

Spatial and Temporal Variations of Meiofaunal Communities from the Western Sector of the Gulf of Batabanó, Cuba.

I. Mangrove Systems

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ABSTRACT: The spatial and temporal variations of meiofaunal communities in mangrove systems were examined. Replicated cores were taken in mudflats between prop roots of *Rhizophora mangle* at five locations within the Gulf of Batabanó, Cuba, during 3 mo. There was a clear seasonality in the water column, but measured abiotic variables did not show obvious relations with meiofaunal patterns. The magnitude of change in salinity for each location appears to influence the meiofauna more than absolute values per se. The meiofauna from southern Pinar del Río showed a higher variation in community structure, suggesting higher levels of stress in comparison with locations in eastern Isla, possibly due to the presence of human settlements, runoff from land, and apparent deterioration of mangroves. The considerable variation in the density and community structure estimates on global (geographical regions) and local (locations in the Gulf of Batabanó) scales could be caused by the high spatial variability in the mangrove microenvironment, coupled with associated methodological differences in the sampling. There was a low density of meiofauna (mean: 101 animals 10 cm⁻²) compared to other shallow tropical habitats. Mangroves from subtropical and temperate regions showed consistently higher meiofaunal densities than tropical mangroves, but causes of this putatively latitudinal pattern require further study. Future strategies for meiofaunal studies in mangrove systems should increase the temporal and spatial replication, include designed field experiments to test ecological hypotheses, and apply a species level approach with regards to nematode assemblages.

Introduction

Mangroves are one of the most widespread coastal estuarine ecosystems in tropical regions that also occupy large areas in the subtropical and temperate zones. These systems have important ecological and economical values (Hogarth 1999) and include unique communities on the earth. The meiofauna (defined as animals passing through a 0.5-mm sieve but retained on a 45- μ m mesh) are the numerically dominant faunal communities within mangrove sediments. Three major ecological roles are played by meiofauna in mangroves (and other estuarine habitats) according to Coull (1999): they enhance nutrient regeneration, they serve as food for a variety of higher trophic levels, and they exhibit high sensitivity to anthropogenic inputs, making them excellent organisms for studying estuarine pollution.

Tropical mangroves are characterized by multi-species assemblages of trees and high primary production (Field 1999). Ecological composition

and structure surveys of meiofauna in tropical mangrove systems have been carried out in several regions: Australia (Alongi 1987a,b,c, 1988; Alongi and Christoffersen 1992), Africa (Dye 1983a; Ólafsson 1995; Ólafsson et al. 2000), Asia (Gee and Somerfield 1997; Somerfield et al. 1998), and America (Hopper et al. 1973). The mentioned studies deal with nematodes (the most abundant taxon in meiofauna) identified to taxonomic level of genus (or species).

Several studies on meiofauna in subtropical and temperate mangrove habitats have been carried out, with diverse topics: assemblages of pneumatophores (Gwyther 2000; Proches et al. 2001; Proches and Marshal 2002; Gwyther and Fairweather 2002, 2005), colonization of azoic sediments (Zhou 2001), temporal and spatial variations of nematode assemblages (Hodda and Nicholas 1986b; Nicholas et al. 1991), and assessment of pollution (Hodda and Nicholas 1986a). Surveys identified nematodes to genus and in certain cases to species.

Cuban mangroves are typically tropical habitats (i.e., latitude 22°N), covering roughly 5,000 km² and constituting 26.6% of the forests in the country (Rodríguez-Otero 2001). Despite its importance,

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studies on marine communities in mangroves are scarce in Cuba, particularly those relating to benthic assemblages. Only one study (Lalana-Rueda and Gosselk 1986) has been published on infauna in mangrove habitats in Cuba; but this study used 0.5 mm as the minimum mesh size.

The research presented here is part of a study on critical habitats and key faunal groups in the Gulf of Batabanó. It is the most important area for spiny lobster (*Panulirus argus*) fisheries in Cuba (Phillips et al. 2000). The landing of spiny lobster has depleted progressively (Phillips et al. 2000), from an average of 11,564 tons in 1978–1989 to 8,845 tons in 1990–1995 (Baisre 2001). The anthropogenic degradation of critical habitats (e.g., mangroves) could be one of the causes of the decline of fisheries. Baseline information of communities in mangroves is essential for assessment of putative human impact affecting them.

