experimental ecology (Hall *et al.* 1990). The cages set up in this investigation modified hydrodynamic patterns as the fly screen on the exclusion cages altered the wave pattern (noticable by less ripple marks) and could have caused different emergence or settlement patterns in control and exclusion cages. But no difference was found in the number of bivalve larvae settling out of the water column between cage treatments and unwanted cage impacts are considered negligible.

Signs of soldiercrab activity were usually seen in control cages and, prior to the attachment of flyscreen, also occassionally within exclusion cages. Thus the actual duration of exclusion was two months. The effectiveness of the exclusions was visible at low tides with soldiercrab activity. Foraging crabs suppress the activity of surface-deposit-feeding macrobenthos such as *Callianassa australiensis* and during low tides with soldiercrab activity no burrow holes of the callianassid shrimps were visible throughout the tidal flat (per. obs.). This was the case outside of cages and in the control treatments, whereas *Callianassa* burrow holes were evident inside exclusion cages. The cages occassionally affected the activity of soldiercrabs and were avoided as visual obstacles. Soldiercrabs can see vertical objects and depending on the contrast between the object and background, and the objects height to width ratio, they are approached or avoided (Kraus & Tautz 1981). It was observed on some days that crabs did not feed in an area of 50 cm around some cages, regardless of the mesh size and seemingly indifferent to the location of the cage. The time of day (sun angle) and the direction from which the crabs approached will have determined which cage, if any, was seen as an obstacle. It remained unknown whether any of the control cages were repeatedly bypassed by crabs.

Disturbance by soldiercrabs: Predation impacts often consist of the combined effects of consumption and disturbance. The predatory grazing of soldiercrabs leads to direct uptake of meiofauna and leaves a disturbed sediment surface behind. Disturbances can cause direct mortality (Palmer 1988) or can alter food availability (Thistle 1981, Reise 1984). The disturbance caused by feeding soldiercrabs, which are raking through the sediment with their chelae, has no immediate effect on meiofauna. Repeated raking on several consecutive days in my experiment had no impact on the infauna. No trophic group response of plathelminthes was apparent and the simulated disturbance did not change the food availability as Reise (1984) showed for experimental small-scale disturbances in temperate tidal flats.

In a study on the effect of *Mictyris platycheles* on the meiofauna in a Tasmanian tidal flat, Warwick *et al.* (1990) suggested that their sediment disturbance changes the abundance of nematodes. However, their sampling scheme fails to distinguish between the effects of burrowing and the effects of feeding by choosing a sample depth of 10 cm. There is also no information given on the persistence of the disturbed and undisturbed patches in their natural experiment. Hoffman *et al.* (1984) showed how fiddler crabs increase meiofaunal densities by providing microhabitats in their burrows, but reduce meiofaunal abundance by feeding. My study concentrated on the feeding of soldiercrabs, as they burrowed away from their feeding grounds and no burrowing site was permanent enough to be choosen for investigations on eventual accomodation of meiofauna in their burrows.

While this study shows the impact of soldiercrabs on meiofauna abundances, we are still far from understanding their role in tropical tidal flats. Their often cryptic behaviour and irregular emergence frequency make it difficult to estimate whether their activity pattern follows an endogeneous rhythm or is related to the abundance of available food. We have to know more on recolonization rates of meiofauna in the tropics and on their seasonal changes in abundance, which so far show high variability unrelated to dry and wet seasons (Alongi 1990 b, Dittmann 1991). The impact of soldiercrabs on meiofauna is further complicated by multilevel interactions with other macrobenthos. Foraging soldiercrabs can inhibit the activity of surface deposit-feeding macrobenthic organisms who are accomodating meiofauna in their burrows. A publication on this indirect effect of soldiercrabs on meiobenthos is in preparation.

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