

COMMUNITY STRUCTURE OF MEIO- AND MACROFAUNA IN SEAGRASS MEADOWS AND MANGROVES FROM NW SHELF OF CUBA (GULF OF MEXICO).

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ABSTRACT

The meio- and macrofauna at 20 stations pertaining to tropical seagrass meadows and mangroves were surveyed for describe their abundance and distribution patterns and also the relationships between these faunal groups. The seagrass meadows presented richer faunal in terms of density and number of taxa when compared to mangroves. The multivariate pattern of communities showed significant differences between habitats possibly due to a higher food availability, habitat complexity and sediment stability in seagrass meadows and the accumulation of tannins in mangrove sediments. Density estimates from other tropical and temperate habitats are consistently higher than our results. There is not conclusive evidence but we consider that very narrow tidal amplitude and also oligotrophic waters would be linked to the diminished infaunal densities at the present study sites. The meiofauna did not changed in the same way that macrofauna across the habitats neither stations suggesting that each community responds to different limiting factors. In mangroves a weak negative relation between these communities appears to exist, possibly accredited to bioturbation or competition for food. The use of the ratio between meio- and macrofauna densities appears to be ecologically meaningless to interpret community patterns in studied ecosystems.

Key words: meiofauna; macrofauna; mangroves; seagrass meadows; ASW, Gulf of Mexico

RESUMEN

Se describen, en hábitats de pastos marinos y manglares, los patrones de abundancia y distribución de la meio- y macrofauna, así como las relaciones entre estos grupos. Los pastos marinos presentaron una fauna más abundante y diversa en comparación con los manglares. El patrón multivariable de la comunidad muestra diferencias significativas entre hábitats posiblemente debido a una mayor disponibilidad de alimento, complejidad de hábitat y estabilidad del sedimento en los pastizales y a la acumulación de taninos en los sedimentos de manglar. Los estimados de densidad en pastizales y manglares de otras regiones tropicales y templadas son consistentemente más elevados que los de este estudio. No existe evidencia concluyente pero la amplitud pequeña de mareas y la oligotrofia de las aguas en la región NW de la plataforma pueden causar la disminución en la densidad de la fauna. La meiofauna no cambia en la misma manera que la macrofauna a través de las estaciones ni de los hábitats, lo que sugiere que cada comunidad responde a diferentes factores limitantes. En los manglares una correlación negativa débil entre las comunidades parece existir posiblemente debido a la bioturbación o competición por el alimento. La proporción entre la densidad de la meio- y la macrofauna es ecológicamente poco útil para interpretar los patrones de la comunidad bentónica.

Palabras clave: meiofauna; macrofauna; manglares; pastos marinos; ASW, Golfo de México.

The Gulf of Mexico is a large marine ecosystem (LME), widely acknowledged for its considerable efforts in conservation and management (Díaz de León *et al.*, 2004).

The northwestern region of the Cuban shelf is probably the less studied area within the Gulf of Mexico and contains a mosaic of tropical ecosystems, including seagrass meadows, coral reefs, mangroves, swamps and muddy flats (González-Sansón and Aguilar-Betancourt, 2004). In order to achieve sustainable management of this

LME, insight on the processes within these habitats and their biological communities must be obtained.

Four major groups of fauna has been defined (Warwick, 1984; Danovaro *et al.*, 2004) in soft-bottom habitats, according to mesh size where animals could be retained (< 45 µm: microfauna; 45 – 500 µm: meiofauna; 0.5 – 4 mm: macrofauna; and > 4 mm: megafauna). Of these groups, meio- and macrofauna are common targets when assessing ecosystem perturbations and

environmental quality, as they provide an integrated response to alterations in the physical and biogeochemical conditions at sampled areas. Meio- and macrofauna are a valuable component of ecosystems with four major roles (Coull, 1999; Danovaro *et al.*, 2004): i) recycling of nutrients and decomposition of organic matter; ii) a link between detritus and higher levels up in the trophic web (e.g. fishes); iii) supplying high secondary production in benthic systems and iv) contributing a high diversity of species. The role of meio- and macrofauna and the interaction between them are particularly important in some tropical habitats (e.g. mangroves and seagrass meadows) where food webs are detritus based (Alongi, 1989; Heymans and Baird, 1995).

The number of ecological surveys on meio- and macrofauna in the tropics has been lower when compared to temperate regions. Recently, the interest of the scientific community has extended towards the tropics with the publication of several recent papers on soft bottom benthic fauna (e.g. De Troch *et al.*, 2005; Nozais *et al.*, 2005; Armenteros *et al.*, 2006). However, current knowledge on the ecology of meio- and macrofauna in tropical habitats is poor. Studies combining the sampling of both meio- and macrofauna in one area at the same time are scarce and almost confined to temperate and subtropical regions (e.g. Wigley and McIntyre, 1964; Elmgren, 1978; Elmgren *et al.*, 1984; Flach *et al.*, 1999; Moodley *et al.*, 2000) due greatly to methodological problems associated with the collection and processing of samples (Albertelli *et al.*, 1999). To our knowledge, relatively few papers (e.g. McIntyre, 1968; Alongi and Christoffersen, 1992; Dittman, 2000) have addressed the combined study of meio- and macrofaunal communities from tropical habitats.

