

# Influence of epibenthos on meiobenthos of the *Ceriops tagal* mangrove sediment at Gazi Bay, Kenya

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**ABSTRACT:** A cage experiment was used to exclude the epibenthos from the *Ceriops tagal* mangrove sediment at Gazi Bay, Kenya. This made it possible to study interactions with the meiobenthos (in terms of predation, food competition and food enhancement). The density of the meiobenthic taxa and nematode genera and a broad range of abiotic variables were followed in a depth profile over 1 yr of caging. There was a significant exclusion effect in the upper sediment layer for total meiofauna, nematodes and oligochaetes during the first 2 mo and for copepods during the last 6 mo of caging. The density of the most common predatory and microalgae-feeding nematodes in particular tended to increase in the surface layers as well as the percentage of muddy detritus and pigment concentration. Food competition with the epibenthos seems to be most important in structuring the nematode community. This is suggested by the parallel exclusion effect on muddy detritus, pigments and nematode composition and the lack of evidence for upward nematode migration in the cage during the experiment. The same can be concluded for the oligochaetes, whereas copepod densities are believed to be controlled more by predation. These findings indicate that the meiofauna community of the *C. tagal* mangrove sediment (consisting of about 95% nematodes and oligochaetes) is part of a rather isolated, detrital food web with only minor predator-prey interactions with the epibenthos.

**KEY WORDS:** Nematodes · Meiobenthos · Epibenthos · Exclusion experiment · Mangroves · Kenya

## INTRODUCTION

Mangroves in Kenya are becoming increasingly subject to anthropogenic impacts, especially uncontrolled dumping of domestic and industrial wastes (Ruwa & Polk 1986). The *Ceriops tagal* mangroves are one of the most extensive and economically important vegetation zones along the coast of Kenya (Kokwaro 1986). A rational management of Kenyan mangroves can only be achieved by analysing structure, function and energy fluxes of the mangrove system and its relation with other ecosystems.

Ecological studies on the meiobenthos in East African mangrove systems are few (Dye & Furstenberg 1978, Dye 1983a, b, Dye & Lasiak 1986, Vanhove et al.

1992, Vanhove 1993, Schrijvers in press). In the present study, the interactions between the epibenthos (consisting mainly of crabs, gastropods, hermit crabs and — to a lesser extent — of shrimps and demersal fishes) and the meiofauna were examined. This could provide some insight into the role of meiobenthos in *Ceriops tagal* mangrove soils.

The role of meiobenthos (generally consisting of about 90% nematodes) in the trophic dynamics of an overall benthic ecosystem has been hypothesized to be 2-fold. (1) The meiobenthos may play an important role in the detrital food web as a self-contained energy sink regulated internally by predation. If this is the case, the meiobenthos depends on, or competes with, the other benthic subsystems (such as the epibenthos) for detrital food (Reise 1979, Heip 1980, Connell 1983, Gee et al. 1985, Olafsson & Moore 1992, Alkemade et al. 1993, Giere 1993, Walters & Moriarty 1993). (2) On the other

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hand, several trophic links with the epibenthos have been recognized, mainly in temperate areas. Predation on meiofauna is either selective or non-selective (Bell & Coull 1978, Reise 1979, Tenore & Rice 1980, Gee et al. 1985, Marinelli & Coull 1987, Gee 1989, Hall et al. 1990, McLachlan & Romer 1990, Castel 1992, Olafsson & Moore 1992, Giere 1993).

For mangrove sediments as well, the potential influence of the mangrove epibenthos in structuring the meiofauna is broad. One can expect that internally regulated meiofaunal communities are mainly affected by competition with, and food enhancement by, the epibenthos (Bell 1980, Sultan Ali et al. 1983, Dye & Lasiak 1986, Alongi 1989, Tietjen & Alongi 1990, Alongi & Christoffersen 1992), whereas meiofauna that is consumed by this epibenthos would be more predator controlled (Bell 1980, Hoffman et al. 1984, Dittmann 1993). Moreover, the physical disturbance and modification of the mangrove sediment by the epibenthos (mainly through tube digging and feeding activities) may also be of importance (Bright 1977, Bell & Coull 1978, Alongi & Tietjen 1980, Bell 1980, Sherman & Coull 1980, Hoffman et al. 1984, Dye & Lasiak 1986, Marinelli & Coull 1987, Alongi 1989, DePatra & Levin 1989).

## MATERIAL AND METHODS

**Study area.** The *Ceriops tagal* mangrove vegetation zone of Gazi Bay, Kenya, is situated 50 km south of Mombasa (4° 25' S and 39° 50' E). It has an area of about 0.5 km<sup>2</sup>. The study site was situated in the non-exploited and patchy *C. tagal* vegetation that borders the west bank of the western creek of the bay. This site is about 2.8 m above mean low water spring level (intermediate in the tidal range) and is inundated during about 65% of the high tides (F. J. Slim pers. comm.). For a more detailed description of the studied area and station see Schrijvers (in press) and Schrijvers et al. (1995) (Stns C2 and G1, respectively).

**Experimental design.** All epibenthic and hyperbenthic animals (hereafter called 'epibenthos') (>2 mm) were excluded from the cages, and the influence on the meiobenthic structure was followed through time. In addition to the full cages (C), 2 control treatments were chosen: true blanks (B) and partial cages (P). 'B' controlled for temporal natural variation while 'P' corrected for possible procedural impacts. Three units were assigned to each treatment. These 9 experimental units were arranged in a randomized block design *sensu* Hurlbert (1984) to obtain an optimal randomization/interspersal ratio, to reduce the probability of chance segregation of treatments and to yield a more sensitive Analysis Of Variance (ANOVA) de-

sign. After rerandomization this resulted in:

Bay		
P	B	P
C	C	B
B	P	C
Land		

Rerandomization consisted of repeated randomization until no possible gradient could be detected in the design. The units were 1 to 2 m apart and had a surface of 1 m<sup>2</sup> each.

Each blank unit was framed with a rope. The partial cages were identical to the regular cages (Fig. 1), but one side of the upper part was not covered with netting so as to avoid exclusion of epibenthos. The epibenthos in the cages was removed manually within the first 5 h of the experiment.

Five samples were taken over time: period 1, before caging (6 August 1992); period 2, after 22 d of caging (28 August 1992); period 3, after 52 d of caging (27 September 1992); period 4, after 139 d of caging (23 December 1992); period 5, after 350 d of caging (30 July 1993).

