Diversity and habitat selectivity of harpacticoid copepods from sea grass beds in Pujada Bay, the Philippines

MARLEEN DE TROCH[1], JENNY LYNN MELGO-EBARLE[2], LEA ANGSINCO-JIMENEZ[3], HENDRIK GHEERARDYN[1] AND MAGDA VINCX[1]

[1]Ghent University, Biology Department, Marine Biology Section, Campus Sterre—Building S8, Krijgslaan 281, B-9000 Ghent, Belgium, [2]Vrije Universiteit Brussel, Ecological Marine Management, Pleinlaan 2, B-1050 Brussels, Belgium, [3]Davao Oriental State College of Science and Technology (DOSCST), NSM Department, 8200 Mati, Davao Oriental, the Philippines

The spatial diversity of meiofauna from sea grass beds of Pujada Bay (the Philippines), was studied with special emphasis on harpacticoid copepods. Sediment cores were obtained from areas adjacent to the different species of sea grasses. Meiofauna was enumerated at higher taxon level and harpacticoid copepods were identified to genus level. Diversity indices were calculated corresponding to the hierarchical levels of spatial biodiversity, i.e. alpha, beta and gamma. Nematodes were the most abundant meiofaunal group in all sediment layers and along the entire tidal gradient (37–92%); harpacticoids were second in abundance (3.0–40.6%) but highly diverse (N_0: 9.33–15.5) at the uppermost sediment layer (0–1 cm) near all beds of sea grass species. There was a sharp turnover of harpacticoid genera along the tidal gradient, thus suggesting a relatively low proportion of shared genera among benthic communities in different sea grass zones. The families of Tetragonicipitidae and Miraciidae were the dominant harpacticoid groups occurring in all sediment layers of all sea grass species. The presence of the epiphytic genera of Metis *at the deepest sediment layers in some sea grass species was striking. Overall, the major contributor to gamma (total) diversity of harpacticoid copepods in Pujada Bay is the high local (alpha) diversity (N_0: 80.6%, H′: 94.7% of total diversity); hence, the habitat heterogeneity among sediment layers in sea grass beds is most relevant for the total diversity and richness of harpacticoid copepod genera in the area.*

INTRODUCTION

Diversity patterns are essential to understand the organization and functioning of organisms present in an ecosystem and their interaction with the environment (Duarte, 2000); this is true also in tropical coastal ecosystems, comprising links between organisms and their habitat, and also among different habitats (e.g. coral reefs, sea grass beds and mangroves). Sea grass meadows provide a complex habitat for the associated organisms, it is the basis of a complex ecosystem that is vulnerable to disturbances both natural and man-made (De Troch et al., 2001a; Gray, 2004; Snelgrove et al., 1997).

The continuum of spatial scales is divided into the following hierachical levels of biodiversity: alpha, beta and gamma diversity (Whittaker, 1972; Magurran, 1988; Ricklefs & Schluter, 1993). Diversity will allow ecologists to describe quantitative changes in species composition and abundances across environmental continua (Whittaker, 1960, 1972, 1975, 1977), e.g. horizontally (between different sea grass species in the tidal zone) and vertically (between sediment layers).

The marine meiofauna (metazoans that pass through a 1 mm sieve but are retained on a 38 μm sieve) and specially harpacticoid copepods, represent an important link between primary producers and higher trophic levels (Sogard, 1984; Fujiwara & Highsmith, 1997; Sutherland et al., 2000). In view of this crucial functional role and their high densities in detritus rich ecosystems, e.g. in sea grass beds (Bell et al., 1988; Bell & Hicks, 1991; De Troch et al., 2001a, b; Nakamura & Sano, 2005) several studies tried to unravel different aspects of their ecology, such as species diversity changes within and between habitats in tropical sea grass beds (e.g. De Troch et al., 2001a), response to small-scale natural disturbance (e.g. Thistle, 1980), feeding behaviour (e.g. De Troch et al., 2005; Gerlach, 1978), reproductive characteristics (e.g. Bell et al., 1988), niche segregation behaviour (e.g. De Troch et al., 2003) and colonization and recruitment of copepods in sea grass mimics (e.g. Bell & Hicks, 1991; Walters & Bell, 1994; De Troch et al., 2005).

Studies on the ecology of harpacticoid copepods in tropical sea grass beds are scarce and restricted to certain regions (e.g. Lakshadweep Atolls of Arabian Sea, Ansari & Parulekar, 1994; Caribbean part of Mexico, Kenyan coast, Zanzibar, De Troch et al., 2001b). Particularly, the Philippines deserve some research effort because it is recognized as an epicentre of biodiversity and evolution (e.g. Carpenter & Springer, 2005). Recent papers have described new species of Copepoda (Suárez-Morales, 2000; Walter et al., 2006) but the benthic meiofauna remains unstudied. In this survey we determine and analyse the spatial levels of biodiversity of harpacticoid

Corresponding author:
M. De Troch
Email: marleen.detroch@ugent.be

copepods within the sea grass bed areas at Pujada Bay, the Philippines.

MATERIALS AND METHODS

Meiofauna samples were collected in May and June 1998 in the sea grass beds near Guang-Guang in Pujada Bay (66°56′N 126°15′–17′E), located at the south-eastern part of the Philippines, on the island of Mindanao (Figure 1). Two transect lines were laid perpendicular to the beach, starting from the lowest pneumatophores of the nearby mangroves down to the subtidal zone and, thus, crossing several meadows of different sea grass species (Figure 2). Both transects were separated approximately 100 m from each other. A total of eight 5×5 m quadrats (area of 25 m²) were positioned along the transect lines in beds of the different sea grass species: *Halophila minor*, *Halodule uninervis*, *Thalassia hemprichii* and *Syringodium isoetifolium* (Figure 2). In each quadrat, triplicate meiofauna samples were collected in bare sediment spots adjacent to the sea grass species using polyvinyl chloride (PVC) sediment cores with an inner diameter of 3.6 cm (area of 10 cm²). This was done by snorkelling within a time range of two hours before to two hours after low tide in an average water depth of 1 to 1.5 m. Subsequently, meiocores were vertically subdivided into different depth layers using a standard Hagge corer (Fleeger *et al.*, 1988): 0–1 cm, 1–2 cm, 2–3 cm, 3–4 cm, 4–5 cm and 5–10 cm. Samples were preserved in 4% buffered formalin. In addition, two samples for nutrient and sediment analysis were taken from each quadrat in between the sea grass plants using a core with an inner diameter of 6.2 cm. These were subdivided into the same six depth layers and stored frozen for further analysis. For chlorophyll-*a* (chl-*a*) analysis, triplicate sediment samples (~1 ml) were taken within each quadrat using a syringe with the lower end cut off, and were subdivided into the same depth layers.

In the laboratory, the meiofauna samples were gradually rinsed with fresh water, decanted ($10\times$) over a 38 μm sieve, centrifuged three times with Ludox HS40 (specific density 1.18), stained with rose Bengal and identified to higher taxon level based on Higgins & Thiel (1988) using a Wild M5 binocular. Harpacticoid copepods were counted, picked out per hundred (as they were encountered during counting) and stored in 75% ethanol. Harpacticoid copepods were identified to genus level using the identification keys and reference books by Boxshall & Hasley (2004) and Lang (1948, 1965) and original genus and species descriptions. Identification of harpacticoid copepods were only restricted to the adult stage.

