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## Zonation and structuring factors of meiofauna communities in a tropical seagrass bed (Gazi Bay, Kenya)

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### Abstract

This study deals with the relation between tropical meiofauna and environmental variables by comparing the ‘benthic’ (i.e. in the bare sediment adjacent to seagrass plants) and the ‘epiphytic’ (i.e. in samples including seagrass plants) meiofauna associated with five seagrass species from the high intertidal to the high subtidal zone in Gazi Bay (Kenya). Ordination and variance analysis revealed three distinct ‘benthic’ and two ‘epiphytic’ meiofauna assemblages. These assemblages corresponded entirely with those identified for the seagrass species: a high intertidal pioneer association (*Halophila ovalis*/*Halodule wrightii*), an intertidal climax assemblage (*Thalassia hemprichii*) and a high subtidal pioneer association (*Halophila stipulacea*/*Syringodium isoetifolium*). These data support the hypothesis that meiofaunal communities correspond to the characteristic zonation of the seagrass vegetation in Gazi Bay.

In beds of the pioneer seagrass species, the close relationship between sediment characteristics and both ‘benthic’ and ‘epiphytic’ meiofauna communities suggests that these pioneer communities were mainly driven by physical factors. The ‘benthic’ communities adjacent to the climax seagrass species *T. hemprichii* were more structured by biogenic factors, e.g. % TOM, chlorophyll *a* and *c*, fucoxanthin, habitat complexity and growth form of the seagrass species. For its associated ‘epiphytic’ meiofauna the latter conclusion was even more striking. These data corroborate the importance of physical factors in disturbed environments (intertidal zone, near pioneer seagrasses) and of biotic factors in more stable conditions (subtidal zone, near climax seagrasses). © 2001 Elsevier Science B.V. All rights reserved.

**Keywords:** Meiofauna; Zonation; Seagrass; Kenya

### 1. Introduction

Due to their importance in coastal ecosystems worldwide, seagrasses and associated fauna have been the subject of a large number of studies (e.g. Lewis and Stoner, 1983; Lewis, 1984; Orth et al., 1984; Schneider and Mann, 1991a,b; Boström and Bonsdorff, 1997). The majority of these studies are

from temperate areas and aim to explain the distribution and abundance patterns of invertebrate communities, particularly macrofauna and their predators. Seagrass morphology (e.g. Connolly and Butler, 1996), species composition (Young, 1981; Stoner, 1983), habitat complexity (Lewis, 1984), biomass (Stoner, 1980; Lewis, 1984), surface area (Stoner, 1983), epiphytic algae (Borowitzka et al., 1990; Schneider and Mann, 1991a,b), food abundance, predation and sediment stability (Orth et al., 1984 and references herein) have all been suggested as

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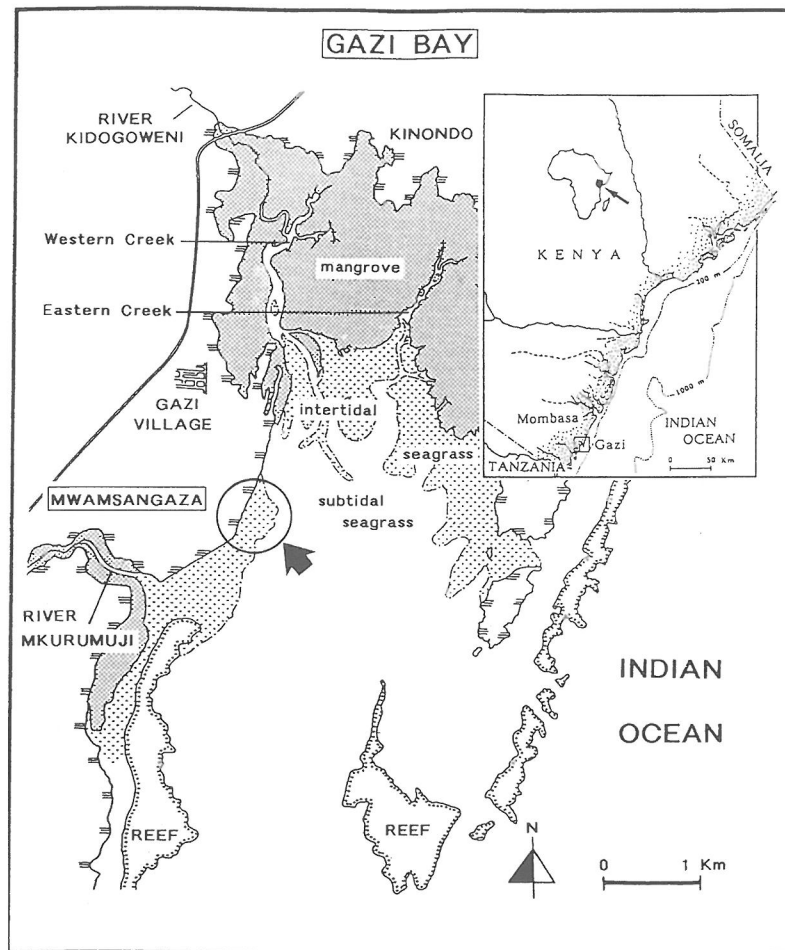


Fig. 1. Location of Gazi Bay and its major biotopes (after Slim, 1993), with an arrow indicating the sampling site at Mwamsangaza beach.

factors structuring assemblages of seagrass macrofauna.

Bell et al. (1984a,b) have pointed out that our knowledge of meiofaunal (here defined as Metazoa in the size range of 38–1 mm) communities in seagrass vegetations is limited, especially when compared to the information available from other shallow habitats or for seagrass macrofauna. A majority of studies to date have been conducted within the continental United States (Bell and Hicks, 1991; Bell et al., 1984a,b). Direct comparison between different studies is often difficult, e.g. because of differences in sampling methodology (Orth et al., 1984).

The present study is part of a research program which aimed to document meiofaunal assemblages from

several seagrass beds in the tropics. To allow comparisons within the tropical zone, we collected meiofauna samples and environmental data on selected seagrass species of the circumtropical *Thalassia* association, as defined by Brazier (1975), in a standardised way. The genera of the *Thalassia* association, such as *Thalassia*, *Halophila*, *Halodule*, *Syringodium*, are common to both the tropical Pacific and/or tropical Atlantic (but are absent from the Mediterranean) and are therefore appropriate to test results of the present study on a broader scale in a further phase of the project.

This study analyses distribution patterns of meiofauna communities among patches of five intertidal seagrass species, characterised by important differences in growth form (i.e. mode of growth,

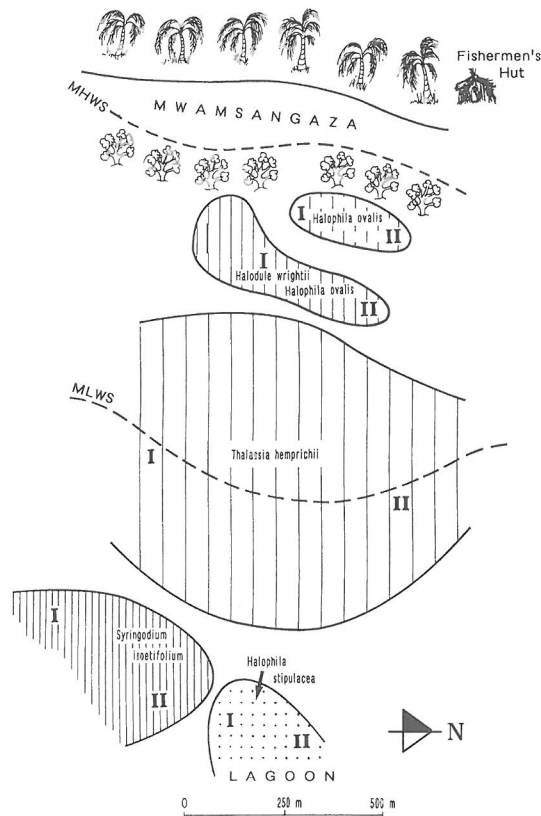


Fig. 2. Map of the intertidal and subtidal zone at Mwamsangaza Beach (Gazi Bay) with indication of both quadrats (I and II) of each sampled seagrass species. MHWS, mean high water level at spring tide; MLWS, mean low water level at spring tide.

branching system, rhizomes/root structure, leaf morphology and surface area available for epiphytic algae and associated fauna). The hypothesis that meiofauna communities would correspond to the characteristic zonation of the seagrass vegetation was tested in Gazi Bay, Kenya. Coppejans et al. (1992) and Van Avesaath et al. (1993) have described a well-marked zonation and succession pattern for the seagrass species in Gazi Bay. This zonation of species coincides with a zonation of different leaf morphologies, different stages in succession and different related environmental factors. Here we explore the importance of seagrass plant morphology and relevant environmental variables as potential structuring factors for the meiofauna, and compare meiofauna structuring factors with available information on driving variables as reported for macrofauna.

