



The effects of the gastropod *Terebralia palustris* on infaunal communities in a tropical tidal mud-flat in East Africa

Anneli Carlén and Emil Ólafsson*

Department of Zoology, University of Stockholm, S-106 91 Stockholm, Sweden; *Author for correspondence (e-mail: emil.olafsson@zoologi.su.se; phone: +48 8 164009; fax: +48 8 167715)

Received 4 May 2001; accepted in revised form 11 November 2001

Key words: Cages, Cyanobacteria, Macrofauna, Meiofauna, *Terebralia palustris*, Tropical mudflat

Abstract

The gastropod *Terebralia palustris* (Linnaeus) is one of the largest prosobranchs found in tropical intertidal habitats. The adults form feeding aggregations and frequently dominate the surface of muddy substrates, where they clearly destabilize the sediment surface. We tested the following hypotheses: 1. The gastropod has negative effects on the density of infaunal animals because of potential food competition and/or surface sediment disturbance. 2. The disturbance exerted by *T. palustris* results in more variable infaunal assemblages, especially where intensity of disturbance is high. To address these hypotheses gastropods were either enclosed or excluded from experimental cages, which were randomly assigned to blocks as far as 300 m apart on an intertidal mudflat in East Africa. After nine weeks of enclosure the gastropod at high densities clearly affected the meiofauna assemblages. Several meiofauna groups were found in significantly reduced densities in the presence of the gastropod compared with control cages without the gastropods, supporting our primary hypothesis. In cages without *T. palustris* a cyanobacterial carpet developed while this was not evident in enclosure cages. *T. palustris* had no significant impact on the macrofauna assemblage. In support of our second hypothesis, multidimensional scaling ordination (MDS) suggested that there was an increased variability of meiofauna within cages with high density of *T. palustris*.

Introduction

Tropical intertidal sediments are generally subjected to considerable variations in physical parameters such as temperature and salinity. This led Moore (1972) and Alongi (1987a, 1990) to advocate that the high physical stress in intertidal tropical areas dominate the biological processes in regulating intertidal communities. A good example of such physically controlled intertidal habitats are hypersaline areas commonly found in the tropics, where the infaunal communities may consist only of a handful of meiofaunal species and being devoid of macrobenthic species (Ólafsson et al. 2000). Nonetheless, a striking feature of tropical intertidal sediments is the presence of abundant macroepifauna which often exert biological pressure on the infauna (e.g. Dittman (1996)).

Experimental work on benthic communities has indicated biological factors as the major forces structuring the infaunal communities. Exclusion studies of macroepifauna have shown significant changes in the meiofauna community structure (Ólafsson and Moore 1992; Dittman 1993; Schrijvers et al. 1995). Exclusion studies have further pointed towards the importance of multi-trophic relationships within the macro- and meiofauna community (e.g. Ólafsson and Moore (1992)). Biological disturbance as habitat modifications may influence the structure of meiofaunal assemblages (Reise and Ax 1979; Thistle 1980; Reidenauer and Thistle 1981; Sherman et al. 1983; Creed and Coull 1984; Warwick et al. 1986; Palmer 1988; Warwick et al. 1990; Ólafsson and Elmgren 1991; Ólafsson and Moore 1992; Dittman 1996). Studies on crab burrows in the sediment of tidal flats in Australia have shown that more infauna is found

alongside burrows than in adjacent sediment (Dittman 1996), while Ólafsson and Ndaro (1997) found very little effects of mangrove crabs on meiofauna communities in soft bottoms.

Since Levinton (1972) theorised that benthic deposit feeding communities are in general limited by food availability, overwhelming evidence for both intra- and interspecific competition for food in soft-bottom communities has been established (see for review Wilson (1991), Ólafsson et al. (1994)). There are, however, few studies on competition for food between meio- and macrofauna or between taxa or species within meiofauna. There are indications of food competition between meiofauna and macrofauna inferred from microcosm experiments (Alongi and Tenore 1985; Ólafsson et al. 1993), but evidence is still circumstantial.

Recent studies indicate that epimacrofauna, like decapods, play an important role in the decomposition of organic material (e.g. Micheli et al. (1991), Lee (1998)), but other detrital feeding organisms such as snails, which may be very abundant in these areas have been given little attention. Previous studies on the prosobranch *Terebralia palustris* Plazait (1977), Shokita et al. (1984), Nishihira (1983), Houbrick (1991), Fratini et al. (2000) suggest that it may play an important role in decomposing mangrove detritus. It has been recorded that *T. palustris* graze on the sediment as well as on mangrove litter, including leaf, stipule, calyx, fruit and propagule (Nishihira 1983; Slim et al. 1997; Dahdouh-Guebas et al. 1998). *Terebralia palustris* is a large prosobranch found in all mangroves around the Indian Ocean (Houbrick 1991). It is often associated with upper intertidal mangrove areas, and is by far the largest prosobranch found in the mangroves (Houbrick 1991). It can attain a shell size of 19 cm, though it usually gains a size of 10 cm (Loch 1987). The adults form feeding aggregations and frequently dominate the surface of muddy substrates of mangrove forests (Nishihira 1983). In some areas adult densities as high as 150 individuals per m² have been recorded (Plazait 1977). The only known predator on *T. palustris* is the mud crab, *Scylla serrata* (Houbrick 1991). The gastropod is also collected by humans and often in great numbers. Several studies indicate that biologically induced surface sediment disturbance may effect the benthic fauna (e.g. Reidenauer and Thistle (1981), Ólafsson and Elmgren (1991), Bonsdorff and Pearson (1997)). In this respect the gastropods contribute to destabilization of the sediment since their heavy shells rearrange the mud