The understanding of the structure and dynamics of ecosystems in the NW Cuban shelf is limited, therefore the description of the distribution patterns and the possible interactions between meio- and macrofauna should provide the basis for further research on the processes governing the functioning of soft-bottom habitats. In Cuba, no other research carried out so far has; namely, i) comparison between habitats based on the communities of meio- and macrofauna and ii) the relation between these communities based on simultaneous sampling with comparable sampling gears. Also, only two papers (Murina *et al.*, 1969; Ibarzábal, 1982) has been published on meio- and macrofauna in the studied region (NW Cuban shelf), thus suggesting that it is possibly one of the

most unknown marine regions in the Cuban archipelago in this perspective.

In this paper we describe the abundance and distribution patterns of meio- and macrofaunal communities in two soft-bottom tropical habitats, and discuss the relation between these faunal communities.

MATERIAL AND METHODS

The sampling was carried out in January, 2004; in the North-western region of the Cuban shelf (Fig. 1). Twenty sampling stations were distributed systematically in order to cover the widest possible area in the shelf. Each sampling station was classified as one of two types of soft-bottom habitat as follows (additional abiotic information available in Table 1):

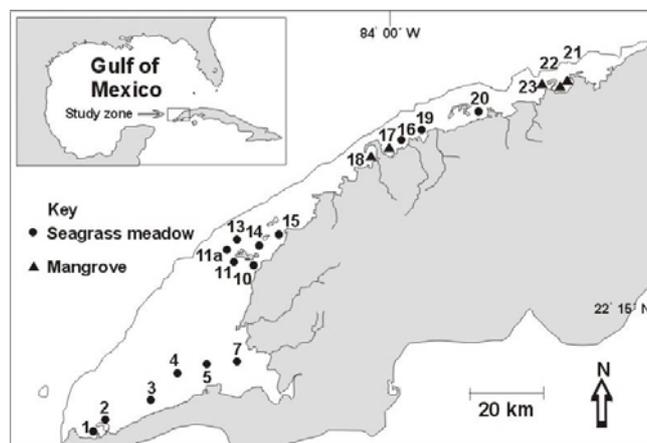


Fig. 1. Study zone. The sampling stations are showed. The contour of shelf break is marked (approximately 200 m depth).

i) Seagrass meadow: Subtidal sand-muddy flat covered in variable degree by the seagrass *Thalassia testudinum*. In some stations other seagrass species (e.g. *Syringodium filiforme* and/or *Halophila decipiens*) were also present. The presence of macroalgae and epiphytes associated with seagrass was common. Accumulation of detritus, presumably from seagrass decomposition, was visually evident in almost all seagrass stations. The sampling stations: 1-5, 7, 10, 11, 11a, 13-16, 19 and 20 were classified as pertaining to this habitat.

ii) Mangrove: Sand-muddy bottom; the sampled zone was the submersed fringe of sediment below prop-roots of *Rhizophora mangle*. The bottom was covered with litter from mangroves in variable

Table 1. Mean values and standard error of abiotic variables in seagrass meadow and mangrove habitats from the NW shelf of Cuba. Number of sampling units: Seagrass meadow (14) and mangrove (5). TOM = Total organic matter.

Habitat	Depth (m)	Temperature (°C)	Salinity (ups)	% Silt/Clay	% TOM*
Seagrass meadow	5.7 ± 0.7	23.0 ± 0.1	37.3 ± 0.1	27.0 ± 3.6	3.5 ± 2.0
Mangrove	0.9 ± 0.1	23.1 ± 0.3	36.6 ± 0.2	24.6 ± 6.2	1.7 ± 0.5

* number of observations: seagrass meadow (10) and mangrove (3)

quantities. The sampling stations in this habitat type were 17, 18, 21, 22 and 23.

The sampling gears used were plastic cylindrical corers (internal diameter: 2.9 cm for meio- and 10.5 cm for macrofauna). Corers were inserted into the sediment to a depth of 10 cm and the material collected in each core was considered a sampling unit (SU). In each sampling station two SU were taken at random for meio- and another two SU for macrofauna. The material from each core was immediately preserved in 4 % formalin buffered with sodium tetraborate (borax). Final concentration of formalin in the samples was not assessed, but the preservation was efficient due to the fact that no decomposition odor was detected and the organisms in the sample were identifiable (i.e. bodies were not decomposed).