## 2. Material and methods

### 2.1. Study area

Gazi Bay or Maftaha Bay ( $4^{\circ}22'S$ ,  $39^{\circ}30'E$ ) (Fig. 1) is located ca. 50 km north of the Tanzanian border and 60 km south of Mombasa Island. The bay is 1.75–3.5 km wide and 3.25 km long and is bordered with mangroves. Two major creeks characterise the system (Fig. 1). The Kidogoweni river enters the bay through the western creek (surface area  $\approx 18$  ha); the eastern creek (2.7 ha) has no freshwater input. Dense seagrass beds occur in both major creeks and in the bay proper (30–100% cover in the creeks and 10–30% in the lagoon). The downstream part of the western creek is characterised by a sparse seagrass vegetation on a sandy bottom (Slim, 1993). Samples (indicated with an arrow in Fig. 1) were taken in the inter- and subtidal zone at Mwamsangaza beach, between the western creek and the Mkurumuji river. The bay experiences semi-diurnal tides, with spring and neap tide ranges of 3.2 and 1.4 m, respectively (Kitheka, 1997). Its salinity regime is influenced by the freshwater influx from both rivers (Kitheka, 1997), but was stable (35) during our sampling campaign.

### 2.2. Seagrass species sampled

Coppejans et al. (1992) identified eleven of the twelve seagrass species known from Kenya in our study area. Meiofauna were sampled from five of them: *Halodule wrightii* Ascherson 1868, *Halophila ovalis* (R. Brown) Hooker F. 1858, *Halophila stipulacea* (Forsskål) Ascherson 1867, *Syringodium isoetifolium* (Ascherson) Dandy 1939 and *Thalassia hemprichii* (Ehrenbergii) Ascherson 1871, all situated in the inter- and subtidal zone.

Six different seagrass morphologies (Den Hartog, 1967) can be found in Gazi Bay, four of which were incorporated in the present study: (1) parvozosterids (e.g. *H. wrightii* = H.w.), characterised by fine linear leaves; (2) halophilids (e.g. *H. ovalis* = H.o. and *H. stipulacea* = H.s.) with small elliptic and ovate leaves; (3) syringodiids (e.g. *S. isoetifolium* = S.i.) with long subulate leaves; and (4) magnozosterids (e.g. *T. hemprichii* = T.h.) with wide linear leaves.

### 2.3. Sampling strategy

Meiofauna samples were taken along the tidal gradient between 16 and 19 July 1996. At high tide, the deepest seagrass species were covered by approximately 4 m water, the shallowest by at the most 1 m. Samples of all seagrass species were taken by snorkelling two hours before to two hours after low tide under a water cover of 1–1.5 m. For each seagrass species, triplicate samples including a single seagrass plant (series 1, 'epiphytic' samples) and triplicate samples excluding seagrass vegetation (series 2, 'benthic' samples) were taken within a quadrat of 5 × 5 m. Series 1 aimed at including the epiphytic meiofauna associated with seagrass plants. Series 2 was taken within a naturally empty spot of about 1 m<sup>2</sup> in each quadrat. In order to assess variance within a seagrass bed, two quadrats (Fig. 2, further numbered as I and II) were sampled. Because of the clear zonation of the seagrass species, these quadrats were situated on more or less straight lines perpendicular to Mwamsangaza beach, starting from the lowest pneumatophores of *Sonneratia alba* (Coppejans and Gallin, 1989; Gallin et al., 1989) down to the subtidal zone. These sampling sites, thus, were situated close to transects 5 and 6 of Coppejans et al. (1992).

Samples were taken using 3.6 cm inner diameter (i.d.) PVC meiocores (surface area of 10 cm<sup>2</sup>), inserted into the sediment to a depth of 10 cm. In sample series 1 (with seagrass plants), cores were carefully placed over a single seagrass plant, i.e. plant and sediment were sampled together. Another technique was used to sample the leaves of *T. hemprichii*; therefore these results are not comparable to the meiocore samples and are not discussed in this paper.

For the sediment samples of series 2 (without seagrass plants), all sediment cores were vertically subdivided on site into the following depth horizons: 0–1, 1–2, 2–3, 3–4, 4–5 and 5–10 cm, using a standard Hagge corer for vertical sectioning (Fleeger et al., 1988). Overlying water was analysed together with the top 1 cm of sediment.

An 8% MgCl<sub>2</sub>-solution was added to all samples including a seagrass plant to improve collection of epiphytic animals (Hulings and Gray, 1971; Hicks, 1977). Sampled seagrass plants were subsequently washed in the field with freshwater over a 1-mm sieve and meiofauna retained on a 38-μm mesh size

sieve. All samples were preserved with warm (60°C) formaldehyde in freshwater to a final concentration of 4%. In the laboratory, samples from both series were rinsed with a jet of freshwater over a 1-mm sieve, decanted ten times over a 38 μm mesh sieve, centrifuged three times with Ludox HS40 (du Pont, specific density 1.18), and finally stained with Rose Bengal. Meiofauna was sorted and enumerated at higher taxon level using a Wild M5 binocular. Taxa identified here were: Cnidaria, Turbellaria, Gnathostomulida, Gastrotricha, Nematoda, Rotifera, Kinorhyncha, Loricifera, Priapulida, Gastropoda, Bivalvia, Polychaeta, Oligochaeta, Sipunculida, Tardigrada, Halacarida, Ostracoda, Copepoda, Amphipoda, Cumacea, Isopoda, 'nauplii' and insect larvae.

### 2.4. Environmental data

Two additional samples were taken from each sampling quadrat for sediment and nutrient analysis. These samples were collected between plants with a 6.2 cm i.d. core and immediately stored frozen. Immediately upon thawing, the interstitial water was analysed for NO<sub>2</sub><sup>-</sup>-N, NO<sub>3</sub><sup>-</sup>-N, NH<sub>4</sub><sup>+</sup>-N, PO<sub>4</sub><sup>3-</sup>-P and SiO<sub>2</sub> concentrations using an A<sub>II</sub> automatic chain (SANplus Segmented Flow Analyser, SKALAR). Part of the remaining sediment was dried at 110°C for 4 h and used for analysis of total organic matter (% TOM), measured as weight loss after combustion at 550°C for 2 h. Sediment grain size was analysed with a Particle Size Analyser (type Coulter® LS100) on gram-aliquots dried at 60°C for 24 h. Characteristics obtained were median grain size, % silt (<63 μm), % coarse sand (850–2000 μm), % gravel (>2000 μm) and skewness.

