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Mangrove pneumatophore arthropod assemblages and temporal patterns

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Arthropod assemblages comprising mites, crustaceans and hexapods are characterized here for mangrove pneumatophores in south-eastern Africa. Initial sampling showed that pneumatophore assemblages differed markedly from benthic sediment assemblages, not only in being more species rich, but also in having lower abundances. Differences among pneumatophore arthropod assemblages were observed in comparisons of two mangrove stands (in the Durban region) and habitats within each stand. Strikingly higher arthropod abundances were found in assemblages associated with pneumatophores on the seaward fringes of the mangrove stands, as compared to those situated inside the mangrove stands or along minor waterways. These differences in abundance are ascribed to differences in physical conditions among habitat types, relating to wetting frequency and sunlight exposure. The assemblages associated with minor waterways varied among themselves according to variations in salinity. Temporal variation in abundance showed that some species peaked in summer and others in winter, indicating effects more closely related to terrestrial seasonal patterns, than to seawater temperature. This study highlights the uniqueness of the mangrove pneumatophore arthropod assemblages, and the need for further investigation into these in order to better understand mangrove meiofaunal ecology.

INTRODUCTION

Mangroves are thought to play a major role in supporting tropical estuarine and coastal marine systems by providing an important source of organic material and acting as nursery grounds and habitats for fishes. The benthic meiofauna, in particular, is postulated to function in litter degradation in high detritus areas and to provide prey for fishes (Alongi, 1987; Gee, 1989). Numerous investigations have documented the composition and abundance of meiofaunal species for a variety of mangrove systems around the world (see Alongi & Sasekumar, 1992 for a review). These highlight the taxonomic complexity and variability of meiofaunas from one region to the next. The current investigation focuses on the meiofauna of the south-eastern African mangroves, the subject of a few previous investigations (Dye, 1983a,b; Ólafsson, 1995; Ndaro & Ólafsson, 1999; Ólafsson et al., 2000).

Most mangrove meiofaunal studies consider the assemblages associated with benthic sediments, with considerably less attention being given to other habitats, such as decaying mangrove litter layers (Gee & Somerfield, 1997) or stems and pneumatophores of mangrove trees. Pneumatophores of the mangrove tree, *Avicennia marina* (Forssk.) Vierh., in particular, not only provide large surfaces for the attachment of epiphytic plants and animals, but accumulate sediment that supports a suite of unattached biota. Additionally, pneumatophores experience considerably more variable physical conditions than benthic sediments. These arise from variable exposure to tidal and sunlight conditions along pneumatophore lengths and between pneumatophores, in relation to their position in a mangrove stand, and are likely to increase microhabitat diversity and hence species richness.

While some investigations on pneumatophores have considered algal communities (Wilkinson et al., 1981; Aikanathan & Sasekumar, 1994; Phillips et al., 1994, 1996), cyanobacteria (Potts, 1980), fungi (Hyde, 1990), barnacles and other sessile animals (Farnsworth & Ellison, 1996; Saturmanatpan et al., 1999) associated with pneumatophores, virtually nothing is known about the meiofaunas inhabiting these structures. Estuarine meiofaunal studies classically consider nematodes and harpacticoid copepods, with relatively less attention given to groups such as mites and hexapods (collembolans and dipterans), even though these are common components of marine intertidal systems (Cheng, 1976; Pugh & King, 1985; Thibaud & Christian, 1997). The only known ecological studies considering estuarine mites concern temperate saltmarsh systems (Luxton, 1966, 1967a,b).

The objectives of the current study were therefore as follows: (1) to characterize the marine arthropod assemblages associated with mangrove pneumatophores; (2) to determine whether these differ from benthic sediment assemblages; and (3) to examine spatial and temporal variability in assemblage structure within and between mangrove stands.

