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Impact of the mangrove crabs *Uca annulipes* and *Dotilla fenestrata* on meiobenthos

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ABSTRACT: To assess the effects of 2 mangrove crabs on benthic meiofauna a laboratory experiment was performed in Zanzibar, eastern Africa. The 2 ocypodidae crab species *Uca annulipes* and *Dotilla fenestrata* are commonly found at mid to high water levels among *Avicennia marina* trees. Both genera are borrowers in soft sediments and feed upon drained surface deposits by forming pseudofaecal pellets. They are efficient bioturbers of the uppermost few mm of the sediment and some *Uca* species may prey directly on meiobenthos. The 2 species were added to microcosms containing sediment with natural meiofauna populations. After 10 d of enclosure, numbers of harpacticoid copepods in the top 1 cm layer were significantly lower in microcosms containing *U. annulipes* than in control microcosms. Two nematode assemblages were found in the microcosms, one in the surface layer and one deeper down. The crabs did not alter the structure of these assemblages. It appears that the nematodes are quite resilient to the reworking of the sediment surface. We conclude that the ocypodid crabs do not regulate resident nematode assemblages, but may inhibit settlement of colonisers that have not adapted to the intense surface disturbance created by these crabs. Such biological control is most likely to be in those areas where tidal water contains relatively high numbers of migrating meiofauna.

KEY WORDS: Nematode assemblage · Meiofauna · Crabs · *Uca* · *Dotilla* · Laboratory experiment · Mangroves · East Africa

INTRODUCTION

Biological factors play an important role in regulating marine benthic communities (e.g. Menge & Sutherland 1976, Ambrose 1984). In soft-bottom habitats the feeding activity of macrofauna on the sediment surface may affect meiofauna in at least 3 ways: first, by direct predation (e.g. Smith & Coull 1987, Palmer 1988); second, by competition for food resources (e.g. Ólafsson et al. 1993); and third, by increased food supply in the form of reworked sediment and faecal pellets (e.g. Bell et al. 1978, Ólafsson et al. 1990). It is likely that such activity mainly affects the surface populations and, to a much lesser extent, the deeper-dwelling meiofauna. Responses to the bioturbation effects of macrofaunal feeding also seem to vary among the major meiofauna taxa. Of the 2 usually most abundant meiofauna taxa, harpacticoid copepods seem to respond more quickly to reworked sediment (Alongi 1985) or faecal casts (Thistle 1980, Ólafsson et al. 1990) than do nematodes.

Macrofaunal assemblages in tropical intertidal habitats differ greatly from those in temperate intertidal habitats. In the tropics, particularly in mangrove sediments, burrowing decapod crustaceans are often the dominant feature of the macrobenthic assemblage (Alongi 1989a, b). Ocypodidae (Decapoda: Brachyura) crabs include the genera *Uca* (fiddler crabs) and *Dotilla*, which are borrowers in soft sediments and feed upon drained surface deposits by forming pseudofaecal pellets (Hartnoll 1975). Both genera are efficient bioturbators of the sediments (e.g. Hartnoll 1973, Katz 1980, Robertson et al. 1980). Direct predation by *Uca* on meiobenthos has been documented (Teal 1962, Robertson & Newell 1982, Reinsel et al. 1996). Fiddler crabs have been excluded or included by using cages in 2 different field experiments, in both of which a considerable reduction in total meiofauna occurred in the

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presence of the crabs (Hoffman et al. 1984, Dye & Lasiak 1986). The results of 4 other field surveys showed that numbers of nematodes increased close to *Uca* burrows while numbers of copepods decreased or remained unaltered (Bell et al. 1978), meiofauna was more abundant in burrows than on the surface of the sediment (DePatra & Levin 1989, Dittman 1996), and numbers of harpacticoid copepods, but not nematodes, were negatively correlated with numbers of burrows (Ólafsson 1995). As far as we know, no other studies have been published on the effects of *Uca* or *Dotilla* crabs on meiobenthos.

Nematodes are generally the most abundant meiobenthic group in marine sediments and commonly represent more than 90% of all metazoans. They are also usually species rich, with representatives of various trophic guilds. In all the studies on the effects of fiddler crabs on meiobenthos mentioned above, nematodes were the dominant taxon. In all but one study (Ólafsson 1995), nematodes were not identified below Phylum. Here, we report on the first laboratory experiment designed to test the hypothesis that meiofauna and the structure of a nematode assemblage are affected by the presence or absence of 2 species of common mangrove crabs.