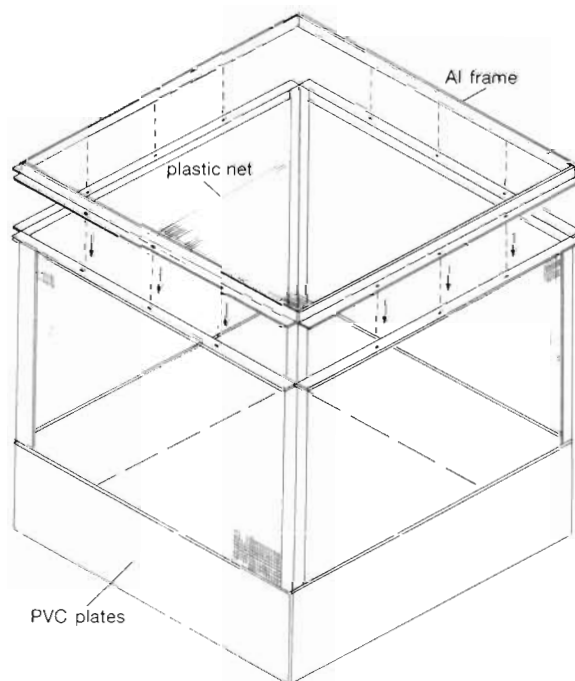


Fig. 1. Model of the cage construction used in the exclusion experiment. It consisted of a lower and upper part. The lower part was composed of four 0.3 m high perforated PVC plates which were completely buried in the sediment. The upper part was composed of an aluminium frame (0.7 m high) that was covered by a plastic net with 2 mm mesh size. The top was detachable to facilitate sampling. (Drawing by Bruyneel 1995)

On each occasion, bottom samples were taken at the same coordinates (randomly chosen) of the surface for each unit and within 10 cm from the edge. Core holes were immediately filled with silicon plugs or sediment bags to avoid influencing the surrounding sediment that was to be sampled later in the experiment (Marinelli & Coull 1987).

The use of partial cages controlled for possible artefacts (fouling, shading, sedimentation, moisture, litter fall and presence of epibenthos) (Hairston 1990).

**Abiotic factors.** One 6 cm diameter core sample was taken in each unit per period. The bottom water in the sample holes was analyzed for bulk values of pH, salinity and dissolved oxygen ( $\text{DO}_2$ ) with a combined, calibrated electrode with consolidated cover, a refractometer and a Clark type 737 electrode, respectively. Other measurements were performed on vertical slices of the core (0–2, 2–4, 4–10, 10–rest cm). Temperature and redox potential were measured in the 3 uppermost slices using a bar thermometer sensitive to  $0.01^\circ\text{C}$  and a combined Hamilton electrode, respectively. For all slices, the % of particulate organic matter (POM) and some granulometric variables were determined. After drying at  $100^\circ\text{C}$ , the POM was quantified via the loss in weight following a  $600^\circ\text{C}$  combustion for 4 h. A Coulter® LS Particle Size Analyser was used to characterize the granulometry of the sediment. This analysis was done both before and after a  $600^\circ\text{C}$  combustion. Before analysis, the gravel fraction ( $>850\ \mu\text{m}$ ) was mechanically separated by sieves.

A 1 cm diameter core was used to estimate the % of organic carbon in the slices 0–2, 2–4 and 4–10 cm with a Carlo Erba NA 1500 series 2 C-analyser. The 2 uppermost slices were analysed for chlorophyll *a* and fucoxanthin pigment concentration (using a Gilson high-performance liquid chromatography (HPLC) chain according to a slightly modified method of Mantoura & Llewellyn 1983).

**Biotic factors.** Samples were obtained by taking 1 handcore (3.6 cm diameter) per unit to a depth of 20 cm and slicing it along a vertical gradient of 0–2, 2–4, 4–10 and 10–rest cm. Each slice was preserved in a hot ( $60^\circ\text{C}$ ) 4% formalin solution. Extraction of meiofauna from the sediment (sieve meshes of  $38\ \mu\text{m}$  and 1 mm) was done by centrifugation ( $2734 \times g$  for  $3 \times 3\ \text{min}$ ) with  $\text{MgSO}_4$  with a density of 1.28, a method that allowed for a fast and easy separation of the target fauna from mangrove roots and detritus. The nematodes and other meiofauna taxa were counted. Densities are expressed as numbers of individuals per  $10\ \text{cm}^2$ .

The nematodes of the 3 cage treatment units for periods 1 and 3 were picked out (mean of  $3 \times 120$  individuals) and identified to genus level. They were classified in trophic groups according to the commonly used feeding types 1A (selective deposit feeders), 2A (epi-

stratum feeders), 1B (non-selective deposit feeders) and 2B (omnivores/predators) (Wieser 1953).

**Statistical analyses.** Non-parametric Spearman rank correlation coefficients were calculated ( $p < 0.05$ ) to determine a relationship between biotic and abiotic variables along the depth gradient and along the horizontal gradient within the upper layer.

An ANOVA was used to test for significant differences of meiofauna densities in different treatments (B, P and C), periods (1 to 5) and slices (the 4 mentioned above). A  $3 \times 4$  (between groups)  $\times 5$  (within subjects) design was constructed, with treatments and slices as groups and periods as subjects repeated over time. Detailed comparison between groups was done by a contrast analysis. Exclusion effects (E) were defined as significant differences between cage and blank-partial cage, while procedural effects (Pr) yielded significant differences between cage-partial cage and blank. The density data were root-root transformed and the % values of abiotic variables were transformed angularly to meet the ANOVA assumptions (normality, homogeneity of variances and non-correlation between means and variances).

## RESULTS

### Spatial distribution patterns

#### Depth profile

The ANOVA for the total slice effect indicated a significant ( $p < 0.05$ ) depth gradient in the sediment for both abiotic and biotic factors. Fig. 2 shows the existence of a prominent gradient from sandy, well-oxygenated, warm and pigment-rich surface layers to muddy, less oxygenated, colder and pigment-poor deeper layers.

Most meiofauna taxa (e.g. nematodes, oligochaetes and copepods) had significantly higher densities in the upper layers. In contrast, the halacaroids did not follow this pattern: they were significantly more abundant in slice 4–10 cm (Fig. 2). Other meiofauna taxa did not show a prominent depth pattern.

