



Effects of intensive seaweed farming on the meiobenthos in a tropical lagoon

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Abstract

Open water aquaculture of the seaweed *Eucheuma spinosum*, imported to Zanzibar from the Philippines in 1989, is presently a large scale operation on the island, with algal farms covering around a 1000 ha of the intertidal area. To assess the effects of the farming on benthic communities both field and laboratory studies were conducted. Two field studies conducted at different times showed that all major meiofaunal taxa were found in significantly lower numbers within the farm area compared with control areas. Multi-dimensional scaling ordination of nematode species, genera and family abundance data separated samples from farmed and control areas. There was a significant difference in the nematode assemblage structure among areas in pairwise comparisons using ANOSIM. The trophic structure of the nematode assemblage was characterised by a high number of epistrate feeders in all areas ranging from 73 to 96% of total numbers in the samples. To test the hypothesis that toxic substances excreted by the seaweed were responsible for lower abundance inside the farm area, a laboratory experiment was conducted. *Eucheuma* plants were added to several microcosms and allowed to grow there for 40 days. The results indicated no effects of the seaweed on the density of the major infauna taxa as no significant difference was found among the treatments. It is concluded that other factors such as increased predation by benthic feeding fish and the mechanical disturbance of the sediments may better explain the observed differences in infauna abundance inside and outside the algal culture farms.

Keywords: Meiofauna; Seaweed aquaculture; Soft-sediment community ecology; Tropical lagoon

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1. Introduction

Since 1989, when seed stock of the seaweed *Euचेuma spinosum* (red algae) was imported from the Philippines, there has been a rapid development in algae aquaculture on Zanzibar. The seaweed is used as raw material for carrageenan manufacture. The *Euचेuma* is cultured in open water areas within lagoons along the Zanzibar coast and is grown on ropes (between two pegs) suspended in water just above the sediment. The farms are usually placed in soft sediment areas which are only exposed during spring low tides, and where seagrass is absent or sparse. The seaweed has exceptionally high growth rates of $\approx 7\%$ per day (Lirasan & Twide, 1993), which is unique in this context. The algae are cultured all year round and are harvested at spring low tides, ≈ 4 wk after implantation. The farms cover an area of ca. 1000 ha along the coast and are represented in almost all places where the conditions for culturing are met.

Despite the rapid expansion of this industry, the environmental impact of such a large scale monoculture of algae has not been assessed. Seaweeds are known to excrete toxic substances as a result of stress, and as part of their life defence mechanism (Philips & Towers, 1982). We know also that *Euचेuma spinosum* grown in Zanzibar excretes halonogenated substances (Collén, pers. comm.). During harvesting of the algae, when plants are broken, and under periods of strong environmental stress, such as high temperatures and little water exchange, the release of such substances may be stimulated leading to an accumulate in the sediments and hence an affect on the infauna.

The conclusion of a recent GEEP workshop (Group of Experts on Environmental Pollution) in Norway has specific bearing on monitoring studies in marine and estuarine habitats. A major finding of the meeting was that of all benthic organisms, the meiofauna (defined here as microscopic metazoan invertebrates, passing 0.5 mm and retained on 40 μm mesh size sieves) were better indicators of environmental perturbation than any of the larger macrofauna (Warwick, 1988; see also Hicks, 1991). Indeed, meiofauna have been increasingly used in pollution studies. This is partly because of the advantages in studying changes at the community level in meso- or microcosm experiments, and partly due to their sensitivity (see for reviews Heip, 1980; Sandulli, 1986; Vincx & Heip, 1987; Moore & Bett, 1989; Coull & Chandler, 1992).

The major aim of this study was to test the null-hypothesis that the large scale culturing of *Euचेuma spinosum* in the tidal flats of Unguja island (Zanzibar) has no effect on the animal communities or on the metabolic processes in the culture area or within the adjacent sediment communities. The second aim was to provide data on the variation in population density for the major meiofaunal taxa and the assemblage structure of free-living marine nematodes. This was done in conjunction with a parallel study on sediment nutrient cycling in the same locations which will be the subject of a later contribution. In this paper we concentrate on meiobenthic populations.

2. Methods

2.1. Study area

Unguja island is the largest island of Zanzibar (Fig. 1) and supports extensive intertidal lagoon flats composed mainly of carbonate sand. The intertidal flat of Paje, $06^{\circ}16'S$, $39^{\circ}32'E$ was chosen as the study site, as it is characteristic of the lagoons on Zanzibar, it is intensively farmed, and it was easily accessible. During spring low tides, this flat extends ≈ 2 km towards the fringing reef. The *Eucheuma* farms are situated parallel to the shoreline and ≈ 400 m from the mean low water line. The farm belt ranges from 10 up to 50 m in width and is several kilometres in length.

