

Alpha and beta diversity of harpacticoid copepods in a tropical seagrass bed: the relation between diversity and species' range size distribution

Marleen De Troch^{1,*}, Frank Fiers², Magda Vincx³

¹Ghent University, Biology Department, Marine Biology Section, K.L. Ledeganckstraat 35, 9000 Gent, Belgium

²Royal Belgian Institute of Natural Sciences, Department Invertebrates, Vautierstraat 29, 1000 Brussels, Belgium

ABSTRACT: Alpha and beta diversity of harpacticoid copepods was studied in a Kenyan seagrass bed (Gazi Bay, Kenya) with a clear zonation of different seagrass species. The application of an appropriate sampling strategy made the interpretation of different spatial diversity levels possible. Alpha diversity was defined as the diversity of harpacticoid copepods associated with 1 seagrass species or 1 subhabitat (roots or leaves). Beta diversity was interpreted as changes in diversity between both subhabitats of 1 seagrass species and between different seagrass species along the tidal gradient. A total of 115 harpacticoid copepod species were recorded in the seagrass samples. Of these, 36 species (31.3%) were restricted to the root subhabitat and 12 (10.4%) were only recovered from leaf samples. Higher diversity was recorded for the deeper seagrass species (*Syringodium isoetifolium*, *Halophila stipulacea*). Copepod communities associated with *Halophila ovalis* and *H. stipulacea* (both pioneer seagrass species) were clearly different from one another in terms of diversity. A trend towards more specialized habitat preference (i.e. a lower ecological range size) was found with increasing diversity. The left-skewed species' range size distribution for the more diverse samples was clearly different from the typical right-skewed curves reported in most terrestrial studies. This may provide evidence for fundamental differences between marine species and terrestrial ones in their range size distribution.

KEY WORDS: Harpacticoid copepods · Seagrass · Diversity · Ecological range size

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INTRODUCTION

There are strong relationships between sampling scale and the processes that influence diversity (Huston 1994). At small scales species are presumed to interact with one another and to compete for similar limiting resources (Gray 1997). To reduce competition between species, they will use different parts of the gradient (Whittaker 1972). This level has been defined as within-habitat or alpha diversity (Fisher et al. 1943, Whittaker 1960, 1967). The extent of change in species composition along an environmental gradient or along different communities in a landscape is defined as between-habitat or beta diversity (Whittaker 1960, 1975, 1977).

These definitions are mainly based on terrestrial ecological studies (e.g. Whittaker 1960, 1975, 1977). At the largest scale (landscape or gamma diversity) (Whittaker 1960, Cody 1986), terrestrial systems show characteristic gradients with high diversity in the tropics and at low altitudes, and low diversity at the poles and at high altitudes. More recently, similar gradients and diversity patterns have been postulated for the marine environment with high diversity in tropical seas and low diversity in polar seas (Gray 1997). Although some groups of organisms appear to reach maximal diversity in polar regions (e.g. mammals), temperate regions (e.g. seaweeds) or the tropics (e.g. corals), for most groups the pattern is unknown, partly because strictly comparative data are lacking (Gee & Warwick 1996). Terrestrial studies showed that species richness is influenced by a number of factors, such as available

*E-mail: marleen.detroch@rug.ac.be

energy or production, habitat heterogeneity and structure, and topographic diversity, rates of immigration, disturbance and time both evolutionary and ecological (Gaston 1996 and references herein). How do these ideas impinge on marine studies? Snelgrove et al. (1997) stated that global biodiversity patterns of marine benthos, the impact of benthos on key ecosystem services and the importance of functional redundancy are poorly understood. In their recent review, Estes & Peterson (2000) concluded that documenting the complex influences of spatial and temporal scales on ecological processes and appreciating intersystem linkages are some of the most pressing needs for future knowledge.

The present paper deals with alpha and beta diversity of harpacticoid copepods in a Kenyan seagrass bed with a clear zonation of seagrass species (Coppejans et al. 1992). The application of an appropriate sampling strategy makes the interpretation of different spatial diversity levels possible. The characteristics of the studied seagrass bed are used to interpret both levels of biodiversity. Alpha diversity is defined as the diversity of harpacticoid copepods associated with 1 seagrass species or 1 of their subhabitats (roots or leaves). Beta diversity can be analysed by comparing both subhabitats of 1 seagrass species. As the habitat selection of seagrass species is quite specific in the sampling site (Coppejans et al. 1992), comparing different seagrass species along the tidal gradient can also be referred to as between-habitat or beta diversity.

In addition to an interpretation of both spatial levels of diversity, the data were also used to interpret 'spot endemism' (*sensu* Schlacher et al. 1998) of harpacticoid copepods in the studied seagrass bed. The lack of

correspondence between hotspots of diversity and hotspots of rarity (Prendergast et al. 1993) is a current challenge for effective conservation strategies. If areas of high species richness fail to coincide with those rich in endemic and rare species, the application of species richness information in conservation may have shortcomings (Schlacher et al. 1998).

This study attempts to target 5 key issues in biodiversity research: (1) spatial interpretation of harpacticoid species diversity (alpha and beta diversity), (2) species turnover along a gradient and its relation to intersite distance (beta), (3) species' range size and possible site or seagrass restriction as a measure for spot endemism (*sensu* Schlacher et al. 1998), (4) relation between diversity and species' range size, and (5) possible causes of (1) to (4) and their value for predictability of biodiversity.

MATERIAL AND METHODS

Study area and sampling strategy. The present study was carried out in Gazi Bay also called Maftaha Bay ($4^{\circ}22'S$, $39^{\circ}30'E$), located ca 50 km north of the Tanzanian border and 60 km south of Mombasa Island. The bay is between 1.75 and 3.5 km wide and 3.25 km long and is bordered by mangroves. A detailed map of the study area is given in De Troch et al. (2001).

