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Meiofaunal Colonization of Decaying Leaves of the Red Mangrove *Rhizophora mangle*, in Southwestern Puerto Rico

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ABSTRACT.— This study targeted the successional, trophic and taxonomic aspects of nematode assemblages inhabiting fallen *Rhizophora mangle* leaves in an experiment repeated during two consecutive years. Four replicates of four leaves each were secured near the mangrove prop roots at Magueyes Island, southwestern Puerto Rico. At biweekly intervals, one leaf from each replicate was removed and selected meiofauna were enumerated. The two most abundant taxa were harpacticoid copepods (max. 228/leaf) and nematodes (max. 182/leaf). Significant differences between sample times were observed. Copepod and nematode densities for these times were compared using a two-way, crossed ANOSIM (global R = 0.327, significance level of 0.1%). Both nematode and copepod densities increased as leaves decayed. The leaf size had no significant effect on meiofaunal densities, an observation consistent with previous studies. We identified 25 nematode species of 25 genera, with the most abundant taxa being *Adoncholaimus* and *Dichromadora*. The most frequently encountered taxa in leaves were *Haliplectus* (58.62%), *Dichromadora* (65.52%), *Adoncholaimus* (41.38%), and *Oncholaimus* (41.38%). When we assigned nematode species to feeding groups, omnivores/predators accounted for >30% of the nematode abundance. Together, the omnivores/predators and the epigrowth feeders accounted for >63% the species richness and >72% of the species abundance. No successional patterns were detected between the nematode feeding groups. Diversity indices were not significantly different within and between years. The successional patterns of colonizing nematodes did not follow the patterns observed in classical succession studies in terrestrial habitats.

KEY WORDS.—nematodes, colonization, meiofauna, mangrove leaflitter, Puerto Rico

INTRODUCTION

Mangroves are mainly tropical ecosystems contributing significantly to both the detritus cycle and export of faunal biomass to adjacent habitats. Up to 30-60% of the primary productivity of mangroves (gross primary productivity 1.4-13.9 $gC \cdot m^{-1}$; in Lugo & Snedaker 1974, Clough 1992) is attributed to the leaflitter (Bunt et al. 1979). The organic carbon found in the mangrove sediments can be overwhelmingly derived from litter decomposition or can be derived from deposited estuarine or marine suspended matter of phytoplankton or adjacent seagrass beds (Bouillon et al. 2003, 2004). Depending on the type of mangrove forest surveyed, the amount of biomass attributed to leaflitter ranges from 323-102,106 kg dry weight · $hectare^{-1}$ (Lugo & Snedaker 1974; Table 1). Mangrove litterfall also supports the detrital food web (Ashton et al. 1999), which indirectly enhances coastal fisheries by providing nutrients to omnivores (e.g. shrimp, crabs, juvenile fish) (Ashton et al. 1999, Hogarth 1999). When mangrove leaves senesce and fall to the forest floor, nutrients are released by the physical and microbial breakdown of the leaves or indirectly by herbivores. The decomposition of submerged fallen mangrove leaves by bacterial and fungal communities (Ashton et al. 1999) supported a diverse invertebrate assemblage, numerically dominated by meiofaunal communities (Alongi 1989, 1990, Gee & Somerfield 1997). Meiofaunal taxa use the biofilm or accumulated materials on the leaf surface as food source (Gwyther 2003). Meiofauna presumably feed on microorganisms on the leaf surface

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TABLE 1. Average number (±SE) of meiofaunal taxa per leaf area (80 cm^2) in 2003 and 2004

	Weeks							
	2		4		6		8	
	2003	2004	2003	2004	2003	2004	2003	2004
Nematodes	0 ± 0.25	3 ± 2.65	35 ± 7.11	16 ± 4.62	32 ± 6.57	72 ± 33.25	104 ± 35.93	57 ± 23.73
Copepods	1 ± 0.50	7 ± 3.59	83 ± 10.09	40 ± 16.72	84 ± 11.68	65 ± 17.17	97 ± 0.88	129 ± 55.73
Polychaetes	3 ± 1.44	2 ± 1.63	27 ± 4.50	4 ± 2.04	15 ± 4.37	9 ± 3.69	7 ± .41	13 ± 5.58

since they feed indiscriminantly on diatoms, bacteria and detritus (Coull 1988). Our study focused on the colonization patterns of one of the most abundant meiofaunal taxa of mangrove leaf litter, nematodes.