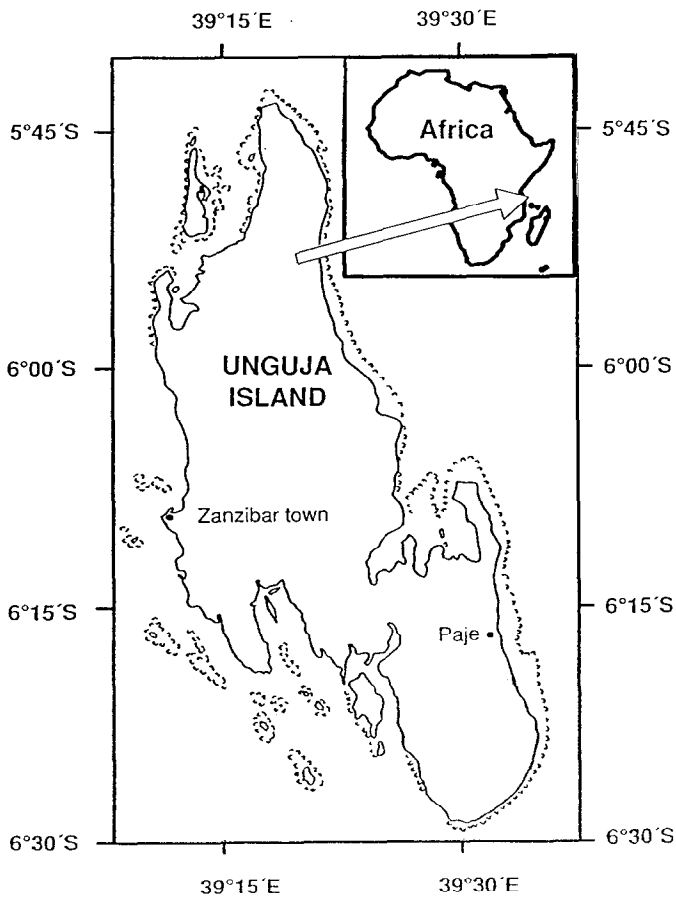


Fig. 1. Map of Unguja island showing the position of Paje the field site and the lagoon areas around the island.

2.2. Field studies

2.2.1. Small scale sampling

Field samples were taken from Paje intertidal sand-flat in April 1992. At the end of the farmed strip (Fig. 2) three sampling areas were defined as follows: *Farm area* (SF), consisting of seven adjacent *Eucheuma* plots each ≈ 2 m wide and 5 m long; *Control areas* situated 5 m away from farm (*Control close*, SC) and 50 m away from farm (*Control away*, SA). Three samples were taken randomly, within a square metre, from each of the seven plots to a depth of 5 cm using polycarbonate tubes with a cross-sectional area of 9.6 cm^2 . In order to reduce within area variance, the samples were lumped together to form one replicate. All samples were immediately fixed in 8% formalin. Sediment samples for grain size analysis were also taken from inside and outside the farm with polycarbonate tubes (54 cm^2 cross-sectional area) as were samples for biogeochemical purposes (Johnstone and Ólafsson, 1995).

2.2.2. Large scale sampling

In November 1994, further samples were taken within and outside the farmed strip from seven locations. At ≈ 300 m interval core samples were taken within the farmed strip (LF), 5 m away (LC) and 50 m away (LA) (Fig. 2). At each location two cores (9.6 cm^2) were taken next to each other, one for animal analysis and