#### Horizontal pattern in the upper layer

To exclude the overriding vertical pattern, the Spearman rank correlation coefficients were calculated for all 0–2 cm layers (Table 1). A clear division could be made between muddy and sandy patches. The former were positively correlated with detritus and pigments, while the latter were characterized by higher temperatures. Copepods, kinorhynchs, oligochaetes and polychaetes



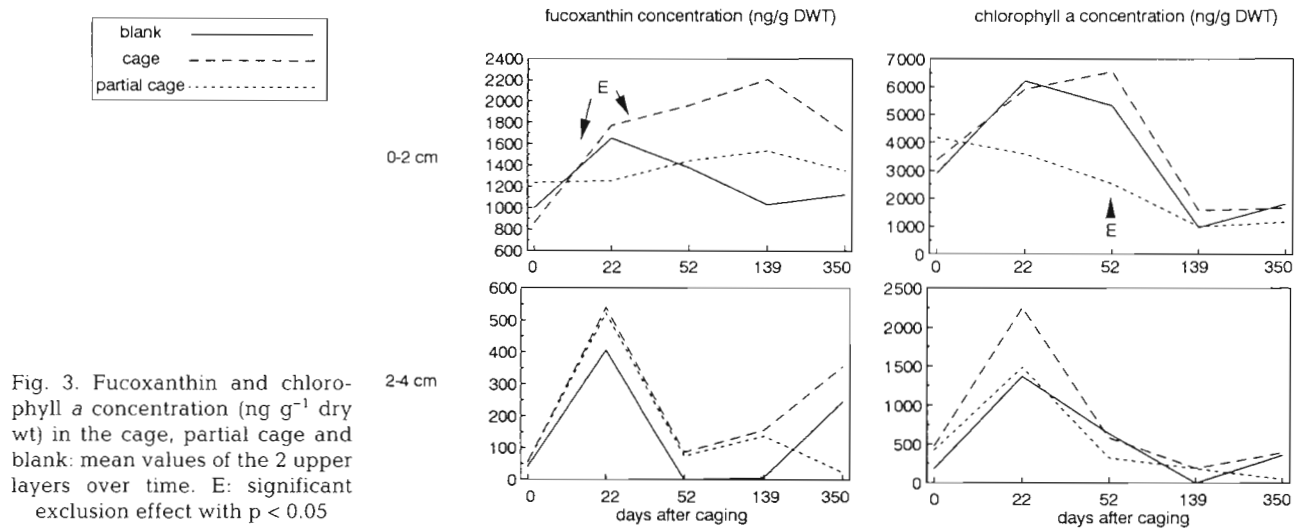


Fig. 3. Fucoxanthin and chlorophyll *a* concentration (ng g<sup>-1</sup> dry wt) in the cage, partial cage and blank: mean values of the 2 upper layers over time. E: significant exclusion effect with  $p < 0.05$

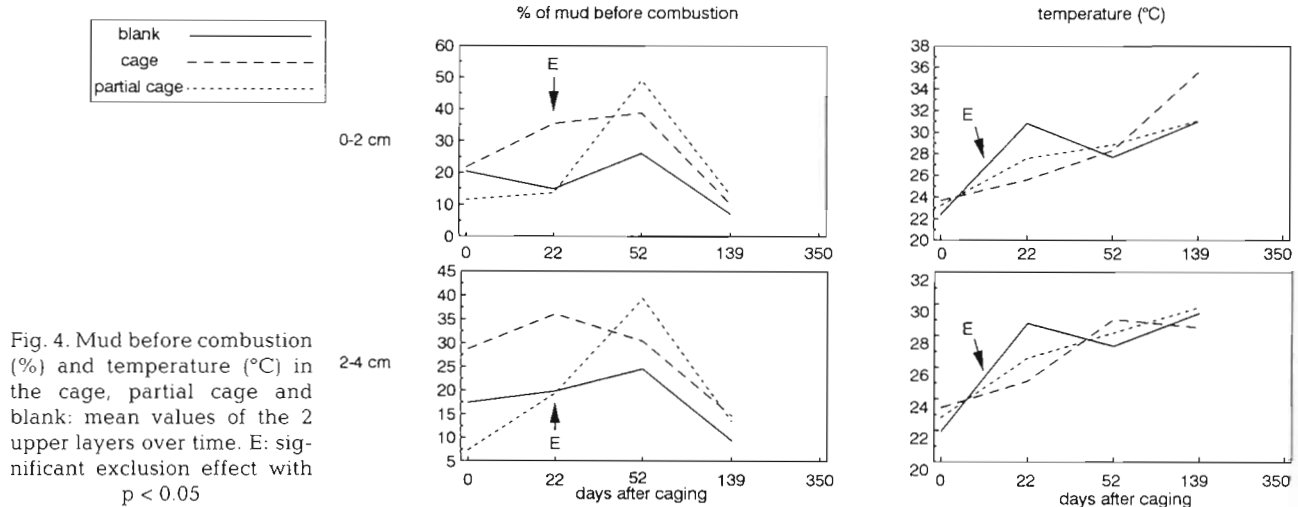


Fig. 4. Mud before combustion (%) and temperature (°C) in the cage, partial cage and blank: mean values of the 2 upper layers over time. E: significant exclusion effect with  $p < 0.05$

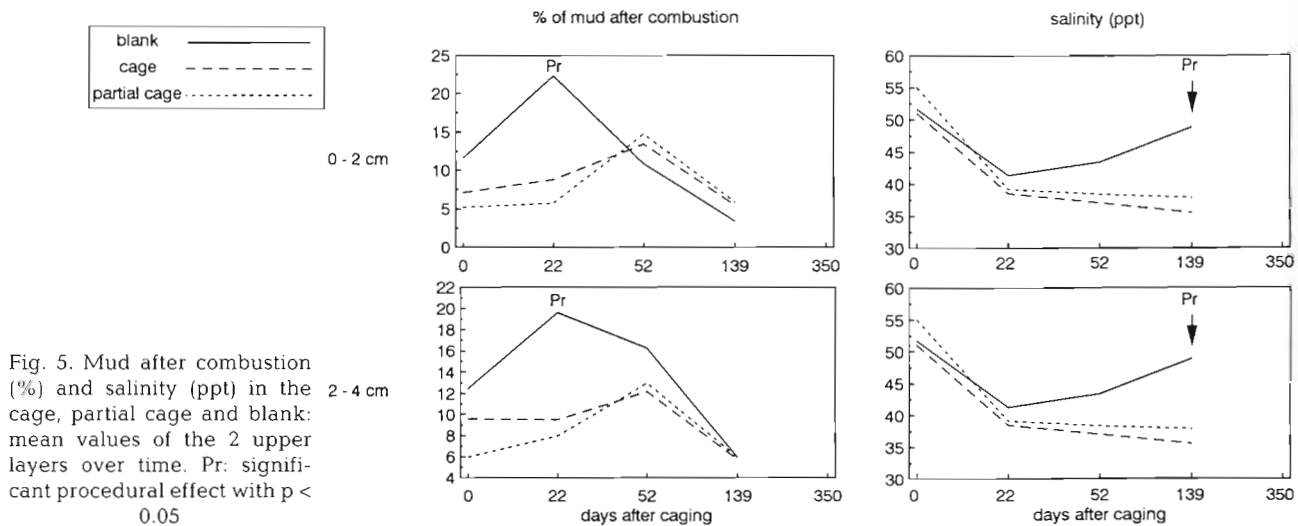


Fig. 5. Mud after combustion (%) and salinity (ppt) in the cage, partial cage and blank: mean values of the 2 upper layers over time. Pr: significant procedural effect with  $p < 0.05$