surface by leaving an approximately 0.5 cm deep track. Such disturbance may therefore stress the infaunal communities, especially those that are confined to the top centimetre such as the vast majority of meiofauna. Increased variability of marine communities has been attributed to stress (Warwick and Clarke 1993).

The aim of current study was to determine if *T. palustris* influences infaunal communities in tropical mudflats. We tested the following hypotheses: 1. The gastropod has negative effects on the density of infaunal animals because of potential food competition and/or surface sediment disturbance. 2. The disturbance exerted by *T. palustris* results in more variable infaunal assemblages, especially where intensity of disturbance is high. To address these hypotheses gastropods were either enclosed or excluded from experimental cages, which were randomly assigned to blocks as far as 300 m apart on an intertidal mudflat. This design was chosen to avoid the effects of possible environmental gradients and to ensure the generality of the results.

Methods

Study site

Chwaka Bay mangrove forest (06 °11'S 39 °25'E) covers an area of approximately 3000 hectares (Ngoile and Shunula 1992) on Unguja island, the largest island of Zanzibar, Tanzania. The study area was situated on a low intertidal mudflat in the Chwaka mangrove delta. The mudflat is inundated on every flood and remains submerged during neap tides. Five to 40 cm thick muddy substrate covers the lime rock and *Terebralia palustris* forms prominent aggregations all over the tidal flat.

Experimental design

Experimental cages (0.23 m²) were constructed of 20 cm high circular steel frame to which 40 cm high plastic garden net (1 cm mesh size) was attached, covering both the sides and the top (Figure 1). The net was kept upright with the aid of several pegs attached to the metal frame. Pilot study showed that the snails stayed within the cages and rarely climbed on the steel frame. Random block design was employed, where eighteen cages were divided into three blocks ca 300 m apart, with two replicate cages of three treatments

in each block situated ca 2 m apart (Figure 1). Cages were pushed 20 cm into the sediment to level the steel frame with the sediment surface. Density of *T. palustris* was estimated by collecting all gastropods within 6 randomly located quadrates (1 m × 1 m) in the vicinity of each block. Adults of similar size (ca 10 cm long) were added to the cages at following densities: 15 individuals (2 × ambient density), 7 individuals (ambient density) and without *T. palustris* (control).

Sediment samples were taken inside the cages at the beginning of the experiment (30th of September 1997), after three weeks and nine weeks during the wet season. At each sampling occasion movement and track building of the snails was examined in haphazardly chosen cages of both treatments. Two sediment cores (10 cm²) were retrieved with a hand-held Perspex tube down to 5 cm in each cage at each occasion. These two subsamples were pooled before further analysis. The samples were instantly fixed with 8% seawater formalin. Sediment water temperature was measured with a mercury thermometer and sediment water salinity was measured with a refractometer. Sediment samples were washed through 500 and 40 µm sieves. All animals retained on the 500 µm sieve were regarded as macrofauna while animals retained on the 40 µm sieve were classified as meiofauna. Meiofauna from the 40 µm sediment fraction was extracted from the sediment by using Ludox (TM colloidal silica) at a density of 1.15 (Platt

and Warwick 1983). The macro- and meiofauna were counted and identified under a stereo dissecting microscope to major taxa, except for the Polychaeta which were identified to the family level. Macrofauna was identified from all three sampling occasions while meiofauna only from the last one.

Statistics

Differences in density were investigated by means of analysis of variance, for treatments, time and blocks. In the case of heterogenous variances (Cochran's test) the data were log₁₀ transformed before analysis. The ANOVA was done by using STATISTICA 5.1 from StatSoft Inc. The taxa abundance data were subjected to non-metric multidimensional scaling ordination (MDS) using the Bray-Curtis similarity measure and ANOSIM (analysis of similarity) used to test for differences in assemblage structure (Warwick et al. 1990). The ordination was done by using PRIMER 4.0 statistical package developed at the Plymouth Marine Laboratory.