Due to the lack of surveys on mangrove faunal communities in the Caribbean area (including Cuba), there is not enough evidence on their role in the dynamics of named ecosystems. Other surveys suggest important roles of meiofauna, such as food for higher trophic levels (Coull 1990; Schmid-Araya and Schmid 2000) and mineralization of detritus (Tietjen and Alongi 1990). The probable importance of meiofauna in the dynamics of mangrove systems in the Gulf of Batabanó led us to conduct a preliminary description of these faunal communities. The objectives were to describe the spatial and temporal patterns of variation in the abundance and composition of communities of meiofauna and to infer the possible causes of these patterns.

Materials and Methods

STUDY ZONE

Five locations were selected in the western sector of the Gulf of Batabanó along the southwest shelf of Cuba (Fig. 1). Three of them (Bacunagua, Dayaniguas, and Coloma) are along the southern coast of the province of Pinar del Río, and two are in the eastern part of the Isla de La Juventud (Isla and Matías). The coastline of these locations is covered by typical Caribbean mangrove trees (i.e., in order from sea to land: *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*). Sediments in these locations are muddy, with a high proportion of silt-clay (S-C). The region is characterized by a narrow tidal range, averaging less than 25 cm (Rodríguez and Rodríguez 1983).

SAMPLING DESIGN

Samples were taken in February, July, and November 2003. Not all locations were sampled during every month (see data analysis below). In

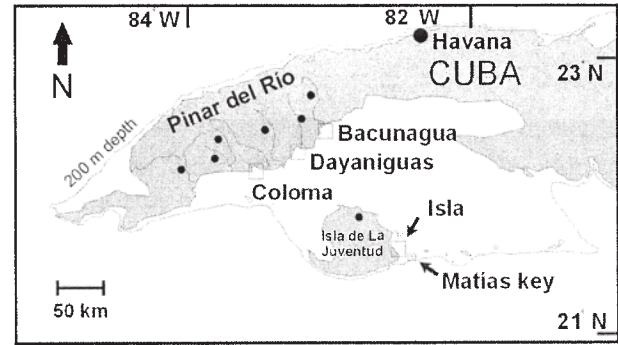


Fig. 1. Study zone. The five locations in the western sector of the Gulf of Batabanó are shown. The shelf break contour (approximately 200 m depth) is indicated with a line. Black dots indicate major human settlements.

February and July two stations were sampled; in November, four stations were sampled. The stations inside each sampled location were located adequately apart from each other (average distance 9 km) to allow an assessment of the community structure on the scale of 10–50 km and to avoid pseudoreplication. Three or four cores were taken for meiofauna in each station in order to assess the small-scale (10–100 m) variability of communities. Cores (plastic syringe of 5.3 cm²) were taken in subtidal flats of bare sediment (sometimes variable quantities of mangrove leaf litter cumulated on the sediment) between prop roots of *R. mangle* up to 10 cm deep. We attempted to select sampling areas with similar sediment characteristics in order to minimize the effects of confounding factors. Temperature, salinity, dissolved oxygen (DO), depth, and pH were measured with an oceanographic probe (Hydrolab 4a of Grant/Ysi). Samples of sediment (upper 10 cm) were taken in November for quantitative assessment of the S-C percentage.

SAMPLE PROCESSING

Samples of sediment were stored in polyethylene bags with formalin. In the laboratory the samples were sieved through 500- μ m and 45- μ m sieves. The sediment retained on the 45- μ m sieve was kept for extraction using the flotation technique in a high density solution (sugar 1.15 g cm⁻³, after Esteves and DaSilva 1998) decanting each sample at least three times. The samples were stained with alcoholic eosin (1%) in order for easier detection of animals (Thiel 1966); the identification to higher taxa (e.g., nematodes, copepods) and the counting of animals was carried out under stereoscopic microscope (56 \times maximum). The percent S-C in sediment samples was determined by wet sieving using a 63- μ m sieve to separate the coarse (sand) and fine (silt + clay) fractions, which were then

TABLE 1. Mean values (\pm standard error) of abiotic variables measured in five locations and during 3 mo in the western part of the Gulf of Batabanó. T = temperature, S = salinity, S-C = silt-clay, and DO = dissolved oxygen. n = 2 for February and July; n = 4 for November. Blank cells indicate that no measurements were taken.

