Journal of the Marine Biological Association of the United Kingdom, 2008, 88(4), 747–758. ©2008 Marine Biological Association of the United Kingdom
doi:10.1017/S0025315408001331 Printed in the United Kingdom

Community structure and microhabitat preferences of harpacticoid copepods in a tropical reef lagoon (Zanzibar Island, Tanzania)

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Three microhabitat types (dead coral fragments, coral gravel and coral sand) were distinguished and sampled at two locations (Matemwe and Makunduchi) in a tropical lagoon (Zanzibar Island, Tanzania), and the community structure, habitat preferences and biodiversity of the associated harpacticoid copepod fauna was investigated. The harpacticoid fauna is affected by sediment granulometry and by the structural differences between coral and both gravel and sediment. The coral fragments contained a specific assemblage composed of typical 'phytal' taxa (Tisbe, Paradactylopodia *and* Dactylopusia) *along with other eurytopic and sediment-dwelling forms (*Ameira, Ectinosoma *and* Amphiascus*), which may be attracted by the sediment retained between the coral branches. The assemblages of coral gravel and upper sediment layer did not differ significantly from each other and had mostly the same dominant genera. The sediment from Matemwe was dominated by the interstitial Paramesochridae and the sediment from Makunduchi by Tetragonicipitidae. The coral fragments from Makunduchi sustained a more diverse assemblage than gravel and the different sediment layers. It was assumed that coral form and complexity, with implications for habitable space, nutritional resources and level of predation, are important in structuring diversity of the associated assemblage.*

Keywords: dead coral substrates, harpacticoid copepods, composition, biodiversity, microhabitats, Indian Ocean

Submitted 18 September 2007; accepted 23 January 2008

INTRODUCTION

In the backreef lagoon of a fringing reef, the seabed floor is commonly composed of eroded deposits from corals and other carbonate-bearing organisms (Alongi, 1989). The physical and biological breakdown of the coral skeletons results in a large variety of substrates with different structural complexity, providing a wide range of potential microhabitats for benthic fauna. Despite the considerable research effort on the meiofauna communities associated with carbonate reef sediments (e.g. Alongi, 1989; Ndaro & Ólafsson, 1999; Netto *et al.*, 1999, 2003; Raes *et al.*, 2007), studies have primarily focused on the associated benthic nematode assemblages, whereas the epimeiofauna inhabiting these hard coral substrates has been ignored. Harpacticoids play an important trophic role in coral sands because of their numerical abundance, capacity to recycle nitrogen and high bacterial ingestion rates (Gray, 1985; Moriarty *et al.*, 1985). Furthermore, they are an important food source for fish larvae and juveniles and for small fish (Hicks & Coull, 1983; Gee, 1989; Coull, 1990; De Troch *et al.*, 1998). However, studies focusing on harpacticoid assemblage structure in the carbonate sands of coral reefs are scarce and geographically restricted to the Bermuda Platform (Coull, 1970; Coull & Herman, 1970), the US Virgin Islands (Hartzband & Hummon, 1974), Mururoa (Villiers *et al.*, 1987; Villiers, 1988) and Fangataufa Atoll (Villiers & Bodiou, 1996), both in French Polynesia. Generally, grain size, controlled by reef hydrodynamics, has been identified as an important structuring factor of harpacticoid communities. Studies about epifaunal harpacticoids are rare and mainly restricted to the phytal assemblages of sea grasses and macroalgae (e.g. Hicks & Coull, 1983; Hicks, 1985; Bell *et al.*, 1988; Bell & Hicks, 1991; De Troch *et al.*, 2001a, 2003). These species-rich assemblages are characterized by a specific faunal composition usually quite distinct from adjacent sedimentary habitats (Hicks, 1985). Different within-plant subhabitats may be occupied by a different suite of species (Hicks, 1977b; De Troch *et al.*, 2001a; Arroyo *et al.*, 2006). Furthermore, the role of structural complexity of the phytal habitat in determining harpacticoid species number and diversity has been documented (Hicks, 1985; Jenkins *et al.*, 2002).

So far, little meiobenthic research has been conducted along the East African coast. Previous studies addressed the associated fauna of sea grass beds, mangroves or the lagoonal soft-bottom in Kenya, Zanzibar and Madagascar (Thomassin *et al.*, 1976; Vanhove *et al.*, 1992; Ólafsson *et al.*, 1995; Ndaro & Ólafsson, 1999; De Troch *et al.*, 2001b; Raes *et al.*, 2007), and mostly focused on the

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nematode assemblage. Harpacticoid copepod studies have mainly focused on their taxonomy, e.g. in Madagascar (Chappuis, 1954), Réunion (Bozic, 1969), Seychelles (Wells & McKenzie, 1973), Mozambique (Wells, 1967), and Kenya (Fiers & De Troch, 2000; Gheerardyn *et al.*, 2006a, b). Recently, De Troch *et al.* (2001a, 2003) also investigated the composition and structure of harpacticoid communities in Kenyan sea grass beds. The East African coast supports extensive intertidal lagoon flats mainly composed of carbonate sand and in Zanzibar these account for approximately 90% of the total coastal area (Ndaro & Ólafsson, 1999). Along the eastern side of the island, fringing reefs span the coastline and are exposed to strong waves and currents, the main ocean current affecting Zanzibar being the East African Coastal Current (Mbije *et al.*, 2002). Ndaro & Ólafsson (1999) examined the meiobenthos of a shallow lagoon along this coast and found distinct nematode assemblages, principally determined by sediment characteristics, in sea grass bed, fine sand and coarse sand habitats. Raes *et al.* (2007) demonstrated the structuring effect of microhabitat type (coral sand, gravel and dead coral fragments) on nematode assemblages along the Kenyan and Zanzibari coasts.

The major aim of this study was to assess the importance of microhabitat type in influencing harpacticoid communities in the lagoon along the east coast of Zanzibar.

MATERIALS AND METHODS

Sampling and laboratory analysis

Meiofauna samples were collected in the lagoon of the fringing reef, between the reef crest and the sand beach, at two locations along the eastern coast of Zanzibar Island (Tanzania): at Matemwe (MAT), located in the north of the island (5°52′S, 39°21′E; 17 August 2004) and at Makunduchi (MAK), in the south of the island (6°25′S, 39°34′E; 22 August 2004) (Figure 1). Distance between both locations is 70 km. At each location, three replicates were taken at a distance of five metres from each other, at approximately 400–500 m from the beach. The sampling area consisted of bare coral sand with patches of coral gravel and dead coral fragments, and was not located adjacent to any sea grass beds, seaweed culture or living coral patches. All material was collected during low tide under a water cover of 0.5 m. For each replicate, a round, metal core (diameter 30 cm) was placed onto the sediment to delimit the sampling area, in which coral sand, coral gravel and dead coral fragments (devoid of any algal covering) were present (see figure 2 in Raes *et al.*, 2007). One 10 cm^2 sediment core for meiofauna was inserted in the coral sand as deep as possible, next to the coral fragments and the gravel patch. Then, coral fragments were taken out manually, coral gravel was gently scooped out with a spoon and each of these substrates was put directly in a plastic bag. Subsequently, the meiocore was collected and vertically subdivided into three different depth horizons (0–1 cm, 1–3 cm and the remaining sediment, ranging from 3–4 cm to 3–9 cm), to study harpacticoid sediment assemblage with changing sediment depth. An additional 10 cm^2 core for granulometric analysis was also taken. Although it was aimed to sample coral fragments which were similar in structural complexity and morphology, the fragments at MAT were generally more eroded, structurally less complex and less protruding from the sediment surface than in MAK. Coral gravel is distinguished from coral sand because small pieces of coral can still be recognized in the former, whereas this is no longer true for the sediment. Abbreviations used in the text, figures and tables: cor, coral fragments; gra, coral gravel; sed1, sed2, sed3, upper, middle and bottom sediment layer, respectively.

After adding $MgCl_2$ to stun the associated fauna, coral fragments and coral gravel were rinsed thoroughly with filtered seawater and sieved through a 1 mm and a 32 μm sieve to separate the macro- and meiofauna. The material was fixed with 4% buffered formalin. Meiofauna was extracted from the sediment by density gradient centrifugation, using Ludox HS40 (specific density 1.18) as

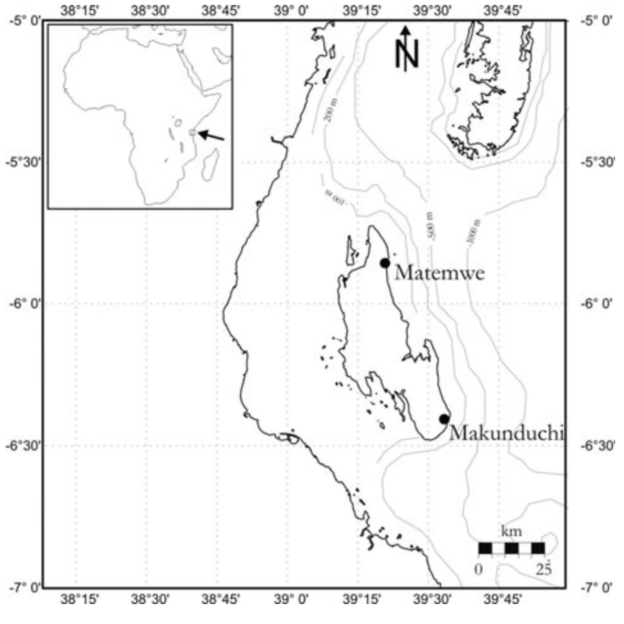

Fig. 1. Map of the study area indicating the sampling sites. The northernmost island is Pemba, the southernmost is Unguja (Zanzibar Island).