MATERIALS AND METHODS

Study area

Sampling was undertaken at two localities (Beachwood and Bayhead Lagoon) near Durban, KwaZulu-Natal, South Africa, between June 1999 and June 2000. The mangrove stand at Beachwood (~44 ha) is located at the mouth of the Umgeni River, while the one at Bayhead (~15 ha) is located in the Durban harbour, ~10 km south of Beachwood (Figure 1; Ward & Steinke, 1982). Nine sites were established at each locality (see Figure 1). Site selection took account of three apparently different sets of environmental conditions that the pneumatophores are likely to experience: the pneumatophores growing at the seaward edge of a mangrove stand (fringe, *sensu* Woodroffe, 1992) experience typical tidal conditions and fairly normal salinities (25–35 psu); those associated with minor waterways such as creeks (riverine) are exposed to reduced salinities (<15 psu) arising from freshwater inflow (Phillips et al., 1994, 1996); and those located deep inside mangrove stands (basin), experience limited sunlight exposure, infrequent wetting and variable salinities. No fringe sites were available at Beachwood, dictating the selection of six riverine and three basin sites there, whereas at Bayhead, three of each habitat type were selected (see Figure 1 for site locations and numbering details).

Sample collection and abundance determination

In the initial study to assess how pneumatophore and benthic sediment meiofaunas compare, samples were collected from the Bayhead fringe and riverine sites (sites 10–15), as they contained the most abundant faunas. The spatial studies included sampling from all 18 sites of the two localities, on three separate occasions (August, October and December 1999). For the assessment of temporal abundance patterns, additional sampling was undertaken at Bayhead (sites 10–15), in February, April and June 2000. On each sampling occasion, five randomly selected replicate samples were collected, comprising the *Avicennia* pneumatophores within a 15×15 cm area, or in the case of benthic sediments, the upper 1 cm of sediment within a disc area of 22.5 cm^2. Pneumatophores were cut at ground level and placed in plastic bags. In the laboratory they were washed over two sieves (5 and 0.1 mm), to retain all the mites, copepods, collembolans, tanaidaceans, isopods, amphipods and dipteran larvae. These arthropods were preserved in 70% ethanol for later identification, sorting and counting.

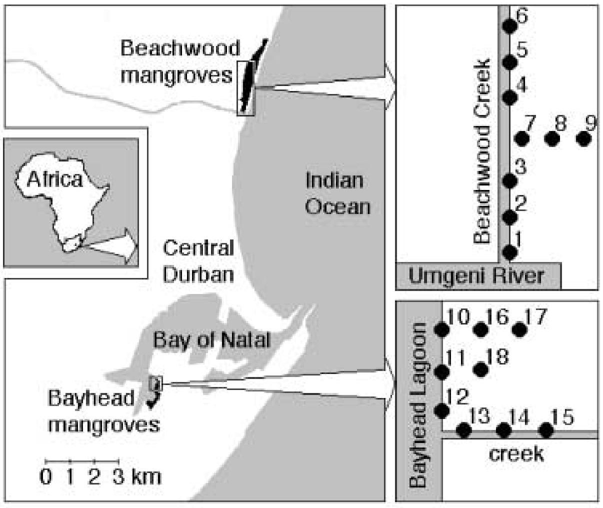

Figure 1. Map of Durban with the position of the collecting sites. The distance between adjacent sites is roughly 50 m.

The extraction procedure followed two steps. Firstly, the mites, tanaidaceans and some insect larvae were extracted from each ethanol sample by hypersaline flotation (Fain & Hart, 1986). The remainder of the sample, which contained mainly copepods and insect larvae, was then brought to a homogeneous aqueous solution of standard volume (50 ml). This was then sub-sampled to give three 5 ml volumes. The number of arthropods in each sub-sample was determined, averaged, and multiplied by ten to obtain an estimate for the entire 50 ml sample. The total number of individuals of the various taxa for the sample was obtained by addition of the numbers in each fraction (hypersaline and aqueous). Benthic samples were treated as above; at the end of the procedure both pneumatophore and sediment values were normalized to 0.1 m^2. Attempts were made to resolve taxa down to species, but in the cases of taxonomically complex groups, more than one species was counted together. Samples were counted under ×100 magnification using a dissecting microscope.

Statistical procedures and data presentation

Using the data for August, October and December 1999, mean abundances (ind 0.1 m^{-2}; N=45) were determined for each group of three sites (1–3, 4–6, 7–9, 10–12, 13–15, 16–18; see Figure 1). Because numbers and lengths of the pneumatophores varied among quadrats, total pneumatophore length was also determined. Paired *t*-tests were used to assess significant differences in abundance of taxa in pneumatophore and benthic sediments. To see how closely the sites were associated with one another in terms of species composition and abundance, a non-metric multidimensional scaling ordination (MDS) was performed from a Euclidean distance model, using 4th-root transformed abundance values to account for rare taxa (Clarke & Warwick, 1994). Plots are given for temporal variations in abundance, as well as for abundances of some Beachwood riverine taxa along a salinity gradient. All statistical procedures were undertaken using SPSS version 9.0 for Windows (1999).