Results

The size of *T. palustris* in the vicinity of the cages was on average 10 cm (±0.4SE) and did not vary significantly among blocks. However, the density of *T. palustris* was significantly different among the vic-

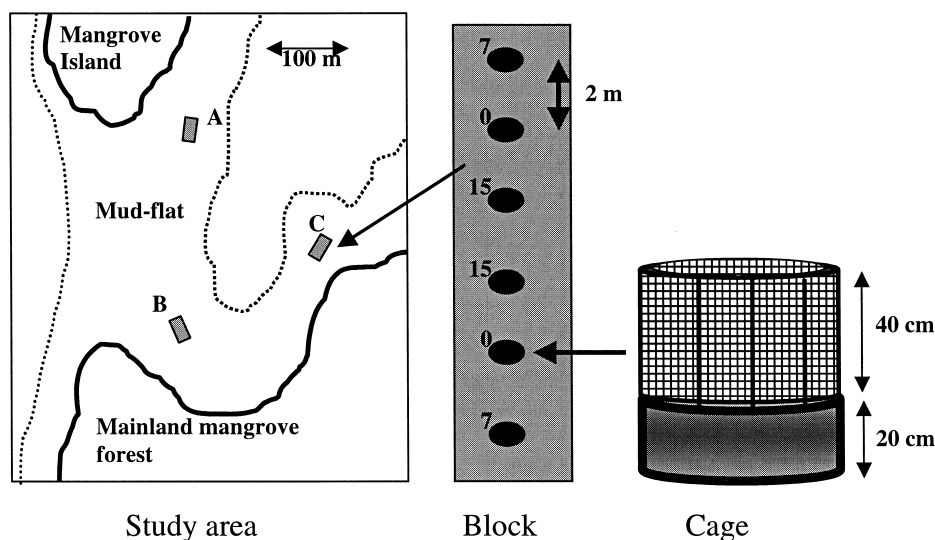


Figure 1. Schematic illustration of the study area (blocks marked A, B and C), a block (figures indicate numbers of gastropods in a cage) and an experimental cage. The dotted lines indicate the sea-ward border of the mudflat at low water during spring tides.

inities of the blocks (1-way ANOVA, $p < 0.001$, Tukey test, Figure 2). The snails inside the cages appeared to behave in the same manner as the free-living snails in the surroundings, i.e. they moved around and created visible tracks on the sediment surface.

The temperature varied little among blocks and sampling occasions, ranging from 28 to 33 °C, while sediment salinity varied significantly among sampling occasions, being on average $43 \pm 3SD$ ppt (initial), $20 \pm 2SD$ ppt (3 weeks) and $29 \pm 1SD$ ppt (9 weeks), but not among blocks (2-way ANOVA, Dates: $p < 0.001$, Blocks: $p > 0.05$, Dates \times Blocks: $p > 0.05$).

After 9 weeks cages without gastropods developed a carpet of cyanobacteria with almost 100% cover except for the cages in the C block where the cover was about 25%. The bacteria consisted of two major colonies of the genera *Lyngbia* and *Spirulina*. Cages with *T. palustris* did not develop such carpets.

Macrofauna

The macrofauna comprised mainly of nematodes (42%), polychaetes (31%) and ostracods (20%) but other groups were found in lower numbers and often infrequently i.e. cumaceans, amphipods, isopods, decapods, platyhelminthes, priapulids and insects. The polychaetes were dominated by the families Capitellidae (25% of total macrofauna numbers), Syllidae (3%) and Sabellidae (2%) while members of other

families accounted for less than 1% of total macrofauna numbers i.e. Terebellidae, Nereidae, Phyllodocidae, Maldanidae and Opheliidae. Average numbers of polychaetes, Capitellidae, Syllidae, Sabellidae, nematodes and ostracods were not significantly ($p > 0.05$) different among treatments and only ostracods showed significant difference among blocks ($p < 0.05$) and dates ($p < 0.05$) while no interactions between factors were found (3-way ANOVA, Table 1). MDS ordination of all the macrofauna data indicates no treatment or time effects (Figure 3). Similar results were found when the typical meiobenthic taxa, Nematoda and Ostracoda, were excluded.

Meiofauna

Nematodes comprised 87% of total meiofauna numbers followed by harpacticoids (7%), polychaetes (4%), kinorhynchans (1%) and others (1%). There was a significant difference in total meiofauna, nematode and polychaete numbers among treatments but not blocks (2-way ANOVA, treatments: $p < 0.05$, blocks: $p > 0.05$, treatments \times blocks: $p > 0.05$) with about two times higher numbers in controls compared to the high density treatment (Figure 4). The MDS ordination of the major meiofauna taxa data separates the control samples without the gastropods from the medium and high *T. palustris* treatments (Figure 5). There was also a significant difference among all the treatments in pair-wise comparisons using ANOSIM