The chronosequence of feeding groups of nematodes has been the subject of several colonization experiments on mangrove leaf litter (Tietjen & Alongi 1990, Somerfield et al. 1998, Gwyther & Fairweather 2002, Gwyther 2003) or mimics of mangrove structures (Gwyther & Fairweather 2002, 2005). These studies assert that during the process of leaf decomposition, changes in the biofilm community influence the assemblage of the feeding groups of nematodes. Marine nematodes can be categorized into four different feeding groups according to the morphology of the buccal cavity and presence or absence of teeth (Jensen 1987). Though meiofaunal climax communities have been attained in submerged leaves, these quickly dissipated (Somerfield et al. 1998). The term "climax communities" may perhaps not be appropriate for use in mangrove litterfall in the same sense as it is applied to terrestrial climax communities. The submerged leaf litter environment is in constant flux because leaves quickly decompose and colonizing meiofauna are presumably forced to switch feeding substrates or to colonize other newly fallen leaves.

There are several ecological investigations of the meiofauna of tropical mangrove environments [see reviews by Por and Dor (1984), Alongi (1989), Alongi & Sasekumar (1992)]. Most pertain to the temperate mangroves of Australia (Gwyther 2000, Gwyther & Fairweather 2002, Gwyther 2003) and South Africa (Dye 1983, Procheş et al. 2001), although several studies have been carried out on the meiofauna of mangrove fringes in tropical Kenya (Vanhove & Vincx 1992, Ólafsson 1995, Schrijvers et al. 1997), India (Krishnamurthy et al. 1984), Malaysia (Sasekumar 1994), and Thailand (Nozawa et al. 1983).

In contrast to the multi-species tropical Pacific mangroves, the Caribbean, *Rhizophora mangle* form monospecific fringing forests. Mangroves in southwestern Puerto Rico cover approximately 1,000 hectares, which represents 15% of the total mangrove coverage (Martinez et al. 1979). A small but significant component (12%) of the mangrove forest biomass in Puerto Rico can be attributed to the leaves (7,780 Kg dry weight · $hectare^{-1}$; Golley et al. 1962). Similar values (7,263 Kg dry weight · $hectare^{-1}$) have been reported from overwash mangroves in Florida. However, here the leaf component comprises 5.6% of the dry weight of the above ground biomass (Lugo and Snedaker 1974). Leaf litter associated meiofauna have been studied in monospecific forests of *Avicennia marina* in the cool-temperate regions of southeastern Australia (Gwyther 2003). There are several important differences between tropical and temperate mangroves that warrant investigation of the meiofaunal colonization processes. Among the most important disparities are the different mangrove and nematode species likely to be encountered and the faster decomposition rate of plant tissue due to higher sea temperatures in the Caribbean. The Caribbean mangrove fringe forests are characterized by one dominant species (*Rhizophora mangle*) and offer an opportunity to assess the chronosequence of colonizing meiofaunal taxa in leaf litter.

In the current study we have addressed the year-to-year variability in an experiment focusing on the trophic and taxonomic aspects of tropical nematode assem-

blages colonizing fallen mangrove leaves. We determined the following: (1) the abundance of major meiofaunal groups colonizing fallen red mangrove leaves, (2) the taxonomic breadth of nematodes on decaying mangrove leaves, and (3) the chronosequence of feeding groups of nematodes as mangroves leaves decayed.