Finally, triplicate (~1 cm<sup>3</sup>) sediment samples were taken from each quadrat using a syringe with the lower end cut off, subdivided into the same depth layers as for meiofauna, and stored frozen. In the laboratory, these samples were thawed and analysed for the phytopigments chlorophyll *a*, chlorophyll *c* and fucoxanthin as a measure for microalgae and diatoms, respectively (Jeffrey and Vesik, 1997). Pigments were extracted in 90% acetone at 4°C in the dark and separated by reverse phase liquid chromatography on a Gilson C-18 HPLC-chain (spectrophotometrical and fluorometrical detection)



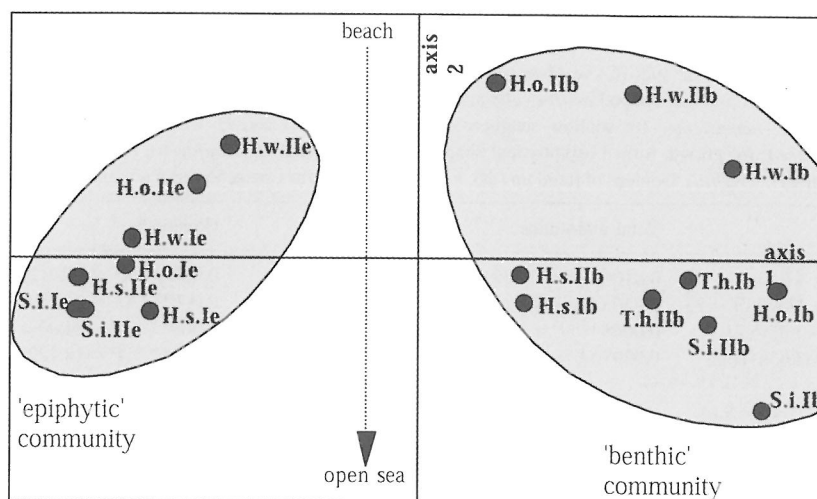


Fig. 3. Results of the correspondence analysis based on all fourthroot transformed meiofauna densities of all taxa (average of three replicates): plot of the sampling quadrats. T.h., *Thalassia hemprichii*; S.i., *Syringodium isoetifolium*; H.o., *Halophila ovalis*; H.s., *Halophila stipulacea*; H.w., *Halodule wrightii*; I, first quadrat; II, second quadrat; e, 'epiphytic' sample; b, 'benthic' sample.

according to a modified protocol of Mantoura and Llewellyn (1983).

## 2.5. Data analysis

The assemblage structure of the meiofauna in relation to environmental factors was analysed using ordination techniques (correspondence analysis (CA) and canonical correspondence analysis (CCA), Ter Braak, 1986). Data were fourth-root transformed prior to analysis in order to scale down the effect of abundant species (Field et al., 1982; Clarke and Green, 1988).

One-way ANOVA was used to compare sample series including and excluding seagrass plants, and to assess the effect of seagrass morphology on the number of higher taxa (as a first indication of diversity) and on the density of total meiofauna, Nematoda and Copepoda. A first analysis combined all seagrass species and all growth forms (elliptic leaf shaped as *H. ovalis* and *H. stipulacea*, slender elongated leaves as *S. isoetifolium* and *H. wrightii*, broad elongated leaves as *T. hemprichii*); separate analyses were performed on the data for the seagrass species at the upper reaches of the bed (*H. wrightii* and *H. ovalis*) and for the deeper species (*T. hemprichii*, *S. isoetifolium* and *H. stipulacea*). All data were  $\log_{10}x$  transformed prior to variance analysis in order to achieve normality and homogeneity of variances. Variance analysis

was performed with the STATISTICA™ software (Microsoft, StatSoft, 1995).

## 3. Results

### 3.1. Meiofauna data

CA (Fig. 3) on all average (of three replicates) densities of meiofauna taxa clearly separated samples including plant material from those without seagrass plants along the first axis (eigen value 0.1518). As mentioned in Material and Methods, epiphytic data of *T. hemprichii* were not included. Hence, our sampling methodology resulted in two major groups, which will henceforth be referred to as 'epiphytic' and 'benthic', respectively. The arrangement of the sampling quadrats along the second axis (eigen value 0.0355) reflects their position along the tidal gradient from beach to open sea.

The most pronounced differences between 'benthic' and 'epiphytic' assemblages were found in the *S. isoetifolium*/*H. stipulacea* association, where total meiofauna, Nematoda and Copepoda densities were significantly higher in the 'epiphytic' (i.e. including plant material) than in the 'benthic' (i.e. only sediment) samples (one-way ANOVA, Table 1). Copepods were five times as abundant in the

Table 1

Significance levels of one-way ANOVA comparison of the effect of: (A) subhabitat (benthic or epiphytic); (B) seagrass morphology on benthic meiofauna densities and number of taxa; and (C) seagrass morphology on epiphytic meiofauna densities and number of taxa for all seagrass species; for all growth forms (elliptic leaf-shaped as *H. ovalis* and *H. stipulacea*, slender elongated leaves as *S. isoetifolium* and *H. wrightii*, broad elongated leaves as *T. hemprichii*); for shallow seagrass species as *H. ovalis* and *H. wrightii*; for deeper seagrass species like *S. isoetifolium* and *H. stipulacea*; for growth form I (elliptic leaf shaped as *H. ovalis* and *H. stipulacea*), for growth form II (slender elongated leaves as *S. isoetifolium* and *H. wrightii*). Degrees of freedom (df), *F*-values and *p*-values are reported; \**p* ≤ 0.05, \*\**p* ≤ 0.01 and \*\*\**p* ≤ 0.001

Effect	Samples	Total meiofauna	Nematoda	Copepoda	# Taxa
(A)	All species df = 47	0.010** ( <i>F</i> = 7.337)	0.673 ( <i>F</i> = 0.181)	0.000*** ( <i>F</i> = 55.712)	0.757 ( <i>F</i> = 0.097)
	Shallow (H.o. + H.w.) df = 23	0.980 ( <i>F</i> = 0.001)	0.025* ( <i>F</i> = 5.793)	0.000*** ( <i>F</i> = 34.499)	0.721 ( <i>F</i> = 0.131)
	Deep (S.i. + H.s.) df = 23	0.000*** ( <i>F</i> = 27.062)	0.000*** ( <i>F</i> = 25.932)	0.000*** ( <i>F</i> = 84.007)	0.953 ( <i>F</i> = 0.004)
	Growth form I (H.o. + H.s.) df = 23	0.029* ( <i>F</i> = 5.503)	0.202 ( <i>F</i> = 1.733)	0.000*** ( <i>F</i> = 18.122)	0.690 ( <i>F</i> = 0.164)
	Growth form II (H.w. + S.i.) df = 23	0.169 ( <i>F</i> = 2.022)	0.215 ( <i>F</i> = 1.631)	0.000*** ( <i>F</i> = 48.599)	0.918 ( <i>F</i> = 0.011)
(B)	All species df = 29	0.610 ( <i>F</i> = 0.684)	0.221 ( <i>F</i> = 1.541)	0.000*** ( <i>F</i> = 17.641)	0.011* ( <i>F</i> = 4.063)
	All growth forms df = 29	0.873 ( <i>F</i> = 0.137)	0.597 ( <i>F</i> = 0.527)	0.034* ( <i>F</i> = 3.832)	0.002** ( <i>F</i> = 7.699)
	Shallow (H.o. + H.w.) df = 11	0.901 ( <i>F</i> = 0.016)	0.676 ( <i>F</i> = 0.186)	0.005*** ( <i>F</i> = 13.059)	0.444 ( <i>F</i> = 0.636)
	Deep (T.h. + S.i. + H.s.) df = 17	0.382 ( <i>F</i> = 1.027)	0.159 ( <i>F</i> = 2.330)	0.131 ( <i>F</i> = 2.088)	0.003** ( <i>F</i> = 8.562)
(C)	All species df = 23	0.061 ( <i>F</i> = 2.916)	0.000*** ( <i>F</i> = 14.582)	0.013* ( <i>F</i> = 4.680)	0.023* ( <i>F</i> = 3.997)
	All growth forms df = 23	0.615 ( <i>F</i> = 0.261)	0.071 ( <i>F</i> = 3.613)	0.211 ( <i>F</i> = 1.666)	0.039* ( <i>F</i> = 4.859)
	Shallow (H.o. + H.w.) df = 11	0.799 ( <i>F</i> = 0.069)	0.013* ( <i>F</i> = 9.499)	0.068 ( <i>F</i> = 4.290)	0.055 ( <i>F</i> = 4.859)
	Deep (S.i. + H.s.) df = 11	0.331 ( <i>F</i> = 1.045)	0.663 ( <i>F</i> = 0.202)	0.236 ( <i>F</i> = 1.588)	0.260 ( <i>F</i> = 1.425)

‘epiphytic’ assemblages (2332 ind. 10 cm<sup>-2</sup>) as in the ‘benthic’ (432 ind. 10 cm<sup>-2</sup>) ones. A similar ratio between ‘epiphytic’ and ‘benthic’ copepod densities was observed for the *H. ovalis*/*H. wrightii* assemblage (554 ind. 10 cm<sup>-2</sup> in ‘epiphytic’ and 109 ind. 10 cm<sup>-2</sup> in ‘benthic’ samples). Copepods exhibited the most pronounced ‘subhabitat effect’ throughout, densities being significantly higher (*p* < 0.001) in ‘epiphytic’ than in ‘benthic’ samples of all seagrass growth forms studied (Table 1). This was also illustrated in the percent composition of the meiofauna in both subhabitats (Fig. 4a and b).