A distinct zonation and succession of seagrass species in Gazi Bay is described by Coppejans et al. (1992). They found 11 of the 12 seagrass species known from Kenya in the study area. Meiofauna samples were taken for 5 of them (Fig. 1): *Halodule wrightii* Ascherson, 1868; *Halophila ovalis* (R. Brown)

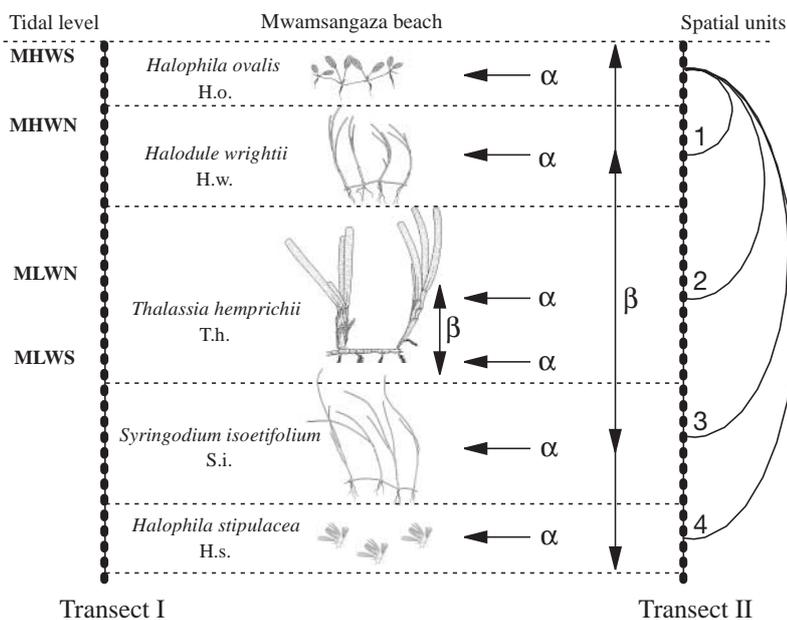


Fig. 1. Schematic presentation of the application of different diversity levels at Mwamsangaza Beach (Gazi Bay) with indication of the sampled seagrass species on 2 transects (I and II). Beta-diversity (β), i.e. comparisons between the different seagrass species along the gradient, is indicated by means of 1 long arrow. The corresponding intersite distance is defined arbitrarily (see text) and indicated as spatial units. 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 level at neap tide

Hooker f., 1858; *Halophila stipulacea* (Forsskål) Ascherson, 1867, *Syringodium isoetifolium* (Ascherson) Dandy, 1939; and *Thalassia hemprichii* Ehrenberg Ascherson, 1871, in the inter- and subtidal zone. There was a well-defined transition from the pioneer association *Halophila ovalis*/*Halodule wrightii* at the upper limits of the seagrass bed, over the *Thalassia hemprichii* climax vegetation in the intertidal zone towards the patches of *Syringodium isoetifolium* and *Halophila stipulacea* in the upper subtidal zone (Coppejans et al. 1992). The same zonation was identified based on meiofauna data at higher taxon level (De Troch et al. 2001).

From each of the 5 seagrass species, triplicate samples were taken between 16 and 19 July 1996. The samples were taken at random within 5 × 5 m quadrats (area of 25 m²) positioned within each seagrass zone. Within each zone, 2 quadrats were selected, situated on 2 transects and separated approximately 500 m from each other. Both transects (Fig. 1) were at right angles to the Mwamsangaza beach as the seagrass zones were parallel to the beach. All samples were obtained by snorkelling under a water cover between 1 and 2 m.

Epiphytic meiofauna was sampled by placing a PVC meiofauna core (inner diameter 3.6 cm, area 10 cm²) over 1 seagrass clump and inserting it into the sediment. Seagrass plants with a minimum of dead leaves were selected at random within each quadrat (see above). For the seagrass species *Thalassia hemprichii* and the first transect of *Halodule wrightii* separate leaf and root samples were collected in each quadrat. The leaves (on average 3 or 4 per sample) were sampled using a plastic bag. A 3.6 cm inner diameter PVC meiocore was inserted into the sediment down to a depth of 10 cm to obtain the roots after cutting the leaves. An 8% MgCl₂ solution was added to all samples with plant material in order to improve collection of epiphytic animals (Hulings & Gray 1971, Hicks 1977); the entire leaves were washed in the field with freshwater over a 1 mm sieve and epiphytic fauna retained on a 38 µm sieve.

Within 2 h after collection, all samples were fixed with warm (60°C) buffered formaldehyde in freshwater to a final concentration of 4%. In the laboratory, samples were rinsed with a jet of freshwater over a 1 mm sieve, then decanted 10 times over a 38 µm sieve, centrifuged 3 times with Ludox HS40 (specific density 1.18) and stained with Bengal Rose. Harpacticoid copepods were enumerated, picked out per hundred (as they were encountered during counting) and stored in 75% ethanol. Due to time-consuming identification, we restricted ourselves to mounting only the first 100 specimens on glycerine slides and identified them to species level.

Data analysis. The spatial distribution of harpacticoid species among the different seagrass species and their related subhabitats was analysed by means of ordination techniques (e.g. correspondence analysis = CA, Ter Braak 1986). Ordination techniques are most accurate for interpretation of community composition in terms of species response to environmental gradients (Ter Braak & Prentice 1988). Data were arcsine transformed (angular transformation, Sokal & Rohlf 1997) prior to multivariate analysis and log₁₀x transformed prior to variance analysis in order to achieve normality and homogeneity of variances. Variance analysis (ANOVA) was performed with STATISTICA™ software (Microsoft, StatSoft 1995).

The ecological range size of a copepod species was defined as the number of quadrats/seagrass species occupied by that species. It can be regarded as the area occupied by a species within the sampled seagrass zone. In this aspect, ecological range size differs from geographical range size as the latter refers to the geographical regions where the species occurs (see 'Discussion'). Here, ecological range size was used to evaluate possible quadrat/seagrass restriction of harpacticoid copepods in relation to sample diversity.

Defining and calculating different spatial levels of biodiversity. The concepts of 'alpha' or inventory diversity and 'beta' or differentiation diversity can be applied to different spatial levels. Differences in the use of these levels appears unimportant if the concepts are clearly defined for each particular study (Whittaker 1977) (Table 1). The definition of alpha diversity as given by Whittaker (1960, 1977) and MacArthur (1965) is interpreted in the present study as diversity of the copepod community associated with an entire plant (α in Fig. 1). For the seagrass species *Thalassia hemprichii*, alpha diversity is defined as diversity of copepods in 1 subhabitat (roots or leaves) (α in Fig. 1).

Changes in diversity between these 2 subhabitats (roots and leaves) provide the first possible interpretation of between-subhabitat or beta diversity (β in Fig. 1).