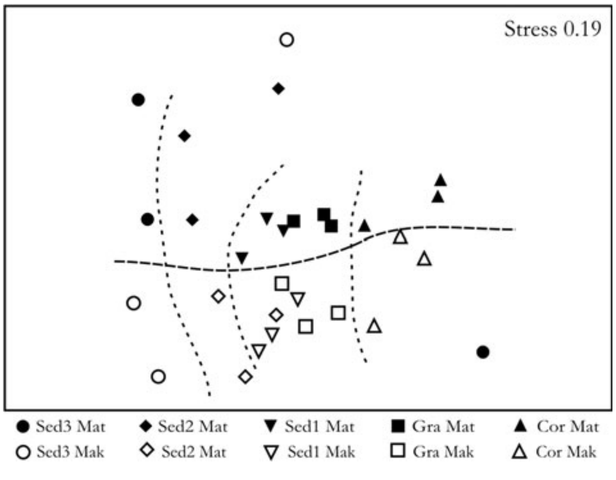

Fig. 2. Multidimensional scaling two-dimensional ordination plot of all samples. Stress value is indicated. The dashed line separates samples from the different locations (MAT: Matemwe; MAK: Makunduchi), the dotted line separates the different microhabitats (cor, coral; gra, gravel; sed1, upper; sed2, middle; and sed3, lower sediment layer) (except samples from gra and sed1).

a flotation medium (Heip *et al.*, 1985; Vincx, 1996). Meiofauna was stained with rose Bengal. From each sample (coral fragment, gravel and the three sediment layers), 200 copepods (or all copepods when less than 200 individuals were present) were randomly picked out and mounted in glycerine. Adult harpacticoids were identified to working species level using Lang (1948, 1965), Boxshall & Halsey (2004) and original descriptions. Assignment of working species to genera and families was in accordance with recent literature. The systematic status of Dactylopusiidae Lang, 1936, Pseudotachidiidae Lang, 1936, Rhynchothalestridae Lang, 1948 and Thalestridae Sars, 1905 follows Willen (2000), the status of Miraciidae Dana, 1846 follows Willen (2000, 2002) and the status of Tisbidae Stebbing, 1910 follows Seifried (2003). Furthermore, each harpacticoid species has been designated to one of the nine body shapes as defined by Coull (1977).

Sediments were analysed with a particle size analyser (type Coulter LS100). The characteristics obtained were median grain size, per cent silt (<63 μm), per cent coarse sand (850–2000 μm), per cent gravel (>2000 μm), kurtosis and skewness.

Statistical analysis

A non-metric, multidimensional scaling, two-dimensional plot (MDS) was produced, using the Bray–Curtis similarity index. Per sample, data were standardized to relative abundance data and arcsin-transformed prior to analysis. The significance of the MDS (differences in copepod assemblage structure between the different groups) was tested through two-way crossed ANOSIM. Similarity of percentages (SIMPER) was used to identify the taxa contributing to the differences found in the ordination analysis. All multivariate tests were performed using the PRIMER5 software (Plymouth Marine Laboratory; Clarke & Gorley, 2001).

Several biodiversity indices were calculated. The Shannon–Wiener index H' and Pielou's evenness J (Pielou, 1975) were calculated for comparison with other studies. Hill's diversity numbers (Hill, 1973) gradually change from indices of species richness to indices of dominance with increasing number: N_0 is identical to the number of species, $N_1 = \exp(H')$ and N_{inf} reflects evenness. Rarefaction curves were constructed from values of the expected number of species (Hurlbert, 1971). Equitability of the copepod fauna was studied based on species' abundance distributions as k-dominance curves (Lambshead *et al.*, 1983).

Parametric analysis of variance (ANOVA) was performed on untransformed or log $(x + 1)$ transformed data if needed to meet the assumptions for ANOVA. Paired *a posteriori* comparisons were carried out with the Tukey test. For non-parametric data, Kruskal–Wallis ANOVA was employed. Post hoc testing of differences was carried out using pairwise Mann–Whitney *U*-tests. Bartlett's and Cochran's tests were used to verify the homogeneity of variances prior to the analysis. All univariate analyses were performed using STATISTICA6 software. Indicator species analysis (ISA) was performed using PC-ORD4 software (McCune & Mefford, 1999). Calculated indicator values were tested for significant values using a Monte Carlo test (Dufrêne & Legendre, 1997). The additive partitioning of species diversity into measures of α- and β-diversity (Veech *et al.*, 2002; Crist *et al.*, 2003) was conducted with PARTITION software.

RESULTS

In total, 4177 copepods were identified. The bulk of the specimens belonged to the order Harpacticoida (79.5%) and Cyclopoida (20.3%). Calanoida were rarely encountered (0.2%, with 9 individuals). Of the 3319 harpacticoid individuals, 55.9% were adults. A total of 119 species, 60 genera and 23 families were recorded in this study (see Appendix). The families Paramesochridae Lang, 1944 (22.2%), Ameiridae Monard, 1927 (14.9%) and Miraciidae (14.9%) dominated and the latter two families showed the highest species number (Table 1). Eight genera (*Ameira* Boeck, 1865, *Apodopsyllus* Kunz, 1962, *Kliopsyllus* Kunz, 1962, *Meiopsyllus* Cottarelli & Forniz, 1994, *Tisbe* Lilljeborg, 1853, *Diagoniceps* Willey, 1930, *Amphiascus* Sars, 1905 and *Parastenhelia* Thompson & A. Scott, 1903) occurred with a relative abundance between 5% and 12.5% and together accounted for 56% of the relative abundance. Most genera (37) were poorly represented (each $<1\%$ of relative abundance). Altogether, 29 species accounted for 80% of the assemblage, with *Ameira* sp. 1, *Kliopsyllus* sp. 1, *Apodopsyllus* sp. 3 and *Diagoniceps* sp. 1 each constituting between 5.2% and 7.4% of relative abundance.

Sediment characteristics

At both locations, the lagoonal soft-sediments are medium to coarse sands with low silt contents (Table 2). Coarse sand percentage was significantly higher at MAK (17.7 ± 1.0% vs 10.8 ± 2.8%), while gravel percentage was significantly higher at MAT (41.2 ± 3.6% vs 12.7 ± 7.4%).

Table 1. Harpacticoid family percentage (%) abundance, number of genera and species in each family identified from the east coast of Zanzibar.

Family	%	Number of genera	Number of species
Paramesochridae	22.22	4	10
Ameiridae	14.94	6	16
Miraciidae	14.89	10	23
Tisbidae	8.47	4	8
Ectinosomatidae	7.93	6	13
Tetragonicipitidae	7.39	2	5
Dactylopusiidae	6.36	3	9
Parastenheliidae	6.09	2	3
Laophontidae	4.26	6	11
Harpacticidae	4.15	3	5
Tegastidae	1.02	1	1
Longipediidae	0.59	1	1
Metidae	0.38	1	2
Canthocamptidae	0.32	2	3
Thalestridae	0.27	1	1
Pseudotachidiidae	0.16	1	1
Cletodidae	0.11	1	1
Louriniidae	0.11	1	1
Rhynchothalestridae	0.11	1	1
Ancorabolidae	0.05	1	1
Canuellidae	0.05	1	1
Normanellidae	0.05	1	1
Peltidiidae	0.05	1	1

Table 2. Mean values and standard deviation, results of 1-way ANOVA and Mann–Whitney *U*-test evaluating differences in sediment characteristics between both locations (MAT, Matemwe; MAK, Makunduchi). Analyses performed on log (x + 1) transformed data. *, $0.01 < P \leq 0.05$.