Sediment for the analysis of meiofauna was sieved through 500 (stainless steel) and 45 µm (fabric) test sieves (supplier Restch). The organisms retained in the 45 µm sieve were considered meiofauna. The extraction from sediment was carried out by a flotation procedure, utilizing a sucrose solution (commercial sugar crystals added to water to a density of 1.18 g cm⁻³). The extract was preserved in 4 % buffered formalin, stained with 1% alcoholic eosin and identified to major taxa (e.g. nematodes, copepods) under a stereomicroscope MBS-9 at a maximum magnification of 56X. The density of meiofauna was expressed as organisms per 10 cm².

Sediment for the analysis of macrofauna was sieved through 4 and 0.5 mm sieves. The sediment and animals retained in the later sieve were preserved in 4 % buffered formalin, stained with 1% alcoholic eosin and identified to major taxa under a stereomicroscope (i.e. no extraction technique was performed). Polychaetes were manually extracted and identified to family level when possible. We analyzed the polychaetes including them in the macrofauna (as major taxon) but also separately as a single assemblage (at the taxonomic level of family). It is common to express macrofaunal density as organisms per m²; but due

to the small area of our sampling device (86.6 cm²) we prefer not to extrapolate to a larger area and therefore express the density as organisms per 0.01 m² (i.e. animals per 100 cm²).

Depth, temperature and salinity of bottom water were measured using an oceanographic multiprobe 4a from Hydrolab Corp. Percent of silt/clay (% S/C) in sediment was determined by wet sieving through 63 µm sieve. Percent of total organic matter (TOM) was determined by the Walkley-Black method after UNEP/IOC/IAEA (1995). This method assesses the organic fraction in sediments utilizing exothermic heating and oxidation with K₂Cr₂O₇ and concentrated H₂SO₄. Samples of abiotic variables were not replicated in each station, therefore statistical tests to determine significant differences between stations could not be carried out. Also, when stations are grouped by habitat, the big difference in number of replicates (i.e. 14 for seagrass and 5 for mangroves) preventing the statistical comparisons among habitats.

Software PRIMER 5.2.9 (Clarke and Warwick, 2001) was used for data analysis. A correlation-based Principal Component Analysis (PCA) was carried out on the data of abiotic variables to determine if a pattern exists across the habitats. The data of faunal density were analyzed independently for meio-, macrofauna and polychaetes assemblages and were transformed using the square root in order to reduce the numerical contribution of dominant taxa (e.g. nematodes and polychaetes) to community structure. A one-way hypothesis test ANOSIM was carried out to identify significant differences in community structure between habitats. A non-metric Multidimensional Scaling (nmMDS) was performed in order to determine the similarity pattern between samples. BIOENV procedure was applied to similarity matrices to link abiotic patterns to multidimensional patterns of fauna. This procedure uses a correlation coefficient to search for possible combinations of abiotic variables (as similarity matrix) that best matches the faunal similarity matrix. The correlation between similarity matrices of meio- and

macrofauna was determined by Spearman rank coefficient, in order to determine the relationship between faunal groups across the samples. Significance of correlation was tested by a permutation procedure RELATE. Spearman's rank correlation coefficient was used to detect relationship between total density of meio- and macrofauna.

RESULTS

Abiotic variables

The ordination plot of the samples (Fig. 2) based on the measured abiotic variables (temperature, salinity, depth and content of silt/clay), suggests differences between mangroves and seagrass meadows. Unfortunately, the % of total organic matter (TOM) could not be measured in all stations, and was not included in the PCA ordination. The mean values of abiotic variables (Table 1) indicate only subtle differences in temperature and salinity. Depth of water was lower in mangroves while higher in seagrass meadows. The differences between both habitats (in absolute values) were more notable in regards to the organic content; that is to say, the % of TOM indicated lower organic content in mangroves (1.7%), whereas seagrass meadow habitats have higher value (3.5%).