METHODS

The study was carried out during the tropical wet seasons of 2003 and 2004 in the fringing mangroves on the east side of Magueyes Island (Figure 1), site of the field laboratories of the Department of Marine Sciences, University of Puerto Rico, Mayagüez. The 2003 experiment started on September 9 and ended November 11. The 2004 experiment started on August 27 and ended on October 25. Magueyes Island (17°58.3′N, 67°2.8′W) has an area of 0.073 km^2 located immediately offshore from the fishing/touristic village of La Parguera, Lajas on the southwest coast of Puerto Rico (Figure 1). The region is classified as a subtropical dry forest (Ewel & Whitmore 1973) with an average maximum temperature of 31.4 °C, average minimum temperature of 22.4 °C, and an average annual precipitation of 74.5 cm (average, 1961-1990). The island is surrounded by mangroves, mainly *Rhizophora mangle*, although *Laguncularia racemosa*, *Avicennia germinans*, and *Conocarpus erectus* occur as well. In other localities, *Rhizophora mangle* can reach up to 30 m in height and 70 cm in diameter with arching stilt roots of 2 to 4.5 m height. However, the red mangroves of Magueyes Island are short, bushy trees with maximum heights of 3 m. Rainfall and trees are similar in structure to those in temperate Australian studies.

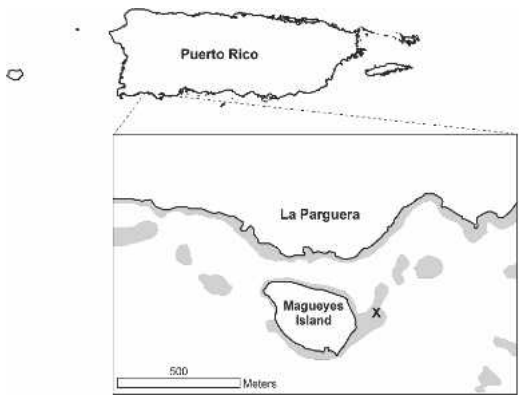

FIG. 1. Map of Island Magueyes, Lajas showing location of the experimental site. Grey areas represent *Rhizophora mangle* forest. The X indicates the location of the experiments.

More than 40 fresh, yellow leaves of *Rhizophora mangle* were hand picked during the same day and washed in freshwater. Five leaves of *R. mangle* were attached at regular intervals (20 cm) to a nylon line by knotting around the petioles. These were then left overnight immersed in freshwater. The following day, four strings of leaves were laid out between the mangrove prop roots (located a few meters apart) by tying the ends of the strings to the roots of trees. At weekly intervals one leaf (i.e. one sample) was removed from each of the four replicates by cutting the petioles, carefully lifting the leaf from the mud surface with forceps, and then placing it into a plastic bag. Filtered seawater was used to rinse the plastic bag as the sample was emptied into a set of 500 μm and 53 μm sieves. The leaves were washed with filtered seawater and then gently rubbed manually to dislodge adhering meiofauna. The retained fauna on the 53 μm sieve was fixed with 10% buffered formalin within 1 h of collection. Nematodes, copepods and ostracods were picked off with a finely hooked needle (a modified Irwin's loop) and placed into vials for later observation and identification. All groups were re-counted and nematodes were identified to at least the level of genus using reference keys for each group (Platt & Warwick 1983, Platt & Warwick 1988, Warwick et al. 1998).

Each leaf was photographed with a digital camera after it was collected and its area was estimated through use of SigmaPlot (SPSS Inc). Correlation analysis was used to examine if leaf size was related to the abundance or diversity of meiofauna. The abundance of each of the three numerically predominant taxa and the total numbers of nematodes and copepods were tested separately by correlation, regression, and for trends related to leaf size. Abundance was

expressed as the numbers of individuals per leaf surface area. Leaf area was standardized to 80 cm^2 because this measurement unit approximates the average total surface area for both sides of the leaf (n = 10, Avg = 78.12, SD = 18.70). Meiofauna inhabit both sides of the leaf. Our study did not examine a potential meiofaunal bias towards the upper or lower leaf side. Previous studies used volume (Gee & Somerfield 1997) or dry weight (Gwyther 2003) of mangrove leaves to estimate density of meiofauna. The submerged leaves changed physically over time, becoming thinner and fragmented due to decomposition. Although leaf volume and dry weight are functions of leaf area, meiofauna inhabit and feed on the surface biofilm. Therefore the area of the leaves is a direct measurement of the available substrate. Leaf area is therefore an alternative, biologically-meaningful, and simple basis for measurement of relative meiofaunal densities.