Total meiofauna densities did not differ between ‘benthic’ and ‘epiphytic’ samples collected from shallow seagrass stands (*H. ovalis*/*H. wrightii*). However, from the absolute densities of copepods and nematodes, it is obvious that higher copepod and concomitantly lower nematode densities in the ‘epiphytic’ samples resulted in the same total meiofauna density (see Figs. 5 and 6; Fig. 9 in Section 4). The influence of the seagrass plant and its leaf morphology, in contrast, resulted in only minor changes in the nematode/copepod ratio.

Total meiofauna density in ‘benthic’ samples

ranged from 2619 ± 457 ind. 10 cm<sup>-2</sup> (H.o.I) to 8478 ± 640 ind. 10 cm<sup>-2</sup> (H.o.II). The percent composition (Fig. 4a) showed a low diversity near the shallow (Fig. 4c) seagrass species (except H.w.I) and copepods contributed less than 2.5% to the total meiofauna of these samples. The importance of copepods was clearly higher near the deeper (Fig. 4c) seagrass species (5–22%) (Fig. 4a). Significant variance within the seagrass bed (between both quadrats) was only found for shallow (Fig. 4c) seagrass species (H.o. and H.w.) (Fig. 5a and b). No significant effect of seagrass morphology on total meiofauna and nematode densities was found (Table 1(B)). A highly significant effect of seagrass morphology was, however, evident for copepod densities, both in analyses covering all seagrasses and in those covering only the shallow species (H.w. + H.o., Table 1). The sediment near *H. wrightii* harboured two (87 ± 15 ind. 10 cm<sup>-2</sup> in quadrat I) to six times (261 ± 69 ind. 10 cm<sup>-2</sup> in quadrat II) as many copepods as the *H. ovalis* sediment (47 ± 18 ind. 10 cm<sup>-2</sup>) (Fig. 5c).

Meiofauna diversity (Fig. 5d), expressed as number of higher taxa, differed significantly (*p* < 0.01)

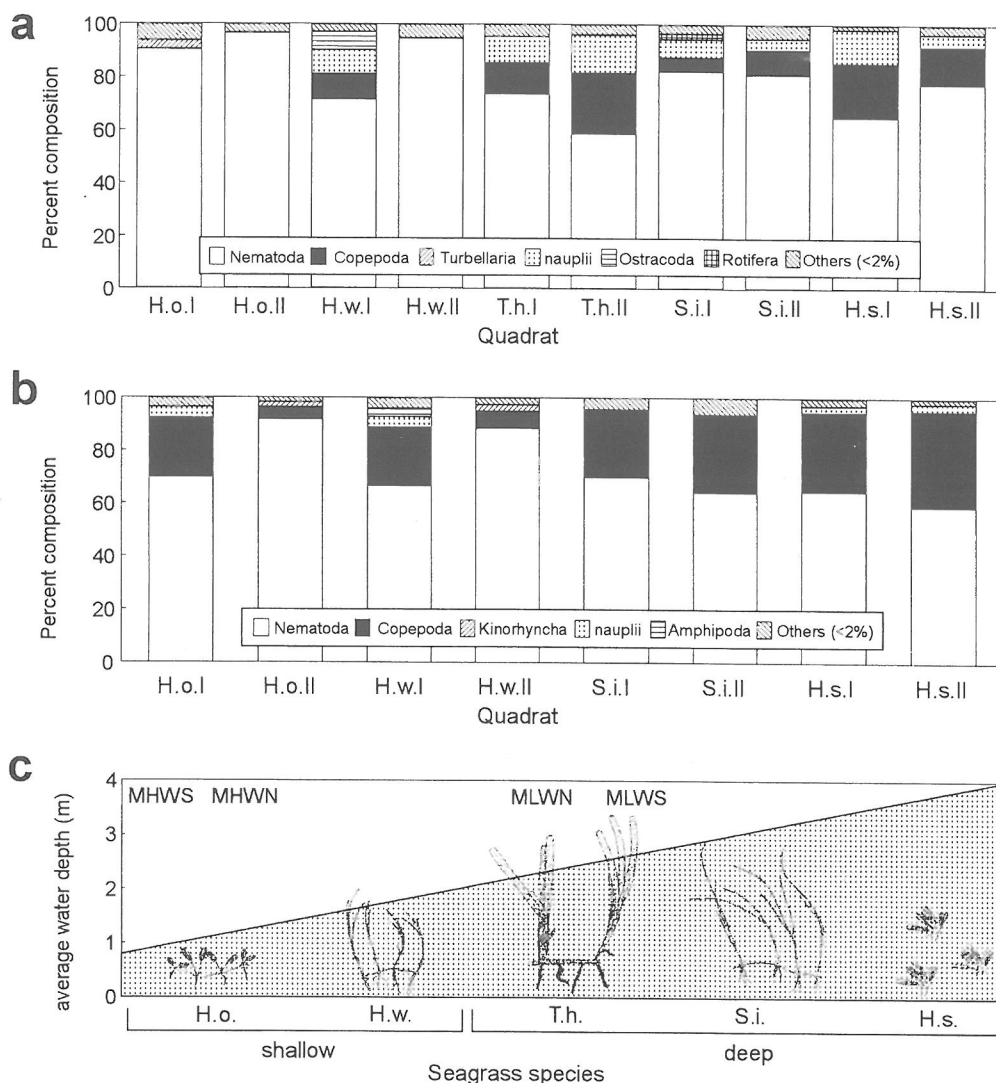


Fig. 4. Percent meiofauna composition for both quadrats (I and II) of (a) 'benthic' and (b) 'epiphytic' samples of *Halophila ovalis* (H.o.), *Halodule wrightii* (H.w.), *Thalassia hemprichii* (T.h.), *Syringodium isoetifolium* (S.i.) and *Halophila stipulacea* (H.s.). (c) Position of each seagrass species along the tidal gradient with indication of the average water cover during high tide.

between different seagrass species and growth forms, both in analyses of all samples together and of the 'subtidal' samples only (Table 1). A gradient of decreasing diversity was observed from *T. hemprichii* (17 taxa) → *S. isoetifolium* (15 taxa) → *H. stipulacea* (13 taxa). In addition, diversity decreased from *T. hemprichii* towards the upper intertidal seagrass species.

Total meiofauna densities in 'epiphytic' samples

ranged from  $3083 \pm 50$  ind.  $10\text{ cm}^{-2}$  (H.w.I) to  $8165 \pm 618$  ind.  $10\text{ cm}^{-2}$  (H.s.II). Copepods associated with the deeper seagrass species accounted for more than 25% of the total meiofauna (Fig. 4b). No significant differences between total meiofauna densities associated with different seagrass morphologies (seagrass growth forms) were found (Fig. 6a). As for the 'benthic' samples, a significant variance within the seagrass bed of *H. ovalis* and *H. wrightii*