	MAT	MAK	1-way ANOVA		Mann–Whitney *U*
			F-ratio	sign. lev.	
silt (%)	2.8 ± 1.5	2.2 ± 0.4	0.254	NS	
median (μm)	408.2 ± 67.9	440.2 ± 57.6	0.283	NS	
coarse sand (%)	10.8 ± 2.8	17.7 ± 1.0	8.99	*	
gravel (%)	41.2 ± 3.6	12.4 ± 7.4			MAT > MAK
skewness	−2.6 ± 0.5	−2.2 ± 0.3	0.536	NS	
kurtosis	12.1 ± 3.9	9.9 ± 2.3	0.432	NS	

sign. lev., significance level; NS, not significant.

Similarity analysis

The MDS ordination indicates that harpacticoid assemblages differ among microhabitats (cor, gra, sed1, sed2, sed3) and between locations (Figure 2). Samples are more separated according to location (averaged over all microhabitat groups), as confirmed by two-way crossed ANOSIM (global $R = 0.379$, $P = 0.001$ among microhabitats; global $R = 0.485$, $P = 0.001$ between locations). Pairwise tests (Table 3) indicated significant differences between cor samples and each of the other microhabitats (gra, sed1, sed2, sed3). Gra samples were significantly different from samples of sed2 and sed3, but not from sed1. Samples from sed2 and sed3 each formed scattered clusters, indicating high variability among replicates.

Multidimensional scaling ordinations at genus and family level (not shown) produced the same pattern of a changing composition across the microhabitats and a clearer separation between locations (indicated by two-way crossed ANOSIM). Pairwise tests indicated significant differences for the same combinations, except that at the genus level there is also a significant difference between gra and sed1 (with $R = 0.296$, $P = 0.05$).

Average similarity among samples in terms of community composition (as indicated by SIMPER) is highest for gra (52.8%) at MAT, and highest for sed1 (48.3%) at MAK. At both locations, average dissimilarity between microhabitats is lowest between gra and sed1 (56.9% and 55%, at MAT and MAK, respectively). Cor samples from both locations are more comparable to each other (dissimilarity value: 64.7%), than they are to the other microhabitats within their respective location (dissimilarity cor–gra at MAT: 66.5%, all other values higher than 75%).

Table 3. Results of ANOSIM pairwise tests: values of the R-statistic and corresponding *P* levels are indicated. **, $0.001 < P \leq 0.01$; *, $0.01 < P \leq 0.05$; NS, not significant. (cor, coral; gra, gravel; sed1, upper; sed2, middle; and sed3, lower sediment layer).

	cor	gra	sed1	sed2	sed3
cor		**	**	**	*
gra	0.778		NS	*	*
sed1	0.889	0.185		NS	*
sed2	0.852	0.296	0.093		NS
sed3	0.565	0.389	0.306	−0.074	

Characterization of the harpacticoid assemblages

At both study sites, four of the five most dominant families in coral fragments were Dactylopusiidae, Ectinosomatidae Sars, 1903, Tisbidae and Ameiridae (Figure 3). These families, together with Laophontidae T. Scott, 1905 and Miraciidae, explained over 90% of similarity among the cor samples and were important in explaining dissimilarity between cor and any other microhabitat (SIMPER). At MAK, the typically phytal family Tegastidae Sars, 1904 explained between 9.5% and 6.7% of the dissimilarity with every other microhabitat (SIMPER). In the gra samples, Ameiridae, Parastenheliidae Lang, 1944, Tisbidae (at both locations), Harpacticidae Sars, 1904 (at MAT) and Miraciidae (at MAK) are the dominant families, which agree well with those from sed1 (i.e. Ameiridae, Miraciidae and Parastenheliidae at both locations). Furthermore, Paramesochridae (20.8% relative abundance) at MAT, and Tetragonicipitidae Lang, 1944 (9.8% relative abundance) at MAK also predominate in sed1. At MAT, sed2 and sed3 are dominated by Paramesochridae (74.4% and 86.6% relative abundance, respectively). At MAK, sed2 is codominated by Tetragonicipitidae, Miraciidae and Ameiridae, while sed3 is dominated by Tetragonicipitidae (67.9% relative abundance).

At both locations, the genera *Dactylopusia* Norman, 1903, *Ectinosoma* Boeck, 1865, *Tisbe* and *Paradactylopodia* Lang, 1944 (at MAT) predominated in cor (Table 4). At Makunduchi, dominant genera in both gra and sed1 are *Paramphiascopsis* Lang, 1944, *Parastenhelia* and *Robertgurneya* Lang, 1944. Both locations differ in dominant genera in sed1 and more distinctly in sed2 and sed3, with mainly paramesochrid genera at MAT, and *Diagoniceps* (Tetragonicipitidae) at MAK. At both locations, *Dactylopusia* and *Ectinosoma* had a significant preference for cor, as shown by indicator species analysis (Table 5). One genus (*Zausodes* C.B. Wilson, 1932) showed a significant preference for gra (at MAT).

Over the complete dataset, the dominant body shapes (as defined by Coull, 1977) are fusiform prehensile (48.4% of the individuals) and vermiform (23.5%). Copepods with fusiform depressed, fusiform compressed and fusiform body shape occur with a relative abundance between 6.7% and 7.7%. The four remaining habitus shapes (depressed, fusiform not prehensile, compressed and cylindrical) are only rarely encountered (less than 4% of relative abundance each). Copepods with a fusiform prehensile body were dominant in cor, gra and sed1 at both locations (ranging between 33.1% and 87.6% of relative abundance), and also in sed2 and sed3 at MAK, due to the presence of Ameiridae, Miraciidae and Tetragonicipitidae (Figure 4). Vermiform copepods were especially dominant in sed2 and sed3 at MAT (over 75% of relative abundance) and increased in relative importance with increasing sediment depth. At MAT, the relative importance of fusiform depressed copepods was significantly higher in cor and gra than in the sediment layers (Kruskal–Wallis ANOVA and Mann–Whitney *U*-tests, $P < 0.05$). Fusiform compressed copepods were

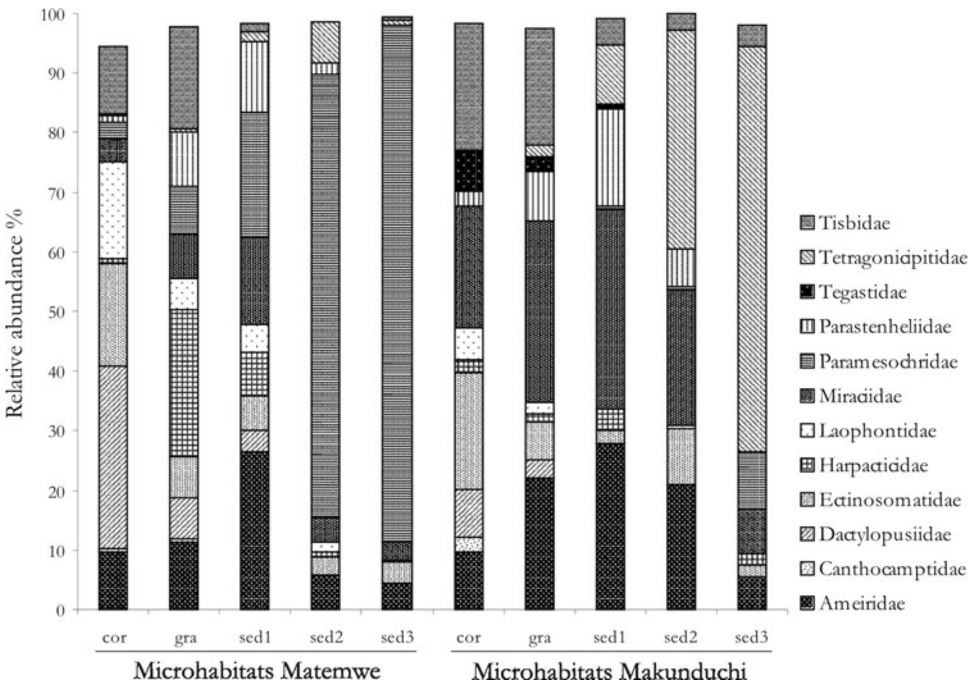

Fig. 3. Harpacticoid family composition per microhabitat at Matemwe and at Makunduchi, based on pooled samples per microhabitat (cor, coral; gra, gravel; sed1, upper; sed2, middle; and sed3, lower sediment layer). Families with a relative abundance >2% in at least one microhabitat are given.

significantly more important in cor than in any sediment layer at MAT (Kruskal–Wallis ANOVA and Mann–Whitney *U*-tests, $P < 0.05$). At MAK, average relative abundance of fusiform copepods (comprising all ectinosomatid genera except *Hastigerella*) was significantly higher in cor than in any other microhabitat (Kruskal–Wallis ANOVA and Mann–Whitney *U*-tests, $P < 0.05$).

