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Epiphytic algal cover and sediment deposition as determinants of arthropod distribution and abundance on mangrove pneumatophores

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We report here an investigation on intertidal mangrove pneumatophores, examining the relationships between arthropod abundance (for ten taxa, mostly belonging to the meiofaunal size-class), algal biomass and sediment cover. There was a strong correlation between the mass of sediment and the mass of macroalgae, supporting the assumption that pneumatophore sediment cover depends on algal growth. These two components of pneumatophore cover were negatively related to elevation, an effect probably relating to desiccation-limited algal growth towards the pneumatophore tips. Total arthropod abundance and that of some taxa (particularly, Uropodidae (Acari), Metidae (Crustacea), Ceratopogonidae (Insecta) and Empidoidea (Insecta)), was negatively correlated with elevation and positively correlated with sediment and algal cover, suggesting a good relationship between abundance and habitat availability. Other arthropod taxa (particularly, Halacaridae (Acari)) however, showed the opposite pattern of relationships. When the pneumatophore cover was physically removed, in an experiment to assess assemblage recovery rates, some arthropod taxa (Halacaridae (Acari), Harpacticoidea (Crustacea) and Ceratopogonidae (Insecta)) had completely recovered by 25 weeks, while others (Tanaididae (Crustacea) and Empidoidea (Insecta)) only partially recovered.

INTRODUCTION

The structure of mangrove habitats is extremely complex and variable between and within systems. Over small scales, this heterogeneity is largely enhanced by the existence of hard substrata (pneumatophores and tree trunks) interspersed in a soft substratum matrix (the benthic sediment) (Beck, 2000). These habitats support vastly differing biota: sediments typically support burrowing organisms, whereas sedentary organisms can attach to pneumatophores. Further variations are caused by the existence of depressions in the benthic sediment, with considerably different physicochemical conditions (Ólafsson et al., 2000). Superimposed on the entire mangrove systems are effects deriving from exposure during tidal cycles in the intertidal zone (variable wetting—see Dye, 1983b).

Although much information is available for mangrove communities, this is skewed towards studies examining the benthic component (Alongi & Sasekumar, 1992; Kathiresan & Bingham, 2001). Much less is known about the pneumatophore component, which can contribute an extensive surface area to mangrove systems. Most studies on pneumatophores concern epiphyte ecology, and particularly the algae (de Oliveira, 1984; Davey & Woelkerling, 1985; Mann & Steinke, 1988; Coppejans & Gallin, 1989; Phillips et al., 1994, 1996), a few having also considered the sessile fauna (Bingham, 1992; Bingham & Young, 1994; Satumanatpan et al., 1999; Satumanatpan & Keough, 2000). With respect to meiofaunal assemblages of mangrove systems (especially nematode and copepod assemblages), those of the benthic sediments have received significant attention (Ólafsson, 1995; Schrijvers et al., 1995; Somerfield et al., 1998; Gee & Somerfield, 1999; Ndaro & Ólafsson, 1999; Ólafsson et al., 2000), with relatively little known about the assemblages associated with pneumatophores (e.g. Gwyther & Fairweather, 2002). A recent study has, however, shown that pneumatophore arthropod assemblages differ markedly from those of benthic sediments (Procheş et al., 2001). Differences are suggested to arise from the steep gradient of drying along the vertical length of pneumatophores, but there is much scope for further investigation here.

Arthropod faunas associated with mangrove pneumatophores are of special interest in that they comprise proportionally more secondary marine taxa (organisms of terrestrial ancestry, such as mites and insects; see Procheş, 2001) than most other intertidal faunas. Therefore, they offer unique opportunities for examining evolutionary constraints on ecological patterns. In addition, they provide opportunities for testing ecological theory over small scales and across narrow physical gradients. Understanding the factors influencing assemblage structure is thus of obvious interest. The current study was undertaken to assess how microhabitat availability affects the assemblage structure of pneumatophore arthropods.