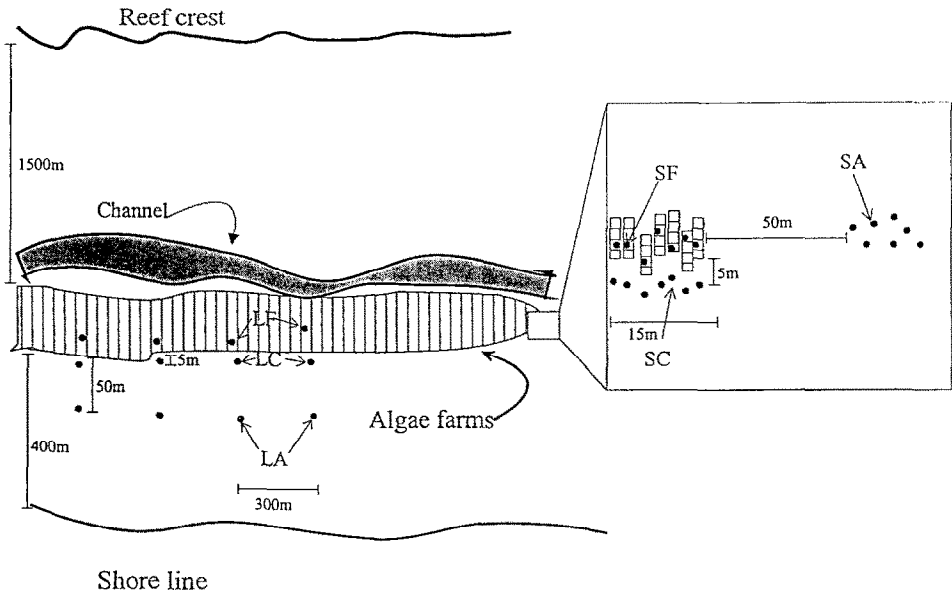


Fig. 2. Schematic representation of the intertidal area of Paje with sampling points indicated with dots (L: large scale field study, S: small scale field study, F: algae farms, C: control 5 m away from farms, A: control 50 m away from farms).

one for grain size analysis. Adjacent to these, further two cores (5 cm²) were taken for chlorophyll analysis. Salinity and temperature were also measured at each location with a refractometer and thermometer.

2.3. Laboratory study

Sediment samples were taken at Paje in October 1992 and used as the sediment material for microcosm experiments. Three sediment cores of 54 cm² were taken randomly in the vicinity of the farm area down to depth of 10 cm and placed carefully in a 5 l plastic jar. Fifteen such jars were generated and then immediately brought to the laboratory. The microcosms were held under in situ conditions using two rows of fluorescent lights providing a 12 h light daily period and air-stones to ensure mixing and oxygenation for the benthos. The water in each microcosm was replaced daily with filtered seawater, and salinity (using refractometre), oxygen tension (using oxygen meter) and temperature were monitored on a daily basis. One week after establishment of the microcosms 70 g of freshly cut *Eucheuma* was added to eight randomly chosen microcosms. The experiment was terminated after 40 days. On termination, 3 cores of 9.6 cm² cross-sectional area were retrieved from each microcosm and lumped together as before to make up a replicate. Additional samples were also taken for grain size analysis.

2.4. Sample processing

Sediment samples were washed in the laboratory through 500 and 40 µm sieves, and the meiofauna extracted from the 40 µm sediment fraction using Ludox colloidal silica at a specific gravity of 1.15. Major meiofaunal taxa were identified and enumerated under a dissecting microscope. From each sample ≈100 nematodes were picked randomly, impregnated with anhydrous glycerine (Platt & Warwick, 1983) and mounted on slides for microscopic species identification. Nematodes were assigned to trophic groups according to the scheme of Wieser (1953). Nematodes were not identified to the species level from the microcosms. Sediment samples for grain size analysis were dried to constant weight at 50°C. The resulting material was then dry sieved through different mesh sizes and the material captured in each fraction was then weighed and calculated as a percentage of the total sample weight (Morgans 1956). Chlorophyll samples were stored directly in 90% acetone and kept dark at 5°C overnight. Chlorophyll *a* was estimated using spectrophotometer and the formula of Parsons et al. (1984)

2.5. Statistical analyses

Differences in density were investigated by means of one-way analyses of variance. Paired a posteriori comparisons of density estimates were carried out with the Tukey test, using 95% confidence limits. Prior to the analysis of variance, all data were first log₁₀ transformed and Cochran's *C* test used to check the assumption of homoscedasticity. When conditions for the use of parametric test

was not fulfilled, Kruskal-Wallis and Mann-Whitney U tests were employed. Species diversity was assessed by using the Shannon-Wiener information function (H'), Pielou evenness (J') (both using \log_2), Simpson's index (D) and the number of species at the 50 individual level using Hurlbert's (1971) rarefaction method (S).

Nematode family, genus and species abundance data were double square root transformed and subjected to multidimensional scaling ordination (MDS) using Bray-Curtis similarity index. The ANOSIM randomisation test was used to test for differences in nematode assemblage structure and the SIMPER computer program used to identify those species contributing to differences observed in the ordination analysis (Warwick et al., 1990a,b). The ordination, the randomisation test and the similarity analysis were done by using PRIMER 3.1. statistical package developed at the Plymouth Marine Laboratory.

3. Results

3.1. Field studies

3.1.1. Small scale sampling

Grain size

Sediment grain size results show no significant difference between the grain size distribution patterns for the areas inside the farms and outside the farms. It should be noted, however, that there was a tendency in the sample from outside the farms to exhibit a higher percentage of particles in the smallest ($<63 \mu\text{m}$) size fraction. Unfortunately, the low number of replicates (3) and the fact that the data represents the mean value over the upper 5 cm, prevents a firmer resolution of the differences.