RESULTS

Species composition and abundance

The mesoarthropod fauna of southern African mangroves comprises three similarly species diverse, taxonomic groups: mites (Acari-mesotigmatids, prostigmatids, and oribatids); crustaceans (copepods, tanaidaceans, isopods and amphipods); and hexapods (collembolans and dipterans) (Table 1). Thirty taxa in total were identified, although this excludes some copepod taxa that were not readily discernible. Of the 22 easily identifiable taxa, 12 were found at both Bayhead and Beachwood, while four and six were exclusive to Beachwood and Bayhead, respectively (Table 1).

Arthropod faunas of the benthic sediment below pneumatophores differed markedly from those associated with the pneumatophores themselves. Of ten taxa, four were

Table 1. *Mesoarthropod taxa occurring in mangrove pneumatophores and benthic sediment.*

Taxa				Further referred to as:
Acari	Mesostigmata	Ascidae	*Leioseius* sp. nov.	*Leioseius*
		Uropodidae	*Uroobovella* sp.	*Uroobovella*
	Prostigmata	Nanorchestidae	*Nanorchestes* sp.	*Nanorchestes*
		Halacaridae	*Copidognathus caloglossae*	*Copidognathus*
			Acarothrix umgenica	*Acarothrix*
			Agauopsis sp. nov.	*Agauopsis*
		Tydaeidae indet.		Tydaeidae
		Tarsonemidae indet.		Tarsonemidae
	Oribatida	Oribatulidae indet.		Oribatulidae*
Crustacea	Copepoda	Harpacticoidea		
		Canthocamptidae	*Amphibiperita* sp.,	
		Diosaccidae	*Robertsonia robusta*, etc.	Non-metid Harpacticoidea*
		Metidae	*Metis* sp. nov.	*Metis*
	Tanaidacea	Tanaididae	*Tanais philetaerus*	*Tanais*
	Isopoda	Sphaeromatidae indet.		Sphaeromatidae
	Amphipoda	Hyalidae	*Hyale grandicornis*	*Hyale*
		Melitidae	*Melita zeylanica*	*Melita*
		Podoceridae indet.		Podoceridae
		Corophiidae	*Corophium triaenonyx*	*Corophium*
Hexapoda	Poduromorpha	Neanuridae	*Anurida maritima*	*Anurida*
	Diptera	Tipulidae indet.		Tipulidae
		Cecidomyiidae	Lestremyiinae indet.	Cecidomyiidae
		Empidoidea indet.		Empidoidea*
		Ceratopogonidae	*Culicoides* sp. nov.	*Culicoides*

*, putative complexes of species.

more abundant on the pneumatophores, two were more abundant in the sediment, and four showed no significant differences between the two habitat types (Figure 2). The most abundant taxon in the sediment (Harpacticoidea, 1900 ind 0.1 m^{-2}) differed by one order of magnitude from the most abundant taxon on the pneumatophores (*Tanais*, 190 ind 0.1 m^{-2}). The mites (Acari) were restricted to pneumatophore habitats. Different groups of crustaceans dominated on the pneumatophores (Tanaidacea), and in the sediment (Harpacticoidea). Generally, dipteran larvae showed similar abundances, both in the sediment and on the pneumatophores, but the Empidoidea were more abundant in the sediment (Figure 2).