Meiofaunal data were analyzed using univariate and non-parametric multivariate techniques as implemented in the PRIMER (Plymouth Routine In Multivariate Ecological Research) version 5.2.9 (Clarke & Warwick 1994). Multivariate data analyses were employed to analyze the change of colonizing meiofaunal assemblages over time (between samples and times). To analyze the abundance of meiofauna with crossed factors (samples, years), a 2-way crossed ANOSIM test was carried out using the similarity matrix Bray-Curtis after transforming the data by log (x+1). To determine the contribution of each taxon to the dissimilarities between different samples and years we used the dissimilarity percentage procedure SIMPER in PRIMER.

Analysis of nematode diversity was performed with the DIVERSE univariate analysis of PRIMER. We determined the Simpson and Shannon diversity indices, Margalef's (d) species richness, and Pielou's evenness (J'). To estimate sample-to-sample and year-to-year variability of the dominant feeding groups as assigned in Jensen (1987), we analyzed nematode diversity with the following combination of factors: time, years, and dominant feeding groups. For this analysis, we employed a 2-way crossed ANOSIM test using the similarity matrix Bray-Curtis after transforming the data with log (x+1). The abundance of nematode species was grouped according to sampling times (2, 4, 6, and 8 weeks), feeding groups, and the 2003 or 2004 years as factors for the analyses. The contribution of nematode species to the dissimilarities between treatments was estimated with the SIMPER procedure of PRIMER. The abundance of each nematode species was arcsine transformed prior to the construction of Bray-Curtis similarity matrices. Nematode abundances were compared with a 2-factor crossed ANOSIM test, where replicate samples were grouped according to collection time (2, 4, 6, or 8 weeks) and by 2003 or 2004 years as factors for the analyses.

RESULTS

Abundance of Meiofaunal Taxa

On 29 leaves we counted 952 nematodes (324 in 2003, 628 in 2004), 1517 copepods (525 in 2003, 992 in 2004), and 228 polychaetes (113 in 2003, 115 in 2004). Turbellarians, ostracods and oligochaetes were scarce throughout the samples ($\leq$16 individuals for both years). Copepods were the most abundant taxon in both years and throughout all stages of leaf decay (Table 1). Nematodes per leaf ranged from 0 to 182, while copepods ranged 0 to 228. No significant correlation was found between the meiofaunal abundance and the size of leaves or between copepod and nematode abundance and leaf size. The densities of copepods, nematodes and polychaetes were compared by a two-way, crossed ANOSIM. A significant difference was recorded between sample time (global R = 0.327, significance level of 0.1%) but not between years (global R = 0.114, significance level of 15.5%). Copepods contributed little to differences between samples (Table 2). The contribution of nematodes to the differences between samples decreased (Table 2) when their abundance increased (Table 1).

TABLE 2. SIMPER analysis showing the contribution % to dissimilarity of the abundance of each taxon between different sampling times.

	Meiofauna	Contribution % to dissimilarity
2 to 4 weeks	Nematodes	36.96
	Copepods	32.95
	Polychaetes	30.09
2 to 6 weeks	Nematodes	38.15
	Copepods	35.62
	Polychaetes	26.23
2 to 8 weeks	Nematodes	39.06
	Copepods	38.35
	Polychaetes	22.59
4 to 6 weeks	Nematodes	30.13
	Copepods	22.20
	Polychaetes	47.67
4 to 8 weeks	Nematodes	33.70
	Copepods	26.59
	Polychaetes	39.71
6 to 8 weeks	Nematodes	29.76
	Copepods	27.66
	Polychaetes	42.58

Species Diversity and Assemblage Structure of Nematodes

We identified 25 nematodes species of 25 genera, which were classified into their respective feeding groups. The frequencies of all identified nematode species are shown in Appendix 1. We used only the identified species for the nematode analysis. Six unidentified species of nematodes with < 3 individuals per species were excluded. Eleven nematodes were destroyed or lost during the process of fixation and slide preparation for identification. Pooling all samples together (years 2003 and 2004), the most numerically dominant taxa were *Adoncholaimus* and *Dichromadora*. The most frequently encountered taxa, *Haliplectus* and *Dichromadora*, were present in 58.62% and 65.52% of all sampled leaves, respectively. These were followed by *Adoncholaimus* and *Oncholaimus*, both present in 41.38% of all sampled leaves.

