Rev. Invest. Mar. (2012), 32(1): 50-61

ISSN: 1991-6086

Habitat heterogeneity effects on macro- and meiofauna (especially nematodes) in Punta Francés coral reef (SW Cuban Archipelago)

Maickel Armenteros[1]*, Alexei Ruiz-Abierno[1], Yimay Sosa[1], José Andrés Pérez-García[1]

(1)Centro de Investigaciones Marinas, Universidad de La Habana, Calle 16, No. 114 entre 1ra y 3ra, Miramar, Playa, Ciudad Habana 11300, Cuba.
(*) Corresponding author: maickel@cim.uh.cu

ABSTRACT

Benthic macrofauna and meiofauna distribution patterns were described in a tropical coral reef (Punta Francés, Cuban Archipelago, Caribbean Sea). Density and main taxa composition for macrofauna and meiofauna and species diversity and organismal traits for free-living nematodes were compared among four habitats: seagrass bed, sand flat, dead coral and hard bottom. Strong spatial patterns of distribution across habitats were detected and explained by a complex combination of habitat features. Signal/noise ratio for macrofauna data of distribution was enough strong to detect changes across habitats but the sizes of sampling devices were not adequate to represent the real patterns in the nature. Meiofauna patterns of distribution were driven by the type of substrate (unconsolidated versus hard bottoms) which surely was in turn dependent of the hydrodynamic regime. Nematodes dominated in seagrass beds and copepods in the other three habitats. Nematode density of species and individuals and species richness were highest in unconsolidated habitats maybe due to higher physical stability, larger spatial niche and more food resource availability. Diversity variation was large and similar between pairs of habitats with the exception of the hard bottom habitat which had lower differentiation. Most of the nematodes living in hard substrates showed adaptive organismal traits to cope with hydrodynamic regime and food availability (biofilm/algal turf), namely small and stout body, teeth for epigrazing, ornamented cuticle and cephalic capsule. Physical control on nematode assemblages was evident but biotic interactions may play a more important role in seagrass beds and sand flats compared to hard substrate habitats. The species diversity of nematodes, both in terms of α- and β-diversity, was high at the scale of the whole Punta Francés coral reef.

Key words: Biological traits; Caribbean Sea; coral reefs; distribution; diversity; macrofauna; meiofauna; nematodes.

RESUMEN

Se describen los patrones de distribución de la macro- y meiofauna en un arrecife de coral (Punta Francés, Archipiélago Cubano, Mar Caribe). La densidad y la composición por taxa para la macrofauna y meiofauna y la diversidad de especies y de caracteres biológicos para nemátodos se compararon entre cuatro hábitats: pastos marinos, arenazo, coral muerto y fondo duro. Se detectaron consistentes patrones espaciales de distribución los cuales fueron explicados por una combinación compleja de características del hábitat. La relación señal/ruido en los datos dedistribución de la macrofauna fue lo suficientemente fuerte para detectar cambios entre hábitats pero el tamaño de los dispositivos demuestreo no fue adecuado para representar los patrones reales en el medio natural. Los patrones de distribución de la meiofauna fueron afectados por el tipo de sustrato (sedimento versus fondo duro) el cual a su vez seguramente depende del régimen hidrodinámico. Los nemátodos dominaron en los pastos marinos y los copépodos en los otros tres hábitats. La densidad de especies e individuos y la riqueza de especie de nemátodos fueron más altas en los hábitats sedimentarios debidos probablemente a mayor estabilidad física, mayor nicho espacial y más disponibilidad de alimento. La variación en la diversidad fue alta y similar entre pares de hábitats con la excepción de los hábitats en fondo duro que tuvieron menor diferenciación. La mayoría de los nemátodos que habitan sobre sustratos duros mostraron rasgos morfológicos que les permiten adaptarse al régimen hidrodinámico y a la disponibilidad de alimento (biofilm/algas), esto es cuerpo pequeño y robusto, dientes para raspar, cutícula ornamentada y capsula cefálica. Fue evidente un control físico sobre las comunidades de nemátodos pero las interacciones bióticas pueden jugar un papel más importante en pastos marinos y arenazos comparado a los hábitats de sustrato duro. La diversidad de especies de nemátodos, en términos de α- y β-diversidad fue alta a la escala del arrecife coralino en Punta Francés.