Major taxa

In all the samples collected the nematodes were the dominant group comprising on average 514, 438 and 875 ind. per 10 cm^2 in sites SF, SC, and SA, respectively. This corresponds to 87, 68, and 78% of the total meiofauna in samples from each respective area. Harpacticoid copepods were usually the second most abundant group and polychaetes were found to be numerically important in the SA site. These three groups taken together comprised on average 98% (SF), 94% (SC) and 97% (SA) of the total meiofauna. Oligochaetes were found in all samples but usually in low numbers. Other groups, Turbellaria, Cyclopoida, Ostracoda, Amphipoda, Cumacea, and Hydroida, were found in low numbers and infrequently.

The total number of meiofauna was, on average, highest in the SA sites and the nematodes were also found in significantly higher numbers at this location (Fig. 3, Table 1). Harpacticoid copepods were approximately twice as abundant in the control areas as in the farm area (Fig. 3) though this was only statistically

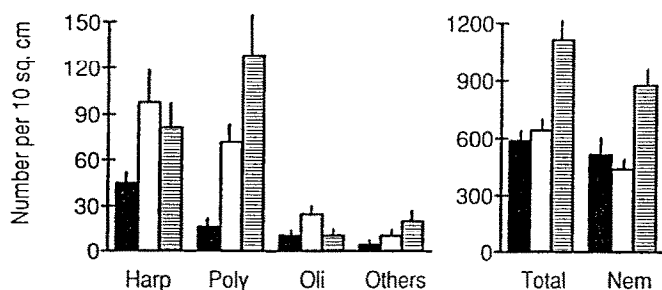


Fig. 3. Average number ($N = 7$) per 10 cm^2 ($+1 \text{ SE}$) of major meiofaunal taxa in the farm area (solid bars), control close (open bars) and control away (hatched bars) (Harp = Harpacticoida, Poly = Polychaeta, Oli = Oligochaeta, Nem = Nematoda) in the small scale study.

significant for the SC site (Table 1). Numbers of meiobenthic polychaetes were highly reduced within the farms (Fig. 3, Table 1) while the numbers of Oligochaetes were not significantly different among areas. The combined number of other taxa were lowest in the farm areas (Fig. 3, Table 1).

Nematode assemblage

A total of 51 nematode species were recorded from the areas around and in the algae farms. The multidimensional scaling ordination of the nematode family, genus and species abundance data clearly separates samples from each area (Fig. 4). There was a significant difference in the nematode assemblage structure among all areas in pairwise comparisons using ANOSIM at the three taxonomic levels (Table 2; family, genus and species).

More than half of the 15 most abundant species displayed significant differences among areas (Table 3). Five species were found in significantly higher number in

Table 1

The results of one-way ANOVA on major meiofaunal taxa data from the two field studies. Farm (SF, LF), control 5m away from farms (SC, LC) and control 50 m away from farms (SA, LA). The results of multiple comparison Tukey a posteriori test, are also presented

	<i>F</i> -ratio	<i>P</i> -value	Tukey
Small scale sampling			
Nematoda	11.83	0.0005	SA > SF, SC
Harpacticoida	4.69	0.0229	SF < SC
Polychaeta	33.71	0.0000	SF < SA, SC
Oligochaeta	*	>0.05	*
Other	10.09	0.0011	SF < SA
Large scale sampling			
Nematoda	5.63	0.0126	LF < LC, LA
Harpacticoida	7.70	0.0038	LF < LC, LA
Polychaeta	17.45	0.0000	LF < LC, LA
Other	8.00	0.0036	LF < LC, LA

* Variance heterogenous, Kruskal-Wallis test employed.

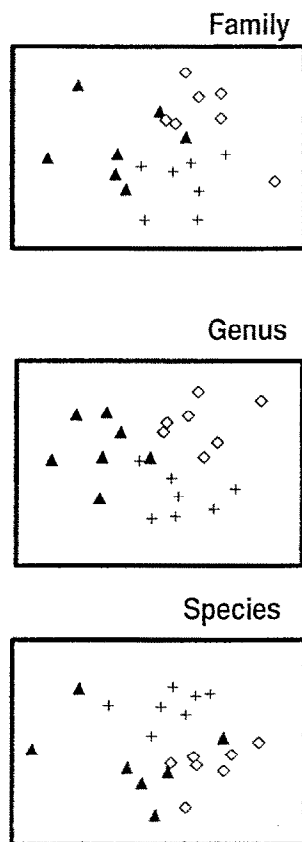


Fig. 4. Two-dimensional configuration (Multidimensional scaling ordination) of nematode species, genera and families, from the three areas in the small scale study. \diamond , Farm; \blacktriangle , control away; +, control near.

either one or both of the control areas compared with the farm area i.e. *Microlaimus* sp. 1, *Dichromadora* sp. 2, *Dichromadora* sp. 3, *Euchromadora* sp. and *Eurystomina* sp. Another two species were found in significantly higher numbers within in the farm area compared to the other areas, i.e.