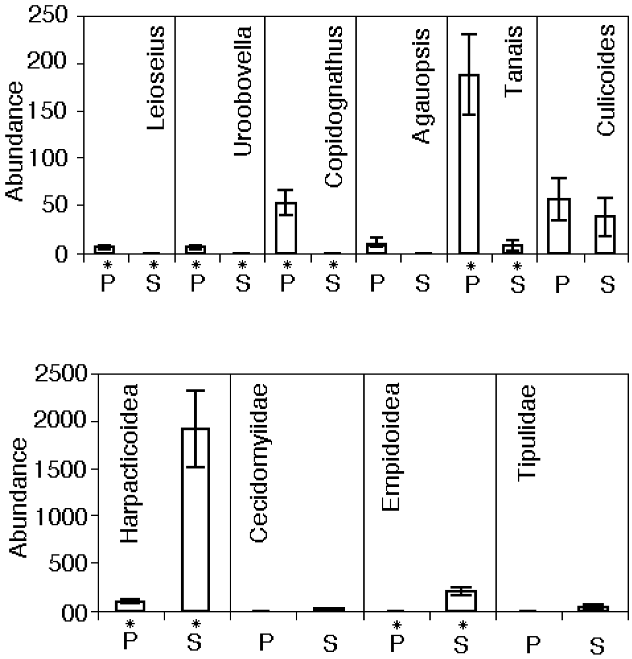

Figure 2. Abundances (mean ±SE for 0.1 m^2; N=30) for arthropod taxa on the pneumatophores (P) and in the benthic sediment (S). *, significant differences between the pneumatophores and the sediment (paired *t*-test, $P > 0.05$).

The crustaceans were the most abundant pneumatophore mesoarthropods (~100 ind 0.1 m^{-2}), followed by the mites (~60 ind 0.1 m^{-2}) and then the hexapods (~30 ind 0.1 m^{-2}). Crustacean abundance was dominated by the abundance of tanaidaceans, though this varied among sites (0–~430 ind 0.1 m^{-2}). The greatest arthropod abundance was found at the Bayhead fringe sites (~900 ind 0.1 m^{-2}) (Table 2). Overall abundances were overwhelmingly influenced by the fringe arthropods and particularly the dominant species of each major taxonomic group, *Copidognathus* (Acari), *Tanais* (Crustacea) and *Culicoides* (Hexapoda) (Table 2). Although total pneumatophore lengths were variable among groups of sites, there was apparently no relationship between total mesoarthropod abundance and total pneumatophore length (Table 2).

Comparisons of assemblages within and between localities

The multidimensional scaling ordination showed a clear distinction between the Beachwood and Bayhead assemblages (Figure 3). This was largely due to differences in species composition at each locality (see Table 2; only 12 of the 20 taxa were common to the two localities).

Table 2. *Abundance of mangrove pneumatophore arthropods.*

	Beachwood			Bayhead			
Taxa	Riverine sites 1–3	Riverine sites 4–6	Basin sites 7–9	Fringe sites 10–12	Riverine sites 13–15	Basin sites 16–18	Grand mean sites 1–18
Leioseius	8.12 ±1.84	4.58 ±0.82	4.56 ±1.06	10.00 ±1.53	6.88 ±1.37	3.51 ±0.85	6.31 ±0.54
Uroobovella	–	0.29 ±0.29	0.30 ±0.22	43.03 ±5.89	3.10 ±1.11	0.61 ±0.34	7.77 ±1.37
Nanorchestes	0.77 ±0.32	2.33 ±0.59	2.14 ±0.60	2.32 ±1.16	–	0.03 ±0.03	1.26 ±0.25
Copidognathus	–	–	–	223.61 ±37.96	16.26 ±6.03	3.92 ±1.33	40.06 ±8.06
Acarothrix	0.77 ±0.40	13.92 ±2.29	3.62 ±1.24	–	–	–	3.10 ±0.54
Tydaeidae	0.77 ±0.32	0.88 ±0.43	5.52 ±1.68	–	–	0.10 ±0.10	1.23 ±0.32
Tarsonemidae	1.06 ±0.35	0.97 ±0.48	0.11 ±0.10	–	–	–	0.36 ±0.10
Oribatulidae	1.16 ±0.57	0.98 ±0.28	1.46 ±0.68	0.61 ±0.23	1.07 ±0.35	0.68 ±0.24	1.00 ±0.18
Total Acari	11.94 ±2.21	24.39 ±2.99	17.97 ±3.46	276.81 ±42.65	27.84 ±7.74	8.00 ±1.70	61.10 ±9.30
Non-metid Harpacticoidea	3.28 ±1.02	0.12 ±0.10	–	26.77 ±5.26	10.35 ±3.07	1.27 ±0.48	7.05 ±1.19
Metis	–	–	–	21.80 ±9.09	15.01 ±6.14	3.39 ±1.64	6.63 ±1.92
Tanais	38.55 ±8.02	1.72 ±0.94	0.12 ±0.10	432.48 ±50.80	15.52 ±4.05	14.82 ±3.07	85.50 ±12.93
Sphaeromatidae	–	–	–	1.41 ±0.56	0.77 ±0.35	0.01 ±0.01	0.36 ±0.11
Hyale	1.45 ±1.00	1.37 ±0.48	2.43 ±1.25	–	–	–	0.89 ±0.28
Melita	6.57 ±2.12	1.21 ±0.72	1.08 ±0.47	0.40 ±0.31	0.50 ±0.21	1.07 ±0.70	1.82 ±0.42
Podoceridae	0.10 ±0.10	–	0.10 ±0.10	–	–	–	0.03 ±0.02
Corophium	0.39 ±0.39	0.01 ±0.01	0.10 ±0.10	–	–	–	0.08 ±0.07
Total Crustacea	51.35 ±10.15	4.25 ±1.72	3.85 ±1.55	494.36 ±53.41	43.00 ±9.16	19.56 ±4.21	102.37 ±14.08
Anurida	–	–	–	23.84 ±6.01	11.23 ±2.76	1.77 ±1.28	6.33 ±1.25
Cecidomyiidae	0.10 ±0.10	1.64 ±1.32	0.03 ±0.03	7.98 ±3.47	0.39 ±0.19	0.17 ±0.12	1.71 ±0.64
Empidoidea	0.29 ±0.17	0.68 ±0.28	2.13 ±2.05	5.05 ±1.49	0.89 ±0.27	1.87 ±1.06	1.82 ±0.47
Culicoides	0.10 ±0.10	0.58 ±0.30	0.30 ±0.17	120.39 ±23.19	2.68 ±1.21	15.86 ±3.41	23.14 ±4.71
Total Hexapoda	0.49 ±0.21	2.96 ±1.35	2.47 ±2.08	158.01 ±28.67	15.41 ±3.03	19.35 ±4.07	32.99 ±5.91
Total mesoarthropods	63.80 ±10.40	31.60 ±4.19	24.29 ±5.57	929.18 ±112.67	86.26 ±11.83	46.91 ±7.97	196.46 ±27.45
Total pneumatophore length (cm)	222.11 ±33.11	285.39 ±42.54	241.35 ±35.98	285.93 ±42.62	224.42 ±33.45	114.03 ±17.00	272.60 ±16.59