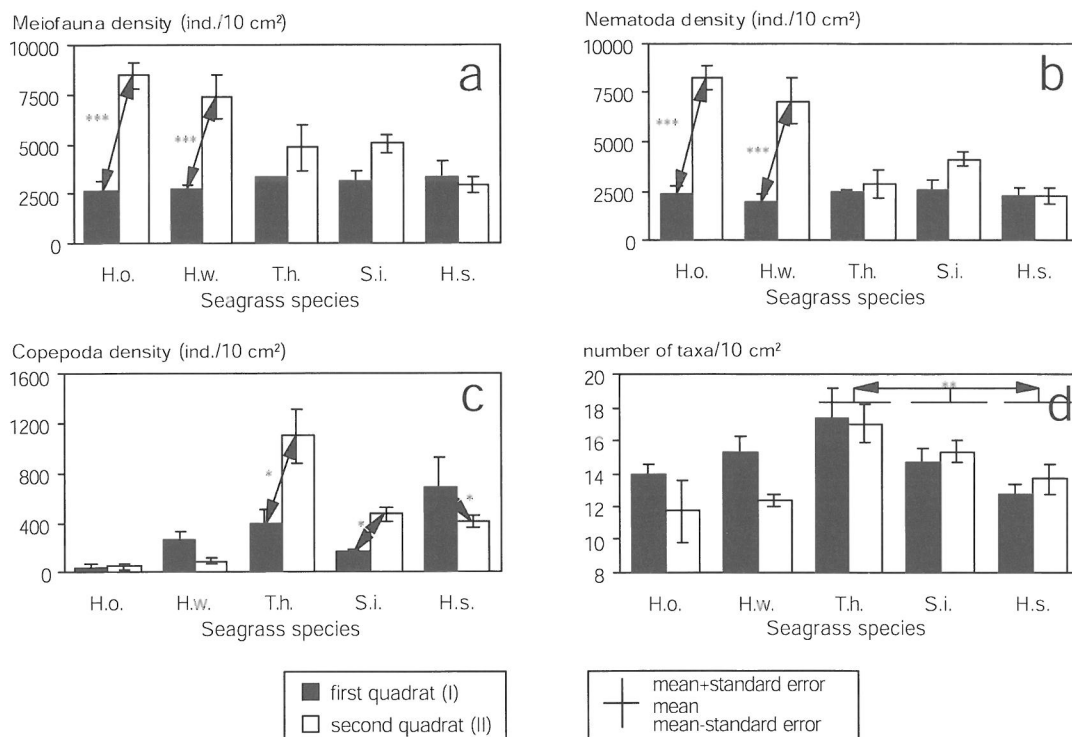


Fig. 5. Main 'benthic' meiofauna densities and number of taxa (mean  $\pm$  1 standard error) for both quadrats (I and II) of *Halophila ovalis* (H.o.), *Halodule wrightii* (H.w.), *Thalassia hemprichii* (T.h.), *Syringodium isoetifolium* (S.i.) and *Halophila stipulacea* (H.s.): (a) total meiofauna; (b) Nematoda; (c) Copepoda; (d) number of taxa. Significance levels indicated by arrows and NS  $p > 0.05$ , \* $p \leq 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

was observed for both total meiofauna and nematode density. Nematode density (Fig. 6b) was significantly different between seagrass species, especially within the shallow zone (H.o. + H.w.). The significant difference in copepod density (Fig. 6c) was mainly explained by seagrass tidal position (Fig. 4c) rather than seagrass morphology. For copepod density, variance within single seagrass beds was important in the shallow seagrass species (H.o. + H.w.). No significant difference in meiofauna taxon diversity (Fig. 6d) was detectable between seagrass species.

CA on 'benthic' meiofauna densities resulted in four groups (Fig. 7a): *H. ovalis* (H.o.I and H.o.II) and *H. wrightii* (H.w.I and H.w.II) were separated as a first assemblage (A). Both quadrats of *H. stipulacea* (H.s.I and H.s.II) (group B) grouped together; so did the quadrats of *S. isoetifolium* (S.i.I and S.i.II) (group C) and of *T. hemprichii* (T.h.I and T.h.II) (group D). There was a clear gradient along the first axis, corresponding to the tidal position of the seagrass species:

*H. ovalis* and *H. wrightii* were separated from the three seagrass species of the deeper subtidal zone (see also Fig. 3). The second axis revealed a gradient within these deeper seagrass species.

(A) *High intertidal pioneer association*: *H. ovalis* and *H. wrightii*. A distinct meiofauna assemblage was associated with *H. ovalis* and *H. wrightii*, two pioneer species at the upper limit of the seagrass bed. At Mwamsangaza beach this is typically the first seagrass association that grows as rather open cover on muddy and sandy patches (Coppejans et al., 1992). The meiofauna associated with these pioneer seagrasses was clearly unstable based on spatial variation, as significant differences were observed among replicates, among quadrats and among both seagrass species. The vertical depth profile (Fig. 8a) was quite uniform. Nematoda were dominant (depth-integrated relative abundance  $>92\%$ ) in all depth layers. Copepods (4.7%) and nauplii (4.0%) were restricted to the upper centimetres. In addition, soft-bodied

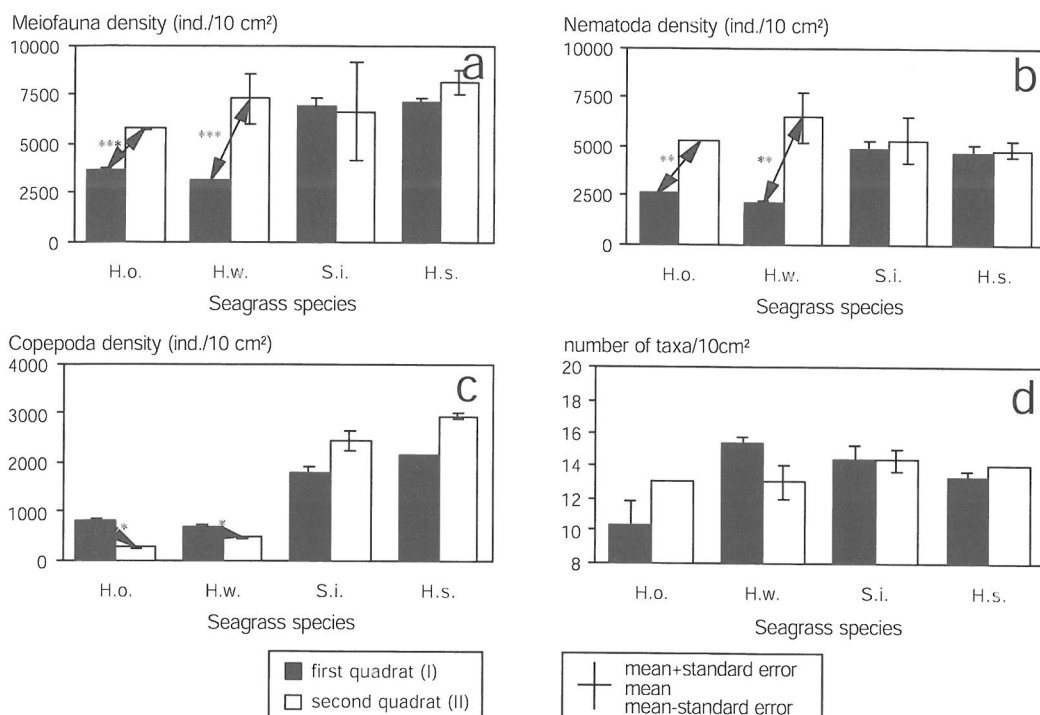


Fig. 6. Main 'epiphytic' meiofauna densities and number of taxa (mean  $\pm$  1 standard error) for the two quadrats (I and II) of *Halophila ovalis* (H.o.), *Halodule wrightii* (H.w.), *Syringodium isoetifolium* (S.i.) and *Halophila stipulacea* (H.s.): (a) total meiofauna; (b) Nematoda; (c) Copepoda; (d) number of taxa. Significance levels indicated by arrows and NS  $p > 0.05$ , \* $p \leq 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ .

(Nematoda, Polychaeta, Turbellaria, Kinorhyncha) and shelled (Bivalvia and Ostracoda) animals were recovered in this community (Fig. 7a).

(B) *High subtidal primary pioneer association: H. stipulacea.* *H. stipulacea* is a fast growing coloniser and sediment accumulator in bare areas on the often eroded banks of the intertidal channel (Coppejans et al., 1992). Meiofauna communities associated with *H. stipulacea* were separated based on the presence of amphipods and isopods in the *H. stipulacea* samples (Fig. 7a). The meiofauna assemblage associated with stands of this species was far more homogenous in terms of spatial variability than that associated with *H. ovalis*. The depth profile of the meiofauna associated with *H. stipulacea* was also clearly different from that of *H. ovalis* meiofauna (Fig. 8b): copepods and nauplii were recovered from all depth layers, while nematodes constituted half of the meiofauna in the top centimetre.

(C) *High subtidal secondary pioneer association: S. isoetifolium.* Newly formed sand bumps between

*Thalassia* plants are usually covered by *S. isoetifolium* (Coppejans et al., 1992) but we sampled an extensive patch of *S. isoetifolium* in the subtidal zone. Cnidaria was a remarkable taxon in these samples (Fig. 7a). The vertical depth profile of meiofauna (Fig. 8c) is less diverse than that of *H. stipulacea* in spite of possible higher detritus input from the larger subulate leaves (maximum 30 cm long) of *S. isoetifolium*. Copepods were only found in the deepest sediment layers. Nematodes were even more important in the top layer than near the other subtidal seagrasses.