The most abundant taxa after four weeks were *Desmolloimidae* (present only in 2004), *Adoncholaimus*, and *Dichromadora*. After six weeks, *Diplolasmelloide* (present only in 2004), *Dichromadora* sp., and *Euchromadora vulgaris* were most abundant. Finally, after eight weeks, *Adoncholaimus* sp., *Dichromadora* sp., and *Haliplectus* sp. were in greatest abundance. In general, nematode numbers increased as leaf decomposition over 8 weeks advanced in both years (Table 1). A comparison using a two-way, crossed ANOSIM showed a difference of nematodes abundance between sampling times (global R = 0.327; significance level 0.1%). However, this was not significant between years (global R = 0.114; significance level 15.5%).

The most important contributors to the dissimilarity between sampling periods were *Diplolasmelloide*, *Euchromadora vulgaris*, *Adoncholaimus*, *Daptonema*, *Dichromadora*, *Oncholaimus*, and *Daptonema* (Table 3). *Diplolaimelloides* and *Haliplectus* were present only during 2004. The six or seven most common species that contributed to the differences between sampling periods are listed in Table 3.

Analysis of feeding groups shows that omnivores/predators were numerically predominant and particularly conspicuous during the 8th week of the experiments (Table 4). The omnivores/predators account for 45% and 30% of the nematode

TABLE 3. SIMPER analysis showing the contribution % to dissimilarity of the abundance of nematodes in different sampling periods.

	Species	Contribution % to dissimilarity
4 to 6 weeks	*Diplolaimelloides**	12.26
	Euchromadora vulgaris	11.16
	Adoncholaimus	9.31
	Daptonema	9.29
	Dichromadora	9.28
	Oncholaimus	7.67
4 to 8 weeks	*Adoncholaimus*	17.49
	Dichromadora	8.76
	*Haliplectus**	8.65
	*Diplolaimelloides**	8.25
	Oncholaimus	7.55
	Euchromadora vulgaris	6.41
6 to 8 weeks	*Adoncholaimus*	18.13
	Dichromadora	9.31
	*Haliplectus**	8.49
	Euchromadora vulgaris	8.25
	Daptonema	8.01
	Oncholaimus	6.64

*These taxa were present in 2004, only.

TABLE 4. Occurrence of feeding groups of nematodes during the colonization experiments.

Feeding groups		# of species	Total # of nematodes				% of total # of nematodes
			2 weeks	4 weeks	6 weeks	8 weeks	
Bacteriovores (1A)	2003	2	0	17	3	7	11.32
	2004	3	2	3	8	29	9.45
Non-selective	2003	1	0	39	9	26	5.66
Deposit feeders (1B)	2004	4	3	4	72	1	18.02
Epigrowth feeders (2A)	2003	5	0	16	34	70	37.74
	2004	6	6	28	58	16	24.32
Omnivores/predators (2B)	2003	8	0	4	18	53	45.28
	2004	6	1	57	14	142	48.20
# of leaves	2003		4	4	3	2	
	2004		4	4	4	4	

abundance (in 2003, 2004, respectively) and consisted of nine species. Together the omnivores/predators with the epigrowth feeders accounted for 81% in 2003 and 63% in 2004 of the species richness, and 83% in 2003 and 72% in 2004 of the species abundance. Bacteriovore nematodes remained at low numbers throughout the experiment, except for the 8th week of 2004, in which *Haliplectus* accounted for 86% of the abundance of the bacteriovores. The proportion of the bacteriovores was 11.3% and 9.5% for 2003 and 2004, respectively.

The diversity indices for Shannon and for Simpson as well as Pielou's species evenness and Margalef's species richness did not reveal any significant relationships with respect to nematodes for the different decomposition stages of the leaves. Nevertheless, as leaves decayed in the 2004 experiment, the nematode diversity reached maximum values at 8 weeks (Figures 2, 3). The richness and evenness values during 2004 exhibited similar trends as that of the species diversity indices (Figure 2). However, all aforementioned trends were not significant. For both experiments, the average Shannon diversity (H') was estimated to be 1.02 ± 0.13 SE with a range from 0 to 1.91.