Palabras clave: Arrecifes de coral; distribución; diversidad; macrofauna; Mar Caribe; meiofauna; nemátodos; rasgos biológicos.

INTRODUCTION

Coral reefs are astounding tropical ecosystems with high biological productivity and species diversity. A huge body of literature about ecological patterns exists related to these ecosystems, but comparatively little research has been done on the small-sized fauna living there and very challenging research questions still to be addressed (Alongi, 1989). Ecological patterns and processes determining the spatial distribution of the benthic fauna in coral reefs are related to the physical scale where organisms occupy their niche. Therefore, small invertebrates (namely, macro- and meiofauna)

probably are ruled by very different habitat architecture and abiotic limiting factors compared with other widely studied invertebrates such as sponges, sclerectinian corals, and larger mobile fauna.

To our knowledge, quantitative studies on the ecology of small invertebrates (says < 1 mm body size) in Caribbean coral reefs are rather scarce. Macrofaunal assemblage structure shows strong spatial variability and depends of the type of habitat, wave exposure, currents within the reef system and larval recruitment (Riddle, 1988; Frouin and Hutchings, 2001). In addition to abiotic controls, feeding predation by fishes exerts significant influence on the macrofauna structure depleting their density and biomass (Alheit, 1981). The availability of epilithic algae and the presence of territorial fishes (pomacentrids) can also exert influence on the small invertebrates living in dead coral and rocks in the coral reef (Klumpp *et al.*, 1988). Macrofauna biomass is also related to abiotic controls in the reef by salinity, granulometry and particulate organic matter in sediments (Nacorda and Yap, 1996).

Reef hydrodynamic affects considerably the sediment granulometry, and both conditions/factors are key ecological drivers of the abundance and diversity of meiofauna (Gamenick and Giere, 1994; Netto *et al.*, 1999a; 1999b; Giere, 2009; Semprucci *et al.*, 2011). These drivers are mediated by the suspension of organisms, the availability to fill interstitial niches and the regulation of vertical gradients of sulfur and oxygen in sediments (Guzmán *et al.*, 1987; Ansari and Parulekar, 1994; Semprucci *et al.*, 2010). Nematodes, as main contributors to meiofauna abundance, are affected by similar ecological drivers. Most of the nematodes from coral reefs are characterized by ornamented cuticle or annulated bodies with somatic setae (Tietjen, 1991; de Jesús-Navarrete, 2007). From a taxonomic point of view they belong to the order Chromadorida being the most common families Desmodoridae, Chromadoridae and Xyalidae (Tietjen, 1991; Boucher, 1997; Raes *et al.*, 2007). Deposit feeding nematodes are dominant in the lagoon and other less physically stressed habitats (Alongi, 1986; Boucher, 1997), although in strongly stressed reefs the predator/omnivore forms can dominate in the less disturbed zones (*i.e.* lagoon and reef pools) (Netto *et al.*, 1999b). Biotic interactions affecting the nematode fauna have been mainly explored related to the predation by larger animals such as shrimps (Alongi 1986) and fishes (St. John *et al.*, 1989). However, the benthic primary production and the ectosymbiotic association with bacteria can also regulate the nematofauna (Ott *et al.*, 1991;Boucher, 1997). Unconsolidated sediments have received most of the attention in macro- and meiofaunal studies in coral reef ecosystems. Hard substrates within the reef with non-coral surface is compose majorly by algal turf which provides shelter and food resources for meiofauna (Logan *et al.*, 2008). Epigrowth feeding nematodes tend to be more abundant in these hard substrates probably due to dominance of microflora and bacteria (Gobin, 2007). The coral degradation zone defines a region in the reef lagoon where dead coral is progressively degraded to smaller pieces (Raes *et al.,* 2007). Coral fragment habitat, located within coral degradation zone, contributes considerably to the biodiversity of meiofaunal species in coral reefs (De Troch *et al.*, 2008; Gheerardyn *et al.*, 2008) and it has been relatively few studied. In these habitats, hydrodynamic regime, the substrate area and the microbial and algal cover drive the nematode structure and their trophic composition (Raes *et al.*, 2007; De Troch *et al.*, 2008).