(D) *Intertidal climax association: T. hemprichii.* The stability of the monospecific seagrass vegetation of *T. hemprichii* was reflected in low spatial variation of the meiofauna assemblage (Figs. 5 and 7a). The composition of the assemblage was characterised by a remarkable preference of crustaceans (except Ostracoda) for *T. hemprichii* and for deeper seagrasses in general (Fig. 7a).

The vertical pattern of 'benthic' meiofauna near the *T. hemprichii* vegetation (Fig. 8d) was well diversified

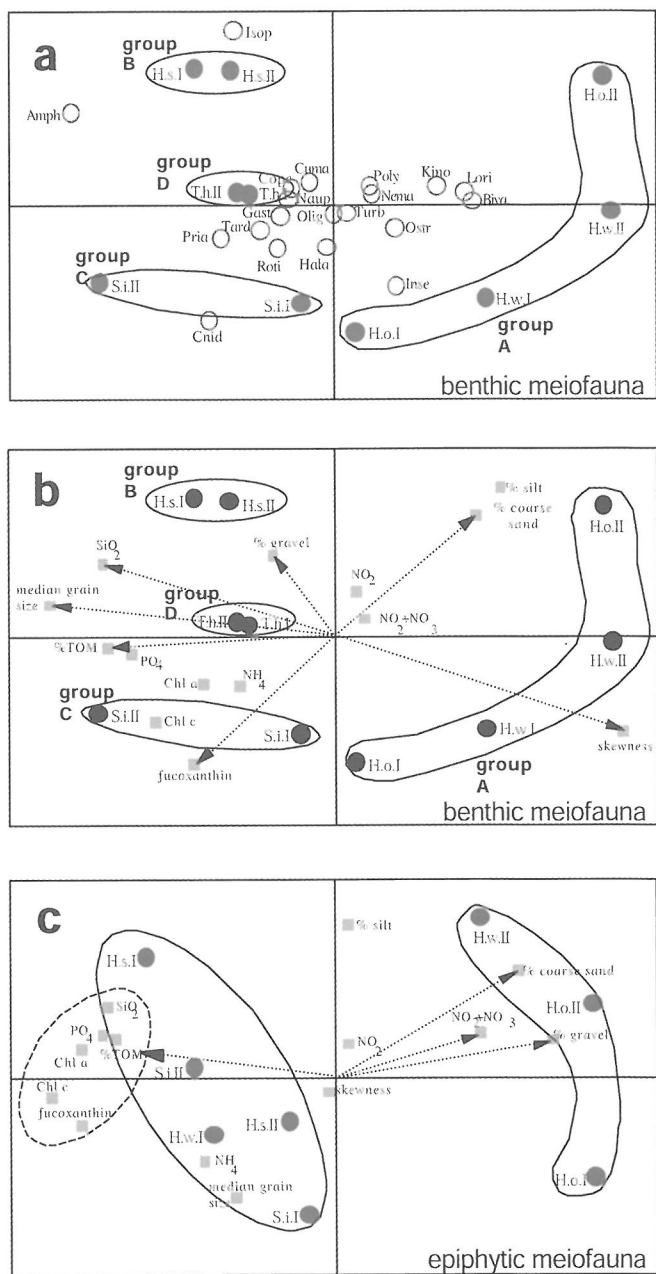


Fig. 7. Canonical correspondence analysis (CCA-ordination) (axis 1 vs. axis 2) based on fourthroot transformed meiofauna densities. For the benthic samples: (a) samples vs. taxa plot and (b) samples vs. environmental variables plot. For the epiphytic samples (c) samples vs. environmental variables plot. ●, quadrats; ■, environmental variables; ★, meiofauna taxa. Environmental variables (see Table 2) are nutrients ( $\text{NO}_2 + \text{NO}_3$ ,  $\text{NO}_2$ ,  $\text{NH}_4$ ,  $\text{PO}_4$ ,  $\text{SiO}_2$ ), pigments (chlorophyll a, c and fucoxanthin), organic matter (%TOM is equal to % total organic matter) and sediment characteristics (median grain size, skewness, % gravel, % coarse sand, % silt). H.o., *Halophila ovalis*; H.w., *Halodule wrightii*; T.h., *Thalassia hemprichii*; S.i., *Syringodium isoetifolium*; H.s., *Halophila stipulacea*. I, first quadrat; II, second quadrat. Isop, Isopoda; Amph, Amphipoda; Cope, Copepoda; Cuma, Cumacea; Naup, Nauplii; Olig, Oligochaeta; Poly, Polychaeta; Gast, Gastropoda; Tard, Tardigrada; Pria, Priapulida; Roti, Rotifera; Hala, Halacarida; Cnid, Cnidaria; Nema, Nematoda; Turb, Turbellaria; Kino, Kinorhyncha; Lori, Loricifera; Biva, Bivalvia; Ostr, Ostracoda; Inse, Insecta larvae.



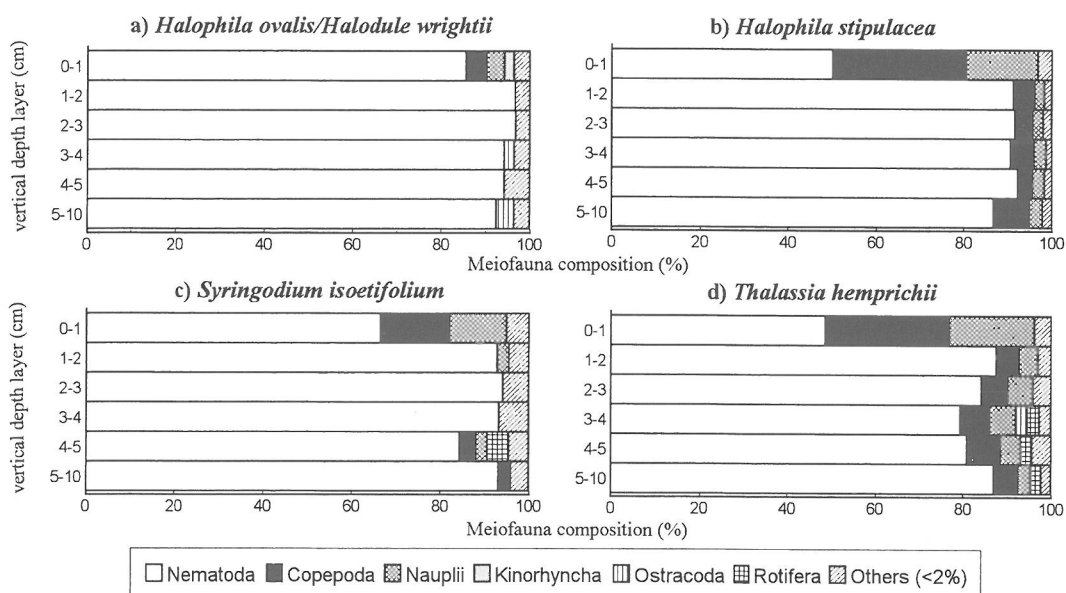


Fig. 8. Vertical distribution of meiobenthos ('benthic' samples) in terms of percentage in the four identified communities (a, b, c, d).

as most meiofauna taxa were found to a depth of 10 cm. In the top centimetre of the sediment, copepods reached 28.3% and nauplii 19.3%. Nematodes constituted almost half (48.6%) of the meiofauna in this layer. In deeper layers their abundance increased to 80%. Copepods and nauplii were present to a depth of 10 cm with an average of 5%. Ostracoda and Rotifera each represented 2.5%.

CA on the 'epiphytic' samples (Fig. 7c) showed two clearly separated assemblages of shallow (*H.o.* and *H.w.*) and deeper (*H.s.* and *S.i.*) seagrass species. The first quadrat of *H. wrightii* grouped together with the deeper seagrasses. This sampling quadrat showed a higher (but not significant) meiofauna diversity on higher taxon level (Fig. 6d). No clear pattern was found in the meiofauna taxa plot (not illustrated).