Table 2

The results of ANOSIM testing with values of the R statistics for pairwise comparisons between farm and control areas of Bray-Curtis similarities from the small scale field study

Areas compared	R -value	Significance level
Farm (SF) vs. Control away (SA)	0.521	$p = 0.001$
Farm (SF) vs. Control close (SC)	0.530	$p = 0.002$
Control close (SC) vs. control away (SA)	0.672	$p = 0.001$

Table 3

Average (AVG) number per 10 cm², (SD) and percentage $N = 7$) of the 15 most abundant nematode species in the three areas; Farm (SF), Control close (SC), Control away (SA) from the scale field study

ANOVA	Farm (SF)			Control close (SC)			Control away (SA)			One-way	
	AVG	SD	%	AVG	SD	%	AVG	SD	%	Sign.	Tukey
<i>Spirina</i> spp.	187	69	36	200	37	46	191	78	22	NS	
<i>Microlaimus</i> sp. 2	14	15	3	106	72	24	310	167	35	***	F < SA, SC
<i>Paracyatholaimus</i>	149	113	29	30	16	7	27	27	3	*	F > SA
<i>Dichromadora</i> sp. 2	5	7	1	2	3	1	62	35	7	***	SA > F, SC
<i>Eurystomina</i> sp. A	1	2	0	18	11	4	42	40	5	***	F < SC, SA
<i>Parecomesoma</i> sp. A	21	24	4	7	8	1	31	28	4	NS	
<i>Molgolaimus</i> sp. B	17	36	3	3	7	1	28	21	3	NS	
<i>Richtersia</i>	11	11	2	1	4	0	30	24	3	**	SA > SC
<i>Promonhystera</i> sp. B	26	28	5	3	5	1	4	6	0	*	F > SC
<i>Subsphaerolaimus</i> sp. A	23	56	4	2	3	0	0	0	0	NS	
<i>Catanema</i>	6	5	1	1	3	0	17	15	2	*	SA > SC
<i>Axonolaimus</i>	6	1	0	10	14	2	11	15	1	NS	
<i>Euchromadora</i> sp. 1	0	0	0	2	3	1	18	21	2	*	SA > F
<i>Dichromadora</i> sp. 3	1	2	0	11	12	2	9	6	1	*	F < SC, SA
<i>Metalinhomoeus</i> sp. 2	7	9	1	2	3	0	8	12	1	NS	
Richness-S	9.06	3.8		9.04	3.49		11.45	4.42		*	NS
Simpson-D	0.72	0.26		0.69	0.25		0.77	0.29		NS	
Shannon-WienerH ^a	2.44	0.94		2.37	0.9		2.91	1.11		NS	
Pielou-J ^a	0.66	0.24		0.63	0.23		0.72	0.25		NS	

^a Using log₂, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. NS = not significant.

Paracyatholaimus sp. and *Promonhystera* sp. (Table 3). Species diversity was highest in the SA sites for all measurements but only significantly for number of species (S; Table 3). The analysis of similarities among areas showed that the replicates from the farms were less similar to each other than from the control areas; the average Bray-Curtis similarity being 51, 59 and 59 from F, SC and SA respectively. The species which were largely responsible for the dissimilarity among areas are presented in Table 4. A number of species were responsible for the observed difference in the nematode assemblage structure between areas. However, whilst most of these species were among the 15 most abundant, some relatively rare species contributed significantly to the dissimilarity, e.g. *Oncholaimus* sp. ranked three according to Bray-Curtis dissimilarity between SA and SF sites; *Daptonema* sp. 2 ranked five between SC and SF sites; and *Trefusia* sp. ranked six between SC and SA sites (Table 4).

The trophic structure of the nematode assemblage was characterised by a high number of epistrate feeders in all areas representing from 73 to 96% of the total numbers in the samples (Fig. 5). Also, epistrate feeders were found in significantly higher numbers in the SA site compared to the other areas (ANOVA $p < 0.001$, Tukey test). In the farm area there were significantly lower numbers of predator/omnivores than in the other areas (ANOVA $p < 0.001$, Tukey test). Selective deposit feeders were in lowest numbers in the control close area (ANOVA

Table 4

Average number (AVG) per 10 cm² and standard deviation (SD) of nematode species in farm and control areas