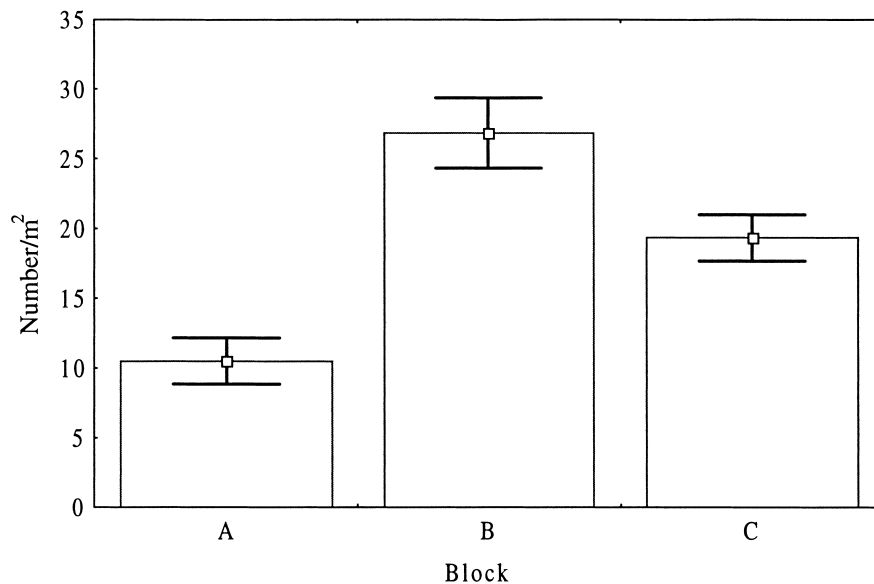


Figure 2. Average numbers ($n = 6$) \pm 1SE of *Terebralia palustris* in the vicinity of block A, B and C.

Table 1. Average numbers (AVG) per 20 cm² (n = 6), standard error (SE) of major macrofauna taxa in the three treatments (Control: 0 gastropods/cage, Ambient: 7 gastropods/cage, 2×Ambient: 15 gastropods/cage) at three different dates.

	Initial Control			After 3 weeks			After 9 weeks											
	Ambient			Ambient			Ambient											
	AVG	SE	2 × Ambient	AVG	SE	2 × Ambient	AVG	SE	2 × Ambient									
Polychaeta total	76	21	110	33	109	23	59	19	49	21	60	21	93	24	52	21	62	9
Capitellidae	39	14	37	14	69	12	53	19	25	9	34	14	39	11	22	8	23	6
Syllidae	6	4	7	4	8	4	5	4	3	3	2	1	10	5	1	1	1	0
Sabellidae	1	0	1	1	6	6	7	5	2	2	2	1	2	1	1	0	0	0
Nematoda	75	21	102	33	93	23	57	19	40	21	43	21	90	24	42	21	44	9
Ostracoda	7	3	9	4	6	2	67	39	15	7	30	11	92	87	12	9	36	30
Others	17	4	15	3	8	2	7	3	10	7	2	1	11	3	16	5	20	9
Total	219	45	281	79	298	47	254	52	144	44	172	49	335	115	146	40	185	51

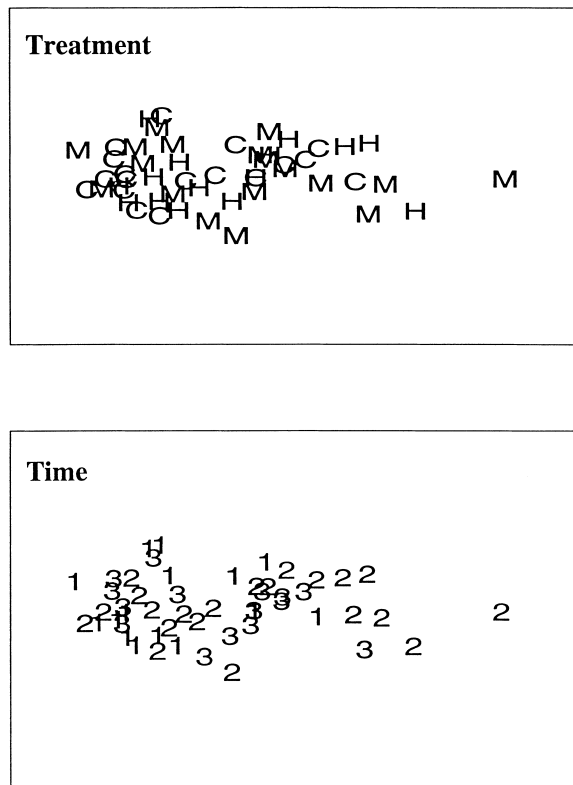


Figure 3. Non-metric multidimensional scaling ordination (MDS) of the macrofauna abundance data, stress = 0.06 (1: sampling at the start, 2: after three weeks, 3: after nine weeks, C: control, M: medium density, H: high density).

($p < 0.05$, Global R:0.2). The replicates of the high density treatment showed highest variability and lowest similarity (Figure 5).