The clear zonation of seagrass species along the tidal gradient (Coppejans et al. 1992) presents a special advantage of the study site: it facilitates interpretation of beta diversity or between-habitat diversity of the seagrass associated copepod fauna along the gradient (β in Fig. 1). The samples along the gradient were taken on 2 transects (see sampling strategy, Fig. 1).

The diversity indices of Hill (Hill 1973) were used to calculate *alpha diversity*:

N_0 equals the number of species. N_0 takes into account all species, independent of their proportional abundance. $N_1 = \exp(H')$, with $H' = \text{Shannon-Wiener diversity index} = -\sum_{i=1}^n p_i \ln p_i$ and $p_i = \frac{N_i}{N_t}$ = relative

Table 1. Definitions and interpretations of alpha and beta diversity

Diversity level	Original definition by Whittaker (1960, 1977), MacArthur (1965)	Concept interpretation in present study
Alpha diversity (within-habitat diversity) (inventory diversity)	For a sample of a community regarded as homogeneous	For individual subhabitats (roots or leaves) of a seagrass species or for individual seagrass species
Beta diversity (between-habitat diversity) (differentiation diversity)	Change along an environmental gradient or among the different communities in a landscape	Changes in species diversity between: – Subhabitats (roots/leaves) of a single seagrass species – Different seagrass species along the tidal gradient

importance of the i th species. N_2 is the reciprocal of Simpson's dominance index. The Simpson's index (Simpson 1949) gives the probability that any 2 individuals drawn at random from an infinitely large community belong to different species, and is calculated as $D = \sum_{i=1}^n p_i^2$ where p_i is the relative importance of i th species (see above). N_∞ is the reciprocal of the proportional abundance of the most common species (reciprocal of Berger-Parker index).

Beta diversity measures the degree of turnover in species composition along a transect or gradient. To interpret the species turnover within the seagrass bed (between different seagrass species and their subhabitats) a spatial scale was defined arbitrarily (Fig. 1): 1 unit for nearest neighbours, 2 units for the second nearest neighbour and so on. Both subhabitats (roots or leaves) of 1 seagrass species are 0 unit separated from each other. We interpreted this level of diversity by means of graphical visualisation instead of a number of indices (for an overview see Magurran 1988). These different indices are based on numbers that are often difficult to estimate exactly, e.g. total number of species recorded in the system. In addition, this mathematical interpretation is often difficult to link to habitat characteristics. However, the graphical presentation provides a lot of information simultaneously: (1) the relation between intersite distance and number of species shared, and (2) the surface is an indirect measure for the specificity of the copepod community associated with a particular seagrass species.

In addition, we calculated the metric version of NESS (normalized expected species shared) (Grassle & Smith 1976) called CNESS (chord-normalized expected species shared) (Trueblood et al. 1994) by means of COMPAH96 (COMbinatorial Polythetic Agglomerative Hierarchical clustering). The measure is based on the expected number of species shared between random samples of size, m , drawn from a population.

RESULTS

A total of 115 harpacticoid copepod species were recorded in the seagrass samples from Gazi Bay. Of these, 36 species (31.3%) were restricted to the root subhabitat and 12 species (10.4%) were only recovered from leaf samples.

Identifying communities by means of gradient analysis

Fig. 2 shows the plot of the sample scores resulting from indirect gradient analysis (correspondence analysis, CA). The identified copepod communities correspond closely to the seagrass distribution along the transects. The first axis (eigenvalue 0.3063) separates the uppermost pioneer seagrass species *Halophila ovalis* and *Halodule wrightii* from the deeper seagrass species based on copepod species composition. In addition, the sample plot illustrates the variance in these more shallow samples (*H. ovalis*, *H. wrightii*). *Thalassia hemprichii* is at an intermediate position along the transect in the seagrass bed (Fig. 1) but grouped together with the deeper seagrass species (Fig. 2).

Alpha or within-habitat diversity

Sample-size dependence of alpha diversity

To evaluate sample-size dependence of the diversity indices of Hill (Hill 1973), 500 copepods of 1 sample (1 replicate of *Halophila stipulacea*, transect II) were identified, starting with 100 specimens at random and adding another 100 at each calculation. The first index of Hill (N_0) was most sensitive to changing sample size as the value doubles with increasing sample size, i.e.

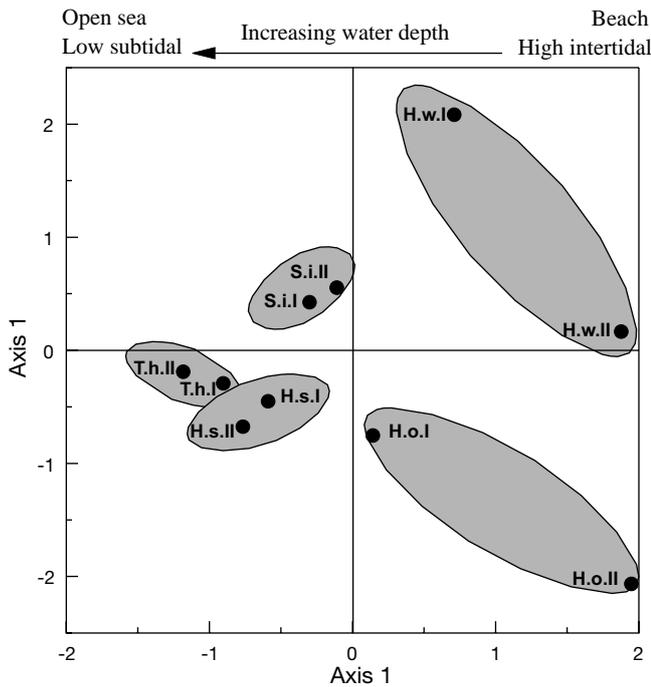


Fig. 2. First 2 ordination axes of a CA (Correspondence Analysis) based on all fourthroot transformed harpacticoid copepod densities in the epiphytic samples of *Halophila ovalis* (H.o.), *Halodule wrightii* (H.w.), *Thalassia hemprichii* (T.h.), *Syringodium isoetifolium* (S.i.), *Halophila stipulacea* (H.s.); first quadrat (I), second quadrat (II)

by adding 100 individuals at each step (Fig. 3). To verify the diversity patterns based on indices of Hill (Hill 1973), the dominance structure of the same sample was analysed by means of k -dominance curves (Lambshhead et al. 1983). It was clear that the latter results were far less sensitive to changing sample size and the overall dominance structure of the sample remained stable irrespective of sample size. When analysing k -dominance curves, care should be taken when interpreting the final number of species identified (species rank, plotted on the x-axis). This final species rank will increase with increasing number of species identified.