Biodiversity

There were significant differences in copepod diversity among microhabitats (Tables 6 & 7), as expressed by indices of species richness (H′, N_0, N_1). However, trends were different between locations. At MAT, diversity (H′) was significantly higher in cor, gra and sed1 than in sed3, and higher in cor

Table 4. Relative abundances (%) of the dominant harpacticoid genera in each microhabitat (cor, coral; gra, gravel; sed1, upper; sed2, middle; and sed3, lower sediment layer), per location. Genera with a relative abundance >2% (calculated over all samples per microhabitat, per location) in at least one microhabitat (per location) are given.

	Matemwe						**Makunduchi**				
	cor	**gra**	**sed1**	**sed2**	**sed3**		**cor**	**gra**	**sed1**	**sed2**	**sed3**
Ameira	9.7	10.3	25.0	5.3	3.5	*Ameira*	9.2	16.4	24.0	9.9	3.8
Amphiascus	0.8	2.9	2.1	0.9	1.0	*Amphiascus*	12.1	13.0	9.3	7.7	
Apodopsyllus				23.8	49.5	*Apodopsyllus*				0.7	7.5
Dactylopusia	12.8	1.1	2.1			*Bulbamphiascus*	3.4	0.5	4.0	5.6	1.9
Diagoniceps		0.6	1.6	6.6	1.0	*Dactylopusia*	6.9	2.4			
Ectinosoma	16.3	4.0	1.6	0.9		*Diagoniceps*			0.9	28.9	60.4
Halectinosoma	0.4	0.6	2.1			*Ectinosoma*	13.8	2.4		4.9	
Hastigerella		2.3	2.1	2.2	3.0	*Halectinosoma*	1.7	3.4	2.2	2.8	
Heterolaophonte	3.9					*Mesochra*	2.3				
Karllangia		5.1	3.6	1.3		*Nitokra*		5.8	2.2	8.5	1.9
Kliopsyllus	2.7	8.0	13.0	22.5	13.9	*Paralaophonte*	4.6	1.0			
Laophonte	2.7	1.1				*Paramphiascopsis*	0.6	10.1	13.8	1.4	1.9
Meiopsyllus			7.8	28.2	22.8	*Parastenhelia*	2.3	7.7	16.4	6.3	
Paradactylopodia	17.9	5.7	1.0			*Phyllopodopsyllus*		1.9	8.9	7.7	7.5
Paralaophonte	8.9	4.0	0.5		0.5	*Psyllocamptus*	0.6		1.3	2.1	
Parastenhelia	1.2	4.0	8.3	0.4		*Robertgurneya*	0.6	5.3	6.2	4.9	1.9
Robertgurneya	0.8	4.0	11.5	2.2	1.5	*Robertsonia*	2.3				
Scutellidium	1.9	2.3				*Scutellidium*	3.4	0.5	0.4	0.7	1.9
Stenhelia (D.)	2.3				0.5	*Tegastes*	6.9	2.4	0.9		
Tapholeon			3.6	1.8		*Tisbe*	13.8	19.3	0.9	0.7	1.9
Tisbe	8.9	14.9	1.6		0.5	*Tisbella*	2.3		3.1	1.4	
Zausodes	0.8	24.6	7.3	0.9		*Zausodes*		1.4	3.6		1.9

Table 5. Indicator genera within each location, as specified by an indicator species analysis. Only taxa with a significant habitat preference are listed. Indicator values, preferred microhabitat (cor, coral; gra, gravel) and significance levels are provided. ***, $P \leq 0.001$; **, $0.001 < P \leq 0.01$; *, $0.01 < P \leq 0.05$.

Genus	Preferred microhabitat	Indicator value	sign. lev.
Matemwe			
Dactylopusia	cor	81,5	**
Paradactylopodia	cor	73	*
Ectinosoma	cor	70,2	**
Laophonte	cor	72	*
Zausodes	gra	62,7	*
Makunduchi			
Dactylopusia	cor	80,4	*
Ectinosoma	cor	64,4	*
Paralaophonte	cor	84,5	*

sign. lev., significance level.

than in sed2. At MAK however, cor was significantly more diverse than any other microhabitat, as shown by N_1. At both locations, N_{inf} is significantly higher in cor and indicates low dominance.

Overall, similar trends were found with K-dominance curves and rarefaction curves based on pooled samples per microhabitat (cor, gra, sed1, sed2, sed3), per location (Figures 5 & 6). At MAT, evenness and species diversity are similar in cor, gra and sed1 (Figures 5a & 6a). At MAK, there is a clear separation in which cor shows the most even distribution (Figure 5b) and the highest diversity (Figure 6b).

Additive partitioning of diversity (Figure 7) indicates that total species richness (γ) is mainly attributed to differences between microhabitats (β_1, 41.4%). Average diversity within microhabitats (α) and β-diversity due to turnover between locations (β_2) contribute 28.8% and 29.8%, respectively. In contrast, 71% of the Shannon index is explained by α-diversity within microhabitats, while β_1-diversity and β_2-diversity contribute less (19.4% and 9.1%, respectively).

The sediment samples contained 69 species, 41 genera and 15 families. Eight families found exclusively in cor and/or gra constituted less than 0.5% of the total assemblage each. Also, 19 genera found exclusively in cor and/or gra samples were relatively rare and, of these, *Heterolaophonte* Lang, 1944 (in cor) and *Laophonte* Philippi, 1840 (in cor and gra) were the most important (with 0.5% and 0.6% of the total assemblage, respectively). Genera restricted to sediment, cor, or gra occurred sporadically, generally representing less than 0.3% of relative abundance (of the total assemblage). Thirteen out of 42 genera occurring in the cor samples are restricted to this microhabitat. Only 3 genera (each found with one individual) out of the 32 genera found in gra samples were restricted to gra. Twelve (of 41) genera were restricted to sediment, with *Tapholeon* Wells, 1967 (with 0.6% of relative abundance), *Apodopsyllus* (with 8.6%) and *Meiopsyllus* (with 6.7%) as the most important. Fifty species were found exclusively in the cor and/or gra samples and, of these, *Paradactylopodia* sp. 3 (occurring in cor and gra) was the most abundant (with 1.9% of the total abundance). Species restricted to one of the microhabitats (35 out of 71 species in cor, 7 out of 51 in gra, 26 out of 69 in sediment) were rare (each constituting less than 1% of the total assemblage), with the exception of *Apodopsyllus* sp. 2 and *Apodopsyllus* sp. 3 (with 2.1% and 5.8%, respectively), and *Meiopsyllus* sp. 2 and *Meiopsyllus* sp. 3 (with 3.5% and 3.0%, respectively).

DISCUSSION

The results of this study indicate that the composition and diversity of the harpacticoid fauna is different in dead coral fragments, coral gravel, and layers (increasing depth into the sediment) of the nearby coral sand. At both locations, there is a trend of changing copepod composition across these

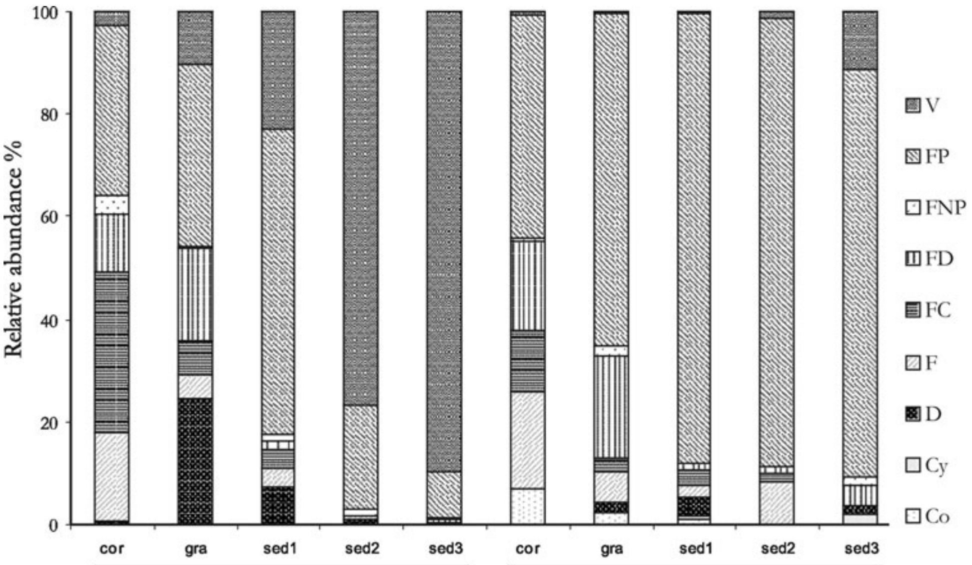

Fig. 4. Composition of body shapes for each microhabitat, per location. Body shapes as defined by Coull (1977). V, vermiform; FP, fusiform prehensile; FNP, fusiform non-prehensile; FD, fusiform depressed; FC, fusiform compressed; F, fusiform; D, depressed; Cy, cylindrical; and Co, compressed.