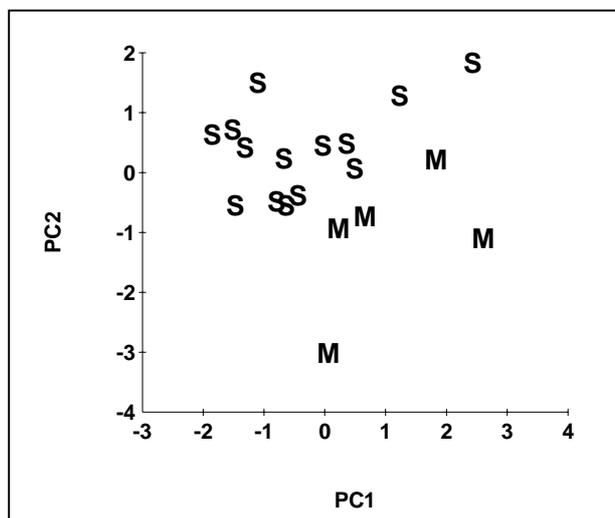


Fig. 2. PCA ordination plot of samples arranged by habitats on the basis of abiotic variables. Explained variance from the two first axes: 72.8 %. Equations of Axes: $PC1 = -0.63T + 0.46 S/C - 0.45d - 0.44S$; $PC2 = 0.62S/C + 0.54S + 0.50d + 0.28T$. T = temperature, d = depth, S = salinity and S/C = percent of silt/clay. Sample labels: S = seagrass meadow, and M = mangrove.

Meiofaunal communities

Eight major taxa of meiofaunal organisms were identified (Table 2). The mean number of taxa recorded in each habitat was (the maximum number recorded in any sample is given in parentheses): seagrass meadows, 5 (8), and mangrove, 4 (5). Nematoda was the dominant taxon in both habitats (71% of total density in seagrass and 59 % in mangroves). The contribution of copepods to the total density was not higher than 6 % in both habitats. Mangrove habitats showed lower values of meiofauna density (mean: 24 ± 11 ind 10 cm^2) while higher values were recorded in the seagrass meadows (mean: 85 ± 12 ind 10 cm^2) (Table 2).

According to the ANOSIM test ($R = 0.36$; $p = 0.001$, 999 permutations), there were differences in community structures of meiofauna between seagrass meadows and mangroves. MDS ordination plot based on density data suggests that mangrove samples had a community structure dissimilar to those from seagrass meadows (i.e. a segregation of samples by habitat was observed in the plot) (Fig. 3). A higher dispersion of samples pertaining to mangroves indicates a greater variability (i.e. samples from mangroves were more dissimilar in regards to each other).

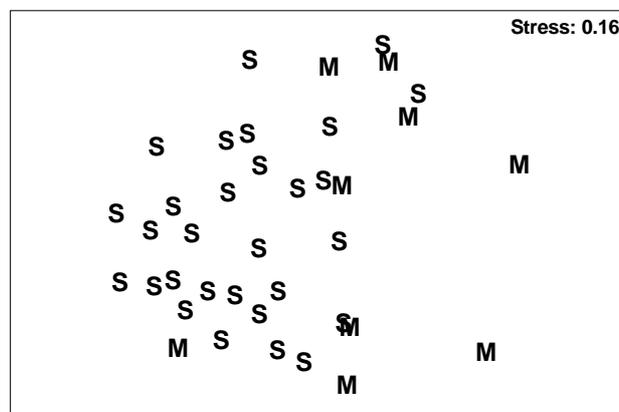


Fig. 3. MDS ordination plot of meiofaunal samples arranged by habitats. Data transformed as square root. Plot labels: S = seagrass meadow, and M = mangrove.

The BIOENV procedure showed a low rank correlation between the multivariate biological pattern of meiofauna and the observed abiotic pattern. The highest values of correlation were obtained with depth ($r = 0.132$); and a combination of depth – temperature ($r = 0.08$).

Table 2. Mean values and standard error of density of meiofauna (individuals 10 cm⁻²) in seagrass meadow and mangrove habitats of NW shelf of Cuba. Number of sampling units: seagrass meadow (29) and mangrove (10). Category "Other" includes: Polychaeta, Tanaidacea, Cumacea, Kynorhyncha and Amphipoda.

Habitat	Nematoda	Copepoda	Ostracoda	Other	Total
Seagrass meadow	75.1 ± 11.3	7.0 ± 1.8	0.9 ± 0.4	2.4 ± 0.7	85.4 ± 11.7
Mangrove	21.7 ± 10.6	1.8 ± 1.0	0.9 ± 0.6	0.5 ± 0.2	24.9 ± 11.1

Macrofaunal communities and polychaetes assemblages

Eleven major taxa were recorded in macrofaunal communities (Table 3). The numbers of taxa in each habitat are as follows (the maximum number of taxa recorded in any sample is given in parentheses): seagrass meadows, 6 (9); and mangroves, 5 (6). In mangroves the dominant taxon was Nematoda (58 % of total density); in seagrass meadows the density of Nematoda and Polychaeta was basically the same (Table 3), each contributing approximately 26% to the total density. The evenness was notably greater in seagrass meadows, i.e. of the total density, 60% is occupied by three taxa (nematodes, polychaetes and tanaidaceans) whereas; in mangroves, this same percentage is integrated by only one taxon (nematodes). The mean total density of macrofauna was very similar for both seagrass meadows and mangroves: 44 and 38 ind 0.01 m² respectively (Table 3).