Values are mean ±SE for 0.1 m^2; N=45 for groups of three sites, n=270 for the grand mean.

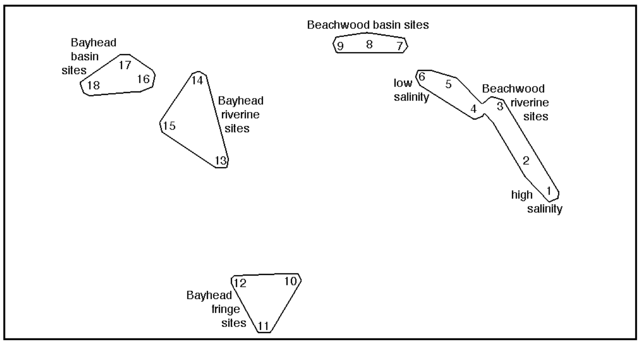

Figure 3. Multidimensional scaling ordination plot for the arthropod assemblages in the 18 sample sites (stress = 0.13).

Although the riverine and basin assemblages were separated at both localities, they were closely spatially associated and showed similar patterns of association for each locality (Figure 3). At Bayhead, the fringe assemblages were, however, widely separated from both the basin and riverine assemblages, an effect attributable to the greater species abundances in the fringe assemblages. Separation of the assemblages at riverine sites in Beachwood, seemed to be influenced by a salinity gradient along the Beachwood Creek. The ordination showed that the assemblages were separated almost linearly from site 1 to site 6 (Figure 3), which respectively represented the highest and lowest salinities of the gradient. Assemblage differences were apparently linked to changing abundances of the

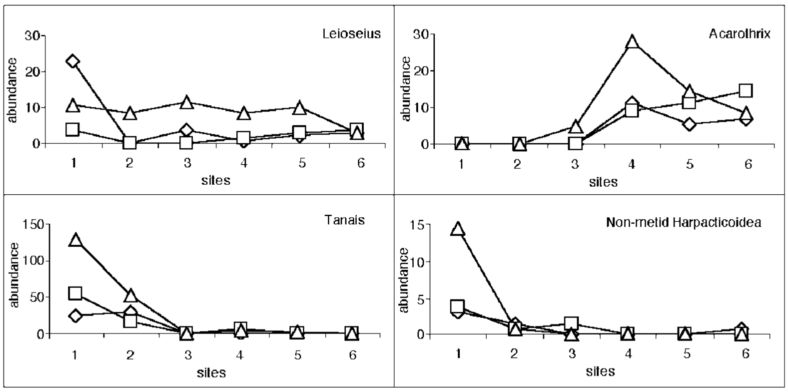

Figure 4. Mean abundance values (0.1 m^2; N=5) for various arthropod taxa at sites 1–6 on three occasions (August, October and December 1999). Salinity decreases from site 1 to site 6. ◇, August samples; □, October samples; △, December samples.