Species	Control away		Farm		δ_i	$\delta_i\%$	$\Sigma \delta_i\%$
	AVG	SD	AVG	SD			
<i>Microaimus</i> sp. 2	310	167	14	15	4.06	7.46	7.46
<i>Dichromadora</i> sp. 2	62	35	5	7	3.05	5.60	13.07
<i>Oncholaimus</i> sp. a	42	40	1	2	2.89	5.30	18.37
<i>Paracyatholaimus</i> sp.	27	27	149	113	2.30	4.23	22.60
<i>Molgolaimus</i> sp. b	28	21	17	36	2.16	3.97	26.57
<i>Promonhystera</i> sp. b	4	6	26	28	2.15	3.95	30.52
<i>Dichromadora</i> sp. 3	9	6	1	2	2.03	3.73	34.25
<i>Parecomesoma</i> sp. a	31	28	21	24	1.91	3.52	37.77
<i>Euchromadora</i> sp. 1	18	21	0	0	1.91	3.51	41.28
<i>Chromadorita</i> sp.	15	19	0	0	1.79	3.28	44.56
<i>Richtersia</i> sp.	30	24	11	11	1.66	3.04	47.60
	<i>Control close</i>		<i>Farm</i>				
<i>Eurystomina</i> sp. A	18	11	1	2	3.08	5.70	5.70
<i>Microaimus</i> sp. 2	106	72	14	15	3.07	5.68	11.38
<i>Promonhystera</i> sp. B	3	5	26	28	2.49	4.60	15.98
<i>Richtersia</i> sp.	1	4	11	11	2.41	4.46	20.44
<i>Daptonema</i> sp. B	14	18	3	6	2.40	4.43	24.87
<i>Dichromadora</i> sp. 3	11	12	1	2	2.34	4.32	29.19
<i>Parecomesoma</i> sp. A	7	8	21	24	2.28	4.22	33.41
<i>Paracyatholaimus</i> sp.	30	16	149	113	2.13	3.93	37.34
<i>Chromadora</i> sp. a	6	7	4	8	2.11	3.89	41.23
<i>Catanema</i> sp.	1	3	6	5	2.08	3.85	45.08
<i>Motgolaimus</i> sp. b	3	7	17	36	2.04	3.77	48.85
	<i>Control close</i>		<i>Control away</i>				
<i>Dichromadora</i> sp. 2	2	3	62	35	3.18	6.25	6.25
<i>Richtersia</i> sp.	1	4	30	24	2.87	5.62	11.87
<i>Daptonema</i> sp. B	14	18	0	0	2.37	4.65	16.52
<i>Mologolaimus</i> sp. b.	3	7	28	21	2.34	4.59	21.11
<i>Catanema</i> sp.	1	3	17	16	2.28	4.47	25.58
<i>Trefusia</i> sp. 1	1	2	11	6	2.14	4.20	29.78
<i>Parecomesoma</i> sp. a	7	8	31	28	2.09	4.10	33.88
<i>Euchromadora</i> sp. 1	2	3	18	21	1.84	3.60	37.48
<i>Microaimus</i> sp. 2	106	72	310	167	1.77	3.48	40.96
<i>Chromadorita</i> sp.	1	3	15	19	1.77	3.47	44.4
<i>Axonolaimus</i> sp.	10	14	11	16	1.40	3.29	47.72

Species are ranked according to average Bray-Curtis dissimilarity (δ_i) between samples from different areas. Mean values representing the contribution of each species (i) to δ are given (δ_i) and also shown as percentage contribution to δ ($\delta_i\%$) and cumulative percentage ($\Sigma \delta_i\%$). A cut-off to the genera list was applied at $\Sigma \delta_i\% = 50\%$. Average Bray-Curtis dissimilarity between Farm and control away was 54.45, between farm and control close was 54.12, and between control close and control away was 50.97. From the small scale field study.

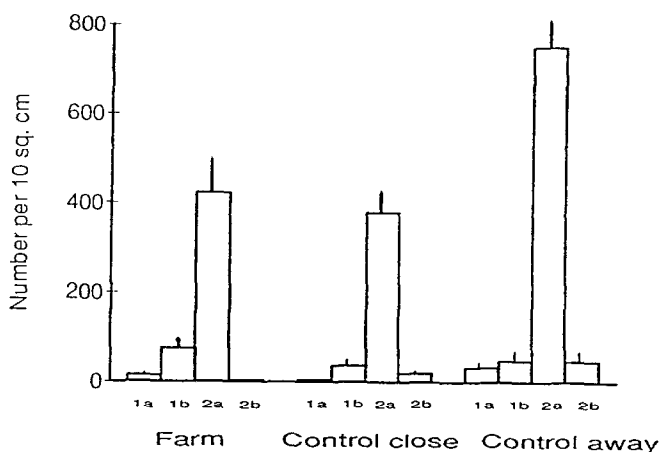


Fig. 5. Average number per 10 cm² (+1 SE) of nematodes in each feeding category (1a = selective deposit feeders, 1b = non-selective deposit feeders, 2a = epistrate feeders, 2b = predators/omnivores) from the three areas in the small scale study.