MATERIALS AND METHODS

Sampling and experimental design. Maruhubi (6° 09' S, 39° 12' E) is a small mangrove forest situated about 1 km north of Zanzibar town, Zanzibar, East Africa. Animals and sediment were collected at mid to high water levels among *Avicennia marina* trees. In the area, *Uca annulipes* dominates the crab fauna, with typically over 100 ind. m^{-2}. *Dotilla fenestrata* is also common in the area, but seems to have a more patchy distribution. During low tide on 22 May 1996, 18 microcosms were established in the following manner. Cores were taken with a 90 cm^2 steel tube to a depth of 9 cm. Care was taken not to take samples directly over a crab hole. Cores were placed into plastic jars of internal diameter 10.7 cm. The bottom of each of the jars had 3 small holes (2 mm in diameter) to allow drainage of water (Fig. 1). The sediment inside the jars was carefully pushed to the sides; this did not break up any vertical stratification of the sediment. Adult crabs were collected by digging by hand in the surrounding sediment. Six individuals, similar in size, of each species were randomly placed in 12 microcosms (jars), i.e. 1 crab per microcosm, while the remaining 6 microcosms served as controls without addition of crabs. Crabs burrowed into the sediment within 10 min of being placed in the microcosms. The opening of each microcosm was fitted with a net (2 mm mesh size) to prevent escape by the crabs (Fig. 1).

Microcosms were placed on a bench in a random block design (Fig. 1) in the backyard of the Institute of Marine Sciences in Zanzibar town. The microcosms were partly exposed to sunlight and rainfall. To simulate the field situation, seawater was added to the microcosms twice a day for the first 4 d, then once a day for the next 3 d and during the last 3 d no water was added. Water was drained off by pulling out the rubber stoppers approximately 1 h after seawater was added. One hour prior to the termination of the experiment, water was added once more to smooth out the sediment surface, which made sampling and sectioning of the cores easier. When water was added, pseudofaecal pellets smoothed out and burrows without crabs became filled with sediment. During the course of the experiment, each microcosm was monitored twice a day for activity by crabs. The numbers of holes were noted and bioturbation was estimated as the percentage of reworked sediment on the surface. After 5 d, a 5 cm deep core (9.6 cm^2) was taken from each microcosm to estimate total organic content. The experiment was terminated after 10 d. From each microcosm, cores were taken for meiofauna (2 cores, 9.6 cm^2, each split into 0–1 cm and 1–5 cm sections), grain size (1 core, 9.6 cm^2, 0–5 cm) and chlorophyll *a* (2 cores, 5.3 cm^2, 0–1 cm). The rest of the sediment was sieved through a 2 mm mesh size sieve and all the crabs were picked out and stored in 4% formalin. The 2 meiofauna cores taken from each microcosm were added together and fixed in 4% formalin. Samples were washed through 500 and 40 µm sieves and meiofauna extracted from the 40 µm fraction using Ludox (colloidal silica polymer) at a specific gravity of 1.15. Meiofauna was enumerated and identified to major taxon in a petri dish

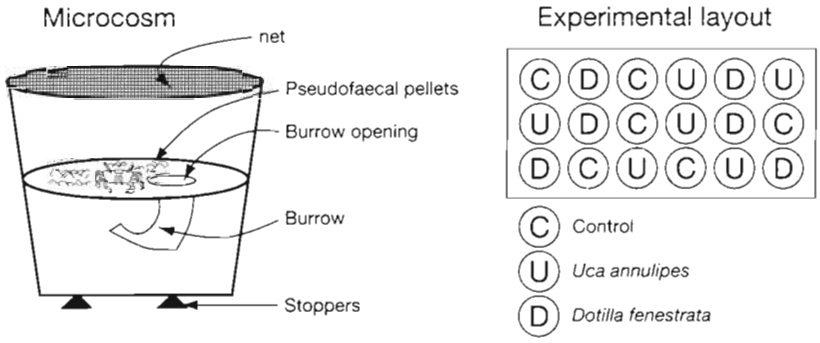

Fig. 1. Schematic representation of a microcosm with a crab, and the layout of the microcosms

under a stereo dissecting microscope. The extracted samples were transferred to glycerine and mounted on slides for identification of nematode genera under a high-power microscope, using the pictorial keys of Platt & Warwick (1983), and nematodes assigned to trophic groups according to the scheme of Wieser (1953). Grain size samples were oven dried at 85°C for 24 h and subsequently sieved through a series of sieves (2, 1, 0.5, 0.25, 0.125 and 0.063 mm) and grain size determined on the basis of the weight of each size fraction (Morgans 1956). The 2 chlorophyll samples taken from each microcosm were combined, placed in an equal volume of 90% acetone, left for 24 h at 4°C and analysed using a spectrophotometer according to Parsons et al. (1984). Organic content was determined by oven drying samples at 85°C for 48 h and then combusting them at 500°C for 5 h (Buchanan 1984).