Relatively few studies about small invertebrate assemblages in coral reefs of Cuban Archipelago have been done (*e.g.* López-Cánovas and Lalana-Rueda, 2001). Spatial patterns of meiofauna distribution in coral reef ecosystems have been described to regional scale, with higher density in reef flats maybe caused by paucity of fishes and macrofauna (Armenteros *et al.*, 2009). The importance of microhabitat (*i.e.* cm- scale) compared to "classical" habitats within the reef (*e.g.* spur and groove, sand flat, patch reef) as explanatory factor for distribution of meiofauna has been stressed by Armenteros *et al.* (2009).

In the current research we tested the hypothesis that the type of habitat is a main driver of the ecological structure of meio- and macrofauna in coral reefs; therefore we predict consistent patterns of variation in the number of taxa/species, abundance, diversity and multivariate composition of assemblages across the four habitats defined *a priori* (seagrass bed, sand flat, dead coral and hard bottom). In order to test the previous hypothesis we propose as objective of this research to compare the ecological structure of macrofauna, meiofauna and free-living nematodes among the four habitats in the coral reef of Punta Francés.

MATERIAL AND METHODS

Study site and sampling

The studied coral reef was located in front of Punta Francés Beach (21°36´N, 83°03´W), Isla de La Juventud, SW region of the Cuban Archipelago and samples were taken on June 2009. The reef ecosystem is relatively far from human settlements therefore pollution and intensive fisheries are negligible disturbances, however paucity of large fishes occurs due to historical artisanal fisheries. The coral reef has the general geomorphology of

other bank reefs in the region, *i.e.* lagoon, back, crest, and front. The measured oceanographic variables were typical of coastal coral reef ecosystems in wet season and they ranged: depth: 1.5 – 2.5 m, dissolved oxygen: 6 – 7 mg/L, salinity: 35 – 36 ppt, and temperature: 28°C. The very clear waters suggested an intense hydrodynamic regime and oligotrophic conditions.

We defined four habitats in the reef according to the minute size of the benthic animals we studied (*i.e.* millimeters) (Figure 1):

(1) Seagrass bed: It is included in the reef lagoon. Soft bottom constituted mainly by fine sand and mud, most of the area was covered by the magnoliophyta *Thalassia testudinum*; and a layer of vegetal debris and macroalgae was present on the bottom. The percentage of carbon in sediment was relatively high 5.7% ± 0.3% (loss by ignition 550°C, *N*= 4);

(2) Sand flat: It is included in the reef lagoon. A strip of carbonate bare sand located between the seagrass bed and the reef crest. There was visual evidence of high exposition to hydrodynamic regime due to the ripples in the sand and scarce accumulation of debris on the bottom. The percentage of carbon in sediment was relatively high 5.2% ± 0.2% (loss by ignition 550°C, *N* = 4);

(3) Dead coral: It is located in the back reef. Areas of coral degradation, just behind of the reef crest. Habitat was characterized by mounds /piles of 1 – 5 cm size fragments of dead coral with growing of macroalgae and crusting organisms on them; and

(4) Hard bottom: It is located in the back reef. Rocky pavement covered by turf macroalgae, just behind of the reef crest.

Replicate samples (*N*= 4) were taken at random by SCUBA diving at each habitat. The very different nature of the bottom did not allow using the same sampling device for all the habitats. Therefore, the final estimates of number of taxa and abundance were standardized per area unit (*i.e.* density) assuming a homogeneous distribution in order to compare the estimates between habitats. For seagrass beds and sand flat, a plastic corer (syringe with end cut-off) of 2.6 cm diameter was pushed within the sediment and a column of 10 cm height of sediment was collected. Dead coral was sampled with the aid of the plastic quadrant of 10 cm x 10 cm placed on the bottom. Coral fragments under the quadrant were carefully collected by hand for a diver and kept in a flask; the collection of the fragments was restricted to the first 4 –8 cm depth into the pile of fragments. To sample at hard bottom a plastic pipe (11 cm diameter) with side windows covered by 38 µm mesh size was placed on the bottom; material on the bottom was gently scratched by hand through the window and kept inside the pipe. Care was put to collect most of the material on the area encircled by the pipe.