Location	Month	Depth (m)	T ($^{\circ}$ C)	pH	S (‰)	% S-C	DO (mg l $^{-1}$)
Bacunagua	February	0.5 (0.05)	29.3 (0.1)	7.77 (0.01)	33.8 (0.8)		5.33 (0.20)
	July	0.5 (0.05)	32.6 (0.4)	8.48 (0.00)	27.3 (1.4)		5.46 (0.35)
	November	0.6 (0.07)	27.3 (0.3)	7.83 (0.04)	25.5 (3.6)	55.7 (9.7)	
Dayaniguas	February	0.5 (0.05)	28.2 (0.4)	7.82 (0.19)	35.2 (1.1)		4.28 (1.19)
	July	0.5 (0.05)	29.5 (0.9)	8.39 (0.14)	22.9 (6.2)		4.85 (0.15)
	November	0.8 (0.1)	26.3 (0.4)	7.84 (0.08)	36.5 (1.2)	73.8 (6.1)	
Coloma	February	2.5 (2.1)	29.6 (0.2)	8.13 (0.05)	36.1 (0.2)		6.34 (0.84)
	July	2.7 (1.9)	30.1 (0.2)	8.62 (0.10)	30.8 (0.6)		7.52 (0.19)
	November	0.6 (0.1)	25.8 (0.5)	7.63 (0.18)	36.3 (0.5)	50.3 (2.8)	
Matías	July	1.1 (0.1)	30.5 (0.0)	8.76 (0.08)	33.4 (0.2)		8.52 (0.27)
	November	0.7 (0.1)				68.1 (17.1)	
Isla	February	2.7 (0.4)	28.1 (0.4)	8.41 (0.04)	36.4 (0.1)		6.93 (0.03)
	July	2.5 (0.4)	29.9 (0.2)	8.42 (0.37)	33.1 (0.1)		8.29 (0.49)

dried at 70 $^{\circ}$ C for 24 h, weighed, and expressed as percent of initial weight.

DATA ANALYSIS

Statistica 6.0 was used for graphical and univariate analysis; density of four meiofaunal taxa was tested by two-way analysis of variance (ANOVA) for differences relating to the fixed factors: month (three levels) and location (five levels). The values of density from each core were used as replicates inside each location-month combination in order to increase the degrees of freedom for the ANOVA. Two combinations of factors (February-Matías and November-Isla) were not sampled causing a design with a lack of efficiency in the assessment of the components of variance. The data were transformed as X^T (using Taylor's power law after Elliot 1971) checking that non-mean-variance correlation was achieved. The values of T in all cases were much closer to zero, so the logarithmic transformation was used (i.e., $\log(x + 1)$). The mean-variance correlation was eliminated only for two variables: density of nematodes and copepods ($r = -0.03$ and 0.41 , respectively). The remainder of the variables (polychaetes and ostracods) maintained high values of correlation ($r = 0.97$ and 0.96 , respectively) after the transformation; due to this, interpretation of ANOVA results should be analyzed with caution.

PRIMER 5.2.9 (Clarke and Warwick 2001) was used for multivariate analyses. An ordination of samples was carried out using a correlation-based principal component analysis (PCA) of abiotic variables; the data were standardized in order to eliminate differences in units of measurement. The ordination of communities on meiofauna data was carried out by non-metric multidimensional scaling (nmMDS). The data set was grouped by months and locations to reveal spatial and temporal changes in meiofaunal communities. The data were square-root transformed in order to reduce the contribution of

nematodes and to increase the importance of less abundant taxa. The Bray-Curtis coefficient of similarity was selected for the construction of similarity matrices. Samples having values of zero were removed from the similarity matrix. An outlier value (1,298 animals 10 cm $^{-2}$) was excluded because its inclusion provoked a collapse of the remainder samples in a unique point in the MDS plots. Two-way crossed similarity analysis (ANOSIM) was performed, using the same similarity matrix of nmMDS, in order to test for statistical differences in the community structure related to the analyzed factors (month and location).

The relationships between multivariate patterns of community structure and abiotic variables were explored using the BIOENV procedure (Clarke and Warwick 2001). It calculates rank correlations between a similarity matrix derived from meiofauna data and other matrices derived from several subsets of abiotic factors. The subsets with more concordance (correlation) are selected as combinations that might best explain the multivariate structure of meiofaunal communities. Univariate correlation analysis using Spearman's rank coefficient was carried out between total density and two abiotic variables (DO and S-C) because they were not measured in all combinations.