Statistics. Differences in density were investigated by means of 2-way analysis of variance (ANOVA), for treatments and blocks. Paired *a posteriori* comparisons of density estimates were carried out with the Tukey test, using 95% confidence limits. Prior to the ANOVA, all data were $\log_{10}$ transformed and Cochran's *C*-test used to check the assumption of homoscedasticity. ANOVA was used on 1 occasion (mean grain size) when the variance was heterogenous, as we had balanced design and no significant difference among treatments (Underwood 1997). Generic diversity was assessed by using the Shannon-Wiener information function (H'), Pielou evenness (J') (both using $\log_2$), Simpson's index (D) and species richness (Margalef) (d). The ANOVA, and the non-parametric test were done by using STATISTICA 5.1 from StatSoft, Inc. Abundances of nematodes were subjected to non-metric multidimensional scaling ordination (MDS) using the Bray-Curtis similarity measure using non-transformed, square root and double square root data. The ANOSIM (analysis of similarity) randomisation test was used to test for differences in structure of nematode assemblage and the SIMPER computer program was used to identify those genera contributing to differences observed in the MDS analysis (Warwick et al. 1990a, b). The ordination, the randomisation test, the similarity analysis and the calculation of diversity indices were done by using the PRIMER 4.0 statistical package developed at the Plymouth Marine Laboratory, England.

RESULTS

Activity of crabs

Crabs of the 2 species all fed at the sediment surface and produced pseudofaecal pellets. *Dotilla fenestrata* usually made 2 to 3 burrows while the *Uca annulipes* made 1 to 2 burrows. Between Days 3 and 7, the daily bioturbation in the microcosms was similar for both *D. fenestrata* and *U. annulipes* or, in other words, on average 69 and 66%, respectively, of the sediment surface was covered with pellets (Table 1). In the control microcosms, bioturbation was minimal and significantly lower than in the crab microcosms (Table 1). The maximal observed daily pellet cover, in the control microcosms, was 10%, due to a juvenile fiddler crab (Table 1).

Organic content, grain size and chlorophyll

There was no significant difference observed among treatments in the mean grain size, organic content or chlorophyll *a* concentrations (Table 1).

Major taxa

Nematodes were the most abundant taxon in the microcosms, comprising 90% of the total numbers, followed by turbellarians (6%), harpacticoids (3%) and other taxa (1%). Most nematodes were found below 1 cm depth while the opposite was true for the harpacticoid copepods, which were more or less confined to the top 1 cm layer (Table 2). Of the major taxa, only the harpacticoids in the top sediment layer showed a significant difference among treatments (Table 2) with

Table 1. Average, maximum and minimum values of the factors measured in the microcosms. Bioturbation as measured between Days 3 and 7 (see text). Mean grain size and chlorophyll *a* were measured after 10 d and organic content after 5 and 10 d. Results of ANOVA and sign test are also shown. ns: not significant

	Control			*Uca annulipes*			*Dotilla fenestrata*			ANOVA	Sign test
	Avg	Max	Min	Avg	Max	Min	Avg	Max	Min		
Bioturbation (%)	3	10	0	69	92	26	66	79	54		$p < 0.01$
Mean grain size (µm)	376	418	326	393	425	363	387	434	324	$p > 0.05^{ns}$	
Chlorophyll *a* (µg l^{-1})	0.50	0.58	0.38	0.52	0.68	0.37	0.43	0.59	0.34	$p > 0.05^{ns}$	
Organic content after 5 d (%)	1.0	1.3	0.7	1.0	1.3	0.7	1.3	1.9	1.0	$p > 0.05^{ns}$	
Organic content 10 d (%)	1.3	2.5	0.7	1.0	1.3	0.6	1.2	2.4	0.8	$p > 0.05^{ns}$	

Table 2. Average numbers per 10 cm^2, standard error (SE) and percentage of total (%) of the major taxa in the mesocoms (N = 6). Results of ANOVA and Tukey *a posteriori* test are also shown. *Significant; ns: not significant