Sediment samples were thawed and the analyses for NO_2, NO_3, NH_4, PO_4 and SiO_2 content were performed using an A_{II} automatic chain (SANplus Segmented Flow Analyser, SKALAR). Part of the remaining sediment samples were dried at 110°C for four hours. These were used for analysis of total organic matter (% TOM), measured as weight loss after combustion at 550°C for two hours. Sediment grain size was analysed with a particle size analyser (type Coulter® LS100) on gram-aliquots dried at 60°C for twenty-four hours. Sediment characteristics obtained were median grain size, silt (<63 μm) content (%), coarse sand (850–2000 μm) content (%) and gravel (>2000 μm) content%). Pigments were extracted with 90% acetone at 4°C in the dark and separated by reverse phase liquid chromatography on a Gilson C-18 high performance liquid chromatography-chain (spectrophotometric and fluorometric detection) according to the modified protocol of Mantoura & Llewellyn (1983).

Hill's (Hill, 1973) diversity indices were used to calculate alpha diversity (see definition in Table 1) using the PRIMER 5 software (version 5.2.8): N_0 = number of genera; N_1 = exp (H′), with H′ the Shannon–Wiener diversity index based on the natural logarithm (ln).

Beta diversity of harpacticoid copepods (see definition in Table 1) represents the range of species turnover along the transect line or gradient. This is measured by the number of harpacticoid genera shared between two sea grass species and all other species of sea grass based on the arbitrarily defined spatial units/intersite distance: 1 unit for the nearest neighbour, 2 units for the second nearest neighbour and so on (see De Troch *et al.*, 2001a). The results were then plotted in a radar chart. The graphical presentation of the radar charts allows an interpretation of the relation between intersite distance and number of genera shared as the surface of the radar chart is an indirect measure for the specificity of the copepod community associated with a particular sea grass species (De Troch *et al.*, 2001a).

Gamma diversity (see definition in Table 1) was analysed based on additive partitioning of the spatial levels of diversity using PARTITION software (true basic edition) (Crist *et al.*, 2003).

Community structure was analysed through non-metric multidimensional scaling (MDS) analyses using the Bray–Curtis similarity index (data were fourth-root transformed prior to analysis) (PRIMER 5 (version 5.2.8)) and canonical correspondence analysis (CCA ordination) (CANOCO (version 4.5)). Relative abundance was expressed as percentages.

RESULTS

Meiofauna in sea grass beds of Pujada Bay

The average total meiofauna density obtained in the sea grass beds of Pujada Bay was 5310 ind/10 cm² (Table 2). A decreasing pattern of meiofauna densities was observed from the top sediment layers towards the deeper layers (Table 2). Likewise, fluctuating meiofauna total densities in each sea grass species were observed from the intertidal to the subtidal zone (Figure 2). Meiofauna assemblages in the intertidal pioneering sea grass species (*H. minor* and *H. uninervis*) showed to be similar and formed one community, whereas the subtidal sea grass species (*T. hemprichii* and *S. isoetifolium*) formed a different community (MDS not shown).

The main meiofaunal groups (>5%) encountered in the adjacent sediments of the sea grass species were Nematoda, Copepoda, nauplii and Polychaeta based on relative composition (Figure 3). Nematodes showed the highest relative abundance (37.0–92.0%) in all sea grass samples and in all sediment layers followed by copepods (3.0–40.6%), nauplii (0.3–15.3%), and polychaetes (0.5–10%). The meiofaunal assemblage associated with *H. minor* in the high intertidal area was nearly homogeneous throughout the sediment layers (below 1–2 cm depth). The relative abundance of Halacarida (0.8–5.5%) was found to be high only in the
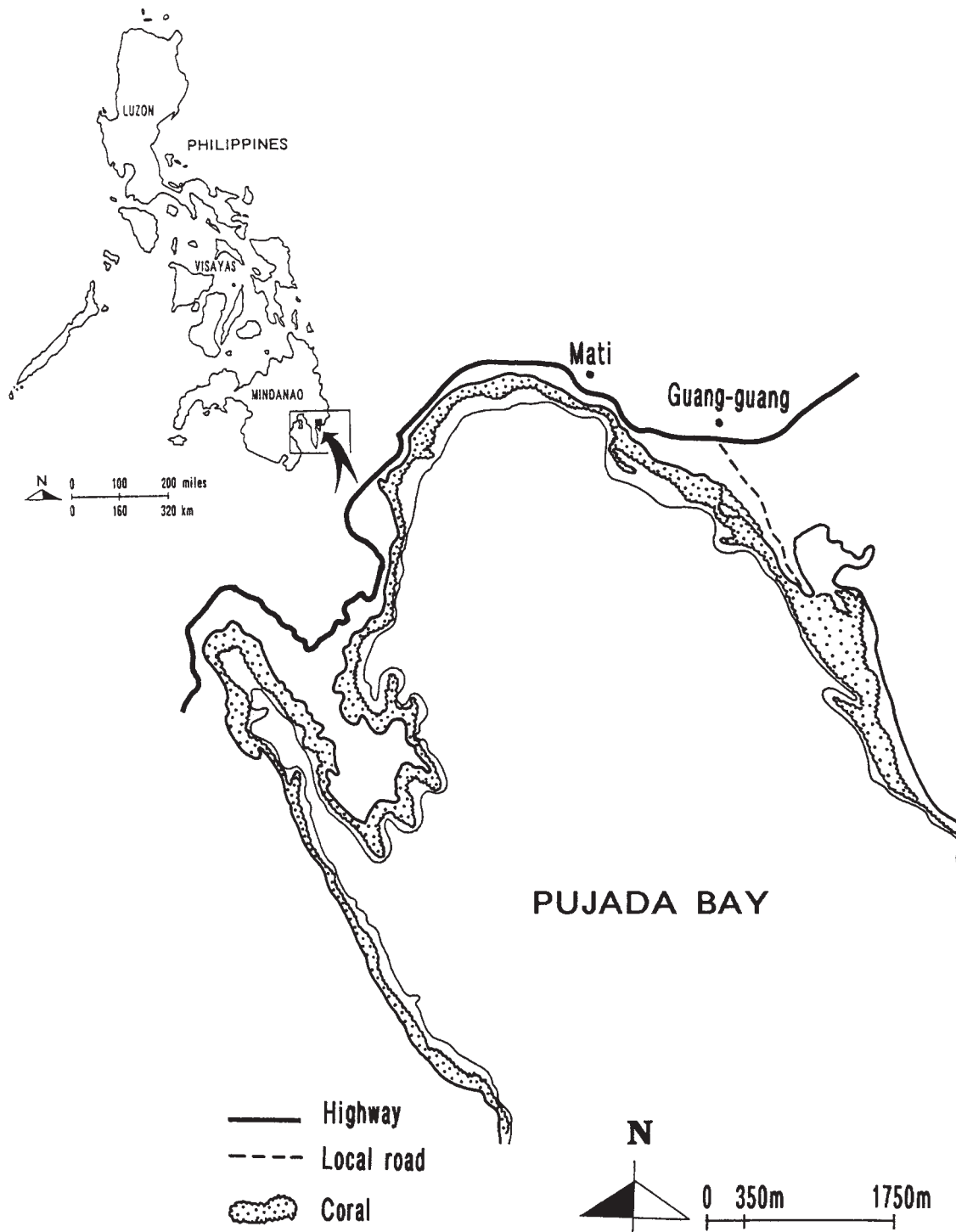
Fig. 1. Map of the Philippines with indication of the sampling site in Pujada Bay.