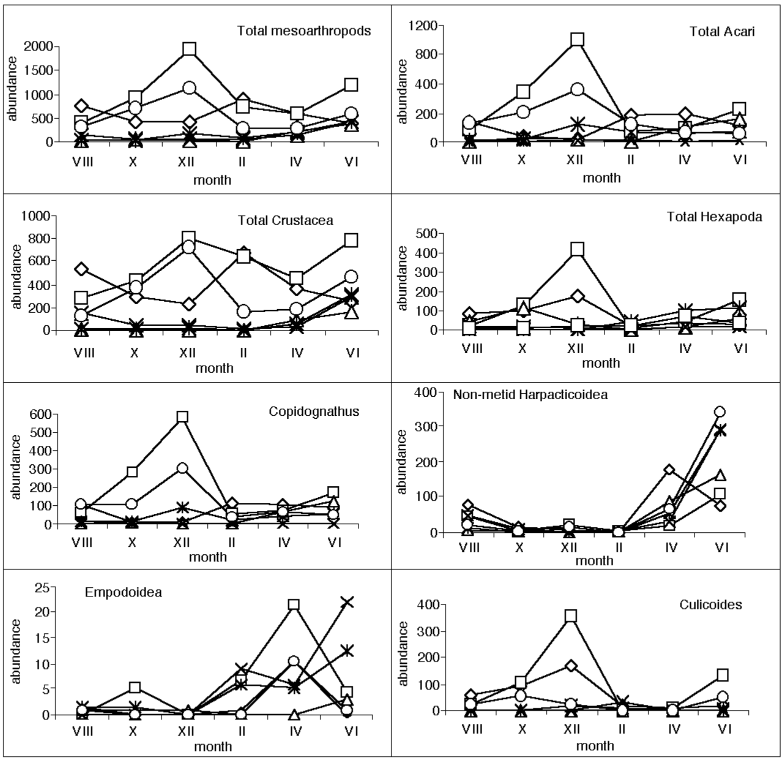

Figure 5. Mean abundance values (0.1 m^2; N=5) for arthropods in sites 10–16 on six occasions (August, October and December 1999, February, April and June 2000). ◇, site 10; □, site 11; ○, site 12; △, site 13; ×, site 14; ✱, site 15.

dominant taxa along this gradient; abundances of the two dominant crustacean taxa decreased (Figure 4), while those of the halacarid mite *Acarothrix*, increased along the gradient of decreasing salinity. Abundances of the predatory mesostigmatid mite, *Leioseius*, were seemingly independent of salinity (Figure 4).

Temporal variation

The abundance values for all the mesoarthropods combined showed a prominent summer and a less prominent winter peak (Figure 5). These patterns were to a large extent influenced by the three most dominant species (*Copidognathus* (Acari), *Tanais* (Crustacea) and *Culicoides* (Hexapoda) (Table 1)). Some of the less abundant species showed slightly different trends (e.g. Empidoidea and Harpacticoidea; Figure 5).

DISCUSSION

Comparisons between pneumatophores and the benthic sediment

We show here that the mesoarthropod assemblages associated with mangrove pneumatophores differ considerably from those of benthic sediments. A new suite of arthropods, containing tanaidaceans and mites, was found exclusively on the pneumatophores investigated, and abundances of other species varied greatly between pneumatophores and benthic sediments. The single known study concerning pneumatophore meiofaunas, shows abundances to be lower on pneumatophores relative to benthic sediments (see Alongi & Sasekumar, 1992), but this excludes mites and tanaidaceans. Even though mites are known to colonize mangrove benthic sediments (Bartsch, 1990; Gee & Warwick, 1996; Chapman, 1998), they were absent from these in the present investigation. Tanaidaceans have been reported in relatively few mangrove meiofaunal studies (Branch & Grindley, 1979; Gee & Warwick, 1996; Chapman, 1998), and the extent to which they colonize benthic sediments remains unclear.