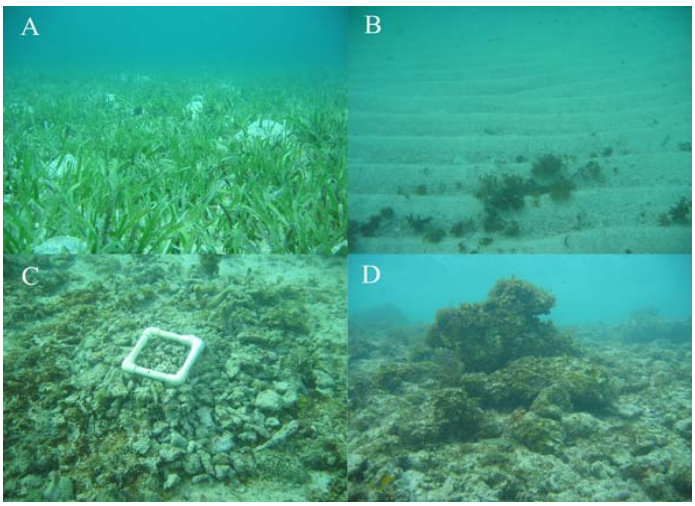

Figure 1. Photos of the four habitats in the coral reef of Punta Francés. (A) Seagrass bed, (B) Sand flat, (C) Dead coral, and (D) Hard bottom.

Sample processing and identification

Sediment from seagrass and sand habitats was mixed with filtered water, the mix gently shook and the supernatant poured onto nested mesh sieves of 500 and 45 µm; this was repeated ten times and the retained material collected. Each dead coral fragment or the whole material (in case of hard bottom) was gently rinsed with water on the nested column of sieves and the retained material was independently (500 µm for macrofauna and 45 µm for meiofauna) stored in 70 v/v ethanol for further identification and counting of animals.

Macro- and meiofauna wereidentified to main taxa (*e.g.* copepods, nematodes) and counted using a stereomicroscope at 56x magnification. Nematodes were pick-up from the samples, fixed in a solution of ethanol – glycerol and permanently mounted on glass slides. For the analysis of nematode assemblages we combined nematodes from macro- and meiofaunal fractions from a same replicate. Nematodes were identified to species using pictorial keys (Platt and Warwick, 1983; 1988; Warwick *et al.*, 1998) and the generic online database NeMys (Deprez *et al.*, 2007).

Each nematode species was classified into a trophic group according to the structure of buccal cavity (Wieser, 1953) in: selective deposit feeder (1A), non-selective deposit feeder (1B), epigrowth feeder (2A), and predator or omnivore (2B). The percentage abundance per trophic group was calculated for each sample. The individual biomass of each nematode was calculated after the modified Andrassy´s formulae proposed in dos Santos *et al.* 2008):

$B=\left(\frac{LW^2}{1700000}\right)*\rho$. Where B is wet biomass (µg), L is body length (µm) without filiform portion of the tail, W is the maximum width (µm) avoiding the vulva protrusion, and ρ is the specific density of body tissue (1.13 µg/nl). The de Man´s ratio (a = body length / body width) was also calculated as a measure of the body shape of nematodes.

Data analysis

Three matrices of taxa x samples were built: Macrofauna, meiofauna and nematodes. Multivariate and univariate techniques were applied to describe differences among the four habitats based on the three assemblages by separate. For each variable, mean value ± standard deviation (SD) were presented. Differences in the density of taxa and individuals were tested by one-way analyses of variance of fixed effects, and in case of significant differences *a posteriori* SNK pairwise tests were performed. The fitness of the data to the assumptions of the parametric ANOVA (*i.e.* homogeneity of variance and normal distribution of residuals) was checked with diagnostic graphs of mean versus variance and residuals versus predicted values. The density data departed notably of the homoscedasticity and they were transformed as logarithm. The transformation improved successfully the fitness of the data to the assumptions, therefore ANOVAs were made on transformed density and the means and SD were back-transformed to the original scale. The unstandardized effect size of the ANOVA factor (*i.e.* habitat) was calculated using the formulae in Nakagawa and Cuthill (2007). Pairwise comparisons of effect sizes were few informative in the context of this study, therefore we calculated the average effect size for each variable, *i.e.* the average of the six pairwise effect sizes among the four habitats (habitat 1 vs. habitat 2, habitat 1 vs. habitat 3, habitat 3 vs. habitat 4) and evaluate the absolute magnitude of these effects.