The ANOSIM test revealed differences in the macrofaunal communities between seagrass meadows and mangroves (R = 0.31; p = 0.01; 999 perm.). The ordination plot of macrofaunal samples agreed with the results of this test (Fig. 4); i.e. mangrove and seagrass samples form separated groups.

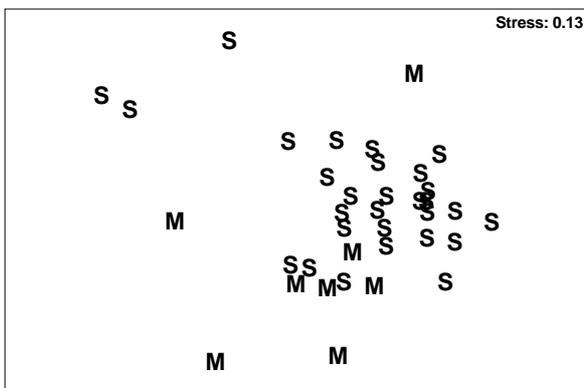


Fig. 4. MDS ordination plot of macrofaunal samples arranged by habitats. Data transformed as square root. Plot labels: S = seagrass meadow, and M = mangrove.

The BIOENV procedure showed a poor relationship between the multivariate macrofaunal pattern and the measured abiotic variables. The best rank correlation was observed with salinity (r = 0.13) and with a combination of salinity - temperature (r = 0.12).

A total of 25 families of Polychaeta were identified. The mean number of families in each habitat (the maximum number of families recorded in any sample is given in parentheses) was as follows: seagrass meadow, 3 (8); and mangrove, 1 (2). The presence of less Polychaeta families in mangroves was clear. However; the ANOSIM hypothesis test does not show differences between habitats according to polychaetes assemblages (R = 0.01; p = 0.44; 999 perm.); this is probably due to the low values of Polychaeta density present in the matrix. An ordination plot showed no clear clustering of samples according to habitats (Fig. 5). The BIOENV procedure showed a poor relationship between the multivariate pattern of density of polychaetes and the abiotic factors. The best values of correlation were with salinity (r=0.27) and with the combination depth - temperature - salinity (r = 0.24).

Relation between meio- and macrofauna

The Spearman rank correlation between square root transformed similarity matrices derived from meio- and macrofaunal data was very low (r = 0.08) and non-significant (p = 0.18; 999 permutations).

The plot of total density of meio- against macrofauna showed non-significant correlation for both habitats (Fig. 6); the values of the correlation coefficient were low for seagrass meadows (r = - 0.22) and half-range (r = - 0.52) for mangroves. The exploration of the total density meio- macrofauna ratio in the present study showed a high variability for both habitats: seagrass meadow (mean: 1191, range: 34 - 9540); and mangrove (mean: 753, range: 0 - 4386).

Table 3. Mean values and standard error of density of macrofauna (ind 0.01 m⁻²) in seagrass meadow and mangrove habitats from the NW shelf of Cuba. Number of observations (cores): seagrass meadow (29) and mangrove (8). Category “Other” includes: Asteracea, Cumacea, Amphipoda, Sipuncula, Oligochaeta and Decapoda.

Habitat	Polychaeta	Nematoda	Copepoda	Tanaidacea	Ostracoda	Other	Total
Seagrass	15.2 ± 2.1	15.0 ± 2.3	2.2 ± 0.5	6.9 ± 1.3	1.4 ± 0.4	3.0 ± 0.9	43.7 ± 5.9
Mangrove	3.6 ± 0.8	30.5 ± 13.3	0.4 ± 0.2	1.7 ± 1.3	0.4 ± 0.4	1.7 ± 0.9	38.4 ± 13.0

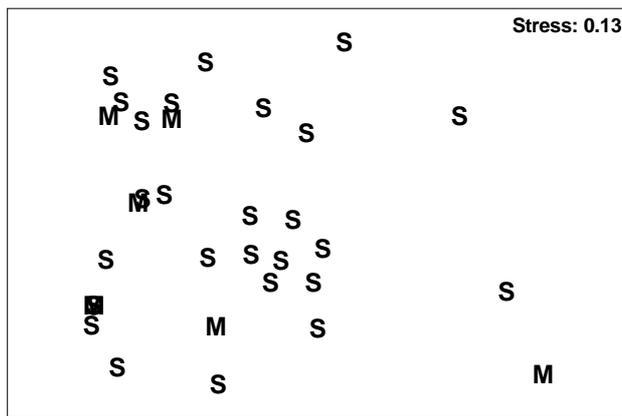


Fig. 5. MDS ordination plot of samples of polychaetes assemblages arranged by habitats. Data transformed as square root. Plot labels: S = seagrass meadow, and M = mangrove.