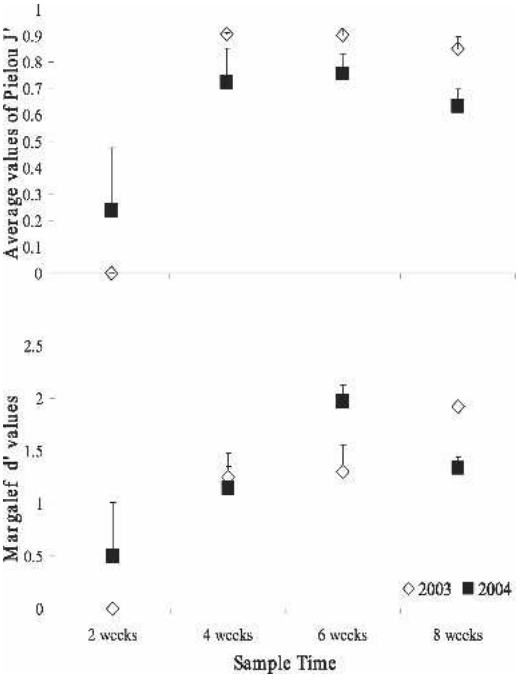

FIG. 2. Pielou's evenness and Margalef's species richness indices of nematodes for 2003 and 2004.

DISCUSSION

Because meiofauna are the most abundant group of metazoans in the mangrove leaf litter, researchers have attempted to quantify the importance of mangrove-associated meiofauna in the decomposition of plant material. Meiofauna has been found to exert strong influence in the cycling of organic matter (Meyers & Hopper 1967, Gerlach 1978, Tietjen 1980, Hicks & Coull 1983, Heip et al. 1985). In other studies, a more limited role has been attributed to meiofauna in the cycling of organic matter (Alongi 1987, Tietjen & Alongi 1990). The many factors involved in the decomposition process of the leaf litter (macro-

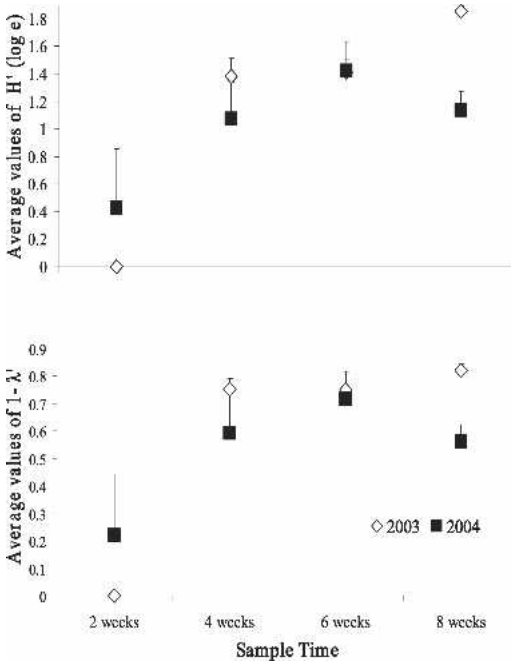

FIG. 3. Shannon and Simpson diversity indices of nematodes for 2003 and 2004.

and meiofauna, fungi, bacteria, temperature, latitude, species composition of the leaf litter) and the complexity of the biological interactions (e.g. meiofauna feed on fungi, bacteria; macrofauna feed on meiofauna) are probably responsible for the contrasting results. It is indeed difficult to resolve single effects. For example, the importance of meiofauna in the decomposition process of detritus in mangroves is under debate. Somerfield et al. (1998) and Gee and Somerfield (1997) concluded that in the soft sediment of tropical mangroves, the meiofaunal communities are more diverse than in temperate soft sediment estuaries and that the communities in mangrove leaf litter are distinctly different from those in the sediment. In this study, meiofauna inhabiting or feeding on fallen leaves of *Rhizophora mangle* consisted mainly of copepods, nematodes, and polychaetes. Contrary to previous research on mangrove litter, nematodes were not the most numerous taxon (Gee & Somerfield 1997, Somerfield et al. 1998, Gwyther 2003). Instead, harpacticoid copepods were predominant throughout all the decay stages of the leaves. Copepod and nematode abundances increased as leaves progressively decayed. Consistent with previous work (Gwyther 2003), no significant effect of leaf size on the meiofaunal densities was detected.