sediment adjacent to *H. uninervis*. Along the vertical sediment profile near *T. hemprichii*, aside from the high relative abundance of nematodes (36.8–90.5%) and copepods (40.6–6.0%), a remarkably high relative abundance of nauplii (15.3–1.4%) was observed. In the adjacent sediment layer of *S. isoetifolium*, relative abundance of nematodes showed no distinct pattern, yet, it still reached high percentages. In addition, relatively high abundances of polychaetes (3.0–10.0%) were observed near *S. isoetifolium* (Figure 3).

Harpacticoid copepod composition and community structure

In total, 35 harpacticoid genera belonging to 18 families were identified in the sediments adjacent to the different sea grass species beds (Table 3). A non-metric multidimensional scaling (MDS, Bray–Curtis similarity index) based on the fourth root-transformed relative abundances/transect data showed no clear correspondence between copepod communities and sea grass zonation (Figure 4A). In this MDS plot,
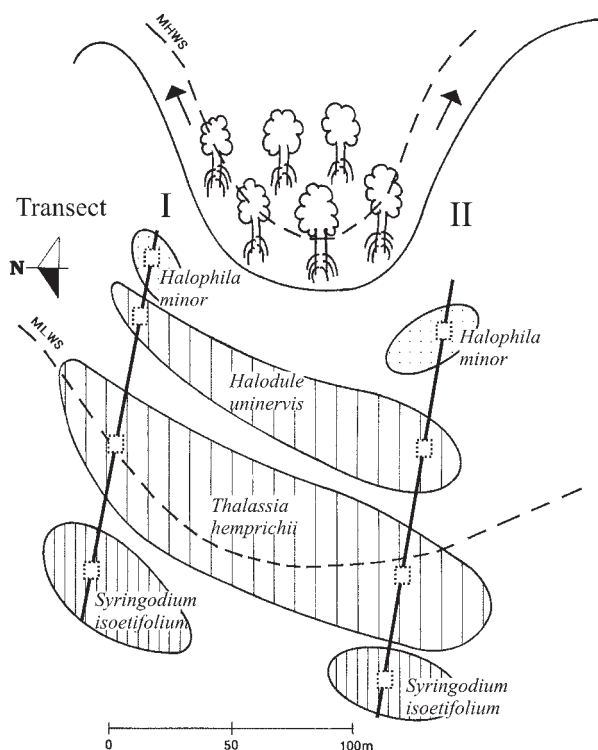
Fig. 2. The sampling strategy scheme applied in the sampling site.

the large distance between the *H. minor* samples illustrates the high variance between both transects in the high intertidal zone (Figure 4A). Although the harpacticoid copepod assemblages observed for each transect *per se* showed indistinct assemblages along the tidal gradient, the pooled results of harpacticoid copepod assemblages (Figure 4B) followed the growth forms of sea grasses; secondary pioneer sea grasses (*H. uninervis* and *S. isoetifolium*) were more similar to each other than to the primary pioneer sea grass (*H. minor*) and the climax sea grass species (*T. hemprichii*).

HIGH INTERTIDAL PIONEER ASSOCIATION:
HALOPHILA MINOR

In the *H. minor* samples, Miraciidae, Tetragonicipitidae, Paramesochridae and Ectinosomatidae were the most abundant families along the sediment profile (Figure 5). The relative abundance of the family Tetragonicipitidae (7.5–24.5%) showed a decreasing pattern with increasing depth, except in the deepest layer. The relative abundance of the family Miraciidae changed only slightly (16.8–33.1%). Higher

variance of the relative abundance of the families Paramesochridae (6.5–32.2%) and Ectinosomatidae (6.5–22.2%), and low relative abundances of Thalestridae (2.4–12.6%) were observed in the different layers. Representatives of the family Tegastidae were found in relatively high abundances in the deeper sediment layers (3 to 5 cm depth). The family Tisbidae was present in some sediment layers, but occurred in very low abundances (<5%).

HIGH INTERTIDAL SECONDARY PIONEER
ASSOCIATION: HALODULE UNINERVIS

The *H. uninervis* zone was situated in the higher intertidal area next to *H. minor* (Figure 2). An increase in relative abundance of Tetragonicipitidae was observed from 0–1 cm to 2–3 cm depth into the sediment (12.7–36.7%) and from 3–4 cm to 5–10 cm depth into the sediment (12.7–0.4%) (Figure 5). Relative abundance of Miraciidae varied in the upper sediment layers of 0–3 cm depth and decreased towards 5–10 cm depth. Likewise, the relative abundances of Tisbidae (8.3–20.2%) and Ectinosomatidae (10.0–10.6%) showed variation along the sediment profile. Cletodidae (2.6–12.2%) and Canuellidae (1.7–8.9%) were not present in the deepest layer (5–10 cm). The family Metidae was present in all sediment layers but with low relative abundances (1.4–6.3%).

SUBTIDAL CLIMAX ASSOCIATION: THALASSIA
HEMPRICHII

The harpacticoid copepods occurring near *T. hemprichii* did not show a distinct vertical change in relative abundance with increasing sediment depth (Figure 5). The families Tetragonicipitidae (15.4–49.0%) and Miraciidae (17.0–38.4%) were relatively abundant in all sediment layers. The other harpacticoid copepod families occurred with lower relative abundances (0.6–20.2%) in the different sediment layers. The family Cletodidae was absent in certain sediment layers.

HIGH SUBTIDAL SECONDARY PIONEER
ASSOCIATION: SYRINGODIUM ISOETIFOLIUM

In the adjacent sediments of *S. isoetifolium*, the family Tetragonicipitidae was relatively abundant in all sediment layers (Figure 5). Representatives of the families Miraciidae and Tisbidae were of second importance but more variance was recorded in these families in comparison to the other sea grass associations. The family Thalestridae was recorded in four sediment layers (2.4–12.6%) but was absent in the sediment layer of 3 to 5 cm depth into the sediment. The families Ectinosomatidae (2.4–7.7%) and Cletodidae (1.8–12.1%) occurred in very low relative abundances along the

Table 1. Definitions and interpretations of different spatial levels of biodiversity.