Cumulative curves of nematode species richness were computed using the program EstimateS 8.2.0 (Colwell, 2006).The four replicates were pooled for each habitat and Mau-Tau function was used for the estimation of the species richness. Curves were built based on 50 permutations without replacement. Data of abundance were used for the computation of curves thus species richness can be compared for a selected value of abundance (says 200 nematodes) but abundance cannot be directly compared among habitats due to the differences in the sampled area (*i.e.* different sampling devices used).

We used the term "variation" for the non-directional change among habitats in the β-diversity (Anderson *et al.*, 2011) but it is equivalent to the term turnover diversity proposed by Gray (2000). The Sorensen index of dissimilarity was calculated between pairs of samples belonging to different habitats. We chose the Sorensen index because it is based on presence/absence data and not on row abundance which is not directly comparable in our study. The values of dissimilarity were pairwise averaged (*e.g.* seagrass bed vs. sand flat, seagrass bed vs. hard bottom, dead coral vs. hard bottom). Computations were done in the EstimateS software (Colwell, 2006).

Analyses of similarity (ANOSIM; Clarke and Warwick, 2001) were performed on each dissimilarity matrix looking for differences between habitats based on the multivariate structure of the assemblages using 999 permutations in each test. To visualize the similarity pattern of each type of assemblage an ordination by non metric multidimensional scaling was made based on the Bray-Curtis dissimilarity matrix.

RESULTS

Macrofauna

The macrofauna density of taxa ranged from 2 to 10 taxa/100 cm^2, with a mean value (± SD) over all samples of 5 ± 3 taxa/100 cm^2. The density of taxa changed significantly among habitats (ANOVA, $F_{3, 12} = 9$, p= 0.002), although the average effect size of the habitat was rather weak (1.5 taxa/100 cm^2). The highest taxa density was in dead coral habitat (9 ± 1 taxa/100 cm^2) and the lowest in the other three habitats (4 ± 2 taxa/100 cm^2) (Figure 2A).

The taxonomic composition of macrofauna assemblages included 13 main taxa, and changes among habitats in the taxonomic composition and density were also evident (Figure 2B). The density of macrofauna individuals changed significantly among habitats (ANOVA, $F_{3, 12}$= 8.5, p= 0.003) although variability was large and the average effect size of the habitat was strong (205 individuals/100 cm^2). Significant differences could only be detected between the lowest density in hard bottom (11 ± 6 individuals/100 cm^2) and the other habitats (160 ± 222 individuals/100 cm^2) (Figure 2B).

The multivariate structure of macrofauna assemblages was significantly different among habitats (ANOSIM, R= 0.59, p< 0.001). The ordination by nmMDS suggests that assemblages living in seagrass beds and sand flats had a different assemblage composition than those living on hard substrate, *i.e.* dead coral and hard bottom (Figure 3A).

Meiofauna

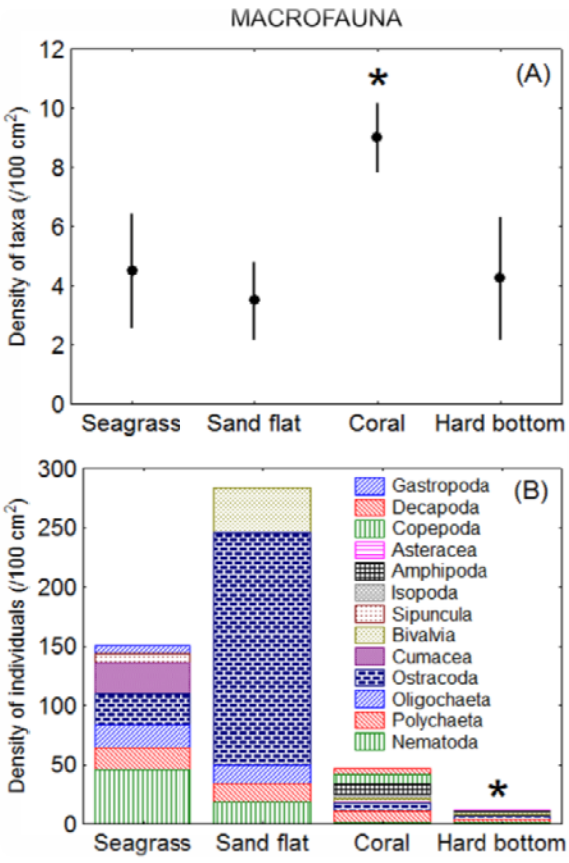

Figure 2. Macrofauna assemblage structure. (A) Mean and standard deviation of density of taxa, (B) Mean stacked density of individuals and taxonomic composition. * indicates significant differences after SNK test.