Table 2. Mean and standard deviation values of some abiotic factors of the 2 upper layers in the 3 treatments (B, C and P) over 5 periods

	Treatment	Period 1	Period 2	Period 3	Period 4	Period 5
<b>Slice 0–2 cm</b>						
Chlorophyll <i>a</i> (ng g <sup>-1</sup> dry wt)	B	2910 ± 687	6199 ± 96	5308 ± 1451	970 ± 991	1795 ± 1365
	C	3377 ± 429	5903 ± 383	6534 ± 897	1556 ± 495	1642 ± 573
	P	4167 ± 1342	3584 ± 1575	2526 ± 1864	982 ± 570	1147 ± 446
Fucoxanthin (ng g <sup>-1</sup> dry wt)	B	1002 ± 357	1649 ± 182	1377 ± 506	1030 ± 390	1125 ± 517
	C	861 ± 92	1771 ± 115	1960 ± 270	2205 ± 291	1703 ± 754
	P	1238 ± 413	1254 ± 341	1441 ± 540	1533 ± 169	1349 ± 224
% of mud before combustion	B	20.49 ± 13.88	14.79 ± 8.12	26.06 ± 3.1	9.01 ± 0.86	
	C	21.66 ± 7.54	35.32 ± 10.52	38.68 ± 7.18	10.20 ± 3.71	
	P	11.51 ± 11.56	13.61 ± 3.97	49.05 ± 12.89	12.99 ± 2.45	
Temperature (°C)	B	22.37 ± 1.87	30.80 ± 2.57	27.67 ± 0.74	30.97 ± 2.04	
	C	23.67 ± 0.66	25.57 ± 1.54	28.33 ± 0.90	29.03 ± 0.05	
	P	23.2 ± 1.10	27.57 ± 3.24	28.83 ± 2.38	31.07 ± 2.48	
% of mud after combustion	B	11.63 ± 0.02	22.26 ± 3.48	10.84 ± 5.76	3.39 ± 0.35	
	C	7.11 ± 3.33	8.76 ± 3.94	13.43 ± 3.09	5.40 ± 1.34	
	P	5.18 ± 2.81	5.73 ± 1.13	14.73 ± 2.10	5.85 ± 1.18	
Salinity (ppt)	B	51 ± 3	41 ± 2	43 ± 3	49 ± 3	
	C	51 ± 5	39 ± 0	37 ± 1	36 ± 0	
	P	55 ± 5	39 ± 3	38 ± 3	38 ± 2	
<b>Slice 2–4 cm</b>						
Chlorophyll <i>a</i> (ng g <sup>-1</sup> dry wt)	B	1826 ± 157	1369 ± 0	633 ± 451	1 ± 2	353 ± 499
	C	478 ± 341	2249 ± 3051	576 ± 497	189 ± 225	388 ± 176
	P	423 ± 368	1485 ± 1742	325 ± 460	186 ± 264	49 ± 69
Fucoxanthin (ng g <sup>-1</sup> dry wt)	B	41 ± 57	405 ± 0	0 ± 0	6 ± 9	246 ± 313
	C	56 ± 79	539 ± 636	87 ± 123	156 ± 117	137 ± 193
	P	54 ± 76	522 ± 738	75 ± 106	137 ± 193	24 ± 35
% of mud before combustion	B	17.47 ± 5.03	19.79 ± 5.83	24.49 ± 1.63	9.43 ± 1.91	
	C	28.67 ± 9.13	36.09 ± 8.62	30.31 ± 6.55	14.67 ± 8.71	
	P	7.3 ± 3.68	19.37 ± 3.3	39.28 ± 11.68	13.47 ± 4.62	
Temperature (°C)	B	21.93 ± 1.75	28.77 ± 2.41	27.33 ± 0.62	29.43 ± 0.62	
	C	23.43 ± 0.61	25.13 ± 1.07	27.73 ± 0.54	28.50 ± 0.16	
	P	22.83 ± 1.38	26.57 ± 2.49	28.17 ± 2.00	29.80 ± 1.98	
% of mud after combustion	B	12.40 ± 3.03	19.60 ± 4.18	16.25 ± 2.89	5.94 ± 1.46	
	C	9.61 ± 3.58	9.50 ± 1.21	12.17 ± 2.49	5.75 ± 1.18	
	P	5.96 ± 2.51	7.97 ± 0.89	12.95 ± 1.25	5.93 ± 0.92	
Salinity (ppt)	B	52 ± 3	41 ± 2	43 ± 3	49 ± 3	
	C	51 ± 5	39 ± 0	37 ± 1	36 ± 0	
	P	55 ± 5	39 ± 3	38 ± 3	38 ± 2	

A significant exclusion effect ( $p < 0.05$ ) on % of mud before combustion was notable in slices 0–2 cm and 2–4 cm (Fig. 4, Table 2). The increase in temperature during the first 22 caging days for slices 0–2 cm and 2–4 cm in the cages appeared as an exclusion effect (Fig. 4, Table 2).

**Procedural effect.** Two variables (Fig. 5, Table 2) underwent a clear cage construction effect.

In contrast with the muddy fraction before combustion, the % of mud after combustion was influenced by the experimental procedure in the upper slices. The evolution of the % of muddy detritus is clearly visible in Fig. 6.

Four months later, the blank salinity was significantly higher than the salinity in both other treatments.

**No effect.** Clear effects on % of POM, % of C, pH, DO<sub>2</sub> and other granulometric factors were not detected.

#### Biotic factors

**Exclusion effect.** Exclusion effects were observed for nematode and total meiofauna density in slices 0–2 and 2–4 cm (Fig. 7, Table 3). It showed an increase of 1.5 to 2× in the cages as compared to control treatments.