Discussion

The results of current study clearly show that the gastropod *T. palustris* has an effect on the meiofauna community. The total meiofauna density decreased significantly in the treatments with 7 and 15 *T. palustris* compared to the treatment without gastropods. Several exclusion studies in both mangrove and other sediment types have shown effects on the density of meiofauna groups (Dye and Lasiak 1986; Hoffman et al. 1984; Dittman 1993; Bell 1980; Schrijvers et al. 1995). In a high intertidal mangrove forest, Schrijvers et al. (1997) excluded macrofauna from the sediment where *T. palustris* was the dominant species. Like in

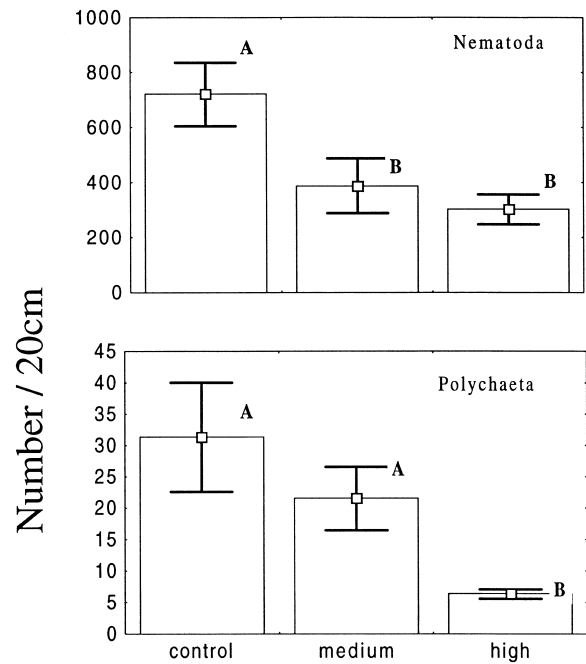


Figure 4. Average number ($n = 6$) \pm 1SE of the two major meiofaunal taxa in the experimental cages. Common letter codes indicate no significant difference (Tukey test).

our study they found also significant effects on the meiobenthos. There are several possible reasons for the negative effects of *T. palustris* on the meiofauna in the current study. Firstly, the physical disturbance from the gastropod movements leave a 5 mm deep track in the mud. This clearly rearranges the habitats of the meiofauna and may stress the individuals so that they may emerge or simply not reproduce as fast as in the cages without *T. palustris*. Another explanation may be a competition for food resources, where microalgae is the dominant food component for gastropods (Houbrick 1991) as well as for the majority of the meiofauna groups (Alongi 1990). Thirdly, it is plausible that breakdown of mangrove detritus by the gastropods enhanced the leaching of tannins, which are known to negatively affect meiofauna in mangrove sediments (Alongi 1987b, 1987c). However, we believe that this was not important here, as mangrove leaves were observed in none of the cages and were rarely found on the mudflat. Finally, the mere presence of cyanobacteria mats in the absence of the gastropods is likely to affect biological, physical and chemical conditions within the sediments and therefore affect the meiobenthos.

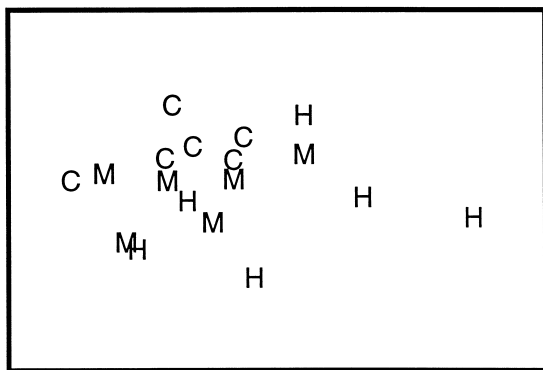


Figure 5. Non-metric multidimensional scaling ordination (MDS) of the meiofaunal abundance data, stress = 0.16 (C: control, M: medium density, H: high density).

The lack of response by the macrofauna component may be due to at least three factors. **Firstly**, the experimental time might have been too short i.e. the generation time of macrofauna is measured in months rather than weeks. However, it is well known that juvenile and adult macrofauna can emergence from the sediment and disperse through the water column (e.g. Lawrie and Raffaelli (1998), Saigusa and Oishi (2000)) and therefore one would have expected at least mobile macrofauna to respond on the time scale we used in this experiment. Also, even if competition between the detrital feeders, such as the capitellids, and the gastropods really occurred in the cages, elevated mortality may take several months before the consequences of food competition, such as suppressed growth, kills off individuals (Dudgeon et al. 1999). **Secondly**, the lack of response can have its explanation in the experimental design itself. The timing of the experiment may not have coincided with the settling of larvae in the area, but data are unavailable on the emergence and settling of soft-bottom macrofauna larvae in the region, let alone the study area. We know, however, that settlement of barnacles and oysters in East Africa is strongly seasonal and linked to Monsoon events (Ruwa and Polk 1994). There are several experimental evidences for habitat choice among macrofauna larvae when settling (e.g. Snelgrove et al. (1999)) so it is also possible that settling larvae avoided the cages even if they could have passed through the relatively large mesh aperture. **Thirdly**, *T. palustris* have simply no effects on the macrofauna. The increased variability of the infauna communities associated with high density of the gastropods can be seen as an effect of a stress put

upon the infauna by *T. palustris*. Warwick and Clarke (1993) showed, for instance, that communities under stress situation are normally more variable than otherwise.