Table 6. Biodiversity indices: Hill's diversity numbers N_0, N_1, N_{inf}, the expected number of species ES (50), the Shannon–Wiener diversity index $H'$and Pielou's evenness J. The average (Avg) value with standard deviation (SD) is given per microhabitat (cor, coral; gra, gravel; sed1, upper; sed2, middle; and sed3, lower sediment layer), per location.

		Matemwe					Makunduchi				
		cor	gra	sed1	sed2	sed3	cor	gra	sed1	sed2	sed3
N_0	Avg	23.67	20.67	19.00	12.00	8.67	27.33	17.00	14.33	16.00	7.33
	SD	5.19	4.03	3.74	5.89	2.05	6.13	5.72	1.89	2.16	4.50
$H'(\log_2)$	Avg	3.95	3.75	3.71	2.69	2.37	4.39	3.19	3.04	3.33	1.91
	SD	0.38	0.19	0.20	0.59	0.10	0.36	0.33	0.24	0.46	0.74
N1	Avg	16.02	13.53	13.20	6.98	5.20	21.66	9.35	8.32	10.56	4.26
	SD	4.49	1.74	1.89	2.60	0.38	5.01	2.14	1.47	2.95	2.07
N_{inf}	Avg	6.32	4.58	5.40	3.45	2.60	8.29	2.99	3.35	4.59	3.47
	SD	1.05	0.77	0.92	0.70	0.66	1.69	0.44	0.41	2.02	2.51
J'	Avg	0.87	0.86	0.88	0.83	0.79	0.93	0.80	0.79	0.84	0.84
	SD	0.03	0.02	0.04	0.09	0.13	0.02	0.02	0.03	0.11	0.23
ES(50)	Avg	18.58	20.38	17.91	13.28		26.85	14.18	12.39		
	SD	3.97	0.67	2.41	3.78		1.32	2.26	1.35		

microhabitats. Multivariate analysis showed that harpacticoid composition of the coral assemblage differs significantly from gravel and sediment layers. The copepod fauna of the gravel samples did not differ significantly from the upper sediment layer, and differed only slightly (but significantly) from middle and lower sediment layers. Furthermore, faunal composition changed with increasing sediment depth.

The harpacticoid fauna associated with the coral fragments was mainly composed of genera typically found in phytal assemblages, such as *Tisbe*, *Paradactylopodia*, *Dactylopusia* (=*Dactylopodia* Lang, 1948) and *Tegastes* Norman, 1903 (at Makunduchi) (Hicks, 1985), along with genera often found among sediments and other epibenthic microhabitats, such as *Ameira*, *Ectinosoma*, *Amphiascus* and *Paralaophonte* Lang, 1944 (Hicks & Coull, 1983). Although species of certain genera (e.g. *Ectinosoma*) occur in a wide range of habitats and are not easily classified as phytal or sediment dwellers, it is not unlikely that sediment-bound forms are attracted by the sediment retained between the coral branches. The meiofauna (including harpacticoids) associated with the holdfasts of macroalgae is not strictly phytal, but a mixture of inhabitants from phytal, epibenthic and interstitial habitats, associated mainly with the sediment retained between the holdfast structure and the variety of niches and refuge provided by them (Moore, 1972, 1973; Hicks, 1977a; Arroyo *et al.*, 2004, 2006). Similarly, the sediment trapped by the coral fragments might provide a microhabitat for sediment-dwellers, while the complex microtopography of the coral branches might be a suitable substratum for true epibenthic or even 'phytal' harpacticoids. The rough surface of coral skeletons may favour copepods with strongly prehensile maxillipeds and first legs for efficient clinging, but is unsuitable for taxa such as Porcellidiidae Sars, 1904 and Peltidiidae Sars, 1904. These families have dorso-ventrally flattened bodies and adapted mouthparts to facilitate adhesion to the smooth, flat thalloid surface of algae (Noodt, 1971; Hicks, 1980, 1985). Klumpp *et al.* (1988) and Preston & Doherty (1994) examined the crustacean cryptofauna associated with dead coral substrata and reported Thalestridae and Peltidiidae as important harpacticoid constituents. In those studies, coral fragments were colonized by filamentous algae and other epiphytes which might explain the presence of a typical phytal family such as Peltidiidae.

Table 7. Results of 1-way ANOVA and Kruskal–Wallis tests for harpacticoid diversity indices between the different microhabitats (cor, coral; gra, gravel; sed1, upper; sed2, middle; and sed3, lower sediment layer), per location. **, $0.001 < P \leq 0.01$; *, $0.01 < P \leq 0.05$; NS, not significant.

	One-way ANOVA		Post hoc	Kruskal–Wallis sign. lev.
	F-ratio	sign. lev.		
Matemwe				
N_0	4.1	*	cor > sed3	
J'	0.5	NS		
$H'(\log_2)$	8.8	**	cor > sed2, sed3; gra, sed1 > sed3	
N_1	6.4	**	cor > sed2, sed3	
N_{inf}	6.4	**	cor > sed2, sed3; sed1 > sed3	
Makunduchi				
N_0	5.2	*	cor > sed3	
J'				NS
$H'(\log_2)$	7.4	**	cor > sed3	
N_1	9.4	**	cor > gra, sed1, sed2, sed3	
N_{inf}				cor > gra, sed1

sign. lev., significance level.

Multivariate analysis proved that gravel is not significantly different from the upper sediment layer (sed1) in terms of community composition. Only one genus, *Zausodes*, showed a significant preference for gravel in Matemwe. *Zausodes*, with its depressed habitus, most likely has an epibenthic lifestyle. The sediment assemblages from both locations differ distinctly in composition, especially in the middle and lower sediment layers, by the occurrence of paramesochrid genera (*Meiopsyllus*, *Kliopsyllus* and *Apodopsyllus*) at Matemwe and of Tetragonicipitidae (especially *Diagoniceps*) at Makunduchi. The granulometric analysis revealed that the coarse sand fraction was significantly more important at Makunduchi, which explains the occurrence of Tetragonicipitidae, generally a conspicuous member of coarse shell-gravel assemblages (Hicks & Coull, 1983). Paramesochridae are typically known as interstitial inhabitants of fine to medium sands. Several studies of carbonate reef-associated sediments also identified sediment granulometry as controlled by reef hydrodynamics (with its

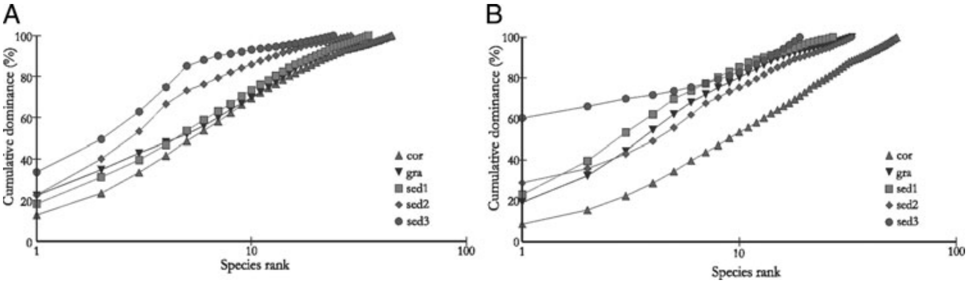

Fig. 5. K-dominance curves of pooled samples per microhabitat (cor, coral; gra, gravel; sed1, upper; sed2, middle; and sed3, lower sediment layer), (A) at Matemwe and (B) at Makunduchi.

effect on other environmental variables) as an important structuring factor of the associated harpacticoid (Coull, 1970; Villiers & Bodiou, 1996) and nematode communities (Ólafsson *et al.*, 1995; Boucher, 1997; Ndaro & Ólafsson, 1999; Netto *et al.*, 1999; de Jesús-Navarrete, 2003). The finer sediment of Matemwe appears to favour vermiform harpacticoids (Paramesochridae and *Hastigerella* Nicholls, 1935), which are adapted to move through narrow spaces between the sand grains. Evidently, the interstitial spaces in the coarser sand at Makunduchi are larger and this explains the pronounced occurrence of harpacticoids with fusiform prehensile body shape (mainly Ameiridae, Miraciidae and Tetragonicipitidae). These harpacticoids are generally larger and have well developed swimming legs, with which they can move through the systems of spaces between the larger sediment particles. Copepods with fusiform and depressed/compressed body shapes (Noodt, 1971; Coull, 1977) were more dominant in the coral and gravel samples.