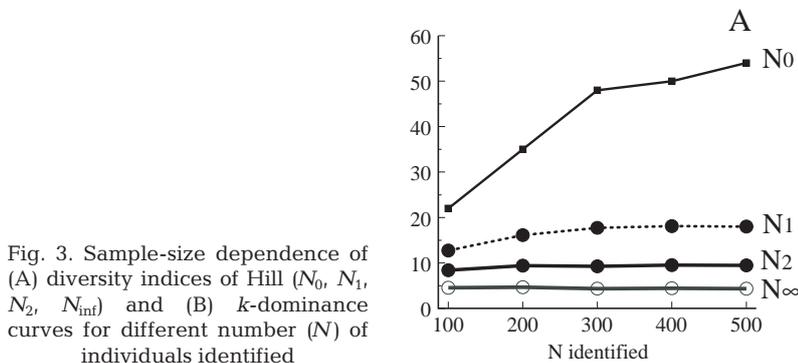


Fig. 3. Sample-size dependence of (A) diversity indices of Hill (N_0 , N_1 , N_2 , N_{inf}) and (B) k -dominance curves for different number (N) of individuals identified

For these reasons and as only the first 100 copepods were identified and incorporated in the present study, all diversity indices will be further interpreted in combination with k -dominance curves (Lambshhead et al. 1983, Platt et al. 1984).

Alpha diversity and dominance structure of copepod communities

Diversity indices of Hill (except N_{∞}) (Fig. 4A, N_2 , N_{∞} not shown) were significantly higher (ANOVA significance levels: $p < 0.001$ for N_0 , $p < 0.01$ for N_1 , $p < 0.05$ for N_2) for copepod samples from deeper seagrass species (*Syringodium isoetifolium*, *Halophila stipulacea*). Copepod communities associated with *Halophila ovalis* and *H. stipulacea* (both pioneer seagrass species) were clearly different in diversity.

The variability between replicates increased with increasing level of diversity index of Hill and was slightly higher for the more diverse associations near the deeper seagrass species.

Overall, very similar patterns are found in the k -dominance plots (Fig. 4B) based on species composition of all samples. *Syringodium isoetifolium* harboured the most diverse copepod community. The same difference between both pioneer species of the genus *Halophila* was detected: the community associated with *H. ovalis* being far less diverse than the one associated with *H. stipulacea*. The curves of the other samples were not comparable in terms of intrinsic diversity as the corresponding k -dominance curves intersected (Lambshhead et al. 1983).

Beta or between-habitat diversity

Diversity of copepods in different subhabitats:
roots versus leaves

The difference of community diversity of 2 adjacent subhabitats, i.e. roots versus leaves, was examined for

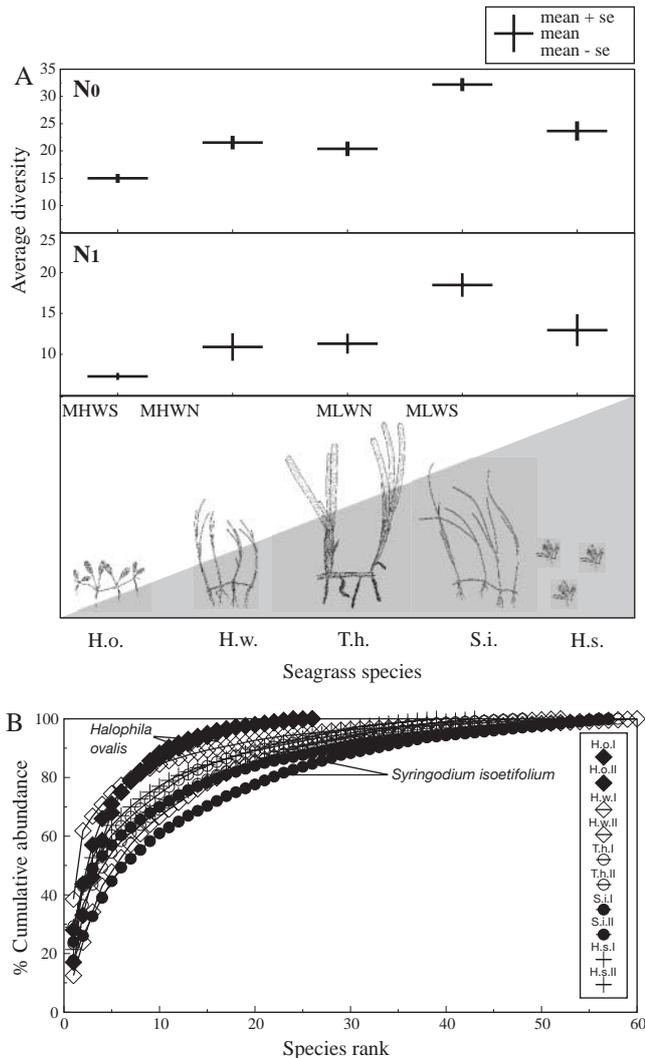


Fig. 4. Alpha diversity of harpacticoid copepods associated with different seagrass species: (A) diversity indices of Hill (mean \pm 1 standard error). Shaded area: relative mean water depth (water cover) along the gradient where the different seagrass species were sampled. (B) Corresponding *k*-dominance curves. *Halophila ovalis* (H.o.), *Halodule wrightii* (H.w.), *Thalassia hemprichii* (T.h.), *Syringodium isoetifolium* (S.i.), *Halophila stipulacea* (H.s.)

the seagrass species *Thalassia hemprichii*. The densities of harpacticoid copepods, nematodes and total meiofauna were significantly (1-way ANOVA significance level: $p < 0.01$) higher in the leaf samples than in the root samples (Fig. 5A). The diversity values (Fig. 5B) showed the opposite trend with copepods being significantly (1-way ANOVA significance levels: $p < 0.01$ for N_0 , $p < 0.05$ for N_1) more diverse in root samples. The variance between replicates was slightly higher for the more diverse samples. The corresponding *k*-dominance curves (Fig. 5C) yielded the same pattern. The % copepod family composition of these samples showed a clear shift from root to leaf. The fam-

ily Thalestridae was dominant in the leaf samples, representing 50% or more of the community. In the root samples, 3 families (Thalestridae, Cletodidae, Diosaccidae) together accounted for 60% of the association. The family Thalestridae is known to exhibit epiphytic habitat preferences (e.g. Hicks & Grahame 1979, Hicks & Coull 1983). Some families were clearly restricted to 1 subhabitat: the families Cletodidae and Tetragnipitidae were only recovered from root samples and epiphytic families as Tegastidae, Porcellidiidae and Harpacticidae only from leaf samples.