### 3.2. Environmental data

Apart from the a priori known position in the tidal zone, no significant differences in field data were found between quadrats (i.e. I and II for each seagrass bed, data analysis not shown). CCA (Fig. 7b and c) was performed to relate meiofauna distribution to

environmental variables as sediment characteristics, pigment and nutrient concentrations (Table 2).

Important environmental variables for the 'benthic' samples (Fig. 7b) were: sediment grain size skewness, median grain size, % TOM and  $\text{SiO}_2$  along the first axis; fucoxanthin concentration and % silt along the second axis. All sediment samples had negative skewness, indicating a large proportion of fine particles (< median grain size). The importance of skewness largely reflects the less negative value for *H. wrightii* sediment. Median grain size was on average larger in stands of the deeper seagrasses: *H. stipulacea* ( $227.1 \pm 45.5 \mu\text{m}$ ), *S. isoetifolium* ( $179.6 \pm 11.0 \mu\text{m}$ ) and *T. hemprichii* ( $210.4 \pm 55.2 \mu\text{m}$ ). The coarser sediment fractions (% gravel and % coarse sand) for *Halophila* sp. and *H. wrightii* can be related to their pioneer function and concomitantly short period of sediment trapping, i.e. sedimentation of suspended matter (Den Hartog, 1967).

The percentage of TOM was twice as high for sediment in stands of *T. hemprichii* (3.6%), *S. isoetifolium* (4.4%) and *H. stipulacea* (3.4%) as in stands of *H. ovalis* (1.7%) and *H. wrightii* (1.7%). Furthermore,

Table 2  
Nutrients, pigments and sediment characteristics in both quadrats (I and II) near the different seagrass species

	<i>H. ovalis</i>		<i>H. wrightii</i>		<i>T. hemprichii</i>		<i>S. isoetifolium</i>		<i>H. stipulacea</i>	
	H.o.I	H.o.II	H.w.I	H.w.II	T.h.I	T.h.II	S.i.I	S.i.II	H.s.I	H.s.II
NO <sub>2</sub> + NO <sub>3</sub> (µg/l)	158.81	294.61	97.97	153.40	447.22	172.95	115.07	248.74	96.35	103.83
NO <sub>2</sub> (µg/l)	54.46	140.41	43.48	35.68	151.34	70.63	30.16	155.63	46.02	69.18
NH <sub>4</sub> (µg/l)	25866.43	36638.92	37212.04	23141.43	36490.39	30469.70	35514.27	41802.05	27532.72	35751.69
PO <sub>4</sub> (µg/l)	919.68	1215.85	1155.66	1301.73	4782.80	1586.81	2386.61	6088.99	4415.15	1691.68
SiO <sub>2</sub> (µg/l)	4243.48	5395.53	4853.27	5306.80	13952.78	8656.13	6743.61	9713.53	10815.94	5374.54
Fucoxanthine (µg/g)	0.87	1.15	3.88	0.28	1.62	4.51	1.83	5.26	2.64	1.56
Chlorophyll <i>a</i> (µg/g)	4.03	6.26	11.03	3.51	6.21	9.65	7.15	17.44	15.72	4.56
Chlorophyll <i>c</i> (µg/g)	0.16	0.19	0.91	0.11	0.42	0.68	0.54	0.94	0.99	0.24
% TOM	1.5	2.0	1.9	1.5	4.7	2.6	3.1	5.7	5.2	1.5
Median grain size (µm)	218.4	117.3	173.4	123.0	155.2	265.6	190.5	168.6	181.6	272.6
Skewness	-1.421	-1.145	-0.198	-0.572	-2.058	-1.263	-1.304	-1.785	-1.413	-1.726
% Gravel (>2 mm)	0.44	0.54	0.08	0.49	0.05	2.07	0.33	0.10	0.30	0.47
% Coarse sand (850–2000 µm)	2.95	3.33	1.31	7.34	0.26	7.20	1.18	0.59	2.70	3.25
% Silt (<63µm)	2.45	9.95	2.19	9.32	7.29	5.25	3.99	9.01	7.07	3.34

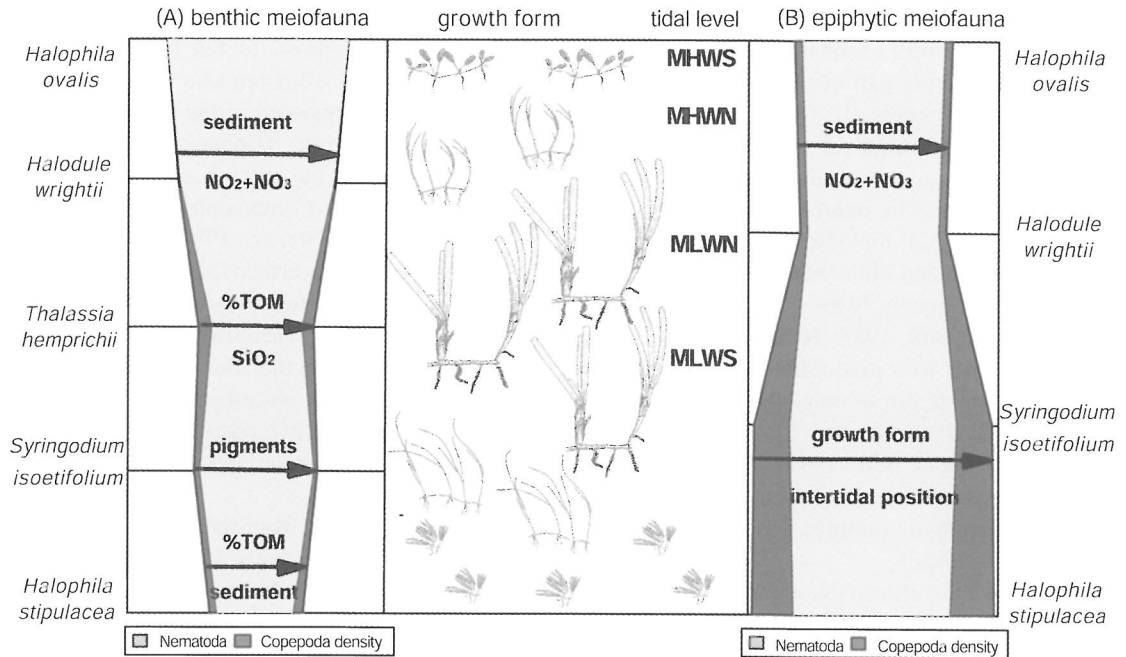


Fig. 9. General patterns of average nematode and copepod absolute densities from (A) 'benthic' and (B) 'epiphytic' samples and their structuring factors. The seagrass species are represented by their growth form and tidal position (MHWS, mean high water level at spring tide; MHWN, mean high water at neap tide; MLWS, mean low water level at spring tide; MLWN, mean low water at neap tide). All absolute densities were plotted on the same scale (max. value  $7500 \text{ ind. } 10 \text{ cm}^{-2}$ ). The arrows indicate the most important environmental factors structuring the associated meiofauna. The length of the arrows is not related to their relative importance.

$\text{SiO}_2$ -values were twice as high for the deeper seagrass samples as in the samples in the upper intertidal zone.

The difference in leaf morphology between both subtidal colonisers (*H. stipulacea* and *S. isoetifolium*) was reflected in only minor differences in copepod and nematode densities (both 'benthic' and 'epiphytic') (Fig. 9). Nevertheless, the related environmental factors were clearly different between both seagrass species. Important factors for the *Syringodium* assemblage were chlorophyll *c* and fucoxanthin, biogenic factors related to the plant and its epiphytes. A physical factor, % gravel, was determinant for the meiofauna assemblage structure associated with the small pioneer species *H. stipulacea*.

The main structuring factors for the meiofauna communities of the 'epiphytic' samples (Fig. 7c) in shallow seagrass beds were % gravel, % coarse sand and  $\text{NO}_2 + \text{NO}_3$  concentrations. For the deeper seagrasses, environmental factors grouped together (Fig. 7c) since they were plant-related: % TOM,

$\text{SiO}_2$  and phytopigments (chlorophyll *a*, chlorophyll *c* and fucoxanthin).