Diversity level	Original definition by Whittaker (1960, 1967, 1972, 1977), MacArthur (1965), Cody (1986)	Concept interpretation in present study
Alpha diversity (within-habitat diversity) (inventory diversity)	Sample of a community regarded as homogeneous	Variance between different sediment layers
Beta diversity (between-habitat diversity) (differentiation diversity)	Change along an environmental gradient or among the different communities in a landscape	Diversity changes between different sea grass species along the tidal gradient
Gamma diversity (total diversity)	Diversity of larger unit, i.e. between transects	Total diversity in Pujada Bay, the Philippines

Table 2. Average total density of meiofauna (ind/10 cm²) between sediment layers and between sea grass species in Pujada Bay, the Philippines. Mean ± standard error.
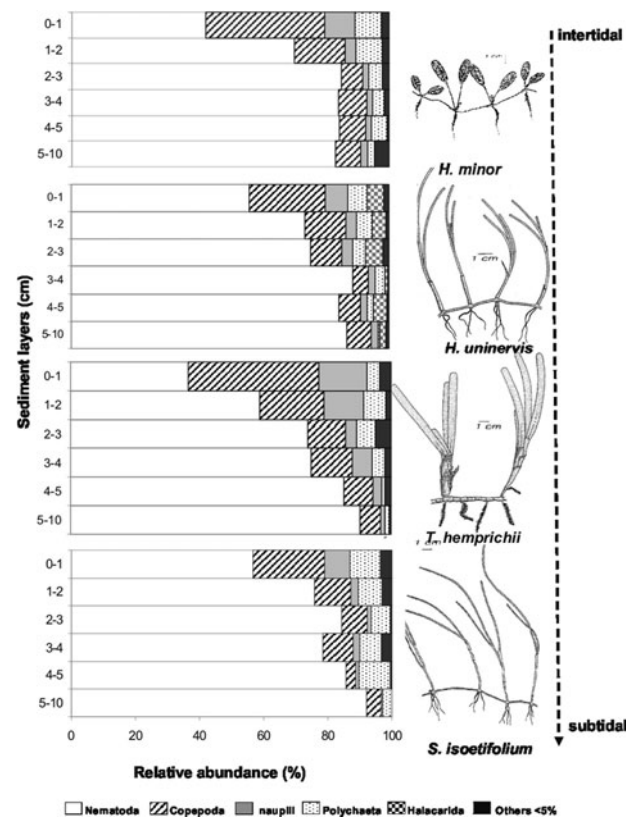
Sediment layer (cm)	Intertidal sea grass species		Subtidal sea grass species	
	Halophila minor (ind/10 cm²)	Halodule uninervis (ind/10 cm²)	Thalassia hemprichii (ind/10 cm²)	Syringodium isoetifolium (ind/10 cm²)
0–1	255 ± 86	567 ± 142	487 ± 79	448 ± 235
1–2	185 ± 18	287 ± 65	337 ± 90	455 ± 239
2–3	123 ± 10	224 ± 79	214 ± 0.70	263 ± 110
3–4	114 ± 50	217 ± 11	111 ± 20	145 ± 50
4–5	90 ± 33	219 ± 20	112 ± 40	147 ± 35
5–10	36 ± 12	130 ± 30	85 ± 44	62 ± 2.60
Average total density/sea grass	802	1644	1345	1519
Total density regardless of sea grass species			5310	

sediment profile. Low relative abundances of the family Metidae were observed between sediment layers, except at depths 4–5 cm, where higher abundance (23.0%) was noted. In addition, the family Canuellidae (4.7–11.7%) was barely encountered in the different sediment layers.

Environmental factors

Based on the CCA analysis (Figure 6), the left side of the CCA ordination plot was largely influenced by silty sediments in the bottom sediment layers of *H. uninervis*, *S. isoetifolium* and *T. hemprichii* (Figure 6). Moreover, the upper sediment

Fig. 3. Average relative abundance (%) of meiofauna in sediment layers adjacent to the different sea grass species. Meiofauna groups with a relative abundance of >5% were shown while taxa with <5% of relative abundance were grouped as 'others'.

layers of these three sea grass stands were also characterized by % TOM, PO_4, chl-*a*, NH_4 and SiO_2. The right side of the ordination plot was mainly characterized by coarse sand, gravel and nitrate concentration. These factors were associated with higher pigment contents which were mostly observed at the surface sediment layers. The sediment where the high intertidal pioneer sea grass species (*H. minor* and *H. uninervis*) grow were characterized mostly by coarser sand and gravel sediments. The adjacent sediments of the subtidal sea grass species consisted of a mixture of coarse sand and gravel in the upper sediment layers and silt in the bottom layers. High silt content governed the copepod communities in the deeper sediment layers, especially in the *S. isoetifolium* sediments (average silt content: 43.9 ± 0.6%). Harpacticoid genera with a higher affinity for silty sediments were *Echinolaophonte*, *Paraleptastacus*, *Diagoniceps*, *Leptocaris* and *Mesochra*, which were commonly found in the deeper sediment layers of *H. uninervis*, *S. isoetifolium* and *T. hemprichii*. While harpacticoid genera such as *Dactylopodia*, *Esola*, *Hastigerella*, *Syngastes*, *Tegastes* and *Apodopsyllus* were mostly found in the coarse sand sediments of *H. minor*.

Alpha diversity: variance of diversity between sediment layers

Diversity within sediment layers was checked with k-dominance curves (Lambshead *et al.*, 1983) since these are less sensitive to differences in sample size (see De Troch *et al.*, 2001a). The k-dominance curves (graphs not shown) revealed the highest diversity in the surface sediment layer. Likewise, Hill's diversity indices showed a high diversity at the upper sediment (0 to 3 cm) layers, as shown by N_0 (3.7–15.5) and N_1 (3.7–11.2). In general, average harpacticoid diversity (N_1) decreased with increasing sediment depth (Figure 7). However, a slight increase of diversity in the deeper layers of sediments was observed in the intertidal zone (*H. minor* and *H. uninervis*) while in the subtidal zone (*T. hemprichii* and *S. isoetifolium*), a distinctly decreasing diversity with sediment depth was observed (Figure 7).

Beta diversity: harpacticoid diversity changes between sea grass species

A change in harpacticoid diversity between sea grass species or along the tidal gradient was observed. The richness and
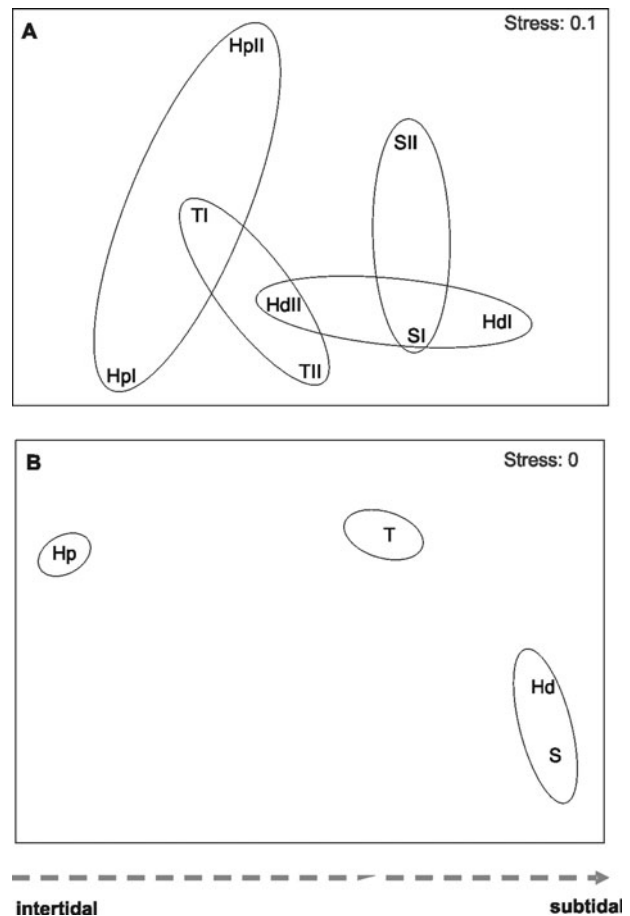
Table 3. Harpacticoid copepod families and genera, found in Pujada Bay, the Philippines.