Beta diversity among seagrass species

To interpret beta diversity along the tidal gradient in Gazi Bay, we calculated the number of copepod species shared between different seagrass species (Fig. 6). The distance between the different seagrass species was arbitrarily defined (see spatial units, Fig. 1) and is

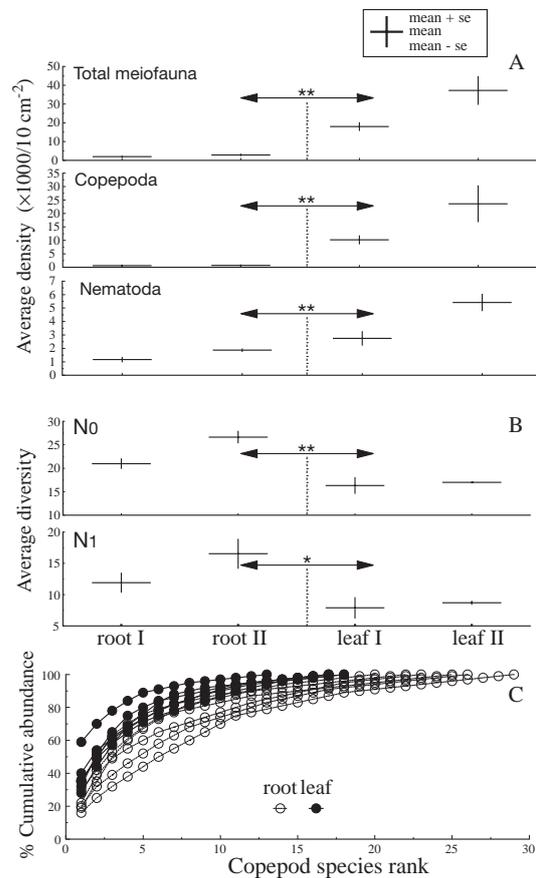


Fig. 5. Beta diversity of copepods in both subhabitats (root and leaf) of *Thalassia hemprichii*: (A) density of total meiofauna and 2 major meiofauna taxa (Copepoda, Nematoda), (B) diversity indices of Hill (N_0 , N_1), and (C) *k*-dominance curves for all replicates. Significance levels indicated by * $p < 0.05$ and ** $p < 0.01$

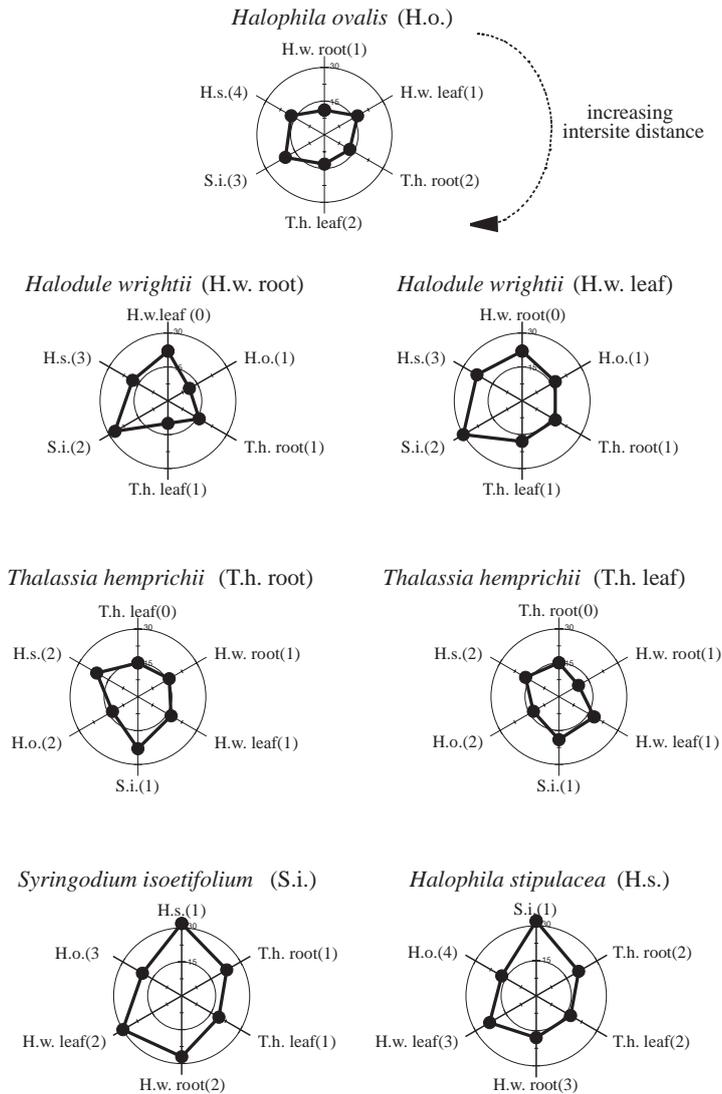


Fig. 6. Circular graphs of number of harpacticoid species shared between 1 seagrass species (indicated above each graph) and the other adjacent seagrass species. The arbitrarily defined distance (see spatial units, Fig. 1) between 2 seagrass species (or subhabitats) is indicated between brackets. *Halophila ovalis* (H.o.), *Halodule wrightii* (H.w.), *Thalassia hemprichii* (T.h.), *Syringodium isoetifolium* (S.i.), *Halophila stipulacea* (H.s.)

indicated between brackets for each seagrass species on the circular graphs. Although the surface of the graphs is not quantified exactly, it gives a general indication of the number of species shared.