The nematode increase in the surface layer of the cage in period 3 was not accompanied by a clear



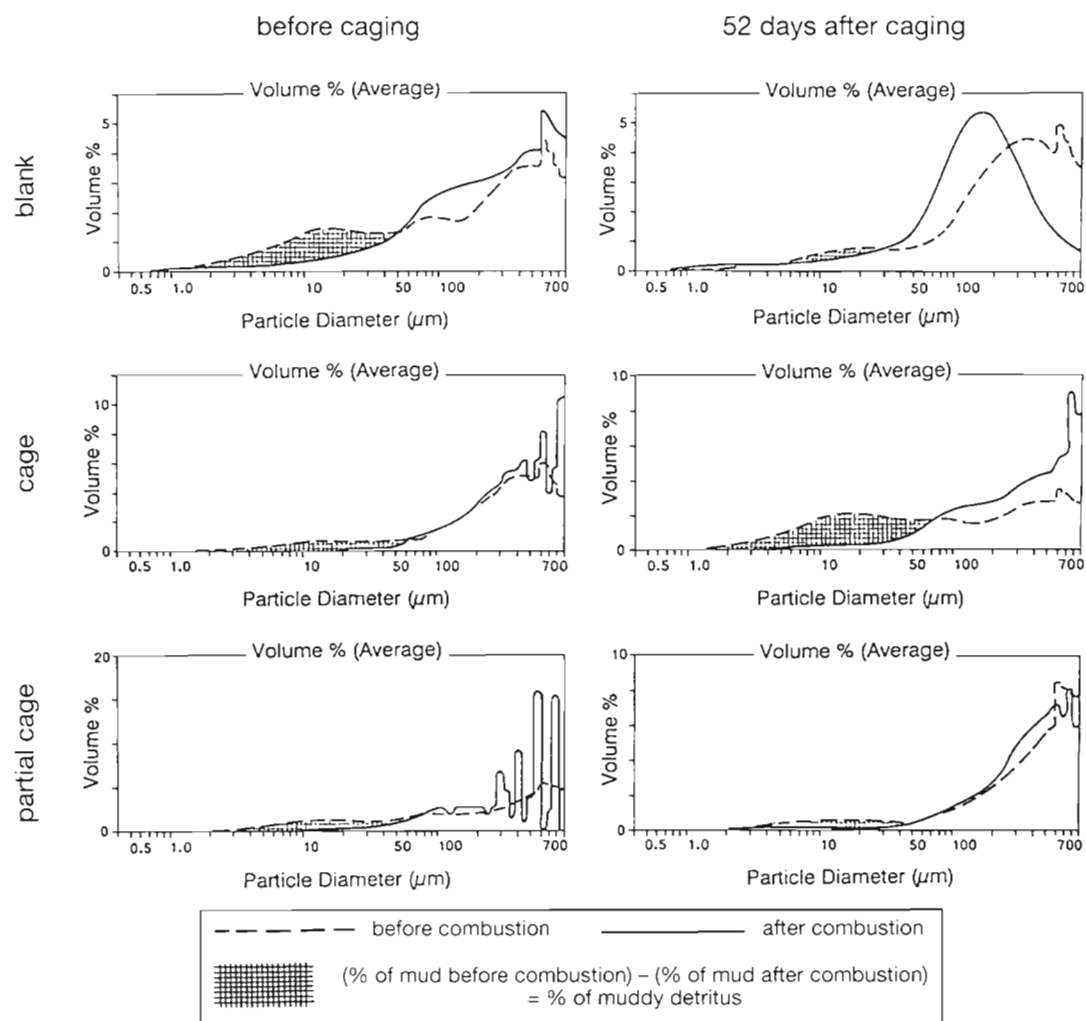


Fig. 6. Grain size composition before and after combustion (volume %) of the surface layer in cage, partial cage and blank sites over 2 periods (with indication of the % of muddy detritus)

Table 3. Mean and standard deviation values of total meiobenthos and nematode density (ind. 10 cm<sup>-2</sup>) of the 2 upper layers in the 3 treatments (B, C and P) over 5 periods

	Treatment	Period 1	Period 2	Period 3	Period 4	Period 5
<b>Slice 0–2 cm</b>						
Total meiobenthos	B	1298 ± 142	1018 ± 531	624 ± 30	700 ± 206	1476 ± 305
	C	1542 ± 142	1865 ± 278	2120 ± 156	1255 ± 584	2676 ± 415
	P	1409 ± 382	1542 ± 153	1024 ± 206	700 ± 206	2089 ± 393
Nematoda	B	713 ± 39	873 ± 446	562 ± 11	627 ± 228	1451 ± 319
	C	1182 ± 204	1663 ± 219	1972 ± 154	1235 ± 497	2620 ± 351
	P	952 ± 151	1354 ± 153	894 ± 174	1084 ± 324	2027 ± 356
<b>Slice 2–4 cm</b>						
Total meiobenthos	B	1195 ± 312	527 ± 359	241 ± 64	420 ± 229	548 ± 120
	C	650 ± 249	582 ± 135	608 ± 338	802 ± 298	849 ± 313
	P	1010 ± 295	439 ± 212	377 ± 212	759 ± 357	965 ± 318
Nematoda	B	481 ± 178	458 ± 309	221 ± 63	403 ± 224	544 ± 117
	C	564 ± 231	554 ± 44	596 ± 343	799 ± 296	845 ± 313
	P	652 ± 205	410 ± 200	359 ± 211	757 ± 356	963 ± 318