Unfortunately we were unable to measure chlorophyll content in the sediment due to failure in the laboratory equipment. However, Branch and Branch (1980) performed a series of caging experiments on the gastropod *Bembicium auratum* to examine their grazing ability on microalgae *in situ*. They found that chlorophyll *a* concentrations increased in surface sediments in the absence of gastropods, remained constant at normal *Bembicium* densities, and decreased at higher densities of the gastropods. Such exclusion effects have been noted in other cage experiments (Gerdol and Hughes 1994; Schrijvers et al. 1995). Several studies indicate a link between meiofauna and microphytobenthos (Blanchard 1990; Decho and Fleeger 1988; Pickney and Sandulli 1990; Ólafsson et al. 1999). Our field observations suggests that cages without *T. palustris* showed signs of overgrowth by cyanobacteria. This implies that *T. palustris* are either effectively engulfing the cyanobacteria or they just simply rearrange the surface to such a degree that no algae can build up carpets due to the frequent and extensive disturbance. Bianchi and Levinton (1981, 1984) showed that cyanobacteria was efficiently grazed upon by the deposit-feeding mud snails *Hydrobia totteni* and *Ilyanassa obsoleta* indicating that the mudwink has at least the potential to utilize the cyanobacteria. We found that cyanobacteria cover was less in control cages in block C, about 25%, than in the other two blocks. The only obvious difference among the block was that the sediment appeared coarser in block C which may have affected the ability of the cyanobacteria to build up extensive mats. This is also in line with our observations in other parts of the bay where cyanobacteria cover seems to be highest in sediments of muddy nature. It is also possible that the control cages themselves induced the formation of the mats. This we find, however, unlikely because of the frequency of such mats in other areas in the bay where the gastropods are absent or in much lower abundances than in our study area.

Cage experiments have been extensively used, criticised and discussed in the literature (e.g. Reise (1985), Jones et al. (1992), Schrijvers et al. (1997)). The main drawback with cage experiments is the potential risk of artefacts caused by the structure of the cage. The problem is not as serious in enclosure experiments compared to enclosure experiments, as

all effects caused by the cage structure are the same in both the treatments and the controls. Also, in low energy areas, like our study site, cage artefacts are less severe than where currents are strong. Because of this, together with relatively large cages and a randomised block design sensu Hurlbert (1984), we conclude that the treatment effects shown in this study are real and not a result of cage artefacts or chance.

Acknowledgements

We thank J. Francis, the former director of the Institute of Marine Sciences in Zanzibar, for making facilities available and the staff for all their help. This study was financed by a grant from the Institution of Tropical Ecology in Uppsala, under the Sida program of Minor Field Studies and from Sida grant nr: SWE-1997-163. Eric Söderbäck helped to identify the cyanobacteria and Fredrik Pleijel confirmed the polychaete identifications. Two anonymous referees are acknowledged for constructive criticism.