The hypothesis that increasing intersite distance results in a decreased number of copepod species shared between seagrass species was tested. No such pattern could be detected from our data. Two types of circular graphs were found: relative small (H.o., T.h. root, T.h. leaf) and larger ones (H.w. root, H.w. leaf, S.i., H.s.). The relative area of the graph gives an indication of the specificity of the copepods associated with

that seagrass species. The plot for *Halophila ovalis* indicates that the species assemblage is quite selective as very few of these species were found on other seagrasses. In the cluster analysis based on CNESS (not illustrated), *H. ovalis* was split off as first station and was characterised by high dissimilarity values in relation to other samples. This corresponds to the position of *H. ovalis* near the high water level at spring tide (MHWS). Copepods associated with *H. ovalis* are exposed to a high degree of stress related to emersion (dry condition, waves, etc) near the beach. We found mainly species of the families Cletodidae (cylindrical body) and Ectinosomatidae (fusiform body). Their body shape is adapted to burrow into the sediments, allowing them to escape from stress conditions during low tide. A similar high level of specialisation was indicated by the small circular graphs corresponding to the copepods associated with both subhabitats of *Thalassia hemprichii*. The number of harpacticoid species shared between both subhabitats of the same seagrass is not significantly higher than the number of species in common between adjacent seagrasses. This was also reflected in the subhabitat-specific copepod composition.

Halodule wrightii (both roots and leaves) shared most copepod species with *Syringodium isoetifolium*. *S. isoetifolium* was characterised by the most diverse copepod community (see alpha diversity, Fig. 4) and hence shared a higher number of species with other seagrasses (see surface circular graph, Fig. 6). Dominant species associated with this seagrass species were *Diarthrodes* n.sp. (Thalestridae) and *Cletodes* aff. *longifurca* (Cletodidae). The large number of species shared between *S. isoetifolium* and *Halophila stipulacea* illustrated the importance of species exchange favoured by the water depth where these seagrass species were collected. This high level of similarity between copepods associated with the 2 latter seagrass species was also proved by a low CNESS dissimilarity value (0.603 with $m = 10$).

Species' range size and its relation with diversity

The range sizes of harpacticoid copepod species are relatively restricted (Fig. 7). Only one (*Diarthrodes* n.sp. 1) out of 115 species occupied the full range of quadrats sampled. By contrast, 25 species (21.7%) were restricted to 1 quadrat. Half of the total community was found in no more than 3 quadrats. These results highlight a high degree of 'spot endemism' in the community. Seagrass species restriction was less

obvious although 30 species (26.1%) were detected on 1 seagrass species only. Half of the copepod species community was associated with no more than 2 seagrass species. We can consider 17 harpacticoid species (14.8%) as non-selective within the seagrass bed as they were found in association with all sampled seagrass species.

From our data, diversity (i.e. number of species in a sample, N_0) highly correlated with the total ecological range size of species in a sample (= sum of ecological range sizes of all species in a sample) (Fig. 8A). To test the hypothesis that species' range size are compressed in diverse communities, the average ecological range size was plotted against the number of species (N_0) (Fig. 8D). The correlation was not significant but a more diverse community tends to harbour more locally rare species. Our data suggest that the diversity (namely number of species) of a sample may be a possible predictor of range size of the comprising species, with species from a diverse sample being generally less widespread than species in a less diverse sample.

The relative distribution of each ecological range (expressed as a discrete value along the x-axis) shows different patterns. Low diversity samples were characterised by a few dominant species with different ecological ranges. In a low diverse sample (Fig. 8B), 3 dominant species were found with ecological range size of 7, 17 and 33.

In a high diverse community a strongly left-skewed distribution was found corresponding to a dominance (in terms of abundance) of more widely spread species (Fig. 8C). In addition, most species were locally scarce.

This corresponds to the lower average ecological range size for this sample (Fig. 8D). Low diverse samples were characterised by more variance in the average ecological range size than high diverse samples.

The same type of plots were made for the other diversity indices of Hill (N_1 , N_2 , N_∞) but the linear negative regression became less significant with increasing order of Hill index and is not discussed further.

DISCUSSION

For our study, harpacticoid copepods were selected as key taxon because of their high abundance and diversity in seagrass beds (Hicks 1980, McRoy & Lloyd 1981). Although harpacticoid copepods and their larvae are generally known as substrate bound metazoans (Dahms 1993), they can actively move between seagrass plants. The remarkable specificity of harpacticoid assemblages (Hicks & Coull 1983) was crucial to test the variation in habitat selection with changing species diversity in the community. In this sense, harpacticoid copepods in a seagrass bed are the aquatic equivalent of, e.g., foliage birds in forest trees (e.g. MacArthur et al. 1966). When contrasting both systems, we must be conscious about the fundamentally different physical conditions under which essential processes like migration and species exchange take place. Patterns of marine biodiversity may not conform to the terrestrial model, because the spectrum of environmental variation in the sea has a longer wavelength over both ecological and evolutionary time

scales than on land. Barriers to dispersal are also weaker because of the continuous nature of the seas and the planktonic dispersal mechanisms of much of the biota (Gee & Warwick 1996).

Furthermore, comparing our results with other studies is difficult in view of the different definitions used for spatial levels of diversity. In addition, most studies focus on alpha diversity (within-habitat or inventory diversity); the interpretation of beta diversity (between-habitat or differentiation diversity) has been mainly restricted to terrestrial communities (e.g. Pandey & Shukla 1999).

Moreover, ecological studies on harpacticoids in seagrass beds are often restricted to 1 seagrass species (alpha diversity) and report densities and seasonal variation only (e.g. Arunachalam & Balakrishnan Nair 1988, Hall & Bell 1993). Arunachalam & Balakrishnan Nair (1988) found a remarkably low alpha or

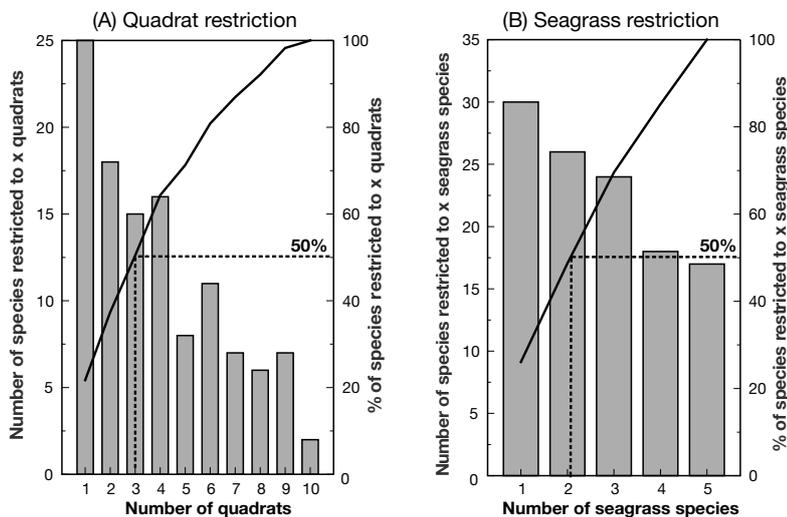


Fig. 7. Distribution of species' range size among harpacticoid copepod species to evaluate possible site (quadrat) and/or seagrass species restriction. Range size is (A) the number of sites or (B) the number of seagrass species occupied by harpacticoid species out of a total of 10 quadrats and 5 seagrass species sampled. Line: cumulative % of species restricted to x sites/seagrass species, with indication of 50% level