Other factors such as variation in the species constitution of the leaf biofilm or chemistry of mangrove detritus could influence the meiofaunal assemblage. Tietjen and Alongi (1990) suggested that the nematode populations were more affected by the chemical composition of the leaves than by the bacterial populations. They concluded that the low field densities (<5) of nematodes per leaf (Alongi 1987) and the inability of nematodes to influence bacterial abundance indicate that meiofauna may not play a major role in the cycling of organic matter in tropical mangrove forests. Gee and Somerfield (1997) questioned the global applicability of Tietjen and Alongi's (1990) conclusions on the role of meiofauna in the detrital cycle of tropical mangroves. Additional experiments were recommended as a remedy to better understand the role of meiofauna in the detrital cycle of mangroves. Gee and Somerfield (1997) also found higher meiofaunal densities on *Rhizophora* leaf litter and adhering sediment (600 nematodes and 70 copepods per leaf in weeks 3-5 of the colonization experiment). We observed 42 nematodes per leaf, ranging from 0 to 104 (standardized leaf area of 80 cm^2). The reported wide range of average nematode abundances is due to the different decomposition stages of the leaves since as the leaves decay the nematode abundance increases (Table 1). The current results are consistent in both 2003 and 2004 and support the hypothesis that the difference in the composition of the leaf biofilm probably determines the meiofaunal assemblage (Gee & Somerfield 1997, Gwyther 2003).

While the feeding groups are comparable across geographical areas, the abundance of nematodes on decaying leaves varies among published studies. Non-selective deposit feeders were one of the predominant feeding groups in mangrove litter from Malaysia (Gee & Somerfield 1997) and northeastern Australia (Tietjen & Alongi

1990). *Diplolaimella,* a non-selective deposit feeder, was reported as abundant in salt marshes and rotting detritus (Somerfield et al. 1998) and associated with mangrove leaves in Florida (Hopper et al. 1973), Africa (Ólafsson 1995), and Hong Kong (Zhou 2001). In Australia, *Diplolaimella* and three other species of non-selective deposit feeders were found abundant on brown leaves of *Avicennia* (Gwyther 2003). During the first four weeks of the 2003 experiment, the non-selective deposit feeding group was numerically predominant, a result comparable with previous findings (Hopper et al. 1973, Ólafsson 1995, Somerfield et al. 1998, Zhou 2001, Gwyther 2003). But contrast to the aforementioned studies, the selective deposit feeding group was not the predominant feeding group in 2004. After the 6th week of our experiments, the predominant nematodes were non-selective deposit (for 2004 only), epistrate, and omnivorous/predatory feeding groups [*Diplolamelloides* (1B), *Euchromadora vulgaris* (2A) *Adoncholaimus* (2B) and *Dichromadora* (2A)]. After eight weeks the predominant groups were epistrate feeders, omnivores/predators, and bacteriovores (*Adoncholaimus* (2B), *Dichromadora* (2A), and *Haliplectus* (1A)). Pooling the data from both years, the epistrate feeders (mainly *Dichromadora*), and the omnivores/predators (mainly *Adoncholaimus*) were the numerically predominant and most common feeding groups. These results differ from previous studies but are consistent with reports that describe the shallow water Chromadoridae as usually being dominated by *Dichromador*a (Lambshead et al. 2003).

We recorded 13 nematodes families that have been found on other sediment and phytal substrates associated with mangroves (Nozawa et al. 1983, Krishnamurthy et al. 1984, Alongi 1987, Jensen 1987, Tietjen & Alongi 1990, Vanhove & Vincx 1992, Sasekumar 1994, Ólafsson 1995, Gee & Somerfield 1997, Schrijvers et al. 1997, Somerfield et al. 1998, Gwyther & Fairweather 2002, Gwyther 2003). During the colonization experiments, the nematode fauna was dominated by Chromadoridae and Oncholaimidae. Our findings are in congruence with the statement that Chromadoridae dominate marine shallow waters (Lambshead et al. 2003). Diversity analysis showed that as leaves decayed, the nematodes species diversity increased and reached a plateau during the 6th week of the experiments (Figure 3). However, we doubt that this constitutes evidence for the presence of climax meiofaunal communities. The richness and evenness values exhibited the same non-significant trends as the species diversity indices (Figures 2, 3). Although we cannot establish any relations between nematode diversity and the decomposition stage of the leaves, our analysis showed a higher Shannon diversity index (1.02 ± 0.13 SE) than the ones reported by Gwyther (2003). These values were 0.38 for yellow leaves and 0.78 for brown leaves. Our estimates of the Shannon diversity index were lower than those reported from other tropical areas, which ranged from 2.0 to 3.2 (Gee & Somerfield 1997). The diversity index is concordant with previously reported values (Gee & Somerfield 1997, Gwyther 2003), where the lower the latitude of the sample location the higher the diversity.