	Control			*Uca annulipes*			*Dotilla fenestrata*			ANOVA
	Avg	SE	%	Avg	SE	%	Avg	SE	%	
Nematoda 0–1 cm	79	16	29	67	10	31	66	10	27	$p > 0.05^{ns}$
Nematoda 1–5 cm	154	11	57	133	29	62	148	45	61	$p > 0.05^{ns}$
Nematoda total	234	23	87	200	33	93	215	43	89	$p > 0.05^{ns}$
Harpacticoida 0–1 cm	13	4	5	1	1	0	7	4	3	$p < 0.05^{*}$, Control > *U. annulipes* (Tukey test)
Harpacticoida 1–5 cm	2	1	1	1	1	0	2	1	1	$p > 0.05^{ns}$
Harpacticoida total	15	5	6	2	1	1	8	4	3	$p < 0.05^{*}$, Control > *U. annulipes* (Tukey test)
Turbellaria 0–1 cm	8	3	3	4	1	2	9	2	4	$p > 0.05^{ns}$
Turbellaria 1–5 cm	9	3	3	6	1	3	6	2	2	$p > 0.05^{ns}$
Turbellaria total	17	4	6	10	2	5	15	2	6	$p > 0.05^{ns}$
Others 0–1 cm	3	1	1	1	0	0	1	1	0	$p > 0.05^{ns}$
Others 1–5 cm	1	0	0	1	0	0	2	1	1	$p > 0.05^{ns}$
Others total	4	1	1	2	0	1	3	1	1	$p > 0.05^{ns}$

larger numbers inside control microcosms compared with the *Uca annulipes* treatment (ANOVA, $p < 0.05$, Tukey test). No block effects were detected.

Nematode assemblage

Altogether 60 species/genera were found in the microcosms. MDS of the nematode species/genera double square rooted data clearly separated samples from the 2 depths (Fig. 2). A pairwise comparison using ANOSIM showed a significant difference in nematode assemblage between the 2 layers (stress value: 0.20, r-value: 0.722, $p \ll 0.001$). Very similar results were obtained when MDS and ANOSIM were performed on non-transformed (stress value: 0.14, r-value: 0.711, $p \ll 0.001$) and square root data (stress value: 0.17, r-value: 0.790, $p \ll 0.001$). Species contributing most to the dissimilarity were *Longicyatholaimus* sp., *Molgolaimus* sp., *Daptonema* sp.1 and *Camacolaimus* sp., which contributed 7.7, 6.1, 4.4 and 3.9%, respectively, of the average Bray-Curtis dissimilarity. All these species, exept *Daptonema* sp.1, were found in greater abundance in the deeper layer, while some species, i.e. *Paracanthoncus* sp., *Leptolaimus* sp.1 and *Daptonema* sp.1, were proportionally more abundant in the top layer (Table 3). The average number of species was greater in the deeper than in the surface layer, although the species diversity indices were similar in the 2 layers (Table 3).

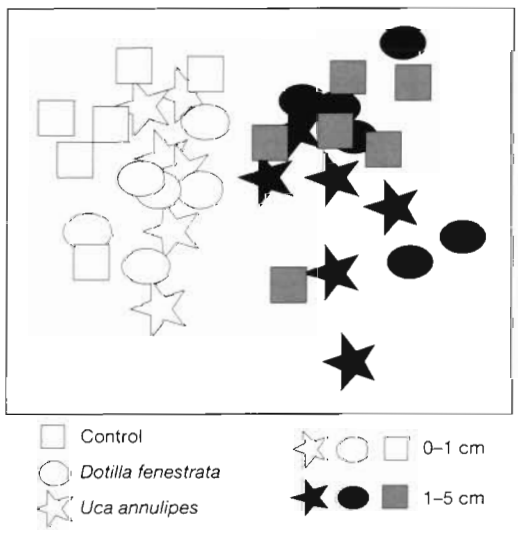

Fig. 2. Two-dimensional configuration (multidimensional scaling ordination) of nematode species/genera in all microcosms and both depth layers

Table 3. Average number per 10 cm^2, standard error (SE) and percentage abundance (%) of the 10 most abundant nematode species/genera in the 2 depth layers (N = 18). Total nematode numbers and diversity indices are also shown