Results

ABIOTIC FACTORS

The averaged depth over all stations and all months was 1.1 m, with maximum and minimum values of 4.6 and 0.3 m, respectively (Table 1). DO was not measured in November; there was not a big change between February and July with averaged values of 5.7 and 6.9 mg l $^{-1}$, respectively. The granulometry was qualitatively assessed in February and July as fine sediment with high content of S-C fraction. This assessment was corroborated by

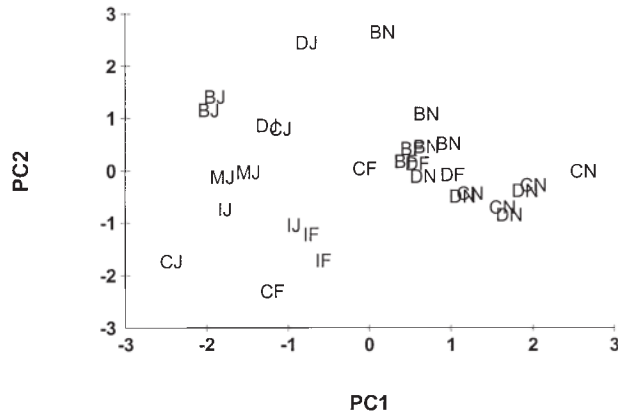


Fig. 2. PCA ordination plot of samples from five locations during 3 mo in the Gulf of Batabanó. Each sample represents a community (combination of location and month). The labels for the samples are location (B = Bacunagua, D = Dayaniguas, C = Coloma, M = Matías, and I = Isla) and month (F = February, J = July, and N = November). The variance explained by the two first PCs is 79.0%. The equations of the axes are $PC1 = -0.65pH - 0.63T - 0.34d + 0.24S$ and $PC2 = -0.73S - 0.66d + 0.15T - 0.07pH$. T = temperature, S = salinity, and d = depth.

determination of S-C percent from the November samples. The mean value (all November's samples averaged) of S-C was 61.6%; the range was from 34.2% to 89.6%.

A PCA ordination constructed using four abiotic variables (depth, salinity, temperature, and pH) explained 79% of the total variance. The remaining two variables (S-C and DO) were not measured in all months. There were clear differences in both space and time on the basis of abiotic variables. The PC1 axis represents a temporal gradient with the three sampled months clearly separated (Fig. 2). The month of July (corresponding with the wet season) had the highest mean values (all locations averaged) of pH (8.5) and temperature (30.5°C). The samples from November and February (corresponding with the dry season) were less clearly

separated; these samples were defined by lower mean values of pH (November: 7.8 and February: 8.0) and temperature (November: 26.5°C and February: 28.8°C).

The PC2 axis suggests the presence of a spatial gradient. The abiotic variables that contributed more to this gradient were salinity and depth; there was not a clear separation of locations on the PC2 axis. Table 1 indicates that the locations from southern Pinar del Río (Bacunagua, Dayaniguas, and Coloma) had relatively lower mean values of DO and depth (5.6 mg l⁻¹ and 0.9 m, respectively) than Matías and Isla (7.9 mg l⁻¹ and 1.7 m, respectively). Differences in salinity between these groups of locations were subtle (31.9‰ southern Pinar del Río versus 34.3‰ eastern Isla).

MEIOFAUNAL COMMUNITIES

In the studied mangrove systems, only five meiofaunal taxa were recorded: Nematoda, Copepoda, Polychaeta, Ostracoda, and Acari. The last, represented by only four animals, was not included in the statistical analyses. Nematoda was present in all samples (Table 2); the dominance of nematodes ranged from 33% to 100%, with a mean value of 88%. The second most abundant taxon was Copepoda, with a highly variable distribution and very low density in Bacunagua. Mean values of total density (all taxa summed) for each core ranged from 0 to 1,298 animals 10 cm⁻², with a total mean for all locations of 101 animals 10 cm⁻². There was a high temporal and spatial variability in the mean density for each location-month combination. The highly significant differences in the interaction of two-way ANOVA (Table 3) for the four tested meiofaunal taxa corroborate this statement.

nmMDS ordination plots did not show a clear pattern of sample clustering (Figs. 3 and 4). There was a notable variability in meiofaunal community structure from Bacunagua, Dayaniguas, and Coloma

TABLE 2. Mean values (\pm standard error) of meiofauna (animals 10 cm⁻²) measured in five locations and during 3 mo in the western part of the Gulf of Batabanó. Blank cells indicate absence of animals.