Family name	Genus name
Ameiridae	*Stenocopia* Sars, 1907
Canthocamptidae	*Canthocamptus* Westwood, 1836
	Mesochra Boeck, 1865
Canuellidae	*Brianola* Monard, 1927
	Canuella T. Scott & A. Scott, 1890
Cletodidae	*Cletodes* Brady, 1872
Darcythompsoniidae	*Leptocaris* T. Scott, 1899
Ectinosomatidae	*Ectinosoma* Boeck, 1865
	Hastigerella Nicholls, 1935
	Noodtiella Wells, 1965
Laophontidae	*Echinolaophonte* Nicholls, 1941
	Esola C.L. Edwards, 1891
	Laophonte Philippi, 1840
	Paralaophonte Lang, 1944
	Quinquelaophonte Wells, Hicks & Coull, 1982
Leptastacidae	*Paraleptastacus* C.B. Wilson, 1932
Longipediidae	*Longipedia* Claus, 186
Metidae	*Metis* Philippi, 1843
Miraciidae	*Amphiascus* Sars, 1905
	Stenhelia Boeck, 1865
	Typhlamphiascus Lang, 1944
Orthopsyllidae	*Orthopsyllus* Brady & Robertson, 1873
Paramesochridae	*Apodopsyllus* Kunz, 1962
	Paramesochra T. Scott, 1892
Porcellidiidae	*Porcellidium* Claus, 1860
Tegastidae	*Syngastes* Monard, 1924
	Tegastes Norman, 1903
Tetragonicipitidae	*Diagoniceps* Willey, 1930
	Laophontella Thompson & A. Scott, 1903
	Phyllopodopsyllus T. Scott, 1906
	Tetragoniceps Por, 1964
Thalestridae	*Dactylopusia* Norman, 1903
	Diarthrodes G.M. Thomson, 1883
	Paradactylopodia Lang, 1944
Tisbidae	*Tisbe* Lilljeborg, 1853

Fig. 4. Multidimensional scaling of harpacticoid benthic copepods of the different sea grass samples in (A) both transects and (B) for pooled data, based on the Bray–Curtis similarities. Data were 4th root transformed prior to analysis. Sea grass species: Hp, *Halophila minor*; Hd, *Halodule uninervis*; S, *Syringodium isoetifolium*; T, *Thalassia hemprichii*. Transects: I, Transect 1, II; Transect 2.

diversity of harpacticoid copepods in the adjacent sediments of *H. uninervis* and *T. hemprichii* showed higher values in comparison to the other sea grasses (Figure 7). Additionally, the calculated number of shared copepod genera between the different sea grass species (based on the arbitrarily defined spatial units, see De Troch et al., 2001a) was plotted in a radar graph (Figure 8). The radar graph of *H. uninervis* shows a relatively larger surface which indicates a high number of shared genera with the adjacent sea grass species (Figure 8). The adjacent sediments of *S. isoetifolium* (located in the subtidal area and distant to other sea grass species) showed a low number of shared harpacticoid genera. There were more shared genera between the adjacent sediments of *H. uninervis* and *T. hemprichii*. In addition, a higher number of shared harpacticoid genera were also observed between the adjacent sediments of *H. minor* and its neighbouring sea grass species (Figure 8).

Gamma diversity: total diversity of harpacticoid copepods in Pujada Bay

Additive partitioning of total diversity showed that alpha diversity (between sediment layers) was an important contributor for total genus richness (N_0: 80.6%) in Pujada Bay

(Figure 9). On the other hand, beta diversity (β_1-diversity: 14.6%, β_2-diversity: 4.9%) showed low contribution to total harpacticoid diversity. Furthermore, when abundance data are taken into account (with H′), the alpha diversity gained an importance (94.7%) whereas beta diversity (β_1-diversity: 5.1% and β_2-diversity: 0.2%) contributed less.

DISCUSSION

In the present study, the total meiofauna density is closer to the highest extreme abundance of the reported ranges of 457 to 8478 ind/10 cm² in tropical sea grass beds (Decho et al., 1985; Ansari & Parulekar, 1994; Aryuthaka & Kikuchi, 1996; Ndaro & Ólafsson, 1999; De Troch et al., 2001a, b). Differences in meiofauna density and diversity patterns between regions (Kenya, Mexico and the Philippines) are mainly due to local processes (e.g. tidal regimes and input of organic matter) (De Troch et al., 2006). The meiofauna communities observed along the tidal gradient differ in sediment grain size, organic matter content and sea grass succession (Hulings & Gray, 1976; Ansari et al., 1991; De Troch et al., 2001b). Furthermore, Da Rocha et al. (2006) found
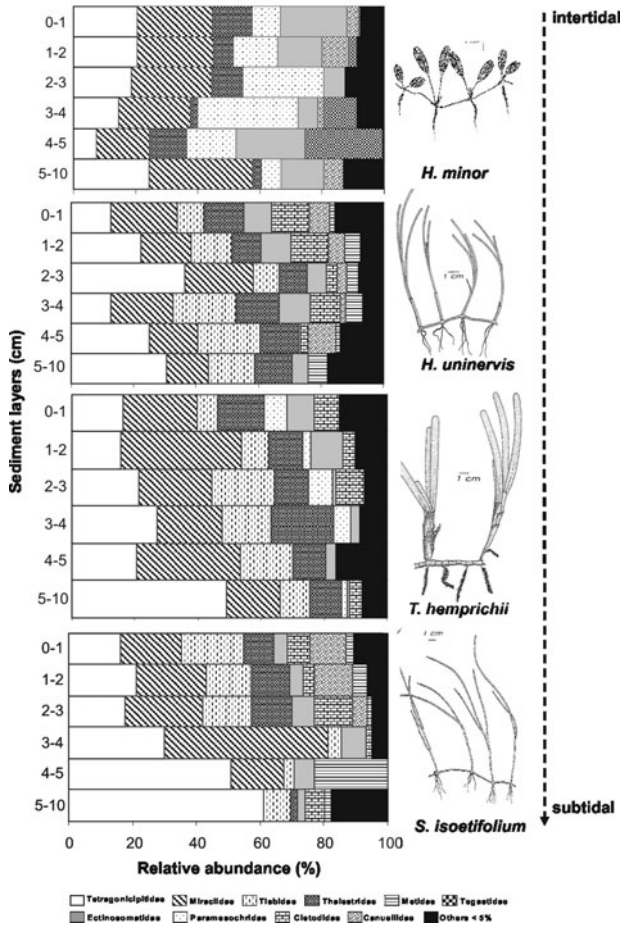
Fig. 5. Vertical distribution of harpacticoid copepods in the sediment layers: relative abundances for the four sea grass communities.