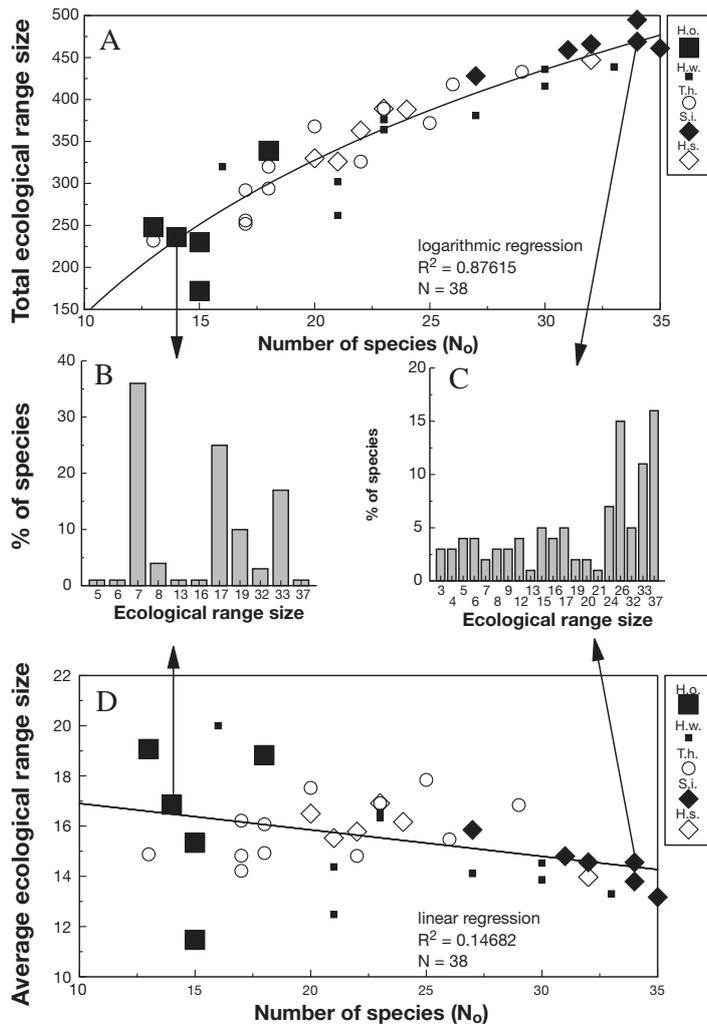


Fig. 8. Relation between diversity (N_0 , number of species) and (A) the total ecological range sizes (i.e. sum of the ecological range sizes of all species in a sample) and (D) the average ecological range size of comprising species (i.e. average number of samples in which the species were represented). Detailed species' range size distribution for a replicate with (B) low and 1 with (C) high number of species. *Halophila ovalis* (H.o.), *Halodule wrightii* (H.w.), *Thalassia hemprichii* (T.h.), *Syringodium isoetifolium* (S.i.), *Halophila stipulacea* (H.s.)

inventory diversity of the epiphytic copepods associated with *Halophila ovalis*, i.e. 19 species belonging to 8 families, although they sampled monthly during 1 year. In the *H. ovalis* samples from Gazi Bay (Kenya), we identified 35 species belonging to 13 families. A possible explanation for this difference may be that Arunachalam & Balakrishnan Nair (1988) did not sample the seagrass roots. Osenga & Coull (1983) reported a positive correlation between number of dead roots and the density of harpacticoid copepod. To our knowledge, the study by Arunachalam & Balakrishnan Nair (1988) is the only one so far on seagrass beds to report data at the species level. Identification at the species

level is often lacking (e.g. Hall & Bell 1993) and this makes comparison extremely difficult. We urge ecologists to identify at the species level because it is necessary for the evaluation of the underlying processes of these diversity patterns recorded by inventory diversity studies.

Such causal processes can be detected by comparing different habitats, a level defined in literature as beta diversity (Whittaker 1960, 1977, MacArthur 1965). Together with this definition, a number of indices based on presence-absence data have been proposed to calculate beta diversity (for an overview see Magurran 1988). In the present study we have chosen to visualise species turnover by means of circular graphs. These graphs permit inclusion of both intersite distance and seagrass morphology in the interpretation of beta diversity patterns. In addition, diversity can never be fully captured by a single number (Purvis & Hector 2000).

From our data, it was clear that seagrass morphology rather than intersite distance was a good predictor of diversity of harpacticoid copepods. High macrofauna species turnover among habitats in a coral reef lagoon combined with independence of beta diversity and spatial scale support this conclusion (Schlacher et al. 1998). More specific, harpacticoid copepods showed a preference for the slender leaves of *Syringodium isoetifolium*. *S. isoetifolium* shared most harpacticoid copepods with *Halodule wrightii*. This can be explained by the comparable growth form of both seagrass species, i.e. both having fine linear leaves (Fig. 1). *S. isoetifolium* belongs to the growth form of the syringodiids with long subulate leaves. It was the only one in this study with leaves rounded in cross-section.

Possible factors determining seagrass selection are, a.o., typology of associated epiphytes, related food availability and probably also the biochemical composition of the plant detritus (Danovaro 1996). No data on epiphytic algae are

included in the present study. Various studies (a.o. Heck & Wetstone 1977, Hicks 1980, 1986) have illustrated that surface and epiphytic cover are positively related to habitat complexity. Several authors (e.g. Kohn & Leviten 1976, Heck & Wetstone 1977, for an overview see Hicks 1980) have stated that increases in micro-spatial complexity allow for linearly related increases in diversity. Greater habitable space, increased nutritional resources and reduced levels of predation contribute to this relationship (Hicks 1980).