DISCUSSION

Three main patterns are evident from our results: i) the ecological structure of benthic soft-bottom communities (meio- and macrofauna) are different between seagrass meadows and mangroves; ii) density estimates from tropical and temperate areas in the world are consistently higher than estimates from the NW region of Cuba; iii) the community structure of the meiofauna did not changed in the same way that macrofauna across the habitats neither stations. Here forth, we discuss each idea.

Differences between seagrass meadows and mangroves

The differences between mangroves and seagrass meadows relating to benthic faunal communities would be linked primarily to differences in four physical-chemical environmental factors:

i) Sedimentary food resources (measured as TOM) in seagrass meadows from the NW shelf are about two times higher than those in the mangrove; this could be an partial explanation for the notable depletion of meiofauna that was observed in mangroves. According to De Troch *et al.*, (2006), the value of TOM is not a reliable measure of food resources available to meiofauna; however, if detritus is primarily decomposed to particulate organic matter we feel that a difference of two-fold in the % of TOM within the sediment should reflect differences in the quantity of food available to detritivores.

Concerning quality, the mangrove detritus has the lowest nutritional value (i.e. high C:N ratio) among marine primary producers (Mann, 2000). Mangrove detritus is unmanageable and inedible by meiofauna, whose communities are known to be affected by the quality of detritus (Albertelli *et al.*, 1999). The total density of macrofauna was somewhat stable between habitats in our study, although individual taxa observed variation, in

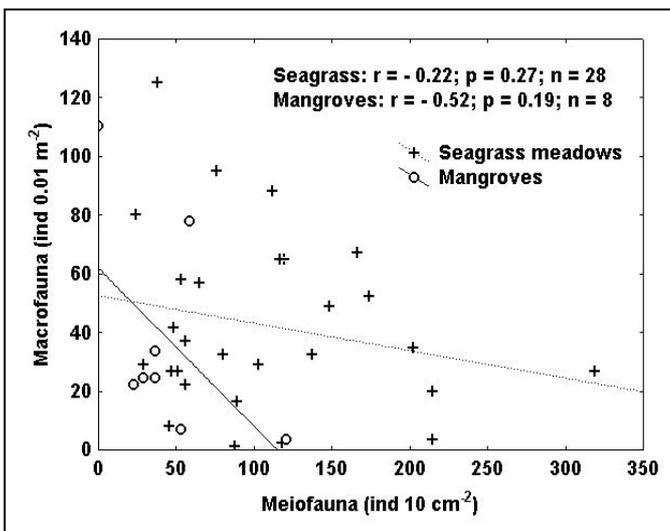


Fig. 6. Total density of meiofauna against macrofauna arranged by habitats. Values of correlation of Spearman and trend line are showed.

spite of differences in quantity and quality of food resources. Webb (1996) reported similar findings, in that there is a lack of response to the macrofauna density to increasing of organic content in sediments.

ii) In terms of habitat complexity, the seagrass meadows offer the benthic community a high variety of microhabitats (sediment, decaying leaf, and low canopy) which are not present in mangrove areas. The prop roots of *Rhizophora mangle* offer a relatively wide area for colonization by meio- and macrofauna (Lalana-Rueda and Gosselck, 1986); however we sampled only the relatively flat area of sediment between prop roots where the spatial complexity in cm-scale was very low. For the three faunal groups (meio-, macrofauna and polychaetes) investigated at the NW shelf of Cuba the number of taxa was higher in seagrass meadows in comparison with seagrass unvegetated areas; this is in agreement with results from both Orth *et al.*, (1984) and Edgar *et al.*, (1994).

iii) Sediment stability – physical disturbance. The reduction of abundance and diversity of soft-bottom benthic communities due to water movement have been expressed by Schratzberger and Warwick (1998) and Netto *et al.*, (1999a; 1999b). In seagrass meadows, the presence of a canopy reduces the erosion from water movement and contributes to the stability of the sedimentary environment, thus reducing suspension processes and washout of the soft bottom fauna (Hall, 1994). The intertidal location of mangrove ecosystems (i.e. having lower water depth than seagrass meadows) allows higher physical disturbance due to tidal currents and waves. Despite the high rate of primary production of mangroves in the Cuban shelf (CARICOMP, 1997); the lower content of TOM reported in the present study (1.7%), when compared to other studied habitats (seagrass: 3.5%; adjacent muddy flats: 3.2%), suggests a relatively low accumulation of litter transported by water movement.

iv) The presence of soluble tannins in mangrove sediments would be a chemical restriction to meio- and macrofaunal communities (Alongi, 1987c; Tietjen and Alongi, 1990; Zhou, 2001); however, the dilution of these tannins in the water would lessen, if not cancel out, their effects on the seagrass communities.