Specifically, the study examined the relationships of arthropod abundances (including mites, insects, copepods and tanaids) with pneumatophore algal growth and sediment cover (the primary elements of microhabitat of these

Table 1. *Arthropod taxa considered in the study.*

Acari	Ascidae	*Leioseius* sp. nov.
	Uropodidae	*Uroobovella* sp.
	Halacaridae	*Copidognathus caloglossae* Procheş
Crustacea	Harpacticoidea	At least 2 spp. (Canthocamptidae; Diosaccidae); Metidae excluded
	Metidae	*Metis* sp.
	Tanaididae	*Tanais philetaerus* Stebbing
Insecta	Cecidomyiidae	Lestremyiinae sp.
	Empidoidea	At least 3 spp. (2 families); not identified
	Ceratopogonidae	*Culicoides* sp.

arthropods). The study also examined rates of arthropod recolonization after the algal and sediment cover is removed from pneumatophores.

MATERIALS AND METHODS

Locality and arthropod taxa

Sampling was undertaken in the Bayhead mangrove forest, Durban, South Africa (29°5′S 30°61′E), between March and December 2000. This forest covers an area of approximately 15 ha (Ward & Steinke, 1982) and experiences a regular tidal cycle with salinity fluctuating between 27 and 35 psu (Begg, 1976). A previous study identified the seaward fringe pneumatophores at Bayhead as comprising the most complex and abundant arthropod assemblages (Procheş et al., 2001). These therefore became the focus of the present study. The nine most abundant arthropod taxa were considered, which included three mite (Acari), two copepod, and three dipteran species, and a single species of tanaid (see Table 1).

Field collections and abundance determinations

Four (× 5 m) transects were established and 50 *Avicennia marina* pneumatophores longer than 10 cm were randomly selected from each transect. The pneumatophores were cut at ground level, and then cut into 5 cm long segments towards the tip, complying with a measurement commonly used in pneumatophore studies (see Davey & Woelkerling, 1985; Coppejans & Gallin, 1989). This gave four elevation levels as follows, 0–5, 5–10, 10–15 and 15–20 cm, with segments above 20 cm being discarded. All transects were parallel to the shoreline, therefore all pneumatophore bases were situated at the same elevation (about 50 cm below high spring tide level). The entire collection procedure for all transects was performed in less than one hour, at low tide (10 to 11 am, 10 December 2000). The segments were bagged and returned to the laboratory.

The pneumatophore segments were washed over a 0.12-mm mesh to retrieve arthropods, macroalgae and coarse sediment. (The study concerning pneumatophore arthropods only, different mesh sizes were used, as compared to typical meiofaunal investigations; see Procheş et al., 2001.) The wash-water was collected and evaporated to retain the fine sediment (particles smaller that 0.12 mm). Samples retrieved in the mesh were transferred to small plastic bottles and treated with 25 ml hypersaline solution (Fain & Hart 1986). Floating specimens (mainly mites, tanaids and insect larvae) were removed from each bottle, identified and counted under a dissecting microscope (×160 magnification). The remaining content of each bottle was brought to a 50 ml aqueous solution, and the arthropods (mainly copepods and insect larvae) in three 5 ml sub-samples of this, were identified and counted. Based on these sub-samples, the number of individuals was determined for the 50 ml volume, and the total number of arthropods for each sample determined by addition of the fractions deriving from the two extraction procedures.

The sediment in both collections (greater than, and less than 0.12 mm particle size) and the algae retrieved with the coarse sediment, were oven-dried at 60°C for 24 h, and weighed. These samples were then burnt for 5 h at 500°C to eliminate the organic component, and re-weighed. Macroalgal dry mass (which dominated the organic biomass) was taken to be the difference between total mass and the inorganic mass of the coarse fraction. The pneumatophore cover components were related to elevation, and Spearman's rank correlation coefficients were determined