	0–1 cm			1–5 cm		
	Avg	SE	%	Avg	SE	%
Chromaspirina sp.	16	3.3	22	49	6.0	34
Longicyatholaimus sp.	0	0.1	0	17	3.2	12
Viscosia sp.	3	0.4	4	8	2.5	6
Camacolaimus sp.	1	0.3	2	8	2.0	6
Molgolaimus sp.	0	0.0	0	8	2.5	6
Paracanthonchus sp.	12	1.4	17	7	1.7	5
Spirinia sp.	2	0.4	2	7	1.3	5
Leptolaimus sp.1	9	1.5	12	6	0.9	4
Microlaimus sp.	3	1.0	4	4	1.2	3
Metalinhomoeus sp.	7	1.3	10	4	0.9	3
Daptonema sp.1	5	1.5	7	2	0.5	1
Halalaimus sp.	3	0.8	4	2	0.4	1
Spilophorella sp.	2	0.5	2	0	0.2	0
Total nematode numbers	71	6.6		145	17.2	
Total number of species	15	0.7		18	0.5	
Richness, *S*	2.26	0.1		2.43	0.1	
Shannon-Wiener, *H'*	3.08	0.1		3.13	0.1	
Pielou evenness, *J'*	0.80	0.01		0.76	0.02	
Simpson, *D*	0.15	0.01		0.19	0.02	

MDS did not reveal any obvious pattern as far as treatments were concerned (Fig. 2). The control samples showed a vague grouping in the upper sediment layer but no significant difference between treatments was detected in the upper or lower sediment layers (ANOSIM, $p > 0.05$). Similar results were obtained with non-transformed and square root transformed data. Of the 13 most abundant nematode species/genera in the upper layer, only one displayed a significant variation among treatments. This species, *Camacolaimus* sp., was the fourth most abundant species in the lower layer (Table 3) and was found in significantly greater numbers in both treatments compared with control ($p < 0.01$, Tukey test). All diversity measures were on average higher in the crab treatments but this difference was not significant ($p > 0.05$). There was no significant difference among treatments and control when numbers in each feeding category were analysed ($p > 0.05$).

DISCUSSION

Our results clearly confirm earlier observations in the mangrove forests of Zanzibar that harpacticoids were negatively correlated and nematodes were not correlated with the number of crab burrows (Ólafsson 1995). In contrast to nematodes, harpacticoids generally move easily, are good swimmers and may actively migrate to the water column (Armonies 1988, Palmer 1988, Walters 1988). They are in general also much quicker to colonise azoic sediments than are nematodes (e.g. Alongi et al. 1983, Sherman et al. 1983, Widbom 1983, Ólafsson & Moore 1990), but this also appears to be species-specific as burrowing and deeper-living harpacticoids have been found to be much slower colonisers than are epibenthic species (e.g. Ólafsson & Moore 1992). Therefore it is quite plausible that the greater abundance of harpacticoids in the control microcosms was due to migrating harpacticoids. At the time of sampling, spring tides prevailed and our sampling station was flooded by the incoming tides. With the tides, epibenthic copepods may have colonised the area and therefore been sampled in the microcosms. Then, the intense surface bioturbation may have contributed to their lower abundance within the crab treatments compared to the controls.

It is obvious that the crabs did not alter the assemblage structure of the nematodes over the experimental period. Even though one species was found in significantly greater numbers in the experimental treatments with crabs compared to the control, this may have occurred by chance, as the probability of Type I error increases with the number of comparisons. Also, this species was relatively rare in all microcosms, making the effect very small for the whole assemblage.

Previous studies where fiddler crabs were either excluded or included by using cages indicated that the crabs have substantial negative effects on numbers of nematodes. The experimental design of these studies makes the evidence less convincing. Dye & Lasiak (1986) based their conclusion on experiments where control cages (without crabs) were designed differently from the enclosure cages. The control cages covered an area about 8 times smaller and were of a shape different to the enclosure cages. All significant difference between the densities could therefore be as easily attributed to the differences in experimental cages as to the presence or absence of the crabs. Similarly, the results of Hoffman et al. (1984) are based on a flawed experimental design. They conducted 2 experiments, one of which was clearly an example of pseudoreplication (2 crab removal plots compared with 1 control plot, using 22 degrees of freedom instead of 2) and the other, a cage experiment, also appeared to have confounding problems because they quoted twice as many replicates as there were experimental units. Further, they did not describe how the cages were placed on the bottom, i.e. random, block, or simple cluster design, which may have a bearing on the interpretation of the data.