Comparisons with estimates from other sites

Research results from tropical mangroves and seagrass meadows (see reviews by Bell *et al.*, 1984 and Alongi, 1989) indicate that density estimates

from meio- and macrofauna are generally low compared to abundances found in similar subtropical and temperate habitats. However, Virnstein *et al.*, (1984) stated that there is a need for caution due to the fact that there is a lack of evidence to support any assumption of the existence of latitudinal patterns within fauna from seagrass habitats. To our knowledge, further evidence proving latitudinal trends does not seem to exist in the present.

The density values of meio- and macrofauna reported in the present study are consistently lower than those found in other studies from tropical seagrass meadows (Table 4, and reviews from Bell *et al.*, 1984; Alongi, 1989). However, macrofaunal density data from tropical seagrass meadows are scarce and when available it is difficult to compare data sets due to the differences in collection and sample processing methods (particularly differences in sizes of sieve mesh). For instance, the comparatively low values of density reported by Murina *et al.*, (1969) and Brook (1977) could have been the result of a larger mesh size (1 and 0.8 mm respectively) and the use of different sampling devices (trawl and dredge) in comparison with the present survey. Edgar *et al.*, (1994) demonstrated that differences in the size of sampler employed (corer) and the habitat sampled, produced notable differences in faunal density estimates in seagrass systems.

Concerning meiofauna, there is a larger data set with relatively few methodological conflicts. Analysis of density estimates suggests that soft-bottom meiofaunal communities in the Gulf of Mexico and the Caribbean Sea are less dense than counterparts from Africa, Asia and Australia. De Troch *et al.*, (2006) argued that tidal movement would be the cause for differences in density and number of taxa within meiofauna communities from tropical seagrass habitats. The limited data sets (i.e. faunal + tidal data) that we have found support this statement; sites pertaining to tropical mangrove and seagrass meadows, in which higher densities of meio- and macrofauna have been reported, are characterized by high tidal range: Dye (1983): 1.35 m, several studies from Ólafsson in E. Africa (see Table 4): approximately 4 m. On the contrary, the Cuban NW shelf presents narrow tidal amplitude (less than 25 cm after Rodríguez and Rodríguez, 1983) complimented with relatively low faunal density estimates. Also, De Troch *et al.*, (2006) suggest an inverse relationship between tidal amplitude and faunal density in seagrass meadows.

Table 4. Estimates of density of meio- (ind 10 cm⁻²) and macrofauna (ind 0.01 m⁻²) reported in sediments from seagrass meadow and mangrove tropical habitats. M = mean; R = range; Max = maximum. For convenience, original units of density have been converted. Additional references have been quoted for seagrass meadows in Bell *et al.* (1984) and for mangroves in Alongi (1989).

Habitat	Group	Density	Place, observations	Author (s)
Seagrass	Meiofauna	M: 1113; R: 836 - 1658	E Africa; reef-lagoon	Ndaro and Ólafsson (1999)
		R: 2619 - 8478	Kenya; E Africa	De Troch <i>et al.</i> , (2001)
		R: 554 - 1351	Arabian Sea; atoll-lagoon	Ansari and Parulekar (1994)
		M: 732	Kenya, E Africa	De Troch <i>et al.</i> , 2006
		M: 254	Yucatán, Gulf of México	De Troch <i>et al.</i> , 2006
		M: 285	Philippines	De Troch <i>et al.</i> , 2006
		R: 5 - 323	Caribbean Sea	López-Cánovas 1990
		M: 85; R: 6 - 302	NW Cuba	Present study
		R: 6 - 19	S Florida	Brook (1977)
		M: 600; R: 530 - 660	E Africa; reef-lagoon	Ndaro and Ólafsson (1999)
		M: 6	NW Cuba	Murina <i>et al.</i> , (1969)
		R: 52 - 91	NW Cuba	Ibarzábal (1982)
		M: 100; 140; 200	Caribbean Sea, reef lagoons	Ibarzábal (1993)
M: 44; R: 1 - 142	NW Cuba	Present study		
Mangrove	Meiofauna	Max: 122	NW Malaysia; nematodes	Somerfield <i>et al.</i> , (1998)
		M: 150; R: 3 - 987	NE Australia; nematodes	Alongi (1987a)
		M: 469; R: 14 - 2454	NE Australia	Alongi (1987b)
		R: 271-656	E Africa	Ólafsson <i>et al.</i> , (2000)
		M: 2700	S Africa	Dye (1983)
		M: 1493; R: 205-5263	E Africa	Ólafsson (1995)
		M : 101 ; R: 0 - 1298	Caribbean Sea	Armenteros <i>et al.</i> , 2006
		M: 25; R: 0 - 121	SE Gulf of Mexico	Present study
		R: 0 - 183	SW Gulf of Mexico; st. 3 and 4 in lagoon;	Hernández-Alcántara and Solís- Weiss 1995
		M: 38; R: 4 - 110	SE Gulf of Mexico	Present study