The differences between communities associated with coral, gravel and upper sediment layer are based in particular on different contributions of the taxa that are present. The coral assemblage is not composed of unique, specific families or genera restricted to this microhabitat, as is often found in algae or hard substrates (containing low levels of deposited sediments) which are distinct (or even largely non-overlapping) from adjacent sedimentary habitats (Hicks, 1985; Atilla *et al.*, 2003). Species restricted to one of the microhabitats occurred only sporadically, with the exception of representatives of *Apodopsyllus* and *Meiopsyllus* in the sediment. However, although dissimilarity between coral samples of both locations is rather high (64.7%), this value is consistently lower than dissimilarity between coral and every other microhabitat within each location. This indicates that coral assemblages from both locations are slightly more comparable to each other in terms of faunal composition than they are to gravel and sediment layers within their respective location.

The harpacticoid fauna associated with different microhabitats investigated in this study appears to be controlled by the structural differences between coral, and gravel and sediment, and by changes in sediment grain size. Not only the nature of the substrate, but also the conditions encountered in these particular microhabitats (e.g. with respect to hydrodynamical stress and food availability) could be important structuring factors. Copepod species living phytally, epibenthically, or in the water column are known to have ecological traits which differ from those of sediment-dwelling species (Marcotte, 1983; Hicks, 1985). The structurally complex dead coral fragments might provide a variety of food resources and meet the feeding requirements of both sediment and phytal taxa, which could also explain their co-occurrence in the coral fragments. In a comparable study of the associated nematode assemblages of coral sand, coral gravel and coral fragments, Raes *et al.* (2007) found that microhabitat type is a major structuring factor. They concluded that nematode communities are even more affected by changes in sediment grain size than by the structural differences between sediment and coral fragments. The coral fragments were considered preferable habitats particularly for nematodes able to withstand the current's eroding effect, such as the epifaunal Epsilonematidae and Draconematidae. Also, current activity can erode detritus from the coral fragments which would explain the low abundance of non-selective deposit feeding nematodes (Raes *et al.*, 2007).

Despite similar changes in harpacticoid composition across microhabitats at both locations, trends in species diversity were different. At Makunduchi, coral fragments sustained a more diverse assemblage (both in terms of species richness and evenness) than gravel and the different sediment layers, whereas at Matemwe, coral was not significantly different from gravel and upper sediment layer.

For phytal assemblages, several studies indicated that an increase in habitat complexity allows for a linear increase in

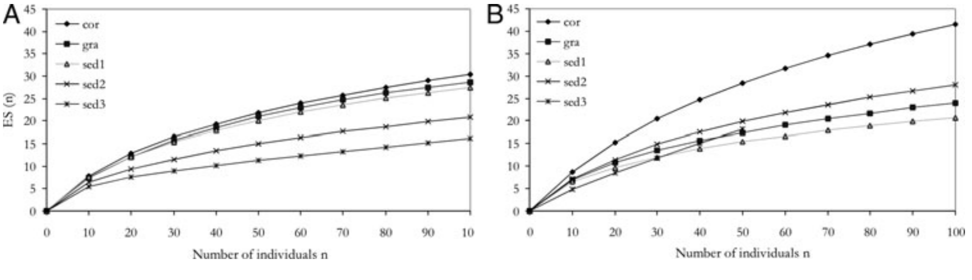

Fig. 6. Rarefaction curves of pooled samples per microhabitat (cor, coral; gra, gravel; sed1, upper; sed2, middle; and sed3, lower sediment layer), (A) at Matemwe and (B) at Makunduchi.

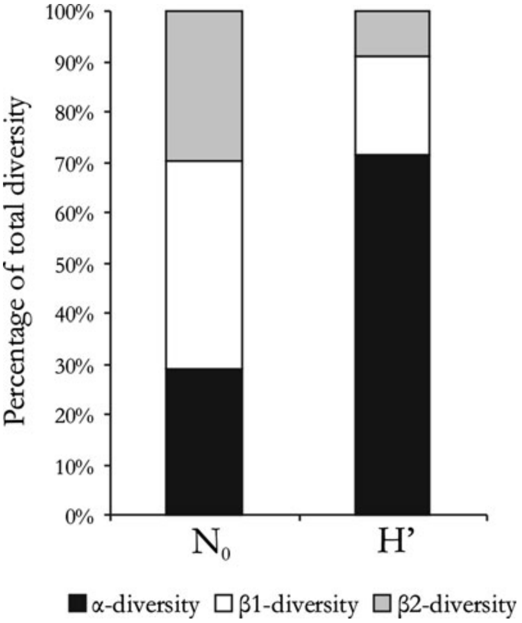

Fig. 7. Additive partitioning of total diversity for the number of species N_0 and for Shannon–Wiener diversity H′. β_1-diversity is the fraction of β-diversity resulting from differences in microhabitat. β_2-diversity is the fraction of β-diversity resulting from differences between locations.

harpacticoid species number and diversity (Hicks, 1980; Gee & Warwick, 1994; Ólafsson *et al.*, 2001; Jenkins *et al.*, 2002). Greater habitable space, increased nutritional resources and reduced levels of predation contribute to this relationship. Coral skeletons at Makunduchi were generally less eroded and structurally more complex than at Matemwe. Although not quantified, it is assumed that the observed differences in complexity might be responsible for the different trends in diversity. Several studies on macrocrustacean cryptofauna have demonstrated that spatial separation of the (living) coral branches influences species abundance and faunal composition (Lewis & Snelgrove, 1990; Vytopil & Willis, 2001). Vytopil & Willis (2001) found greater abundance and species richness of macro-epifauna in tightly branched coral species in comparison to their rarity or absence in open-branched species and related this to the higher protection afforded by the more complex habitat structure. Similarly, the level of structural complexity of certain coral fragments might be high enough for the associated meiofauna to provide refuge against predation. Furthermore, coral form may have implications for the associated epifauna, including increased potential for niche separation (Begon *et al.*, 1990) and modification of the local hydrodynamical environment (Helmuth *et al.*, 1997) with consequences for the nutritional resources available.

This is the first study that includes coral degradation products (such as coral fragments and coral gravel) as a habitat for harpacticoid copepods. It is clear that by including these additional microhabitats, total species diversity of the tropical lagoon is increased substantially. As indicated by additive partitioning of diversity, these added species, however, are generally rare.

In conclusion, microhabitat type is important in structuring the associated harpacticoid assemblages. The coral fragments support a specific assemblage composed of epibenthic or phytal taxa with an addition of sediment-dwelling species. The observed differences in growth form and complexity of the coral fragments, with implications for habitable space, nutritional resources and level of predation might be important in structuring diversity of the associated assemblages.

ACKNOWLEDGEMENTS

The authors wish to thank Dr A. Dubi, Dr D.C.P. Masalu and the staff from the Institute of Marine Sciences in Zanzibar (University of Dar es Salaam, Tanzania). Dr M. Raes, Drs K. Guilini and R. Teerlynck (Marine Biology Section, Ghent University, Belgium) helped during sampling. Special thanks go to B. Beuselinck, D. Schram and A. Van Kenhove (Marine Biology Section, Ghent University, Belgium) for technical support. Two anonymous referees and the Executive Editor are kindly thanked for critically reading the manuscript and providing constructive remarks. The first and second authors acknowledge grants, as aspirant and postdoctoral fellow respectively, from the Fund for Scientific Research (FWO-Flanders, Belgium). The sampling campaign in Zanzibar was organized in the frame of the research project G.0199.03 'A Comparative Study of the Meio-Epifauna Associated with Tropical and Cold-Water Coral Reefs' sponsored by the Fund for Scientific Research (FWO-Flanders, Belgium). This study was partly conducted in the frame of UGent-BOF-GOA research project 01GZ0705 'Biogeography and Biodiversity of the Sea'.

REFERENCES

Alongi D.M. (1989) The role of soft-bottom benthic communities in tropical mangrove and coral reef ecosystems. *Aquatic Sciences* 1, 243–279.

Arroyo N.L., Maldonado M., Pérez-Portela R. and Benito J. (2004) Distribution patterns of meiofauna associated with a sublittoral *Laminaria* bed in the Cantabrian Sea (north-eastern Atlantic). *Marine Biology* 144, 231–242.

Arroyo N.L., Maldonado M. and Walters K. (2006) Within- and between-plant distribution of harpacticoid copepods in a North Atlantic bed of *Laminaria ochroleuca*. *Journal of the Marine Biological Association of the United Kingdom* 86, 309–316.

Atilla N., Wetzel M. and Fleeger J. (2003) Abundance and colonization potential of artificial hard substrate-associated meiofauna. *Journal of Experimental Marine Biology and Ecology* 287, 273–287.

Begon M., Harper J.L. and Townsend C.R. (1990) *Ecology. Individuals, populations and communities*, 2nd edn. Boston: Blackwell Scientific Publications.

Bell S.S. and Hicks G.R.F. (1991) Marine landscapes and faunal recruitment: a field test with seagrasses and copepods. *Marine Ecology Progress Series* 73, 61–68.

Bell S.S., Hicks G.R.F. and Walters K. (1988) Active swimming in meiobenthic copepods of seagrass beds: geographic comparisons of abundance and reproductive characteristics. *Marine Biology* 98, 351–358.