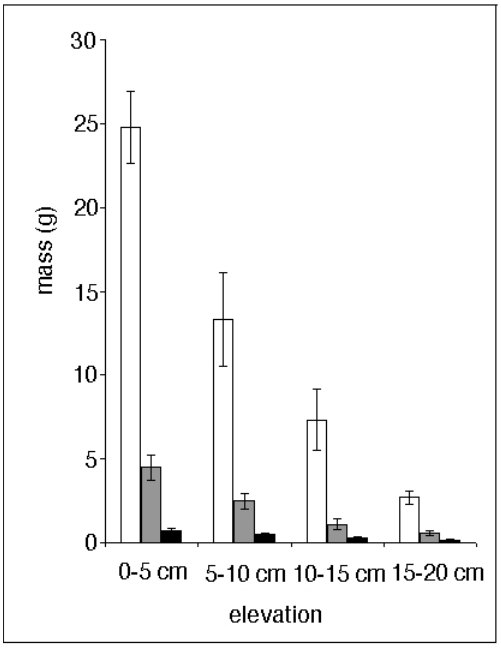

Figure 1. Variation in three factors defining microhabitat conditions along the length of the pneumatophores: fine sediment (white), coarse inorganic sediment (grey) and macroalgae (black). The values represent grams of dry mass (for N=4 sets of 50 pneumatophore segments each).

Table 2. *Abundance of arthropods (mean ±SE, N=4, per sets of 50 pneumatophores) at four levels of elevation on mangrove pneumatophores. All pneumatophores were longer than 15 cm, but some less than 20 cm in length, so the three lower levels represent abundances/50 pneumatophore segments, while the top level (15–20 cm) contained various numbers of segments (<50).*

	0–5 cm	5–10 cm	10–15 cm	15–20 cm
Ascidae	0.00 ±0.00	3.50 ±2.02	0.83 ±0.83	9.05 ±7.01
Uropodidae	9.00 ±4.38	8.50 ±2.99	2.78 ±1.84	0.83 ±0.83
Halacaridae	0.00 ±0.00	22.75 ±11.39	69.92 ±35.16	149.44 ±122.78
Cecidomyiidae	4.00 ±2.12	4.00 ±2.12	6.64 ±3.61	13.71 ±9.97
Empidoidea	57.50 ±11.08	21.00 ±10.30	5.56 ±5.56	1.25 ±0.80
Ceratopogonidae	101.00 ±40.44	32.50 ±9.54	0.83 ±0.83	0.00 ±0.00
Harpacticoidea	10.50 ±7.79	14.75 ±9.82	6.89 ±4.67	4.89 ±3.77
Metidae	80.00 ±28.37	16.50 ±12.35	2.03 ±2.03	0.83 ±0.83
Tanaididae	312.00 ±73.52	375.00 ±123.19	244.90 ±115.69	533.60 ±294.95
Total	574.00 ±132.47	498.50 ±133.93	340.39 ±130.93	713.62 ±384.85

Table 3. *Spearman's rank correlation values for abundance of the arthropod taxa against: (1) elevation level on the pneumatophores; (2) mass of sediment; and (3) mass of macroalgae. Asterisks indicate significant relationships ('table-wide', according to the sequential Bonferroni technique, see Rice, 1989).*

	Elevation	Sediment	Macroalgae
Ascidae	0.280	−0.227	−0.252
Uropodidae	−0.589	0.760*	0.694
Halacaridae	0.573	−0.491	−0.517*
Cecidomyiidae	0.192	−0.183	−0.053
Empidoidea	−0.748*	0.777*	0.676
Ceratopogonidae	−0.764*	0.787*	0.760*
Harpacticoidea	−0.209	0.149	0.052
Metidae	−0.789*	0.688	0.618
Tanaididae	−0.255	0.391	0.492
Total	−0.376	0.518	0.526

for relationships between the abundance of each taxon and elevation, sediment dry mass, and algal dry mass (using data from the 16 samples—4 transects×4 elevation levels). The significance level (*P*) was set at 0.0015, using the sequential Bonferroni technique (Rice, 1989) with an initial α of 0.050, for 33 correlation values (10 taxa×3 environmental factors; three further values among the environmental factors). The package SPSS ver. 9.0 (1998) was used throughout.

Assemblage recovery experiment

This experiment was intended to monitor the temporal changes in arthropod assemblages after clearing pneumatophores of their sediment and algal cover. Six experimental and six control plots, of 60×60 cm each, were established. These were randomly selected at similar elevation on the shoreline, around 3 m apart from one another. In the experimental plots, the sediment and algal cover was removed from all pneumatophores using abrasive Velcro material. Ten pneumatophores were randomly chosen from each experimental and control plot. The pneumatophores were cut at their bases, placed in bags and returned to the laboratory. The site was revisited after 1, 4, 12 and 25 weeks, to undertake further sampling. The samples were processed according to the procedure described above, and the abundances (mean and SE) were plotted for both experimental and control plots. Samples were comparable in total pneumatophore length (130 and 160 cm), eliminating the need to correct for possible discrepancies arising from differences in habitat availability.