References

- Alongi D.M. and Tenore K.R. 1985. Effect of detritus supply on trophic relationships within experimental benthic food webs. 1. Meiofauna-polychaete (*Capitella capitata* (Type I) Fabricius) interactions. *Journal of Experimental Marine Biology and Ecology* 88: 153–166.
- Alongi D.M. 1987a. Intertidal zonation and seasonality of meiobenthos in tropical mangrove estuaries. *Marine Biology* 95: 447–458.
- Alongi D.M. 1987b. The influence of mangrove-derived tannins on intertidal meiobenthos in tropical estuaries. *Oecologia* 71: 537–540.
- Alongi D.M. 1987c. Inter-estuary variation and intertidal zonation of free-living nematode communities in tropical mangrove systems. *Marine Ecology Progress Series* 40: 103–114.
- Alongi D.M. 1990. The ecology of tropical soft-bottom benthic ecosystems. *Oceanographic and Marine Biology Annual Review* 28: 381–496.
- Bell S.S. 1980. Meiofauna-macrofauna interactions in a high salt marsh habitat. *Ecological Monographs* 50: 487–505.
- Bianchi T.S. and Levinton J.S. 1981. Nutrition and Food Limitation of Deposit-Feeders. II. Differential Effects of *Hydrobia totteni* and *Ilyanassa obsoleta* on the Microbial Community. *Journal of Marine Research* 39: 547–556.
- Bianchi T.S. and Levinton J.S. 1984. The importance of microalgae, bacteria and particulate organic matter in the somatic growth of *Hydrobia totteni*. *Journal of Marine Research* 42: 431–443.
- Blanchard G.F. 1990. Overlapping microscale dispersion patterns of meiofauna and microphytobenthos. *Marine Ecology Progress Series* 68: 101–111.
- Bonsdorff E. and Pearson T.H. 1997. The relative impact of physical disturbance and predation by *Crangon crangon* on population density in *Capitella capitata*: An experimental study. *Ophelia* 46: 1–10.
- Branch G.M. and Branch M.L. 1980. Competition in *Bembicium auratum* (Gastropoda) and its effect on microalgal standing stock in mangrove muds. *Oecologia* 46: 106–114.
- Creed E.L. and Coull B.C. 1984. Sand dollar, *Mellita quinquesperforata* (Leske), and sea urchin, *Renilla reniformis* (Cuvier) effects on meiofaunal abundance. *Journal of Experimental Marine Biology and Ecology* 84: 225–234.
- Dahdouh-Guebas F., Verneir M., Tack J.F., Van Speybroeck D. and Koedam N. 1998. Propagule predators in Kenyan mangroves and their possible effect on regeneration. *Marine and Freshwater Research* 49: 345–350.
- Decho A.W. and Fleeger J.W. 1988. Ontogenetic feeding shifts in the meiobenthic harpacticoid copepod *Nitocra lacustris*. *Marine Biology* 97: 191–197.
- Dittman S. 1993. Impact of foraging soldiercrabs (Decapoda: *Mictyridae*) on meiofauna in a tropical tidal flat. *Revista de Biología Tropical* 41: 627–637.
- Dittman S. 1996. Effects of macrobenthic burrows on infaunal communities in tropical tidal flats. *Marine Ecology Progress Series* 134: 119–130.
- Dudgeon S.R., Steneck R.S., Davison I.R. and Vadas R. 1999. Coexistence of similar species in a space-limited intertidal zone. *Ecological Monographs* 69: 331–352.
- Dye A.H. and Lasiak T.A. 1986. Microbenthos meiobenthos and fiddler crabs: trophic interaction in a tropical mangrove sediment. *Marine Ecology Progress Series* 32: 259–264.
- Fratini S., Cannicci S. and Vannini M. 2000. Competition and interaction between *Neosarmatium smithi* (Crustacea: Grapsidae) and *Terebralia palustris* (Mollusca: Gastropoda) in a Kenyan mangrove. *Marine Biology* 137: 309–316.
- Gerdol V. and Hughes R.G. 1994. Effect of *Corophium volutator* on the abundance of benthic diatoms, bacteria and sediment stability in two estuaries in south-eastern England. *Marine Ecology Progress Series* 113: 109–115.
- Hoffman J.A., Katz J. and Bertness M.D. 1984. Fiddler crab deposit-feeding and meiofaunal abundance in salt marsh habitats. *Journal of Experimental Marine Biology and Ecology* 82: 161–174.
- Houbrick R.S. 1991. Systematic review and functional morphology of the mangrove snails *Terebralia* and *Telescopium* (Potamididae, Prosobranchia). *Malacologia* 33: 298–338.
- Hurlbert S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187–211.
- Jones G.P., Ferrell D.J. and Sale P.F. 1992. Fish feeding and dynamics of soft-sediment mollusc populations in a coral reef lagoon. *Marine Ecology Progress Series* 80: 175–190.
- Lawrie S.M. and Raffaelli D.G. 1998. In situ swimming behaviour of the amphipod *Corophium volutator* (Pallas). *Journal of Experimental Marine Biology and Ecology* 224: 237–251.
- Lee S.Y. 1998. Ecological role of grapsid crabs in mangrove ecosystems: a review. *Marine Freshwater Research* 49: 335–343.
- Levinton J. 1972. Stability and trophic structure in deposit-feeding and suspension-feeding communities. *The American Naturalist* 106: 472–486.
- Loch I. 1987. A tremendous *Terebralia*. *Australian Shell News*, No 58.4.
- Micheli F., Gherardi F. and Vannini M. 1991. Feeding and burrowing ecology of two East African mangrove crabs. *Marine Biology* 111: 247–254.