Fig. 6. Canonical correspondence analysis ordination plot of harpacticoid copepods relative abundance data and environmental variables. Symbols: Δ, harpacticoid copepods; ●, sea grass species and their corresponding sediment depth. The arrows indicate the environmental variables. Sea grass species: Hp, *H. minor*; Hd, *H. uninervis*; S, *S. isoetifolium*; T, *T. hemprichii*. Sediment depth: 1 = 0–1 cm, 2 = 1–2 cm, 3 = 2–3 cm, 4 = 3–4 cm, 5 = 4–5 cm, 6 = 5–10 cm. Harpacticoid copepods genera: Long, *Longipedia*; Bria, *Brianola*; Can, *Canuella*; Ect, *Ectinosoma*; Has, *Hastigerella*; Noo, *Noodtiella*; Tis, *Tisbe*; Dia, *Diarthrodes*; Par, *Paradactylopodia*; Dac, *Dactylopodia*; Ste, *Stenhelia*; Amp, *Amphiascus*; Typ, *Typhlamphiascus*; Met, *Metis*; Para, *Paramesochra*; Apo, *Apodopsyllus*; Phy, *Phyllopodopsyllus*; Lao, *Laophontella*; Tet, *Tetragoniceps*; Dia, *Diagoniceps*; Mes, *Mesochra*; Cantho, *Canthocamptus*; Cle, *Cletodes*; Echi, *Echinolaophonte*; Paralao, *Paralaophonte*; Laoph, *Laophonte*; Qui, *Quinquenlaophonte*; Orth, *Orthopsyllus*; Teg, *Tegastes*; Syn, *Syngastes*; Lep, *Leptocaris*; Paralep, *Paraleptastacus*; Steno, *Stenocopia*; Por, *Porcellidium*. Environmental variables: nutrients ($NO_2 + NO_3$, NO_2, NH_4, PO_4, SiO_2); pigments (chlorophyll-*a*); total organic matter; and sediment characteristics (% gravel, % coarse sand, % silt).

different nematofauna assemblages in macrophytes and adjacent sediments. The homogeneous distribution of the meiofauna observed in the lower layers of the adjacent sediment of the small pioneer sea grass plant, *H. minor*, could be explained by its position in the high intertidal zone where it is mostly affected by local disturbance (e.g. tidal currents and desiccation). However, a higher relative abundance of harpacticoid copepods was observed at the surface sediment layers of *H. minor*. According to Coull (1999), coarse sand sediments are dominated by copepods and to a lesser extent by nematodes. The leaves of *H. minor* overlap during low tide in order to minimize water loss (Björk et al., 1999), thus, protecting both the associated fauna and the underlying sediment from desiccation. The climax subtidal sea grass *T. hemprichii* is known to store a significant amount of carbon and TOM in the sediments which represents an available food source and habitat (Duarte, 2000). This would explain the relatively high abundance of meiofauna in these sediments.

Among the meiofauna groups, the Nematoda, exhibited the highest relative abundance in the different sediment layers and sea grass species along the tidal gradient, followed by the harpacticoids. Their resilience to withstand perturbations (Guerrini et al., 1998) and their tolerance to low oxygen content (Steyaert et al., 2005) in deeper sediment layers explain their dominance in the sediment layers examined. The rest of the meiofauna groups occurred
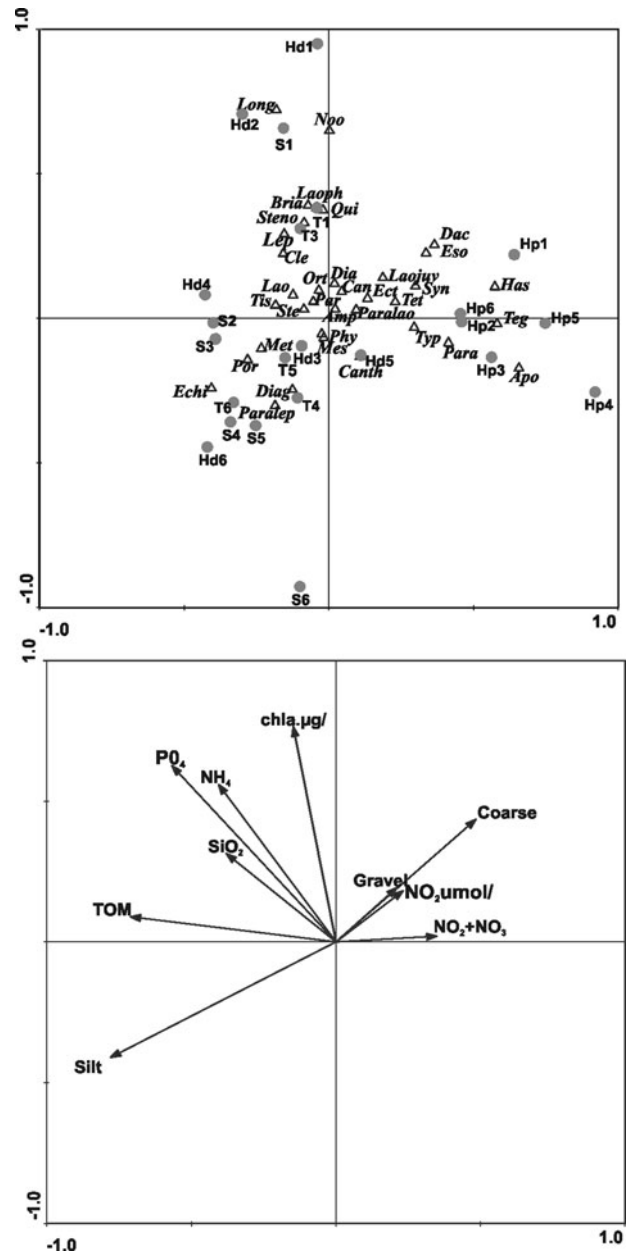
in low relative abundances (e.g. nauplii, Polychaeta, Halacarida, Tardigrada and Ostracoda) and were mostly limited to the oxygenated, upper sediment layers. Nauplii
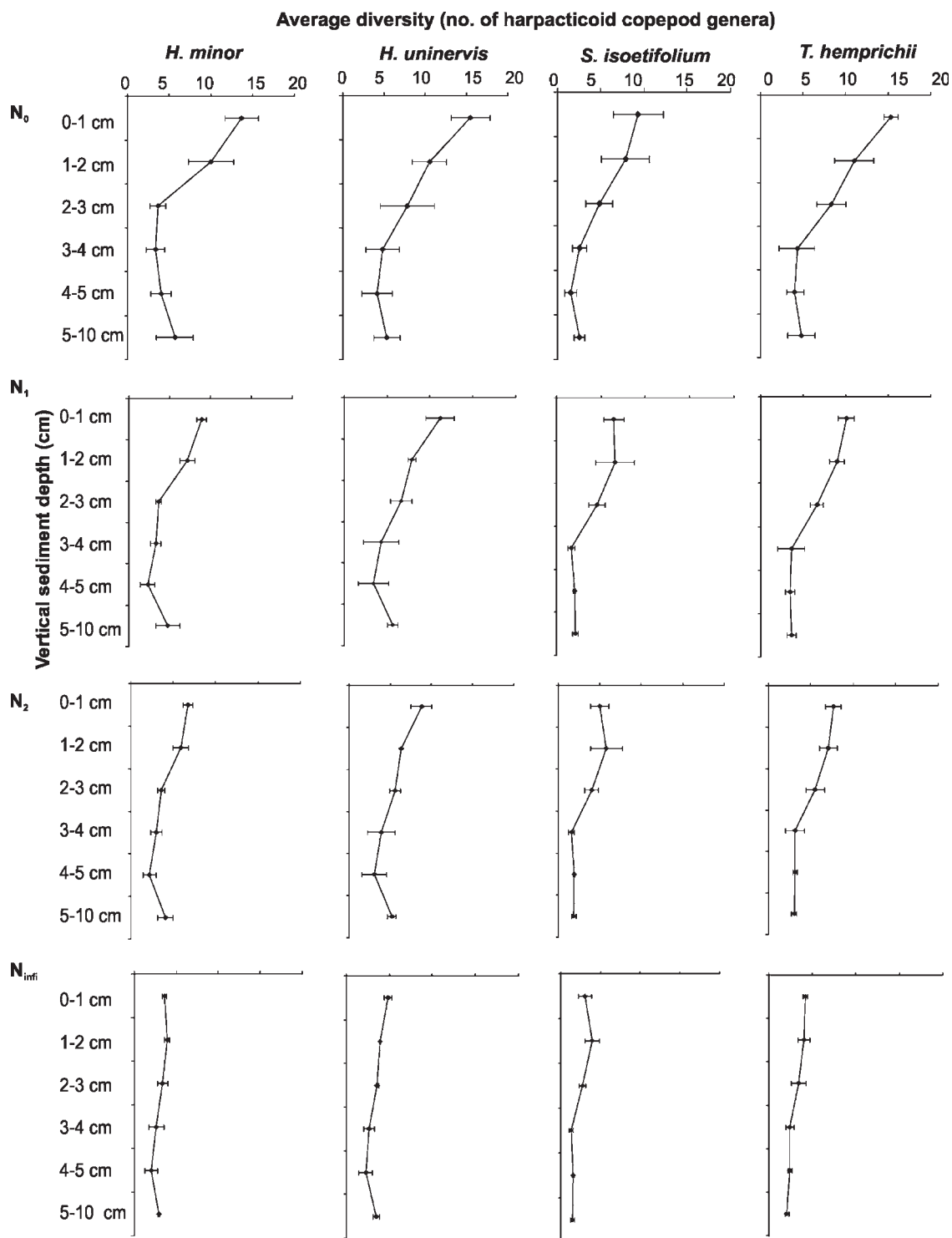
Fig. 7. Average harpacticoid diversity within the different sediment layers, as shown by Hill's indices (N_0, N_1). N_0 indicates the number of genera, N_1 denotes the harpacticoid copepod diversity.