$p < 0.001$, Tukey test), while there was no significant difference detected in the numbers of non-selective deposit feeders among areas.

3.1.2. Large scale sampling

Grain size, chlorophyll a, salinity and temperature

Medium grain size was not significantly different between the farmed area (average: 134 μm) and control close (average: 198 μm) (Mann-Whitney U test, $p > 0.05$) or between control areas (Mann-Whitney U test, $p > 0.05$). However medium grain size was significantly lower in the control areas away (average: 101 μm) compared with farmed areas (Mann-Whitney U test, $p > 0.05$). The percentage of silt (<0.125 μm) varied among the areas being 54, 63 and 73% in LF, LC and LA, respectively, though this difference was not significant (ANOVA, $p > 0.05$). Chlorophyll a content was on average lower in the farmed area than the others though not significantly so (ANOVA $p > 0.05$). Salinity and temperature measurements were very similar between areas, around 36‰, and 32°C, respectively.

Major taxa

The same group dominated the samples as in the small scale field sampling, i.e. together Nematoda, Harpacticoida and Polychaeta accounted for 98, 96 and 96% of all the fauna in the farm area, close to farm and far away, respectively. Nematodes were on average 3 times lower in numbers within the farm area compared with the control areas while harpacticoids and polychaetes were on average 5 times lower in number (Fig. 6, Table 1). There were no significant differences observed for the major groups between the control areas (Table 1).

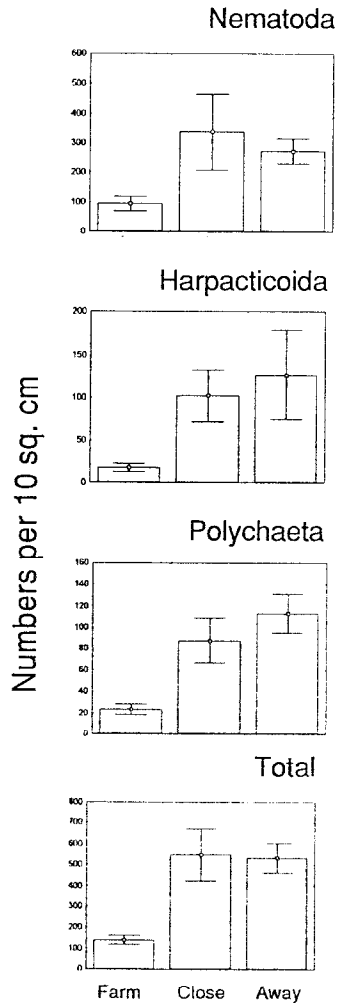


Fig. 6. Average number ($N = 7$) per 10 cm^2 ($+1 \text{ SE}$) of major meiofaunal taxa in the farm area (LF), control close (LC) and control away (LA) in the large scale study.

3.2. Laboratory study

The average numbers of the major meiofaunal taxa in the microcosms are presented in Table 5. Numbers of nematodes and polychaetes were of the same magnitude as in the field samples while other groups were found in much lower numbers inside the microcosms. It is clear that the presence of *Eucheuma* had no effects on the density of the major meiofaunal taxa in the laboratory (Table 5). Fluctuations in grain size, salinity, temperature and pH were very similar in all microcosms and not significantly different between treatments ($p > 0.05$).

Table 5

Average (AVG) number ($N = 7$) per 10 cm² and standard error (SE) of the major meiofaunal taxa in the mesocosms

	With <i>Eucheuma</i>		Without <i>Eucheuma</i>	
	AVG	SE	AVG	SE
Nematodes	657	82	662	47
Polychaetes	30	3	28	3
Harpacticoida	3	0.4	3	1
Oligochaeta	1	0.2	2	0.5
Turbellaria	1	1	1	0.3
Ostracoda	1	0.8	1	0.1
Other	1	0.4	0.1	0.1

4. Discussion

The field investigations show clearly that the algae farms accommodate different meiobenthic assemblages than closely adjacent areas, and they exhibit poorer fauna in terms of numbers and altered assemblage structure. Several explanations may account for this pattern including:

(1) *Toxic substances from the algae accumulate in the sediment directly under the algae farms resulting in reduced population density.*

A number of field and laboratory studies have shown that under pollution pressure the meiobenthos may be found in lower numbers (see for review Coull & Chandler, 1992) and that the effect of pollutants can depend very much on the pollutant type as well as their level of exposure. We do not know if there were any toxic substances excreted by the *Eucheuma* and certainly the results from the microcosm study strongly indicate that if such excretion occurred the effects on the fauna are negligible. With diurnal tides and relatively strong currents the farm areas are subjected to rapid exchange of water minimising the risk of toxic accumulation. On the basis of the laboratory experiment we therefore reject the hypothesis that toxic substances account for reduction in population densities of meiobenthos inside the farms.