Location	Month	Nematoda	Copepoda	Polychaeta	Ostracoda	Acari	Total
Bacunagua	February	33.7 (6.0)			7.6 (3.3)	0.6 (0.4)	41.9 (8.7)
	July	29.9 (9.9)	0.3 (0.3)				30.2 (9.8)
	November	6.1 (3.1)			0.5 (0.5)		6.6 (3.3)
Dayaniguas	February	75.1 (40.7)	1.7 (1.7)	0.2 (0.2)			77.0 (42.0)
	July	51.6 (37.5)		0.5 (0.5)	0.5 (0.3)		52.6 (37.2)
	November	21.7 (7.5)	0.9 (0.9)	1.9 (1.3)	0.9 (0.9)		24.6 (8.3)
Coloma	February	66.6 (38.2)	0.5 (0.5)	0.2 (0.2)			67.3 (38.6)
	July	591.2 (38.2)	2.7 (0.6)				593.9 (283.1)
	November	61.0 (30.6)	13.7 (11.2)	1.9 (1.3)	2.8 (1.6)		67.3 (38.6)
Matías	July	112.0 (31.0)	15.1 (3.8)	0.7 (0.5)			127.8 (32.6)
	November	117.8 (28.1)	10.7 (3.5)		0.6 (0.6)		129.2 (25.9)
Isla	February	175.7 (19.4)	7.6 (1.0)	4.4 (2.3)		0.6 (0.4)	188.4 (21.0)
	July	5.0 (1.5)	0.2 (0.2)				5.2 (1.4)

TABLE 3. Results of two-way ANOVA on density of meiofaunal taxa (transformed as $\log(x + 1)$). F ratios and probabilities (in parentheses) are presented. df = degree of freedom. df for error is 68.

Factor	df	Nematodes	Copepods	Polychaetes	Ostracods
Location	4	3.14 (0.02)	23.74 (< 0.01)	1.55 (0.20)	6.06 (< 0.01)
Month	4	1.16 (0.32)	1.39 (0.26)	2.57 (0.08)	5.35 (< 0.01)
Interaction	6	4.65 (< 0.01)	7.14 (< 0.01)	3.06 (0.01)	10.62 (< 0.01)

for each sampled month (Fig. 3), i.e., replicates from the same location were separate in the plot more than those from different locations. A lower variability in community structure appears to exist in February in comparison with the remaining months. The clustering of samples from Matías and Isla (i.e., samples from a same month are clustered closer) suggests a lower variability in their communities. There was no tendency in the temporal variation of communities for each location (Fig. 4). Only Isla appears to have a clear separation between months; a subtle separation between months appears in Bacunagua.

Using two-way ANOSIM global tests on density of taxa revealed significant differences in location ($R = 0.29$, $p = 0.001$, and 999 permutations) and month ($R = 0.14$, $p = 0.015$, and 999 permutations). The results of pairwise tests showed significant differences between all locations, except Bacunagua and Dayaniguas, Dayaniguas and Coloma, and Coloma and Matías (Table 4). The only location different from the rest was Isla. Pairwise tests of the three sampled months indicated no differences between November and July ($R = -0.073$, $p = 0.76$); there were differences between February and July ($R = 0.24$, $p = 0.001$); and February and November ($R = 0.24$, $p = 0.022$).

LINKING COMMUNITY STRUCTURE TO ABIOTIC FACTORS

The BIOENV procedure showed a very poor agreement between the multidimensional pattern of meiofauna and the set of abiotic factors measured in water column. The abiotic factor that best matched the biotic pattern was depth, but the correlation value was very low (0.12); the second combination was depth-pH ($r = -0.018$). Two abiotic factors (DO and % S-C) were not included in BIOENV procedure because they were not measured in all months.

A correlation using Spearman's rank coefficient between total density and DO ($n = 18$) showed a low ($r = 0.14$) and nonsignificant ($p = 0.56$) value of correlation. A correlation between total density and % S-C ($n = 15$) showed similar results ($r = 0.07$, $p = 0.80$).

Discussion

In the present study seasonal variation was found in the mangrove environment (fundamentally con-

cerning pH, DO, and temperature); seasonal variations in tropical mangroves have also been reported by Dye (1983a) and Alongi (1987b). The seasonal changes in pH affect the redox potential (Dye 1983a) and possibly the meiofauna, but this trend is not evident. Possible explanations would be changes in pH and other factors in the water column (e.g., DO) do not have a direct relation with the sedimentary environment and there are nonmeasured confounding factors affecting meiofauna (e.g., organic content).