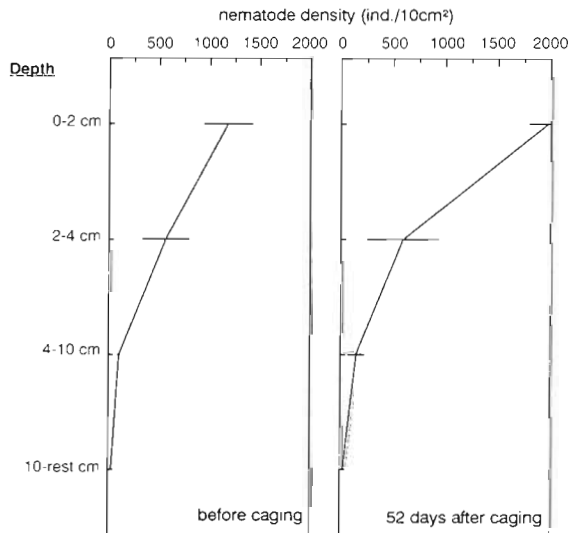
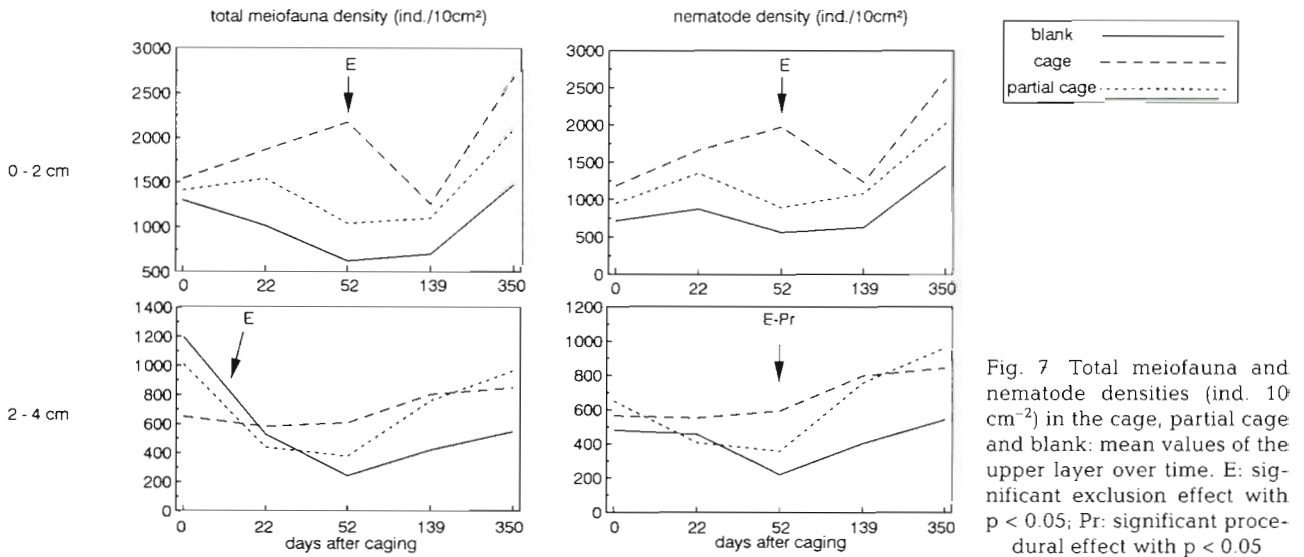


Fig. 8. Depth profile of the mean nematode density in the cage over 2 periods

Table 4. Mean density values (ind. 10 cm<sup>-2</sup>) of the most common nematode genera of the surface and deepest layer in the cage over 2 periods

	Feeding type	Slice 0-2 cm		Slice 10-rest cm	
		Per. 1	Per. 3	Per. 1	Per. 3
<i>Chromaspirina</i>	2B	43.4	294.2	98.7	95.1
<i>Microaimus</i>	2A	43.5	185.5	246.7	268.8
<i>Daptonema</i>	1B	154.1	64.0	33.0	116.0
<i>Ptycholaimellus</i>	2A/2B	158.1	179.1	32.9	—
<i>Sphaerolaimus</i>	2B	71.1	95.9	—	—
<i>Spirinia</i>	2A	71.1	121.5	16.4	—
<i>Desmodora</i>	2A	142.3	179.1	82.3	54.5

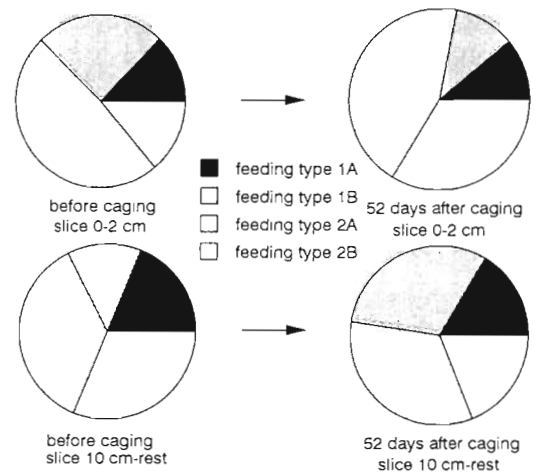


Fig. 9. Mean relative composition (%) of the nematode feeding types (Wieser 1953) of the surface and deepest layer of the cage over 2 periods

decrease in the deeper layers (Fig. 8), which indicated that upward vertical migration could not explain the observations.

After 5 mo (period 4) and 1 yr (period 5) the exclusion effect was no longer detectable, density differences between treatments having fallen back to their original levels.

For nematode feeding guilds 2 parallel (though non-significant) trends were observed in the cages over time (Fig. 9). There was a general increase of feeding type 2B (omnivores/predators) in slice 0-2 cm at the expense of type 1B (non-selective deposit feeders) and there was no change for type 2A (epistratum feeders). In the deepest layer an opposite change in feeding types occurred with a decrease in 2B and an increase in 1B.



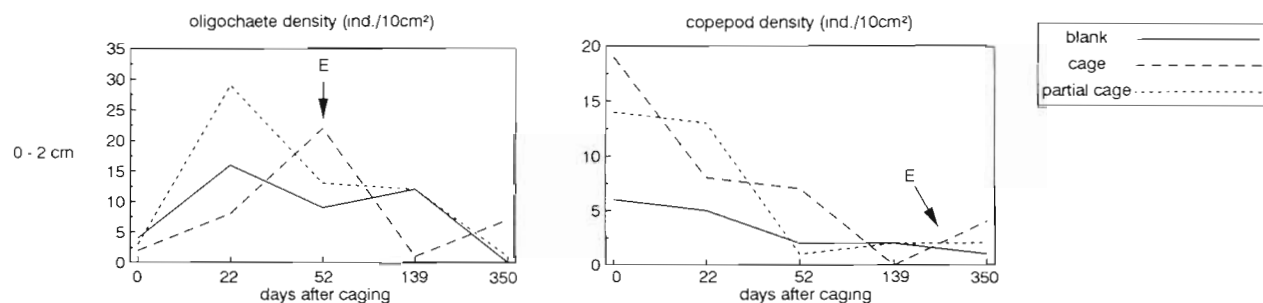


Fig. 10. Oligochaete and copepod densities (ind. 10 cm<sup>-2</sup>) in the cage, partial cage and blank: mean values of the upper layer over time. E: significant exclusion effect with  $p < 0.05$

As for the most common nematode genera, *Chromaspirina* and *Sphaerolaimus* (type 2B) and *Ptycholaimellus* and *Spirinia* (type 2A) increased conspicuously in the surface layer, whereas *Daptonema* (type 1B) increased in the deepest layer (Table 4).

As for the other meiofauna taxa, exclusion effects were demonstrated for copepod and oligochaete densities in the upper layer (Fig. 10, Table 5). The oligochaete response was observed as a density increase in the upper slice of the cage after 2 mo (10×). Copepod densities showed a general decline over 1 yr. ANOVA only showed a significant exclusion effect during the last half year of caging. The upward trend during this period was significantly stronger in cages (4×) than in partial cages and blanks.

**No effect.** No procedural effect could be demonstrated for the patterns in nematode, oligochaete or copepod densities. Neither procedural nor exclusion effects could be detected for polychaetes, ostracods, halacaroids and kinorhynchs.