RESULTS

Both sediment deposition and algal cover were negatively correlated with elevation along the pneumatophore. At the uppermost elevation, the mass of pneumatophore cover (sediment and algae) was less than a fifth of that at the base. At each elevation, the ratio of fine sediment, to coarse inorganic sediment, to macroalgae was approximately 25 : 5 : 1 (Figure 1). The rank correlation between the mass of the fine sediment and the coarse inorganic sediment was 1, indicating no differential deposition of the two sediment fractions at different elevations. The total mass of sediment (the sum of the two sediment fractions) was therefore used in further correlations with arthropod distribution and abundance. There was also a strong correlation (r=0.925) between the mass of the sediment and that of the macroalgae.

Abundances were remarkably variable among the taxa, for example the range of the 15–20 cm elevation level (for 50 pneumatophores) was from 533 individuals in the case of Tanaididae, to no individuals for the Ascidae and Ceratopogonidae (Table 2). The abundances of most taxa were negatively correlated with elevation, with the exception of the Ascidae, Halacaridae and Cecidomyiidae (Table 3). Although the most abundant taxon, the Tanaididae, showed a negative correlation with elevation, some samples gave extraordinary high abundance values at the uppermost pneumatophore level. Despite the good correlations between elevation, sediment deposition and algal growth (Figure 1), the invertebrate taxa responded differently to the three factors. The Empidoidea, Ceratopoginidae and Metidae showed significant negative correlations with elevation, but only in the former two can this be attributed the larger amount of sediment deposited at lower elevations, and only in Ceratopogonidae was the correlation with algal biomass significant. Two additional correlation