- Moore H.B. 1972. Aspects of stress in the tropical marine environment. *Advanced Marine Biology* 10: 217–269.
- Ngoile M.A.K. and Shunula I.P. 1992. Status and exploitation of the mangrove and the associated fishery resources in Zanzibar. *Hydrobiologia* 247: 229–234.
- Nishihira M. 1983. Grazing of the mangrove litters by *Terebralia palustris* (Gastropoda, *Potamididae*) in the Okinawan mangal, preliminarily report. *Galaxea* 2: 45–58.
- Ólafsson E. and Elmgren R. 1991. The effects of biological disturbance by benthic amphipods *Monoporeia affinis* on meiobenthic community structure: a laboratory approach. *Marine Ecology Progress Series* 7: 179–184.
- Ólafsson E. and Moore C.G. 1992. Effects of macroepifauna on developing nematode and harpacticoid assemblages in a muddy habitat. *Marine Ecology Progress Series* 84: 161–171.
- Ólafsson E., Elmgren R. and Papakosta O. 1993. Effects of the deposit-feeding benthic bivalve *Macoma balthica* on meiobenthos. *Oecologia* 93: 457–462.
- Ólafsson E. and Ndaró S.G.M. 1997. The impact of the mangrove crabs *Uca annulipes* and *Dotilla fenestrata* on meiobenthos. *Marine Ecology Progress Series* 158: 225–231.
- Ólafsson E., Modig H. and van de Bund W.J. 1999. Species specific uptake of radio-labelled phytodetritus by benthic meiofauna from the Baltic Sea. *Marine Ecology Progress Series* 177: 63–72.
- Ólafsson E., Carlström S. and Ndaró S.G.M. 2000. Meiobenthos of hypersaline tropical mangrove sediment in relation to spring tide inundation. *Hydrobiologia* 426: 57–64.
- Ólafsson E.B., Peterson C.H. and Ambrose W.G. Jr 1994. Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: The relative significance of pre- and post-settlement processes. *Oceanography and Marine Biology: An Annual Review* 32: 65–109.
- Palmer M.A. 1988. Epibenthic predators and marine meiofauna: separating predation, disturbance and hydrodynamic effects. *Ecology* 69: 1251–1259.
- Pickney J. and Sandulli R. 1990. Spatial autocorrelation analysis of meiofaunal and microalgal populations on an intertidal sandflat-scale linkage between consumers and resources. *Estuarine Coastal and Shelf Science* 30: 341–353.
- Platt H. and Warwick R.M. 1983. Free-living marine nematodes. Part 1. British Enoplids. In: Kermack D.M. and Barnes R.K.S. (eds), *Synopsis of the British fauna (New Series)*. Cambridge University Press, Cambridge, pp. 1–307.
- Plazait J.C. 1977. Les certhides tropicaux et leur polymorphisme lie a l'ecologie littorale des mangroves. *Malacologica* 16: 35–44.
- Reidenauer J.A. and Thistle D. 1981. Response of a soft-bottom harpacticoid community to stingray (*Dasyatis sabina*) disturbance. *Marine Biology* 65: 261–267.
- Reise K. and Ax P. 1979. A meiofaunal 'thiobios' limited to the anaerobic sulphide system of marine sand does not exist. *Marine Biology* 54: 225–237.
- Reise K. 1985. *Tidal flat ecology*. Springer, Berlin.
- Ruwa R.K. and Polk P. 1994. Patterns of spat settlement recorded for tropical oyster *Crassostrea cucullata* (Born 1778) and the barnacle, *Balanus amphitrite* (Darwin 1854) in a mangrove creek. *Tropical Zoology* 7: 121–131.
- Saigusa M. and Oishi K. 2000. Emergence rhythms of subtidal small invertebrates in the subtropical sea: nocturnal patterns and variety in the synchrony with tidal and lunar cycles. *Zoological Science* 17: 241–251.
- Schrijvers J., Okondo J., Steyaert M. and Vincx M. 1995. Influence of epibenthos on meiobenthos of the *Ceriops tagal* mangrove sediment at Gazi Bay, Kenya. *Marine Ecology Progress Series* 128: 247–259.
- Schrijvers J., Schallier R., Silence J., Okondo J.P. and Vincx M. 1997. Interactions between epibenthos and meiobenthos in a high intertidal *Avicennia marina* mangrove forest. *Mangroves and Salt Marshes* 1: 137–154.
- Sherman K.M., Reidenauer J.A., Thistle D. and Meeter D. 1983. Role of natural disturbance in an assemblage of marine free-living nematodes. *Marine Ecology Progress Series* 11: 23–30.
- Shokita S., Limsakul S. and Karnjanagesorn C. 1984. Distribution and abundance of the giant potamid snail *Terebralia palustris* (Gastropoda) in the Thai mangal. In: *Mangrove estuarine ecology in Thailand*. Thai-Japanese co-operative research project on mangrove productivity and development. 1983–1984, 39–53.
- Slim F.J., Hemminga M.A., Ochieng C., Jannink N.T., Cocheret de la Moriniere E. and Van der Velde G. 1997. Leaf litter removal by the snail *Terebralia palustris* (Linnaeus) and sesarmid crabs in an East African mangrove forest (Gazi Bay, Kenya). *Journal of Experimental Marine Biology and Ecology* 215: 35–48.
- Snelgrove P.V.R., Grassle J.P., Grassle J.F., Petrecca R.F. and Ma H. 1999. In situ habitat selection by settling larvae of marine soft-sediment invertebrates. *Limnology and Oceanography* 44: 1341–1347.
- Thistle D. 1980. The response of a harpacticoid copepod community to a small scale natural disturbance. *Journal of Marine Research* 38: 381–395.
- Warwick R.M. and Clarke K.R. 1993. Increased variability as a symptom of stress in marine communities. *Journal of Experimental Marine Biology and Ecology* 172: 215–226.
- Warwick R.M., Clarke K.R. and Gee J.M. 1990. The effect of disturbance by soldier crabs *Mictyris platycheles* H. Milne Edwards on meiobenthic community structure. *Journal of Experimental Marine Biology and Ecology* 135: 19–33.
- Warwick R.M., Gee J.M., Berge J.A. and Ambrose W. 1986. Effects of the feeding activity of the polychaete *Streblosoma bairdi* (Malmgren) on meiofaunal abundance and community structure. *Sarsia* 71: 11–16.
- Wilson W.H. 1991. Competition and predation in marine soft sediment communities. *Annual Review of Ecology and Systematics* 21: 221–241.