## DISCUSSION

### Spatial distribution patterns

The study shows a correlation of the meiobenthic community structure with physical gradients in the sediment. This may reflect a typical rigid system of abiotic factors regulating infaunal community structure in extreme eu littoral habitats (Hulings & Gray 1976). Especially in mangrove sediments the pigment gradient is very conspicuous (Alongi 1989, Ming-Yi et

Table 5. Mean and standard deviation values of oligochaete and copepod density (ind. 10 cm<sup>-2</sup>) of the surface layer in the 3 treatments (B, C and P) over 5 periods

Treatment		Slice 0–2 cm				
		Period 1	Period 2	Period 3	Period 4	Period 5
Oligochaeta	B	4 ± 1	16 ± 8	9 ± 6	12 ± 8	0 ± 0
	C	2 ± 3	8 ± 5	22 ± 1	1 ± 2	7 ± 4
	P	3 ± 2	29 ± 2	13 ± 8	12 ± 8	1 ± 1
Copepoda	B	6 ± 1	5 ± 3	2 ± 2	2 ± 2	1 ± 1
	C	19 ± 11	8 ± 5	7 ± 7	0 ± 0	4 ± 1
	P	14 ± 10	13 ± 9	1 ± 0	2 ± 2	2 ± 2

Table 6. Qualitative observations (–: absent, +: present, ±: intermediate) of possible artefacts in the 3 treatments (B, C and P) after 1 and 5 mo of caging with procedural evaluation

	After 1 mo of caging			After 5 mo of caging			Evaluation
	B	C	P	B	C	P	
Fouling	–	–	–	–	–	–	OK
Shading	–	+	±	–	+	±	± Procedural
Sedimentation	–	–	–	–	–	–	OK
Moisture	–	–	–	–	+	+	Procedural
Litter fall	+	–	±	+	–	±	± OK
Epibenthos	+	–	+	+	–	+	± OK

al. 1994). Most meiofauna taxa have been shown to prefer subsurface O<sub>2</sub> rich layers (Dye 1983a, Alongi & Sasekumar 1992). It is therefore not surprising that they are found to be positively correlated to characteristics such as chlorophyll *a* concentration that are typical for these layers.

### Experimental design

The meiofauna are useful subjects in cage exclusion experiments because of their short generation time and benthic larval stage (Bell 1980). Exclusion was achieved by removing large epibenthic organisms such

as crabs and gastropods by hand. Besides the observed permanent epibenthos (which is dominant during low tide), the exclusion of the visiting epibenthos (hyperbenthos and demersal fishes) was also of importance.

The experimental procedure allowed us to study the overall effects of competition, predation and food enhancement by epibenthos. Since old biogenic structures (burrows) persisted throughout the experiment, the effects of physical modification and bioturbation prior to caging could not be assessed. Moreover, removal of epibenthos and sampling led to an artificial disturbance of the sediment.

Until now, most exclusion experiments have concentrated on interactions at the species level (Kneib 1988, Martin et al. 1989, Kneib 1991). However, Walters & Moriarty (1993) advocated the use of amalgam species groups (e.g. higher taxa or functional groups), especially when the detailed species composition and trophic structure of the system are not known and when omnivory is important because of the absence of competitively dominant predators.

Exclusion approaches have limitations (difficulty of selective exclusion and faster development of artefacts) compared to enclosures (Hall et al. 1990). However, possible artefacts (Hairston 1990) were taken into account by a detailed follow up in the field (Table 6) and by using a randomized block design with procedure controls (Hurlbert 1984).

The initial emplacement and burying of the lower cage wall in the sediment did not cause a major disturbance. It was gradually pushed down into man-made grooves between the roots without influencing the caged area.

## Experimental results

### Abiotic factors

**Exclusion effect.** Some sediment characteristics (% of mud before combustion) and pigment concentration showed an exclusion effect in the upper layer. In general, there was an evolution in the cages to a muddier and pigment-rich sediment after 52 d. The increase of the % of mud was due to detritus accumulation since the % of mud after combustion did not show a parallel increase. As the total organic material (% of POM and C) in the sediment did not change, this detrital increase was most probably restricted to the muddy fraction of the detritus (Fig. 6).

Effects on the pigment concentration (chlorophyll *a* in particular) are correlated with changes in microalgae and diatoms (Gerdol & Hughes 1994).

**Procedural effect.** It is obvious that the sediment of the treatments P and C became moister through time

than that of treatment B as a result of the cage construction (Table 6). This resulted in lower temperatures and, later in the experiment, in lower salinities. Indeed, the exclusion effect on temperature could, in fact, be a procedural effect of the cage shadow which was less conspicuous in the partial cage (one side was open).

### Nematode and total meiofauna density

An exclusion effect on nematode and total density was also reported by Dye & Lasiak (1986) (an increase of 2× to even 5×), by Hoffman et al. (1984) (10×) and by Dittmann (1993) (5×). Bell (1980) only found an exclusion effect for total meiofauna density.

**Competition.** The epibenthos in the *Cerriops tagal* vegetation was dominated by the crab *Uca lactea annulipes* (2 to 26 ind. m<sup>-2</sup>) and the gastropod *Terebralia palustris* (6 to 70 ind. m<sup>-2</sup>). According to Bell (1980) and Dye & Lasiak (1986), competition with the nematodes is the driving force: the dominant epibenthos and pelagic fauna are thought to be important grazers on detritus and the associated bacteria, protozoans and fungi (Gerlach 1978, Alongi 1989). Stomach content analyses of *Uca polita* and *Uca vocans* and fiddler crabs in general revealed bacteria, microalgae and protozoans to be the dominant dietary items (Dye & Lasiak 1986). The diet of gastropods in mangroves is limited to microalgae, bacteria and fungi (Branch & Pringle 1987 in Alongi 1989). As in the present study, caging and exclusion of gastropods has been shown to cause an increase of chlorophyll *a* in a study of Branch & Branch (1980) (in Alongi 1989).

Consequently, the exclusion effect as a conspicuous increase of pigment concentration and muddy detritus could not have been entirely caused by the cage construction. Moreover, this exclusion effect was parallel to that on nematodes and total meiofauna (i.e. after 52 d of caging). Therefore, the nematodes and the epibenthos in this study are believed to compete for food.

**Predation.** With respect to the predation hypothesis, *Uca pugnax* and juvenile crabs in general have been shown to ingest nematodes (Bell 1980, Hoffman et al. 1984). Dittmann (1993) was convinced that consumption of, and predation on, the meiofauna by the dominant crab *Mictyris longicarpus* was the structuring factor.