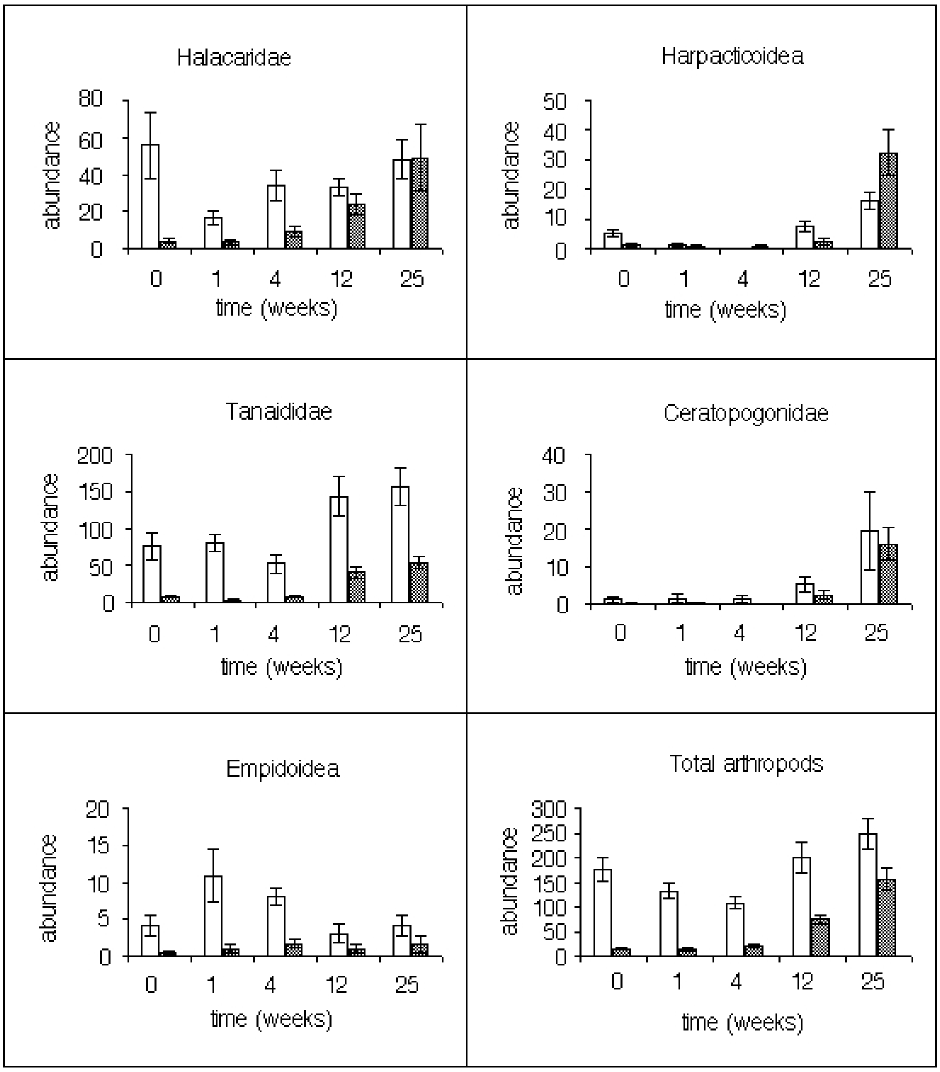

Figure 2. Variation in arthropods abundance (mean and SE, N=6) for the five most abundant arthropod taxa and total arthropods in plots where pneumatophore cover was experimentally removed (grey bars) and in control plots (white bars).

values were significant: the Uropodidae were positively correlated to the sediment, and the Halacaridae were negatively correlated to the macroalgae. Total arthropod abundance was negatively correlated with elevation and positively correlated with sediment and algae, though none of these correlations was significant (Table 3).

Experimental removal of the pneumatophore cover eliminated 90% of the arthropods (Figure 2). Although there was high temporal variability for the abundances in control plots, there was a general trend of recovery in the 25 week period considered. Total arthropod abundance on experimental pneumatophores after 25 weeks was almost ten times greater than the initial abundance following removal of cover, and 60% of the control abundance. The Halacaridae showed the most rapid recovery (there was no significant difference between experimental and control pneumatophores at 12 and 25 weeks), with complete recovery also seen for the Harpacticoidea and Ceratopogonidae, after 25

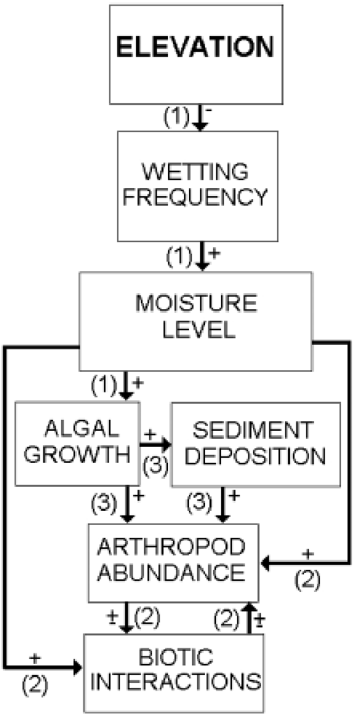

Figure 3. (*Opposite*) Interrelationships among physical and biotic components of the mangrove pneumatophore environment, based on Phillips et al., 1996 (1); Procheş et al., 2001 (2); and Gwyther & Fairweather, 2002; present study (3).

weeks. The most abundant taxon (the Tanaididae) showed relatively slow recovery (Figure 2).

DISCUSSION

Mangrove pneumatophores provide ideal surfaces for the attachment of sedentary biota, for example, algae and barnacles. These biota are considerably variable taxonomically and ecologically (in terms of biomass and abundance), between mangrove stands and from one geographical region to the next. Whereas eukaryotic life growing on pneumatophores may comprise as little as filamentous algae, in other instances this contributes a biomass similar to that of the pneumatophores themselves. For example, epiphytic macrobiotic assemblages on pneumatophores are dominated by filamentous and lamellar algae in southern African estuarine systems (see Phillips et al., 1994, 1996), by barnacles and oysters in some Australian bay systems (see Bayliss, 1993; Ross & Underwood, 1997), and by an array of sponges, hydrozoans, and ascidians in the open sea mangrove islands of Florida (Bingham, 1992; Bingham & Young, 1994). Depending on the nature of the biotic covering, in estuarine systems in particular, it potentially traps fine sediment. Both the biotic and sediment covering of pneumatophores support a variety of motile meiofauna and arthropods, the distributions of which, in some southern African mangroves, have been the subject of recent investigations (Procheş et al., 2001).