Temperature is an important seasonal abiotic factor in mangroves, but its effects on meiofauna are somewhat contradictory based on literature. Richer populations of nematodes in warmer sediments are expected (Hopper et al. 1973; Heip et al. 1985) since temperature affects nematode reproduction, but Alongi (1990) reported more meiofauna (nematodes) in cooler seasons than during the hottest months of the year. An inverted relationship between temperature and redox potential in sediment has been reported by Dye (1983b). As a result, the effects from temperature (positive on reproduction and negative on oxygenation of sediment) probably cancel each other out, and the seasonal fluctuations would be caused by other factors (e.g., local input of organic matter or predation) that are largely random. The confounding effects of other physical factors with temperature have been pointed out by Alongi (1990) in tropical Australian mangroves.

Clear variations of abiotic factors (salinity and depth) and meiofauna were present in spatial scales of tens of kilometers (e.g., between locations) in the present study. The runoff from land could be a major cause of low mean salinity in southern Pinar del Río, although the damming of rivers and creeks is one of the more harmful disturbances of ecosystems in this region (Piñeiro 2003). The wider monthly variation of pH and the higher number of rivers and creeks in southern Pinar del Río in comparison with Matías and Isla suggest that runoff is more intense in this region; the input of water from land would cause the dilution of substances (e.g., phenols and humic acids) increasing the pH.

In the present study, spatial variations in salinity were not clearly linked with the meiofaunal communities. Changes in meiofaunal community structure relating to salinity in tropical mangroves has

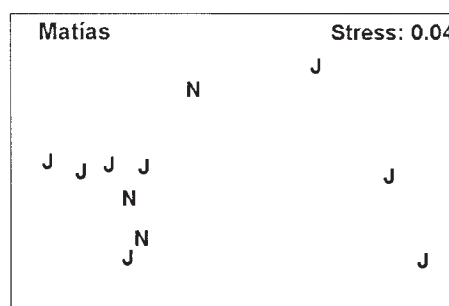
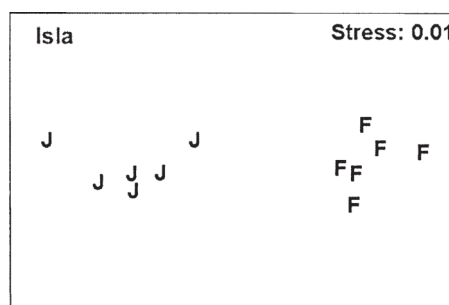
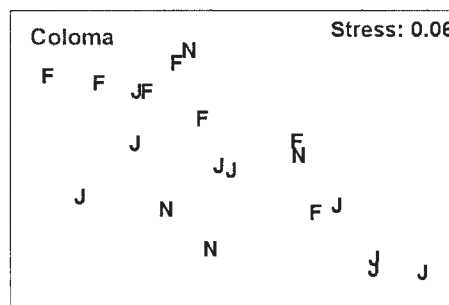
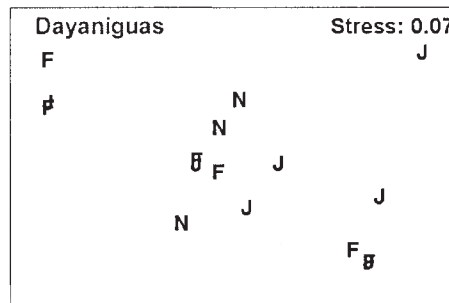
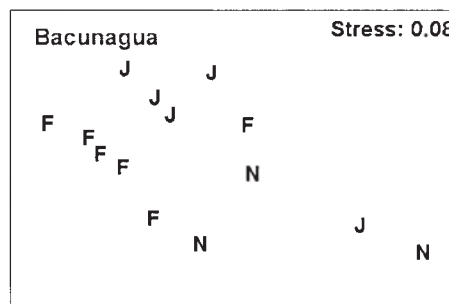
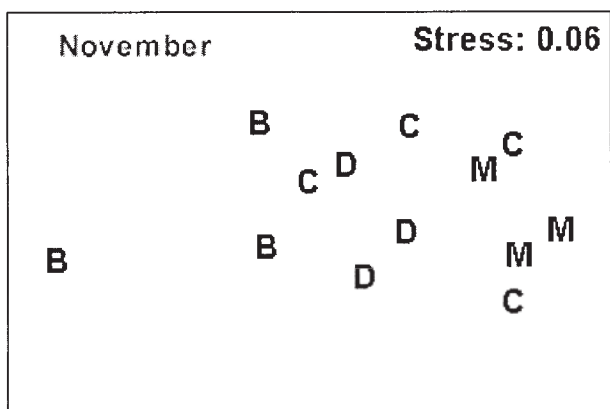
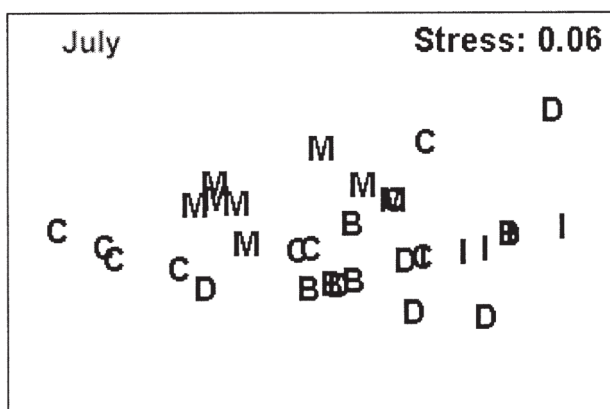
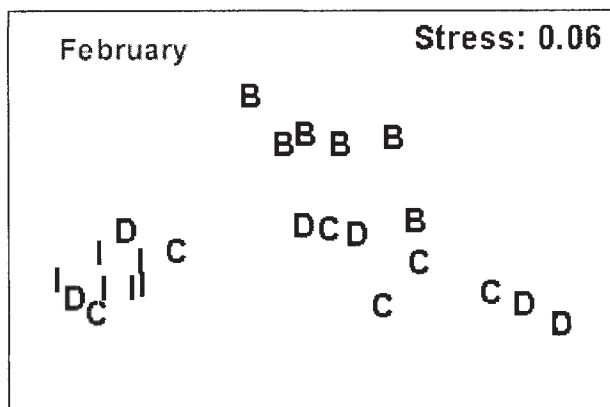