Boucher G. (1997) Structure and biodiversity of nematode assemblages in the SW lagoon of New Caledonia. *Coral Reefs* 16, 177–186.

Boxshall G.A. and Halsey S.H. (2004) *Copepod orders and families. An introduction to copepod diversity*. London: Ray Society.

Bozic B. (1969) Copépodes Harpacticoïdes de la Réunion VI. *Bulletin du Musée d'Histoire Naturelle de Paris* 41, 867–882.

Chappuis P.A. (1954) Recherches sur la faune interstitielle des sediments marins et d'eau douce à Madagascar IV Copépodes Harpacticoides psammiques de Madagascar. *Mémoires de l'Institut Scientifique de Madagascar* 9, 45–73.

Clarke K.R. and Gorley R.N. (2001) *PRIMER v5: User Manual/Tutorial*. Plymouth: PRIMER-E.

Coull B.C. (1970) Shallow water meiobenthos of the Bermuda platform. *Oecologia* 4, 325–357.

Coull B.C. (1977) Marine flora and fauna of the northeastern United States. Copepoda: Harpacticoida. *NOAA Technical Report NHFS Circular* 399, 1–48.

Coull B.C. (1990) Are members of the meiofauna food for higher trophic levels? *Transactions of the American Microscopical Society* 109, 233–246.

Coull B.C. and Herman S.S. (1970) Zoogeography and parallel level-bottom communities of the meiobenthic Harpacticoida (Crustacea Copepoda) of Bermuda. *Oecologia* 5, 392–399.

Crist T.O., Veech J.A., Gering J.C. and Summerville K.S. (2003) Partitioning species diversity across landscapes and regions: a hierarchical analysis of α β and γ diversity. *American Naturalist* 162, 734–743.

de Jesús-Navarrete A. (2003) Diversity of Nematoda in a Caribbean atoll: Banco Chinchorro Mexico. *Bulletin of Marine Science* 73, 47–56.

De Troch M., Fiers F. and Vincx M. (2001a) Alpha and beta diversity of harpacticoid copepods in a tropical seagrass bed: the relation between diversity and species' range size distribution. *Marine Ecology Progress Series* 215, 225–236.

De Troch M., Fiers F. and Vincx M. (2003) Niche segregation and habitat specialisation of harpacticoid copepods in a tropical seagrass bed. *Marine Biology* 142, 345–355.

De Troch M., Gurdebeke S., Fiers F. and Vincx M. (2001b) Zonation and structuring factors of meiofauna communities in a tropical seagrass bed (Gazi Bay Kenya). *Journal of Sea Research* 45, 45–61.

De Troch M., Mees J. and Wakwabi E. (1998) Diets of abundant fishes from beach seine catches in seagrass beds of a tropical bay (Gazi Bay Kenya). *Belgian Journal of Zoology* 128, 119–154.

Dufrêne M. and Legendre P. (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67, 345–366.

Fiers F. and De Troch M. (2000) New Tetragonicipitidae (Copepoda Harpacticoida) from the Indo-Pacific. *Hydrobiologia* 434, 97–144.

Gee J.M. (1989) An ecological and economic review of meiofauna as food for fish. *Zoological Journal of the Linnean Society* 96, 243–261.

Gee J.M. and Warwick R.M. (1994) Metazoan community structure in relation to the fractal dimensions of marine macroalgae. *Marine Ecology Progress Series* 103, 141–150.

Gheerardyn H., Fiers F., Vincx M. and De Troch M. (2006a) *Peltidiphonte* gen n a new taxon of Laophontidae (Copepoda:Harpacticoida) from coral substrates of the Indo-West Pacific Ocean. *Hydrobiologia* 553, 171–199.

Gheerardyn H., Fiers F., Vincx M. and De Troch M. (2006b) Two new genera of Laophontidae (Copepoda:Harpacticoida) without sexual dimorphism in the endopods of the swimming legs. *Zootaxa* 1327, 41–62.

Gray J.S. (1985) Nitrogenous excretion by meiofauna from coral-reef sediments—Mecor-5. *Marine Biology* 89, 31–35.

Hartzband D.J. and Hummon W.D. (1974) Sub-community structure in subtidal meiobenthic Harpacticoida. *Oecologia* 14, 37–51.

Heip C., Vincx M. and Vranken G. (1985) The ecology of marine nematodes. *Oceanography and Marine Biology: an Annual Review* 23, 399–489.

Helmuth B.S.T., Timmerman B.E.H. and Sebens K.P. (1997) Interplay of host morphology and symbiont microhabitat in coral aggregations. *Marine Biology* 130, 1–10.

Hicks G.R.F. (1977a) Species associations and seasonal population densities of marine phytal harpacticoid copepods from Cook Strait. *New Zealand Journal of Marine and Freshwater Research* 11, 621–643.

Hicks G.R.F. (1977b) Observations on substrate preference of marine phytal harpacticoids (Copepoda). *Hydrobiologia* 56, 7–9.

Hicks G.R.F. (1980) Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. *Journal of Experimental Marine Biology and Ecology* 44, 157–192.

Hicks G.R.F. (1985) Meiofauna associated with rocky shore algae. In Moore P.G. and Seed R. (eds) *The ecology of rocky coasts*. New York: Columbia University Press, pp. 36–55.

Hicks G.R.F. and Coull B.C. (1983) The ecology of marine meiobenthic harpacticoid copepods. *Oceanography and Marine Biology: an Annual Review*, 21, 67–175.

Hill M.O. (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology* 54, 427–432.

Hurlbert S.H. (1971) The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52, 577–586.

Jenkins G.P., Walker-Smith G.K. and Hamer P.A. (2002) Elements of habitat complexity that influence harpacticoid copepods associated with seagrass beds in a termerate bay. *Oecologia* 131, 598–605.

Klumpp D.W., McKinnon A.D. and Mundy C.N. (1988) Motile cryptofauna of a coral reef: abundance distribution and trophic potential. *Marine Ecology Progress Series* 45, 95–108.

Lambshead P.J.D., Platt H.M. and Shaw K.M. (1983) The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. *Journal of Natural History* 17, 859–874.

Lang K. (1948) *Monographie der Harpacticiden I & II*. Lund: Håkan Ohlssons Boktryckeri.

Lang K. (1965) Copepoda Harpacticoidea from the Californian Pacific coast. *Kungliga Svenska Vetenskapsakademiens Handlingar* 10, 1–566.

Lewis J.B. and Snelgrove P.V.R. (1990) Corallum morphology and composition of crustacean cryptofauna of the hermatypic coral *Madracis mirabilis*. *Marine Biology* 106, 267–272.

Marcotte B.M. (1983) The imperatives of copepod diversity: perception, cognition, competition and predation. In Schram F.R. (ed.) *Crustacean phylogeny*. Rotterdam: AA Balkema Publishers, pp. 47–72.

Mbije N.E., Wagner G.M., Francis J., Ohman M.C. and Garpe K. (2002) Patterns in the distribution and abundance of hard corals around Zanzibar Island. *Ambio* 31, 609–611.

McCune B. and Mefford M.J. (1999) *PC-ORD. Multivariate analysis of ecological data, Version 4.32*. Gleneden Beach, OR, USA: MjM Software.

Moore P.G. (1972) Particulate matter in the sublittoral zone of an exposed coast and its ecological significance with special reference to the fauna inhabiting kelp holdfasts. *Journal of Experimental Marine Biology and Ecology* 10, 59–80.

Moore P.G. (1973) The kelp fauna of northeast Britain. II. Multivariate classification: turbidity as an ecological factor. *Journal of Experimental Marine Biology and Ecology* 13, 127–163.

Moriarty D.J.W., Pollard P.C., Alongi D.M., Wilkinson C.R. and Gray J.S. (1985) Bacterial productivity and trophic relationships with consumers on coral reefs (Mecor I). *Proceedings of the 5th International Coral Reef Symposium* 3, 457–462.

Ndaro S. and Ólafsson E. (1999) Soft-bottom fauna with emphasis on nematode assemblage structure in a tropical lagoon in Zanzibar eastern Africa: I. spatial variability. *Hydrobiologia* 405, 133–148.

Netto S.A., Attrill M.J. and Warwick R.M. (2003) The relationship between benthic fauna carbonate sediments and reef morphology in reef-flat tidal pools of Rocal Atoll (north-east Brazil). *Journal of the Marine Biological Association of the United Kingdom* 83, 425–432.

Netto S.A., Warwick R.M. and Attrill M.J. (1999) Meiobenthic and macrobenthic community structure in carbonate sediments of Rocas Atoll (North-east Brazil). *Estuarine, Coastal and Shelf Science* 48, 39–50.