Ecological distributions and species abundances, in general, are influenced by habitat suitability (physicochemical conditions), biotic interactions, and life history patterns (Rosenzweig, 1997). Species vertical distributions in the intertidal zone (particularly upper limits) are largely determined by tolerance of physical conditions relating to air exposure, such as desiccation (Underwood & Denley, 1984, but see Pugh & King, 1985, for Acari). We show here that this also relates, in some instances, to habitat availability, as the primary habitat available to the pneumatophore meiofauna (comprising the algal and sediment cover) decreases upwards from ground level. This pattern probably relates to a desiccation-induced reduction in algal growth (Phillips et al., 1994, 1996) (Figure 3).

The abundance of some arthropod taxa (particularly, Uropodidae, Empodiodea, Ceratopogonidae and Metidae) corresponds with the reduction in habitat availability by decreasing along the vertical height of the pneumatophore. This pattern suggests a causal relationship between arthropod abundance and habitat availability (the Uropodidae and Ceratopogonidae are typically interstitial organisms; Krantz, 1976; Linley, 1976). The other meiofaunal taxa either showed a clear negative relationship (in the case of the Halacaridae) or, were weakly positively or negatively related to habitat availability.

The arthropod community had not completely recovered during the investigation period, with rate of recovery being highly variable among taxa. Whereas abundances of some arthropod groups had recovered after 25 weeks, the total arthropod abundance remained below that of the controls by this time (though this was largely due to the dominant taxon—Tanaididae). Extrapolation of the consistent temporal increase in our abundance data indicates that complete recovery should be effected by around 50 weeks. Eston et al. (1992) found epiphytic algal communities on pneumatophores to recover in four to eight months. While our study does not prove conclusively the connection between algal recovery and arthropod recovery, the similarity between their respective recovery times is unlikely to be incidental, and the connection is also supported by a recent independent study (Gwyther & Fairweather, 2002; concentrating on pneumatophore copepods and nematodes).

Intuitively it would follow that taxa whose populations had recovered completely, prior to full recovery of the habitat, are more general in their utilization of habitat than those taxa showing partial recovery. This situation was found to be applicable to the rapidly recovering Halacaridae (strongly negatively related to habitat availability) and the Harpacticoidea (weakly related to habitat), but not to the Ceratopogonidae (strongly correlated to habitat) (see Table 3 and Figure 1). These contrasting results indicate factors other than habitat utilization in influencing population and assemblage recovery. The most obvious and important are factors pertaining to life history and dispersal characters. The temporally consistent increase in abundance of the Halacaridae suggests that their recovery relates to growth of the remnant population on the pneumatophores (as not all individuals were removed during the experiment), whereas harpacticoid copepods could recolonize from benthic sediments where they occur in relatively high abundance (Alongi & Sasekumar, 1992; Procheş et al., 2001). Insects, however, (represented in our samples by larvae) have flying adults, enabling them to disperse efficiently (Cheng & Frank, 1993), but not necessarily uniformly across available habitat. This would explain the variability in spatial and temporal distribution and abundance on pneumatophore of insects in general, and particularly, the Ceratopogonidae. With respect to the taxa showing poor recovery, the design of the current experiment does not permit inference regarding the extent to which their life histories vs habitat and niche availability and utilization, limit population growth.

Even though they offer considerable opportunities for ecological study, in that they can be readily quantified and their spatial patterns be easily identified, mangrove pneumatophore meiofaunas have been poorly explored. The current study suggests that utilization of the habitat comprising macroalgae and sediment varies considerably among the arthropod species. In addition to habitat availability, development of the meiofanal arthropod populations on pneumatophores depends on life history characteristics of the specific taxa as well as other factors, including biotic interactions. Given the diversity of mangrove systems worldwide, there is considerable scope for comparing the effects of pneumatophore cover on the ecology of meiofaunal arthropods, by considering other types of mangrove systems, which support vastly different pneumatophore components (see Bayliss, 1993; Lambert et al., 1994; Bingham & Young, 1994; Ross & Underwood, 1997), and from other geographical regions.

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