(crustacean larvae) and cnidarians were slightly abundant in the subtidal zone, where pigments, nutrients and TOM contents were high.

Harpacticoid copepods community structure

TIDAL GRADIENT

Harpacticoids constituted approximately 13% of the total meiofauna in sea grass beds in Pujada Bay. There was no clear assemblage structure per transect in the adjacent sediments of the different sea grass species (Figure 4). This indistinct pattern could be due to the emergence of harpacticoid copepods, since sampling was done at shallow depths (at most 1.5 m). Differences in the assemblage structure of copepods in the *H. minor* plots might be related to the position of this sea grass at the highest intertidal fringe, clearly exposed to physical and chemical disturbances. Moreover, the generic distribution of harpacticoids corresponded to the different
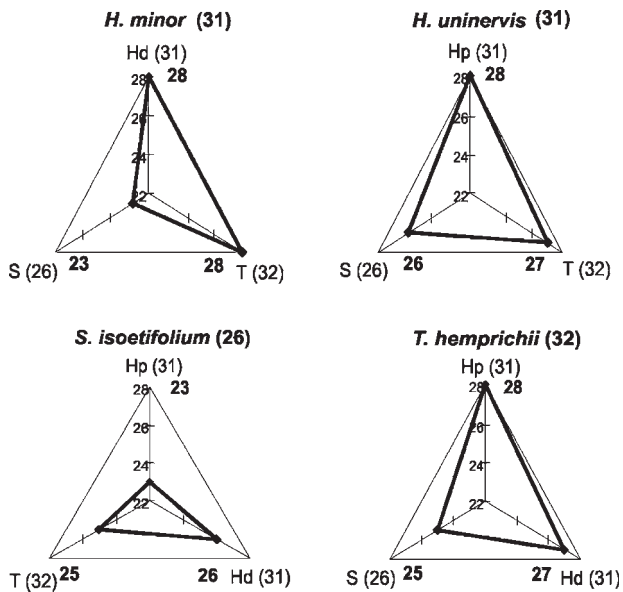
Fig. 8. Radar charts depicting the number of copepod genera shared between each sea grass species and all other sea grass species. The total number of copepod genera in the sediment adjacent to each sea grass species is indicated in parentheses. Sea grass species: Hp, *Halophila minor*; Hd, *Halodule uninervis*; S, *Syringodium isoetifolium*; T, *Thalassia hemprichii*.

sea grass species surveyed: *H. minor, H. uninervis, T. hemprichii* and *S. isoetifolium*.

VERTICAL GRADIENT

Harpacticoid abundance and diversity was highest at the top sediment layers; both were progressively lower at deeper sediment strata (Figures 6 & 7). The slight increase of diversity related to the bottom sediment layer of the intertidal sea grass species (*H. minor and H. uninervis*) could be explained by the larger grain size of the sediment (e.g. coarse sand), which is known to enhance water pore permeability and habitat complexity of microbial flora (Ravenel & Thistle, 1981). This feature implies an advantageous effect for the meiobenthic fauna.