#### 4. Discussion

The maximum meiofauna density in this study was  $8478 \text{ ind. } 10 \text{ cm}^{-2}$ . This is among the highest densities reported for tropical seagrass beds: average densities reported in literature range between 634 and  $6251 \text{ ind. } 10 \text{ cm}^{-2}$  (Decho et al., 1985; Ansari and Parulekar, 1994; Aryuthaka, 1991; Aryuthaka and Kikuchi, 1996; Ndaro and Ólafsson, 1999). Duineveld et al. (1997) found only  $1029 \text{ ind. } 10 \text{ cm}^{-2}$  in the lagoon in Gazi Bay at an average depth of 50 m. These studies reported a general trend of higher total meiofauna densities in seagrass vs. bare sediment. The opposite trend, with higher meiofauna (Decho et al., 1985; Aryuthaka and Kikuchi, 1996) or copepod (Iwasaki, 1999) densities in bare sediment vs. seagrass samples, has only been reported in these three studies.

In our study, the highest meiofauna densities were found in ‘benthic’ samples near the shallow seagrass species and in the deeper part of the tidal gradient for the ‘epiphytic’ samples (Fig. 9). The effect of submergence was highly significant for copepods in general and for all meiofauna near the deeper seagrass species. No difference in number of taxa between ‘benthic’ and ‘epiphytic’ meiofauna was observed.

Nematodes dominated both ‘benthic’ and ‘epiphytic’ samples. This is generally the case in marine sediments (Hicks and Coull, 1983; Hicks, 1985; Heip et al., 1985), but shifts to a predominance of harpacticoid copepods and nauplii in epiphytic samples have been reported in the literature (e.g. Lewis and Hollingworth, 1982; Hall and Bell, 1993). We reported a comparable pattern with an increasing importance of copepods in the epiphytic samples, especially near the deeper seagrass species.

Several studies have shown the importance of vegetation providing shelter for macrofauna and their predators (Lewis, 1984; Orth et al., 1984; Bird and Jenkins, 1999). Coull and Wells (1983) proved the protective role of phytal habitats for meiofauna. The importance of crustaceans in samples from the deeper subtidal zone probably also reflects the protecting influence of the *T. hemprichii* leaves: many crustaceans, including harpacticoid copepods, are direct food for juvenile fishes (e.g. Sogard, 1984; Gee, 1989; Coull, 1990; De Troch et al., 1998), and may therefore seek the shelter of larger plants because of their higher habitat complexity. Heck and Wetstone (1977) found that above-ground plant biomass of *Thalassia testudinum* was significantly correlated with both macroinvertebrate species number and abundance, while Stoner (1980) demonstrated that the relative abundance of crustaceans was a function of both seagrass species and biomass. Hicks (1980) showed how harpacticoid species number and diversity increased linearly with increasing microspatial complexity over a range of habitats generated by different species of algae. Here we report a seagrass species-specific effect on density of copepods in the ‘benthic’ samples and of nematodes in the ‘epiphytic’ samples. The effect of seagrass morphology on diversity, however, was only significant for the deeper seagrasses.

The role of the above-ground habitat complexity was reflected in a more profound vertical distribution

of meiofauna in the sediment. *Thalassia* is the climax vegetation found down to the highest parts of the subtidal zone and is known as a slow growing genus which is firmly anchored in the substratum by well-developed rhizomes (Copejans et al., 1992). Although biomass has often been identified as a key organising factor in macrophyte-associated faunal assemblages (e.g. Stoner, 1980; Lewis, 1984), we found a comparable vertical distribution of meiofauna in the sediment near two seagrass species with clearly different biomass (*T. hemprichii* and *H. stipulacea*). The strong erosion in the zone colonised by *H. stipulacea* and the active bioturbation by amphipods and isopods (Fig. 7a) are two possible factors diversifying the sediment and the vertical depth profile of meiofauna.

The detritus input from the large *Thalassia* plants contributed to a relatively high organic matter (% TOM) in the adjacent bare sediment but resulted in a lower meiofauna density and higher diversity in the ‘benthic’ samples of the more subtidal seagrasses than in the shallow samples. This detritus input was of major importance to discriminate between shallow and deeper seagrass species, since both density and diversity of meiofauna of the adjacent deeper seagrasses were affected by this input. Moreover, the meiofauna assemblages associated with the deeper seagrasses (*T. hemprichii*, *S. isoetifolium*, *H. stipulacea*) were structured by biogenic factors, particularly organic matter (% TOM) (as discussed before) and pigments. The nutritional importance of seagrass plants for meiofauna is probably largely indirect, and the result of detritus–bacteria–meiofauna interactions (e.g. Pollard and Kogure, 1993b; Danovaro, 1996). Fenchel (1970) indicated that micro-organisms on detritus constitute the real food source for the detritivores rather than the nitrogen-poor residues of the macrovegetation. Meiofauna densities in seagrass beds were significantly related, with a time lag, to changes in bacterial standing stock, indicating that microbes may be an important resource (Danovaro, 1996). Tenore et al. (1977) illustrated an enhanced utilisation of seagrass detritus by polychaetes following stimulation of microbial growth by other meiofauna. In addition, epiphytic algae and benthic diatoms on seagrass leaves play an important role as primary producers (e.g. Kikuchi and Pérès, 1977; Dauby and Poulicek, 1995). Pollard and Kogure

(1993a) reported that epiphytic algae accounted for more than four times the above-ground primary production of *S. isoetifolium*.

Besides shelter and food, tidal disturbance clearly affected both composition and variability of meiofauna assemblages associated with the shallow seagrass species (*H. ovalis* and *H. wrightii*). Meiofauna associated with the pioneer species *H. ovalis* (i.e. the first species to establish on bare sediment) was a low diverse assemblage (but high benthic densities) dominated by nematodes. These seagrass species and associated fauna have to withstand significant stress in the high intertidal zone, e.g. desiccation at low tide and strong wave action. Harpacticoid copepods are known to be sensitive to low pore water content, regardless of the oxygen concentration (Hicks and Coull, 1983). Nematodes apparently exhibit a greater ability to withstand perturbations (Guerini et al., 1998). This difference can be a possible explanation for the low portion of copepods in the 'benthic' samples near these seagrasses. The higher density of copepods in the corresponding 'epiphytic' samples (Fig. 9) can be explained by the fact that the leaves of *H. ovalis* and *H. wrightii* overlap during low tide so as to minimise water loss (Björk et al., 1999). Shelled animals were abundant near the shallow seagrasses probably because of their ability to survive this episodic stress, e.g. by closing their shell. The importance of soft-bodied and burrowing taxa in this upper margin of the tidal zone can be explained by their ability to escape from stress conditions into the bottom. Our results, thus, suggest that this shallow meiofauna assemblage was largely structured by sediment characteristics (Fig. 9).

In contrast, meiofauna found in the deeper subtidal zone was mainly structured by plant-related environmental factors. We found higher concentrations of chlorophyll *c* and/or fucoxanthin, indicative of diatoms (Van den Hoek et al., 1995), near the deeper seagrasses. Reyes-Vasquez (1970) found that sediment characteristics can greatly affect the diatom flora of *T. testudinum*. In addition, higher SiO<sub>2</sub>-values were reported in the deeper zone, which can also favour diatoms (Sommer, 1996); on the other hand, SiO<sub>2</sub> is probably not limiting in tropical sediments with concentrations usually within millimol range (Alongi, 1990). These favourable conditions for diatoms provide a possible explanation for the impor-

tance of crustaceans feeding on diatoms (e.g. Hicks and Coull, 1983) in these samples.

Our data thus support the theory of 'biotic factors in stable environment' by Hulings and Gray (1976), which states that biological interactions control meiofauna abundances on atidal beaches, while on tidal beaches, sediment characteristics are major controlling factors.

From these results, we can conclude that within a given area, the overall effect of leaf morphology and related biomass of the seagrass species on meiofauna is indirect. Meiofauna is structured by environmental conditions as selected and partly created by the seagrass species, which indirectly means a seagrass species selection. The habitat selected by the seagrass species, in view of its role in the succession, in terms of grain size, organic matter and pigments determines the associated meiofauna. The variation within the meiofauna assemblage is also linked to the specific habitat requirements of the seagrass species: a high variation for a eurytopic coloniser and a low variation for a stenotopic (i.e. having a restricted range of distribution) climax vegetation.

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