Tides provide auxiliary energy to benthic communities by permitting greater food availability to these faunal components, thus increasing their productivity. Integration of ecological information from the NW region of Cuba (González-Sansón and Aguilar-Betancourt, 2004) suggests that it is an oligotrophic area (i.e. very scarce run-off from land) with low tidal energy (i.e. low energy supply). When compared with other more productive tropical areas, these recognized differences would be the cause, at least partially, for lower faunal density estimates found in the present investigation (see Table 4 for references). No conclusive evidence exists that explains the role of tidal amplitude on densities of faunal communities in studied habitats; we recommend sampling fauna across other sites with a wide range of tidal amplitude in an effort determine one.

Relationship between meio- and macrofauna densities

Meio- and macrofauna are communities coexisting in time and space, hence suggesting that some kind of relation between these faunal groups would be expected. Results obtained did not confirm this belief and none of the performed tests indicate a clear association or trend between these groups of fauna for either habitat.

In seagrass meadows, macrofauna seems to be more directly related to the structural architecture of this habitat than in the case of meiofauna (Paula *et al.*, 2001); therefore, the local variations among seagrass stations (e.g. height of canopy, density of seagrass leaves and shoots) would influence the community structures of macrofauna more than the meiofauna. Orth *et al.*, (1984) reported that in

seagrass meadows the relationships predator-prey could be important in structuring the infaunal community; however, named review includes very few reports from tropical habitats. Results from highly productive temperate salt-marshes (similar in some features to tropical seagrass meadows) indicate that predation on meiofauna by macrofauna is not always a regulating factor probably due to availability of food resources (detritus) (Fleeger *et al.*, 1982). Additional processes, e.g. rate of macrofaunal recruitment from temporal meiofauna or bioturbation, are probably very important in studied seagrass meadows but our study design did not allow us to include them in the analysis.

In the case of mangroves, the calculated correlation's coefficient was low and non-significant possibly due to a low number of observations ($n = 8$). Other studies (see Alongi, 1989 for review) showed evidence of negative interactions between both faunal groups; however, the decline of meiofauna in the presence of macrofauna should not be related directly to predation by the latter since tropical mangroves seem to have very low densities of potential macrofaunal predators (Alongi, 1987b). Biological interactions such as bioturbation and competition for food and space would be equally plausible to explain negative relations between meio- and macrofauna (Alongi, 1989; Albertelli *et al.*, 1999).

Almost all manipulative studies (in field and/or laboratory) indicate some effects of macrofauna on meiofauna communities (see Ólafsson, 2003 for review). The processes underlying this relation and the types of effects (e.g. changes in density or diversity) particularly in tropical habitats are not completely understood. Further controlled studies in the field (e.g. Peachey and Bell, 1997; De Troch *et al.*, 2005) are necessary to clarify the dynamics of meio- and macrofauna in these systems.

Macrofauna - meiofauna ratios have been computed in some surveys, but no estimates of this ratio were found in the reviewed literature for tropical ecosystems. These ratios seem to be ecologically important concerning biomass (e.g. Elmgren, 1978; Elmgren *et al.*, 1984; Albertelli *et al.*, 1999). When applied to density, several reports on the macrofauna - meiofauna ratio are quoted for temperate and/or deep waters (e.g. Wigley and McIntyre, 1964; McIntyre, 1968; Flach *et al.*, 1999). Only two patterns have been identified regarding the macro:meiofauna ratio: i) A notable constancy (1:170) between different areas from Europe and inshore New England waters, although

in many cases the taxonomic composition and biotope features differed remarkably (Wigley and McIntyre, 1964). ii) A lineal relation between ratio and water depth along continental slopes from NW Atlantic Ocean (Flach *et al.*, 1999). The joint analysis of ratios computed in other papers (e.g. Elmgren *et al.*, 1983; 1984; Moodley *et al.*, 2000; Netto *et al.*, 1999b) and those from the present study shows a very wide range of variation and no interpretable patterns. When a strong environmental factor (e.g. fluxes of carbon on deep water benthos after Flach *et al.*, 1999) alters the community structures of both meio- and macrofauna in similar ways, it is expected that there would be a meaningful change in the ratio; however, if each community responds in a different manner to ecological factors then the changes in the ratio can not be interpreted in terms of community structure.

In summary, due to marked different abiotic environments in each habitat, we found notable differences in community structure between seagrass meadows and mangroves in terms of major meio- and macrofaunal taxa. Also, tidal amplitude along with ecosystem productivity would be the cause of lower estimates of faunal density in the study area when compared to other tropical and temperate sites. Finally, no relation is evident between meio- and macrofauna in terms of community structure, thus suggesting that each faunal group responds to different key ecological factors.

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