However, Dye & Lasiak (1986) stressed that exclusion of predation as a driving force would lead to an upward vertical migration of nematodes. No evidence for this was found in our study, stressing the lack of predatory control (Alongi 1989).

**Bioturbation.** A third interaction possibility is disturbance due to bioturbation (Alongi 1989) caused by

burrowing (Bright 1977, DePatra & Levin 1989) or feeding activities or by the production of (pseudo)fecal pellets (Sherman & Coull 1980, Hoffman et al. 1984, Dye & Lasiak 1986, Dittmann 1993). As mentioned before, exclusion of bioturbation was probably not a driving force in our experiments.

*Procedure.* In this study, the effect of the cage construction itself was reflected in a decrease in the muddy fraction (after combustion), salinity and temperature in the cages and partial cages.

The potential effect of these changes is believed to be marginal as compared to the obvious exclusion effect on nematodes. Bell (1980) found no experimental effect on the muddy fraction, whereas Virnstein (1977) and Alongi (1989) found an increase due to water stagnation.

#### Nematode genera composition

Although the overall 2A type % did not change, an increase of the most common type 2A nematode genera (epistratal microalgae feeders) and an overall increase of type 2B (omnivores/predators) in the upper layer was evident. It was followed by a new equilibrium in nematode density. Epistratum feeders were reacting to the microalgal abundance and could be rapidly grazed down by nematode predators that were partly coming from deeper layers. The presence of type 2B could also be a reason for the decrease of type 1B nematodes, which were not or only slightly affected by competition. These findings support the competition hypothesis. Unfortunately, we did not compare these data with the evolution of feeding types in partial cage and blank treatments. A comparison would probably indicate possible significant exclusion and procedural effects on genus composition and trophic structure of the nematode community.

#### Oligochaete density

Hoffman et al. (1984) found a 4-fold increase of annelids in general, while Dittmann (1993) showed a 5-fold increase in oligochaetes.

*Competition.* From the 5 food categories for oligochaetes (Giere & Pfannkuche 1982) the most important dietary item for interstitial tubificids and enchytraeids is believed to be organic matter enriched with bacteria rather than microalgae, which were found to be most important for nematodes (Giere 1975). Organic matter is particularly plentiful in littoral sands and muds. Indeed, it was this muddy detritus that showed a conspicuous exclusion effect in the experiment, indicating that the removal of epibenthos

turned out to favour the oligochaetes in terms of competition for food.

*Predation.* Nevertheless, a decrease of predation by crabs (Dittmann 1993) or by juvenile fish can also be a possible factor. In temperate regions, there is evidence that young demersal fish (e.g. gobiids) prey upon oligochaetes (Giere & Pfannkuche 1982). Virnstein (1977), on the other hand, showed with a cage experiment in a temperate shallow estuarine bottom that the dominant tubificid was largely unaffected by predation of crabs or fishes.

*Bioturbation.* It is known that the production of burrows and food and fecal pellets by crustaceans may have a positive effect on oligochaete numbers (Bell & Coull 1978, Reise & Ax 1979, Alongi & Tietjen 1980, Dittmann 1993). Indeed, the exclusion could possibly lead to a decrease in oligochaetes in the cages. However, this kind of effect was not observed in this experiment.

*Procedure.* As mentioned above, the 3 abiotic factors influenced by the cage construction were salinity (after 6 mo), and % of mud (after combustion) and temperature (after 1 mo). The detailed composition of the oligochaete fauna is not known, which makes it difficult to analyse the response to changes in the abiotic environment.

#### Copepod density

Bell (1980), Hoffman et al. (1984) and Dittmann (1993) showed a similar exclusion effect on harpacticoid copepods.

*Competition.* With respect to competition regulation, only juvenile crabs were mentioned as possible competitors of copepods (Bell 1980). Their food is assumed to consist mainly of detritus, but selective grazing on single food particles has also been observed (Marcotte 1984 in Hicks & Coull 1983).

*Predation.* Reise (1979) and Webb & Parsons (1991) believed that predation has little or no influence. In contrast, Hoffman et al. (1984) and Dittmann (1993) proposed that it is mainly predation by epibenthos (such as crabs) that influences copepod numbers. The late effect in the present study (only in period 5) accords with the study of Bell (1980), who only found an effect on copepods after an exclusion lasting 9 mo. Hicks & Coull (1983) thought that, especially for muddy or detrital substrata, juvenile fishes are primary predators on harpacticoids. These fishes were also excluded in our experiment. Hicks & Coull (1983), Gee (1989) and Giere (1993) mentioned that, whereas nematodes and oligochaetes are certainly important in remineralization of organic matter and may be food items for epibenthic deposit-feeders, copepods seem to



be the major taxon in terms of fish food and/or biomass transfer to the demersal-pelagic realm.

**Bioturbation.** It has been postulated that sediment reworking activities are an alternative structuring force (Bell & Coull 1978, Reise 1979, Webb & Parsons 1991, Olafsson & Moore 1992). Our experiment did not show this kind of effect.

#### Other taxa densities

In contrast with our study, in which there was no effect on polychaetes, Bell (1980) and Hoffman et al. (1984) mentioned a significant increase.

The absence of an effect on polychaetes led to the question whether our experimental design was adequate to detect possible effects in the first place. Therefore, the techniques of power analysis (Cohen 1977) were employed for a *post hoc* determination of the sensitivity of our experiment. The parameters significance level (0.05), effect size (0.274 calculated from ANOVA variances) and sample size (3) permitted us to estimate a power level of 11% via power tables provided by Cohen (1977). Such a low power value was also common in subtidal caging experiments, and it limits the detection power of effects on polychaetes severely (Hall et al. 1990).

The same can be concluded for effects on ostracod (18%), halacaroid (32%) and kinorhynch (13%) numbers.

#### CONCLUSION

Exclusion of all epibenthos from a *Cerriops tagal* mangrove sediment clearly influenced the nematode, oligochaete and copepod densities, i.e. the dominant part of the total meiobenthos. The excluded permanent epibenthos was dominated by detritivores. Besides a possible sheltering effect, the absence of epibenthos in particular led to an increase in muddy detritus and microalgae in the surface layer. This was followed by a higher abundance of diatom-feeding nematodes (type 2A) and oligochaetes and a subsequent increase in predatory nematodes (type 2B). Eventually, it brought the system to a new equilibrium.

The structure of the meiofauna community is regulated not only by the physical environment, but mainly by biological, competitive interactions with the epibenthos. These findings indicate that the meiofauna community of mangrove sediments is part of an isolated, detrital food web with only minor predator-prey interactions with the epibenthos. The impact of epibenthos on meiofauna is further complicated by multilevel interactions with other infaunal macrobenthos. A publication on this effect is in preparation.

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