However, the higher habitat complexity of the seagrass *Thalassia hemprichii*, compared to that of other seagrasses investigated in this study, did not result in a

higher diversity of leaf associated copepods. In view of the low number of species in common with other nearby seagrass species, a lower diversity of the community associated with the leaves was linked to a high degree of seagrass selection of the harpacticoid species. We can conclude from our data of the *Thalassia* community that species composition rather than diversity was affected by seagrass growth form and related complexity.

The impact of tidal height on diversity patterns was highlighted in the present study. Exchange of copepod species between deeper seagrass species was linked to higher turbidity in these subtidal zones. Within the deeper communities (i.e. *Syringodium isoetifolium* and *Halodule wrightii*), diversity differences are well predicted, if not largely determined, by the structural complexity of individual seagrass species (see Hicks 1980 for algae).

From terrestrial studies (e.g. on forest birds), it is clear that vertical and horizontal habitat selection could be less subtle in different sites. The degree of habitat selection varies with species diversity (MacArthur et al. 1966). The key-taxon in our case study, harpacticoid copepods, showed a high degree of habitat selection both in terms of quadrat and seagrass species restriction (Fig. 7). The data on seagrass restriction can be used to indicate the number of seagrass species needed to include a certain fraction of the diversity within a seagrass bed. On a larger scale, this method can be useful to test the effect of adding seagrass species to a protected area and to predict diversity patterns. In view of the considerable worldwide loss in the area of seagrass beds (a.o. Hutchings et al. 1991), this kind of information is essential to evaluate the impact of these losses.

Finally, the present study also addresses the hypothesis that species' range sizes increasingly become compressed as communities become more diverse. So far, this hypothesis has not received sufficient documentation, especially not in marine ecosystems. Most studies on 'range size' refer to 'geographical range size' of species, often meaning nothing more than a description of the regions in which its individuals have been recorded (Gaston 1991). The origins of biogeography lie in systematics (Myers & Giller 1988) and a historical, and regional or global view of the determinants of distributions is a dominant theme. On the other hand, ecology is more concerned with the interactions between organisms and their environment (Begon et al. 1996), typically at local scales. In particular, in this context, it is concerned with the role of prevailing conditions (abiotic and biotic) in determining distribution. Therefore, we discuss 'ecological' range sizes as our study addresses local and ecological analyses.

Until recently, there has been little interest in species range size distribution, whereas much more attention has been paid to the closely related species abundance distribution (Gaston, 1996). However, in the present study we have the data at hand to evaluate the importance of the ecological range size of the species, its distribution on a local scale and correlation, if any, with diversity.

The diversity-ecological range size correlation of the comprising species was mainly clear for the total sum of these range sizes. The higher total range size in more diverse samples may appear quite self-evident in view of the high number of species in a more diverse sample. The other option, where a constant sum of ecological range sizes can be found for all samples irrespective of diversity, i.e. with an extremely strong decline in individual species' range as the overall diversity increases, was not applicable.

A trend towards further habitat selection with increasing diversity was only demonstrated with a slight decrease in average ecological range size. This further speciation was also illustrated by the left-skewed species range size distribution (Fig. 8C), i.e. half of the species are generalists (recovered from >65% of the samples) and the other half was characterised by a small ecological range size. A left-skewed species' range size distribution on this smaller scale contrasts with the typical strongly right-skewed distribution at larger scales (macro-ranges and meso-ranges), as reported in several terrestrial surveys (e.g. Gaston 1994, 1996, 1998, 1999 and references herein). The tendency for marine species on average to be more widely distributed than terrestrial (Rapoport 1994) is associated with a lower species diversity in marine compared to terrestrial systems (May 1994, Gaston & Williams 1996). Gaston (1998) summarized the major explanations for the 'general' right-skewed log-normal shape of the range size distribution: (1) the rather crude fashion in which geographical range sizes are typically measured, (2) the fact that many published species range size distributions concern continental faunas or (3) the influence of human activities on the occurrences of species. Hitherto, no detailed range size distributions have been reported for marine species. Our results, thus, provide the first evidence for fundamental differences between range size distributions of marine and terrestrial species. The potential problem of underestimation of narrowly distributed species in relation to sampling strategy has to be carefully considered. In addition, one should take into account the specific biology and related speciation of the selected key taxon and the characteristics of the marine habitat (as discussed before). The copepod communities tend to a high level of speciation in order to allow a maximum number of species in the favour-

able conditions of the phytal habitat. This was illustrated by the high level of specificity of the copepod community of the *Thalassia* leaves as only a few species were shared with adjacent seagrass species. In contrast, Fenchel (1993) stated that small organisms tend to have wider or even cosmopolitan distribution, higher dispersal efficiency, lower rate of allopatric speciation and lower local and global extinction rates than larger organisms do.

This study underlines the relation between rarity and diversity for small organisms (i.e. between 38 µm and 1 mm, meiofauna). Rarity was measured by means of species' range size and was thus irrespective of local density and population size. In this sense, rare species are 'spot endemics' but may or may not be locally abundant (Schlacher et al. 1998). Our data support the assumption that samples with high species richness coincide with those rich in rare species (Prendergast et al. 1993), although Kerr (1997) and Schlacher et al. (1998) have proved that this does not always hold. The level of rarity in species-rich sites ('hotspots') is essential for conservation. Lawton et al. (1994) illustrated that recent conservation priorities have shifted from rare species towards greater emphasis on conserving areas of high diversity. If rarity coincides with high diversity, as documented by our data, decision-making for conservation management becomes evident.

Whether the results of this case study can be generalised for the marine environment as a whole remains open to debate and should be further substantiated by future research. The large portion of undescribed species (more than half of the harpacticoid species recovered in the study area are new to science, De Troch unpubl. data) and other taxonomy problems hamper estimates of global diversity patterns and their underlying factors. Marine species patterns correlate well with historical disturbance (e.g. glaciation), sediment grain size, organic content, depth and temperature (Snelgrove et al. 1997). Ongoing research focuses on diversity of copepod communities in different seagrass beds worldwide (gamma diversity, De Troch et al. unpubl. data) in order to analyse parallelism and underlying factors of global marine diversity patterns.

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