The diversity decrease at increasing sediment depths along the subtidal sea grass species (*T. hemprichii and S. isoetifolium*) might be caused by the silty, low permeability
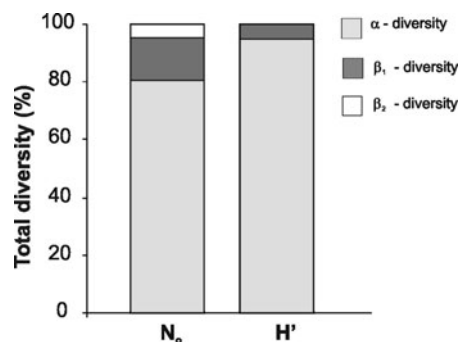

Fig. 9. Additive partitioning of gamma diversity of harpacticoid copepod genera for the number of genera (N_o) and Shannon–Wiener diversity H'. α-diversity refers to the harpacticoid composition and diversity in the different vertical sediment layers. β_1-diversity is the proportion of β-diversity due to the differences between sea grass species; β_2-diversity is the proportion of β-diversity due to the differences between transects.

sediments, with lower nutrient availability. The variation of the physical properties in the sediment (Jansson, 1966; Gray, 1968; McLachlan *et al.*, 1977) and the unequal distribution of food items (Joint *et al.*, 1982) affect the vertical distribution of meiobenthic animals. Altogether, the granulometric characteristics of the sediment and food availability were important structuring the vertical distribution of the harpacticoid communities.

Harpacticoid copepods diversity and distribution

ALPHA DIVERSITY

Members of the families Tetragonicipitidae and Miraciidae were widely dominant, they occurred in all sediment layers of all sea grass species. Representatives of these families have cylindrical, slender, or fusiform body shapes that favour burrowing, even in the deepest silty sediments of the deeper layers. The same is true for the generalist torpedo-shaped body of the family Ectinosomatidae which is well-adapted to burrowing (Hicks, 1980; De Troch *et al.*, 2003), also recorded in all sediment layers as well. Representatives of the families Canuellidae (e.g. *Canuella*) have an elongated or cylindrical body shape that allows them to burrow in sediments in order to escape stress and predation during low tide (De Troch *et al.*, 2003). As expected, the epiphytic Metidae, Tegastidae, Tisbidae and Porcellidiidae (Hicks & Coull, 1983; Bell *et al.*, 1987; De Troch *et al.*, 2003) were dominant at the top sediment layers. Some of these epiphytic genera, however, were recorded even at the deepest sediment layers (e.g. *Metis* (Metidae) and *Tegastes* (Tegastidae)). Other harpacticoid families such as Thalestridae, Cletodidae, Canuellidae, Laophontidae and Longipediidae were restricted to certain sediment layers, thus confirming their ability to segregate niches (De Troch *et al.*, 2003). These groups of harpacticoids are capable of swimming in the water column but are also considered active burrowers in detritus-rich sediments (Hicks, 1986; Huys *et al.*, 1996; De Troch *et al.*, 2003). The importance of the family Paramesochridae (e.g. *Apodopsyllus*) based on high relative abundance at the intertidal zone might be linked to their ability to dwell in anoxic conditions (Wieser *et al.*, 1974; Coull & Hogue, 1978) and to avoid the high-density communities of the uppermost sediment layers (Hicks & Coull, 1983; De Troch *et al.*, 2003). This could also be true for the genus *Paraleptastacus* (Ameiridae) that occurred in deeper sediment layers near *H. minor* and *H. uninervis*. The presence of *Leptocaris* (Darcythompsoniidae) is typically linked to high concentrations of organic matter (Ravenel & Thistle, 1981) and decomposing material (Huys *et al.*, 1996); these premises were found to be supported by our data, this genus was found only near the climax sea grass species *T. hemprichii*.

BETA DIVERSITY

Harpacticoid copepods are conspicuous emergers (Thistle, 2003; Sedlacek & Thistle, 2006). Bell *et al.* (1984, 1988) documented the migration of harpacticoid copepods from the water column to the sediment and to other habitats (e.g. sea grass leaves) for feeding and as a strategic mechanism to avoid predation and competition (Hicks, 1986; De Troch *et al.*, 2003). Also, hydrological factors (i.e. tidal rhythm) favour the exchange of harpacticoid copepods among habitats

along the tidal gradient (De Troch *et al.*, 2001, 2003), thus partitioning the community structure (Wisheu, 1998). The high number of shared genera between the adjacent sediments of *H. uninervis* and *T. hemprichii* and the low number of shared genera between *H. uninervis* and *S. isoetifolium* could be attributed to hydrological factors (e.g. tidal currents) and distance between habitats (Figure 8). The adjacent sediments of *H. uninervis* were mainly composed of gravel and coarse sand in the upper sediment layers and silt in the deepest stratum. This zone is strongly structured by physical and chemical variables, but has high concentrations of fresh organic material (e.g. chl-*a*, % TOM), possibly originated from the adjacent detritus-rich habitat of *T. hemprichii*. The large sea grass plant, *Thalassia hemprichii* produces higher amounts of organic matter from its leaf litter (Terrados *et al.*, 1998; Duarte, 2000), thus offering a more complex habitat for the associated fauna. In Kenya, the harpacticoid assemblage associated with *S. isoetifolium* (both roots and leaves) showed the highest diversity and hence shared a high number of copepod species with other sea grass species (De Troch *et al.*, 2001a). In the present study, the highest number of shared genera with other sea grass species, as deduced from the larger surface of the radar chart, was recorded near *H. uninervis*, whereas this surface was clearly smaller for the *S. isoetifolium* community indicating a lower number of shared species. This could be attributed to differences in sediment grain size. In Kenya, the highly diverse harpacticoid community associated with *S. isoetifolium* was found in coarse sand sediments (De Troch *et al.*, 2001a,b) whereas the local community of *S. isoetifolium* occurred at areas with higher silt percentage, which effected a decrease of the detrital load (Ravenel & Thistle, 1981), an important food source for harpacticoids. Moreover, different sea grass species with vertical and horizontal stems growth (e.g. *Halodule* and *Syringodium*) exhibit seasonality effects towards sedimentation (Vermaat *et al.*, 1997). In these studies, temporal changes have been excluded, and higher harpacticoid diversity might be expected when different seasons or diurnal samplings are included. Nonetheless, *H. uninervis* and *S. isoetifolium* are similar in growth forms and both are characterized by high diversity of harpacticoid copepods in their surrounding sediments.

GAMMA DIVERSITY

Overall, alpha (α) diversity (between sediment layers) of harpacticoids was a major contributor to the total diversity (γ-diversity) in Pujada Bay. This implies that the heterogeneous vertical distribution of the grain sizes greatly influenced the high harpacticoid diversity and composition in the sediment layers. However, the relatively smaller contribution of sea grass species (β1-diversity) to the total copepod diversity should not be neglected. The growth strategy and the role of the sea grass species in the colonization process are vital in structuring the harpacticoid copepod community as they represent the base of the detritus production. Sea grasses provide a complex habitat and available food. A comparable study in Kenyan sea grass beds (De Troch *et al.*, 2001b), had a lower total diversity of harpacticoid genera. The relatively high gamma diversity of harpacticoids in the Philippines supports the hypothesis of an extraordinary high diversity in the East Indies Triangle (Carpenter & Springer, 2005).

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Correspondence should be addressed to:
Marleen de Troch
Ghent University
Biology Department
Marine Biology Section
Campus Sterre—Building S8
Krijgslaan 281
B-9000 Ghent
Belgium
email: marleen.detroch@ugent.be