Noodt W. (1971) Ecology of the Copepoda. *Smithsonian Contributions to Zoology* 76, 97–102.

Ólafsson E., Ingolfsson A. and Steinarsdottir M.B. (2001) Harpacticoid copepod communities of floating seaweed: controlling factors and implications for dispersal. *Hydrobiologia* 453/454, 189–200.

Ólafsson E., Johnstone R.W. and Ndaro S.G.M. (1995) Effects of intensive seaweed farming on the meiobenthos in a tropical lagoon. *Journal of Experimental Marine Biology and Ecology* 191, 101–117.

Pielou E.C. (1975) *Ecological diversity*. New York: Wiley-Interscience.

Preston N.P. and Doherty P.J. (1994) Cross-shelf patterns in the community structure of coral-dwelling Crustacea in the central region of the Great Barrier Reef. II. Cryptofauna. *Marine Ecology Progress Series* 104, 27–38.

Raes M., De Troch M., Ndaro S.G.M., Muthumbi A., Guilini K. and Vanreusel A. (2007) The structuring role of microhabitat type in coral degradation zones: a case study with marine nematodes from Kenya and Zanzibar. *Coral Reefs* 26, 113–126.

Seifried S. (2003) *Phylogeny of Harpacticoida (Copepoda): revision of 'Maxillipedasphalea' and Exanechentra*. Göttingen: Cuvillier.

Thomassin B.A., Vivier M.H. and Vitiello P. (1976) Distribution de la méiofaune et de la macrofaune des sables coralliens de la retenue d'eau épirécifale du grand récif de tuléar (Madagascar). *Journal of Experimental Marine Biology and Ecology* 22, 31–53.

Vanhove S., Vincx M., Van Gansbeke D., Gijselinck W. and Schram D. (1992) The meiobenthos of five mangrove vegetation types in Gazi Bay Kenya. *Hydrobiologia* 247, 99–108.

Veech J.A., Summerville K.S., Crist T.O. and Gering J.C. (2002) The additive partitioning of species diversity: recent revival of an old idea. *Oikos* 99, 3–9.

Villiers L. (1988) Density and biomass of macro- and meiofauna in lagoon sands at Mururoa atoll French Polynesia. *Proceedings of the 6th International Coral Reef Symposium* 2, 45–51.

Villiers L. and Bodiou J.Y. (1996) Community structure of harpacticoid copepods in a tropical reef lagoon (Fangataufa Atoll—French Polynesia). *Oceanologica Acta* 19, 155–162.

Villiers L., Christien D. and Sevère A. (1987) Investigations sur l'écologie des sables lagonaires biogènes de l'atoll de Mururoa (Tuamotu-Polynésie française). *ORSTOM Tahiti Notes et Documents d'Océanographie* 36, 1–98.

Vincx M. (1996) Meiofauna in marine and freshwater sediments. In Hall G.S. (ed.) *Methods for examination of organismal diversity in soils and sediments*. Wallingford: CAB International, pp. 187–195.

Vytopil E. and Willis B.L. (2001) Epifaunal community structure in *Acropora* spp (Scleractinia) on the Great Barrier Reef: implications of coral morphology and habitat complexity. *Coral Reefs* 20, 281–288.

Wells J.B.J. (1967) The littoral Copepoda (Crustacea) of Inhaca Island Mozambique. *Transactions of the Royal Society of Edinburgh* 67, 189–358.

Wells J.B.J. and McKenzie K.G. (1973) Report on a small collection of benthic copepods from marine and brackish waters of Aldabra Indian Ocean. *Crustaceana* 25, 133–146.

Willen E. (2000) *Phylogeny of the Thalestridimorpha Lang, 1944 (Crustacea Copepoda)*. Göttingen: Cuvillier.

and

Willen E. (2002) Notes on the systematic position of the Stenheliinae (Copepoda Harpacticoida) within the Thalestridimorpha and description of two new species from Motupore Island Papua New Guinea. *Cahiers de Biologie Marine* 43, 27–42.

APPENDIX

List of identified families and genera (with number of morphospecies in parentheses) from the eastern coast of Zanzibar.

Ameiridae Monard, 1927
- *Ameira* Boeck, 1865 (9 sp.)
- *Nitokra* Boeck, 1865 (3 sp.)
- *Praeleptomesochra* Lang, 1965 (1 sp.)
- *Psyllocamptus* T. Scott, 1899 (1 sp.)
- *Stenocopia* Sars, 1907 (1 sp.)
- Ameirinae gen. 1 (1 sp.)

Ancorabolidae Sars, 1909
- *Laophontodes* T. Scott, 1894 (1 sp.)

Canthocamptidae Sars, 1906
- *Mesochra* Boeck, 1865 (2 sp.)
- Canthocamptidae gen. 1 (1 sp.)

Canuellidae Lang, 1944
- *Brianola* Monard, 1926 (1 sp.)

Cletodidae T. Scott, 1905
- *Enhydrosomella* Monard, 1935 (1 sp.)

Dactylopusiidae Lang, 1936
- *Dactylopusia* Norman, 1903 (5 sp.)
- *Paradactylopodia* Lang, 1944 (3 sp.)
- Dactylopusiidae gen. 1 (1 sp.)

Ectinosomatidae Sars, 1903
- *Ectinosoma* Boeck, 1865 (5 sp.)
- *Halectinosoma* Lang, 1944 (2 sp.)
- *Halophytophilus* Brian, 1917 (1 sp.)
- *Hastigerella* Nicholls, 1935 (1 sp.)
- *Pseudobradya* Sars, 1904 (1 sp.)
- *Sigmatidium* Giesbrecht, 1881 (3 sp.)

Harpacticidae Sars, 1904
- *Harpacticus* Milne-Edwards, 1840 (1 sp.)
- *Perissocope* Brady, 1910 (2 sp.)
- *Zausodes* C.B. Wilson, 1932 (2 sp.)

Laophontidae T. Scott, 1905
- *Esola longicauda* Edwards, 1891
- *Heterolaophonte* Lang, 1944 (1 sp.)
- *Laophonte cornuta* Philippi, 1840
- *Laophonte ciliata* Noodt, 1964
- *Laophonte inornata* A. Scott, 1902
- *Paralaophonte* Lang, 1944 (3 sp.)

Paralaophonte congenera (Sars, 1908)
Tapholeon tenuis Gheerardyn & Fiers, 2007
Laophontinae gen. 1 (1 sp.)

Longipediidae Sars, 1903
Longipedia Claus, 1863 (1 sp.)

Louriniidae Monard, 1927
Lourinia Wilson, 1924 (1 sp.)

Metidae Sars, 1910
Metis Philippi, 1843 (2 sp.)

Miraciidae Dana, 1846
Amphiascoides Nicholls, 1941 (2 sp.)
Amphiascus Sars, 1905 (8 sp.)
Bulbamphiascus Lang, 1944 (1 sp.)
Haloschizopera Lang, 1944 (1 sp.)
Paramphiascella Lang, 1944 (1 sp.)
Paramphiascopsis Lang, 1944 (1 sp.)
Robertgurneya Lang, 1944 (4 sp.)
Robertsonia Brady, 1880 (1 sp.)
Stenhelia (Delavalia) Boeck, 1865 (3 sp.)
Typhlamphiascus Lang, 1944 (1 sp.)

Normanellidae Lang, 1944
Normanella Brady, 1880 (1 sp.)

Paramesochridae Lang, 1944
Apodopsyllus Kunz, 1962 (4 sp.)
Kliopsyllus Kunz, 1962 (1 sp.)
Kliopsyllus furcavaricatus (Kunz, 1974)
Meiopsyllus Cottarelli & Forniz, 1994 (3 sp.)
Scottopsyllus Kunz, 1962 (1 sp.)

Parastenheliidae Lang, 1944
Karllangia Noodt, 1964 (1 sp.)
Parastenhelia Thompson & A. Scott, 1903 (2 sp.)

Peltidiidae Sars, 1904
Peltidium Philippi, 1839 (1 sp.)

Pseudotachidiidae Lang, 1936
Sentiropsis Huys & Gee, 1996 (1 sp.)

Rhynchothalestridae Lang, 1948
Rhynchothalestridae gen. 1 (1 sp.)

Tegastidae Sars, 1904
Tegastes Norman, 1903 (1 sp.)

Tetragonicipitidae Lang, 1944
Diagoniceps Willey, 1930 (1 sp.)
Phyllopodopsyllus T. Scott, 1906 (4 sp.)

Thalestridae Sars, 1905
Eudactylopus A. Scott, 1909 (1 sp.)

Tisbidae Stebbing, 1910
Scutellidium Claus, 1866 (2 sp.)
Tisbe Lilljeborg, 1853 (3 sp.)
Tisbella Gurney, 1927 (2 sp.)
Tisbidae gen. 1 (1 sp.)

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