Fig. 3. MDS ordination plots of meiofaunal samples (i.e., replicas = cores) for each sampled month. Data of density are square-root transformed. B = Bacunagua, D = Dayaniguas, C = Coloma, M = Matias, and I = Isla.

Fig. 4. MDS ordination plots of meiofaunal samples (i.e., replicas = cores) for each sampled location. Data of density are square-root transformed. F = February, J = July, and N = November.

TABLE 4. Results of pairwise two-way ANOSIM tests on density of meiofaunal taxa (square-root transformed) related to location factor (data averaged across all months). R values and probabilities (in parentheses) are presented. Number of permutations is 999 for each comparison.

	Bacunagua	Dayaniguas	Coloma	Isla
Dayaniguas	0.077 (0.15)			
Coloma	0.23 (0.017)	0.033 (0.26)		
Isla	0.51 (0.002)	0.23 (0.002)	0.39 (0.001)	
Matías	0.42 (0.004)	0.38 (0.005)	0.13 (0.093)	0.64 (0.03)

been reported by Somerfield et al. (1998) and Alongi (1987a), the magnitude in the change of salinity values appeared to be more important in its effect on meiofauna than absolute values per se. Our results supported this statement; the months with a wide range of salinity (17‰ and 23‰ in July and November, respectively) showed higher spatial variability (i.e., samples were not clustered by location) in their communities after MDS ordination plots. February had the narrowest range (3‰) and the lowest spatial variation within communities.

Alongi (1987a,b) stated that environmental factors such as temperature and granulometry are the main factors influencing the spatial distribution of meiofauna in tropical mangrove systems. In our survey the spatial variation of temperature (i.e., between locations within a same month) were narrow and did not appear to be the cause of significant changes found in meiofauna. The granulometric composition of sediment would be a causal factor of distribution of meiofauna (see Coull 1999 for review). The lack of evident relations between grain size and meiofauna in this study could be caused by: the amount of variation in S-C percentages not being large enough to influence the structure of meiofauna in any important way; and the measured S-C percentage not reflecting true granulometric conditions for benthic infauna (e.g., pore space; Dernie et al. 2003).