(2) *Population reduction of meiobenthos inside the farms was due to increased predation rates.*

Underwater observations during high tides indicate that juvenile fishes seek shelter in the farms (Giegold, pers. comm. and pers. obs.). The dominant juvenile fish species in Paje belong to the Gerreidae, with *Gerres oyena* being far the most abundant, but Gobidae, Carangidae, Clupeidae and Lethrinidae also being well represented (pers. obs.). Examination of gut content of *Gerres oyena* revealed that it fed almost exclusively on polychaetes and harpacticoid copepods but had also consumed some nematodes (Ndaró and Ólafsson, 1995). It is very plausible

that fish predation inside the farms accounted partly or fully for the lower abundance of the major taxa inside the farm areas, though we can only at present offer circumstantial evidence.

(3) *Mechanical alteration of the sediments by the cultured algae.*

As mentioned earlier, the *Eucheuma* cultivation involves the setting out of the algae along thin ropes stretched between two poles anchored in the bottom. Whilst this in itself does little to the benthos, often currents which pass through the farms over the tidal cycle cause the ropes and algae to energetically brush against the sediment surface. The effect that this may have on the incorporation of fine particulate organic matter (POM) into the sediments could be substantial; as is suggested by the difference seen in the finest grain size fraction from each of the sediment areas. Also, we have never observed any form of microalgal build up on the sediment surface or zones of accumulation which can often be seen outside the farms. Thus it is plausible that the amount of POM available to sediment fauna is reduced within the farm areas.

(4) *Epiphytic nematodes may explain to some degree the difference in the assemblage structure of the nematode fauna.*

Two species of nematodes were found in highest abundance inside the farm area, i.e. *Paracyatholaimus* sp., the second most abundant species within the farm area and *Promonhystera* sp.. Species belonging to *Paracyatholaimus* have been associated with algae in tropical waters (Wieser, 1954). It is plausible that the high density of the *Paracyatholaimus* species inside the farms was due to affinity for the seaweed.

(5) *The difference in the abundance and composition of meiobenthos between the three areas reflects a spatial variation between the areas existing before the farms were established.*

When we have a strip of farms extending several kilometres along the intertidal region it is difficult to choose reference sites in an impact study. By taking samples either landwards or seawards of the farmed strip may result in differences that cannot be related to the “treatment”, since they could equally well result from natural spatial variability across the beach. In our large scale study this could well be the case between the control away (LA) and the farms (LF). The median grain size was for example different and this area is longer exposed than the farms. The control close (LC) was at same intertidal level as the farms and should therefore provide useful comparison. In the small scale field study we were however able to choose reference sites at the end of the farmed strip that were relatively far away from the farms but at the same intertidal level. As both field studies show basically the same pattern we believe that the differences in numbers and assemblage structure were indeed due to the algae farms.

It is clear that the difference in the assemblage structure of the nematode component between the three areas in the field was detected at family, genus and species level. However at the major taxon (phylum) level the nematodes were found in very similar numbers close to the farms and within the farms. This is in an agreement with Heip et al. (1988), Warwick et al. (1988) and Ólafsson (1992) who found that at taxonomic levels above the family rank meiofaunal community response to environmental change was difficult to detect.

Variations in the density of the major meiofaunal taxa in this study fall within variations recorded in previous investigations on meiofaunal numbers in carbonate sand sediments (see Alongi, 1989a,b for reviews). The nematode assemblage structure was characterised by high numbers of epistrate feeders and relatively low species diversity. The dominance of epistrate feeders in all samples (73 to 96%) may be best explained by the nature of the sediment, being medium to coarse sand. Both in temperate (e.g. Wieser, 1959; Heip et al. 1983) and tropical habitats (Alongi 1986) epistrate feeders have shown affinity for sandy sediments as they possess teeth capable of rasping food particles off large sand grains or of cracking open algal cells and sucking out cell fluids (Alongi & Tietjen, 1980). The relatively low nematode species diversity in the current study is in sharp contrast with studies conducted in quartz sand habitats where diversity tends to be the highest (see Heip et al. 1985 for review). However, in carbonate reef sand habitats low nematode diversity appears to be common (Decreamer & Coomans, 1978; Rao & Misra, 1983; Alongi, 1986). Alongi (1986) suggested that low diversity of nematodes in reefal sands probably reflects the low rates of deposition of organic matter to reef seabeds.

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