It is debatable whether bacteria or fungi contribute more to the decomposition of mangrove leaves (Cundell et al. 1979, Robertson 1988, Wafar et al. 1997, Mahasneh 2002). Regardless of the relative contribution of microorganisms, a microbial biofilm is developed on the leaf surface and this provides the prime food source of meiofauna. The present study suggests that patterns of meiofauna colonization are different from study to study. Examination of all available data on colonization patterns of leaf litter nematodes reveals that no general conclusions can be drawn about the colonization trends of feeding groups, abundance, and diversity of meiofauna. If community patterns of nematodes vary from study to study, use of the community-based maturity index (Bongers et al. 1991, Bongers & Ferris 1999) in environmental monitoring might only be of local utility. The variability of our results reflects possible changes in the microbial communities established on the decaying leaves of mangroves systems (Alongi, 1987, Jensen 1987, Ólafsson 1995). Further studies are needed

to determine how the multifactorial dynamics governing the development of this microbial matrix affect the nematode assemblages. We suggest that colonization patterns of leaflitter nematodes do not fit classical succession models (Connell & Slatyer 1977) and are therefore not characterized by consistent succession patterns that have been established through studies of glacial moraines in southeast Alaska (Lawrence 1958), the sand-dunes of Lake Michigan (Olson 1958), or algal species transitions in the rocky intertidal of California (Souza 1979).

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APPENDIX 1. Feeding groups of nematodes for 2003 and 2004 combined.

Species	Family	Feeding groups	% frequency	Presence (p) or absence (a) by weeks			
				2	4	6	8
Adoncholaimus	Oncholaimidae	2B	41.38	a	p	p	p
Bathyeurystomina	Enchelidiidae	2B	3.45	a	a	p	p
Chromadorella	Chromadoridae	2A	6.9	a	a	p	p
Cricolaimus	Leptolaimidae	1A	6.9	a	a	a	p
Daptonema	Xyalidae	1B	24.14	p	p	p	p
Desmodora	Desmodoridae	2A	17.24	p	p	p	p
Dichromadora	Chromadoridae	2A	65.52	p	p	p	p
Diplogasteridea 1	Diplogasteridae	2A	6.9	a	a	p	a
Diplolaimelloides	Monhysteridae	1B	17.24	a	p	p	p
Draconema	Draconematidae	1B	3.45	a	a	p	a
Epsilonema	Epsilonematidae	1A	6.9	a	a	p	p
Euchromadora vulgaris	Chromadoridae	2A	37.93	p	p	p	p
Eurystomina	Enchelidiidae	2B	20.69	p	a	p	p
Haliplectus	Haliplectidae	1A	58.62	p	p	p	p
Microlaimus	Microlaimidae	2A	3.45	a	p	a	a
Oncholaimellus	Oncholaimidae	2B	10.34	a	a	p	p
Oncholaimus	Oncholaimidae	2B	41.38	a	p	p	p
Paroxystomina	Oxystominidae	1A	3.45	a	p	a	a
Polygastrophora	Enchelidiidae	2B	17.24	a	p	p	p
Polysigma	Desmodoridae	2A	6.9	a	a	p	p
Prochromadorella	Chromadoridae	2A	10.34	a	p	p	a
Symplocostoma	Enchelidiidae	2B	13.79	a	p	p	p
Symplocostomella	Enchelidiidae	2B	3.45	a	p	a	a
Theristus	Xyalidae	1B	10.34	a	a	p	a
Viscosia	Oncholaimidae	2B	10.34	a	p	p	a