There could be several explanations for why we did not detect any effects on the most abundant taxon, the nematodes. The following are the 2 most likely explanations:

(1) The nematode fauna is well adapted to the intense bioturbation and is not effectively eaten by crabs. This is perhaps the most logical explanation, because in areas where there are crabs the bioturbation is continuous and widespread, often leaving no or only a very limited area untouched. The nematodes must therefore tolerate both the bioturbation and possible predation. This they can do with well-adapted species that do not rely on the very first 2 mm of sediment for food source or oxygen uptake. It is clear from this experiment that the assemblages were quite different between the top 1 cm layer and the 1–5 cm deep layer. It is quite plausible that the nematodes either stay below the layer of bioturbation (0–2 mm) or migrate downwards when crabs are active on the surface. By doing this, they may completely avoid the destructive bioturbation or predation. Several studies indicate that surface bioturbation has little or no effect on nematode assemblage (Sherman et al. 1983, 1993, Ólafsson et al. 1990, Ólafsson & Elmgren 1991). Further, some studies indicate that nematodes can be quite resilient to human disturbance with small or no changes in assemblage structure (e.g. Alongi et al. 1983, Gee et al. 1985, Lambshead 1986, Warwick et al. 1988). Unfortunately,

there have been few studies where nematodes have been identified to taxon level lower than Phylum, which limits the applicability of generalisations.

(2) Crabs do control the nematode assemblage, but this was not detected because of experimental limitations. First, the experiment ran for only 10 d, which may not have been sufficient time for the nematodes in the microcosms without crabs to regenerate. Many nematode species do, however, regenerate within hours or a few days, especially when the temperature is moderately high (Heip et al. 1985). The only way to find out if there has been sufficient time for regeneration is to carry out a similar experiment over a longer period of time. Second, we had a limited number of species in the experimental units due to the absence of immigration. This may have hampered the establishment of nematode fauna which is sensitive to bioturbation/predation by these crabs. Third, species sensitive to disturbance by crabs might also be sensitive to microcosm manipulation.

Two other studies on the effects of decapods on soft-bottom meiofauna have been performed. Warwick et al. (1990a) examined the effects of disturbance of sediment by soldier crabs using a natural experiment in Tasmania, Australia. Soldier crabs appear to disturb the sediment in a similar fashion to the crabs in the present study, i.e. they are deposit feeders which scoop and rework sediment with their mouthparts and deposit pseudofaecal pellets on the sediment surface. Within the same beach, around mid-tide level, zones where the crabs were abundant were compared with zones where they were absent. Although average density of the nematodes was similar in both habitats, the nematode assemblage structure differed significantly between the zones. The authors point out that the flaw in such an experimental approach is that its validity rests on the assumption that the places or times differ only in the intensity of the selected factor. They believe that the patchiness of disturbed and undisturbed sediment is most likely a reflection of the gregarious behaviour of the crabs rather than a response to an unspecified environmental factor (Warwick et al. 1990a). Nevertheless, the evidence remains circumstantial. Dittman (1993) carried out an experiment in a tropical tidal flat in northeast Australia where soldier crabs were excluded by cages. She found a significant reduction in nematode and other meiofauna numbers within the exclusion cages compared with control cages. She also mechanically disturbed the sediment to simulate bioturbation by crabs and found that such disturbance had no effects on the meiofauna. She concluded that the soldier crabs were therefore reducing meiofauna populations by predation. The exclusion cages had a much finer mesh size (1 × 2 mm) than the procedural control cages (50 mm). Obviously modification of sediment inside cages with a very fine mesh size is likely to be different than with a coarse mesh size, especially in intertidal areas (e.g. Virnstein 1978, Hulberg & Oliver 1980, Reise 1985). Therefore the elevated numbers of nematodes inside the exclusion cages could just as well be a result of modifications of sediment as due to predation by crabs.

Three other studies have indicated that the burrows or the sediments directly in the vicinity of fiddler crabs contain larger numbers of nematodes than are found in the surrounding sediments (Bell et al. 1978, DePatra & Levin 1989, Dittman 1996). The reason for this pattern is not quite clear, but Bell et al. (1978) attributed it to increased food resources, while DePatra & Levin (1989) showed that meiofauna was passively deposited in natural and artificial burrows. Regrettably, none of the authors identified the nematodes to a level lower than major taxon and therefore we cannot say if their findings are due to colonisers that did not survive predation/disturbance on the surface or due to enhanced resident nematode fauna as a result of increased food resources.

We conclude that the ocypodid crabs do not regulate resident assemblages of nematodes, but may inhibit settlement of colonisers that have not adapted to the intense surface disturbance or predation by these crabs. Such biological control is most likely to be in those areas where tidal water contains relatively large numbers of migrating meiofauna.

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