Spatial and temporal variability in marine meiofaunal assemblages has been attributed to a variety of biotic factors (including food availability) and habitat conditions. For example, in lotic systems, biotic interactions include large-scale effects resulting from fish predation and small scale effects resulting from meiofaunal predation (Swan & Palmer, 2000). Another example for deep-sea sediments, ascribes variability to worm-related disturbance (Gage, 1997). Habitat conditions of relevance include sediment particle size, habitat salinity and the potential for dehydration (Alongi & Sasekumar, 1992; Ólafsson et al., 2000). Salinity is known to vary considerably in relation to position on the shore, and depressions in the sediment (Phillips et al., 1996; Chapman, 1998; Ólafsson et al., 2000). Probably the greatest cause of the observed increase in species richness on pneumatophores relative to benthic sediments, derives from the physical and structural attributes of the pneumatophores. Pneumatophores introduce a unique structural feature to the physical environment of mudflats, which significantly increases habitat complexity (Beck, 2000). Additionally, they provide surfaces for the attachment of sessile biota (e.g. algae and barnacles), which form a habitat for other smaller biota (e.g. mites). Furthermore, pneumatophores experience differential dehydration along their lengths during air exposure (following tidal recession). The exclusive occurrence of some taxa on pneumatophores may well relate to their enhanced capacities to withstand dehydration.

Comparisons of assemblages between and within mangrove stands

A second definitive result is that the meiofaunal arthropod assemblages of pneumatophores vary remarkably among mangrove stands, and within stands depending on the position relative to the edge, and to minor waterways. The way in which assemblages change in tandem with changes in salinity between Bayhead and Beachwood, and between sites at the latter, suggests that salinity plays a predominant role in structuring these assemblages. Numerous other studies have suggested how salinity influences mangrove meiofaunal assemblages (Ólafsson, 1995; Somerfield et al., 1998; Ndaro & Ólafsson, 1999, Ólafsson et al., 2000). Differences between the fringe and basin pneumatophore assemblages apparently also relate to differences in habitat conditions; fringe pneumatophores experience a higher frequency of wetting and are often exposed to direct sunlight. At least the former condition is likely to yield greater algal productivity, and thus support larger meiofaunal colonies. This would explain the considerably greater arthropod abundances associated with fringe pneumatophores relative to basin pneumatophores. The lower species richness of fringe assemblages is probably explained by the loss from these assemblages of dehydration intolerant species, as exposure to direct sunlight causes rapid dehydration of these pneumatophores, compared to basin pneumatophores which are shaded by the tree canopy.

Temporal patterns

The temporal patterns of the mangrove pneumatophore arthopods are open to interpretation in terms of terrestrial or marine variations in climatic conditions. Because there is very little variation in the seawater temperature conditions during the year (the warm Agulhas current in the region keeps the temperature >20°C all year round; Bolton & Anderson, 1997), the observed patterns are more likely to relate to terrestrial conditions. Summers in Durban are considerably hotter and wetter than winters (when temperatures often fall below 15°C; Cockcroft & Forbes, 1981). The observed differences among taxa in seasonal abundances may relate to their different preferences of the conditions prevailing at different times of the year. However, the occurrence of summer peaks in taxa which apparently prefer relatively low salinity conditions as well as those which prefer relatively high salinity conditions, suggest that salinity variation caused by summer rains can be discounted as a factor influencing abundance variation among taxa.

Concluding remarks

In summary, we show that mangrove pneumatophores provide an additional dimension of habitat to the mud surface below them, and that the physical characteristics of this habitat explain differences between pneumatophore and sediment assemblages. While we show that pneumatophore arthropod assemblages differ at two different spatial scales—between and within mangrove stands—it is obvious that complex gradients of habitat conditions must exist over a variety of spatial scales. There is certainly scope to investigate much finer scales than those considered here. For instance, it would be interesting to know whether vertical gradients of assemblages exist along the pneumatophore length, considering the potential for differential dehydration along pneumatophores. Even more challenging would be to consider the scale of the sediment particle, which presumably represents the actual habitat space of some of the smaller meiofauna, like nematodes and copepods. Indeed, this preliminary investigation shows not only the usefulness of studying mangrove pneumatophore meiofaunal assemblages, but also highlights our lack of understanding of these assemblages.

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