The larger variability in the structure of meiofauna from southern Pinar del Río suggests the existence of a higher intensity of disturbance in comparison to the locations in eastern Isla. The increase of variability in meiofaunal community structure (particularly nematodes) has been pointed out as a symptom of environmental stress on biota (Lambshhead and Hodda 1994). Runoff from land, the higher number of human settlements in southern Pinar del Río (Fig. 1), and the noticeable deterioration of mangroves in the area (Armenteros personal observation) support this idea; in what way the disturbance is anthropogenic, it is not yet clear. Very little information on pollution-related variables in studied mangroves exists; performed surveys to date on organochlorine pesticides (Dierksmeier et al. 1996) and heavy metals (Armenteros unpub-

lished data) are not enough to state environmental qualities in studied mangroves.

The density of meiofauna (particularly nematodes) in tropical mangroves tends to be lower than in other coastal ecosystems around the world (Alongi 1988) and their community structure shows considerable variation both on global and local scales (Ólafsson 1995). Somerfield et al. (1998) reported no more than 122 nematodes 10 cm^{-2} in a site from a tropical Malaysian mangrove forest, and Alongi (1987b) has pointed out densities as low as 0.1–100 animals 10 cm^{-2} . The present study showed low values of density (general average: 101 animals 10 cm^{-2}). Higher abundances have been recorded in African tropical mangroves by Dye (1983a), Ólafsson (1995), and Ólafsson et al. (2000): 2,700, 205–5,263, and 271–656 animals 10 cm^{-2} , respectively.

Practical difficulties for standardizing the sampling, fundamentally the selection of sampling sites, could be an important cause of variation in estimates of community structure. There are different types of substrate, such as bare sediment, leaf detritus, fallen leaves, and biotic surfaces (e.g., pneumatophores, prop roots). The meiofaunal communities on each type of substrate within the mangroves would be significantly different (Gee and Somerfield 1997) and the substrates often are patchy in small spatial scales (centimeters to meters) due to this; sampling in relatively homogeneous substrates would be difficult or impossible. In tropical mangroves, a complex zonation is often present with narrow fringes of microenvironments (i.e., sediment under canopy, prop roots from *Rhizophora*, pneumatophores from *Avicennia*; Alongi 1987b). The mangroves are intertidal systems where the water depth and the distance from land (i.e., from influence of runoff or anthropogenic inputs) are determined by tidal amplitude for a particular location. These features point out a high spatial variability in the microenvironment in mangrove habitats with associated methodological difficulties in the application of sampling strategies.

Two additional features that could account for high variability in density estimates of meiofauna in tropical mangroves are: biogeographical patterns showing African mangroves' meiofauna more abundant than in Caribbean and Asian regions (no further information about this topic appear to exist) and local environments operating within habitats (e.g., organic matter, tidal currents, accumulation of tannins).

The ecological causes of low densities in some tropical mangroves include poor nutritional quality of derived mangrove detritus (Alongi 1989; Tietjen and Alongi 1990; Alongi and Christoffersen 1992); high tannin content of the sediment in mangroves,

which have a significant negative effect on fauna (Alongi 1987c; Tietjen and Alongi 1990); suspension of meiofauna in the water column by physical reworking due to tidal currents and waves (Alongi and Christoffersen 1992; Dernie et al. 2003); and high temperatures of sediment strengthening the anoxic conditions in mangrove sediment (Alongi 1990) affecting the reproduction of nematodes (Heip et al. 1985).

Several studies in subtropical and temperate mangroves (Hodda and Nicholas 1985; Nicholas et al. 1991; Gwyther 2000; Zhou 2001) recorded values of meiofauna densities consistently higher than the tropical surveys quoted in this paper. The first three ecological causes discussed above can affect meiofauna in nontropical mangroves, but the extension and importance of them is not clear. To our knowledge, latitudinal patterns of meiofaunal communities in mangroves have not yet been proposed.

The statement of Ólafsson (1995) on the impossibility to enunciate generalizations on the basis of a few studies regarding meiofaunal structure and abiotic control factor in mangrove habitats would be true still. This study constitutes an initial approach to the study of meiofaunal communities in mangrove systems from southwest Cuba. Future strategies for meiofaunal studies in mangrove systems include increasing the temporal and spatial replication in order to find patterns of variation, implementing manipulative field experiments on meiofauna to test for ecological hypotheses, and applying a species-level approach for assessing the diversity of nematode assemblages and isolating the abiotic factors that structure these assemblages.

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