The meiofauna density of taxa ranged from 5 to 12 taxa/10 cm², with a mean value over all samples of 8 ± 2 taxa/10 cm². The density of taxa changed significantly among habitats (ANOVA, $F_{3, 12} = 36$, $p < 0.001$), but the average effect size of the habitat was rather weak (3 taxa/10 cm²). The highest density of taxa was in dead coral habitat (12 ± 1 taxa/10 cm²), followed by hard bottom (8 ± 1 taxa/10 cm²), and the lowest was in the sand flat (6 ± 1 taxa/10 cm²) (Figure 4A).

The taxonomic composition of meiofauna assemblages was constituted by 15 main taxa and changed notably among the habitats (Figure 4B). The relative abundance of nematodes was higher in seagrass beds compared to the other three habitats where copepods had higher relative abundance. The density of meiofauna individuals (transformed as logarithm) changed significantly among habitats (ANOVA, $F_{3, 12} = 32$, $p < 0.001$), and the average effect size was strong (194 individuals/10 cm²). The meiofauna living on soft bottoms (*i.e.* seagrass bed and sand flat) had significantly higher density (222 ± 95 individuals/10 cm²) than meiofauna living on hard substrates (50 ± 9 individuals/10 cm²).

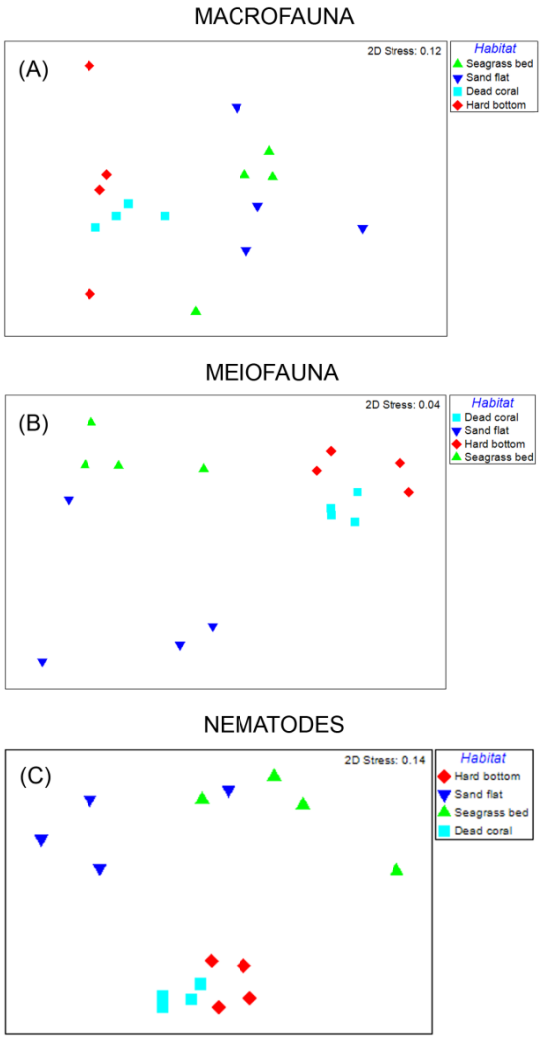

Figure 3. Ordination by nmMDS of samples from four habitats of Punta Francés reef based on the multivariate assemblage structure of (A) macrofauna, (B) meiofauna, and (C) nematodes.

The multivariate structure of meiofauna assemblage was significantly different among habitats (ANOSIM, $R = 0.78$, $p < 0.01$). The ordination of samples suggested a clustering of samples by type of substrate, with samples from hard bottom and dead coral having a higher similarity in the assemblage structure. Samples belonging to soft bottoms showed a higher dispersion in the plot suggesting a notable variability in the assemblage structure (Figure 3B).

Nematodes

The nematode density of species ranged from 9 to 37 species/10 cm²; the mean value over all samples was 26 ± 9 species/10 cm² without differences among habitats (ANOVA, $F_{3, 12} = 3$, $p = 0.07$) (Figure 5A).

The nematode density of individuals ranged from 11 to 178 individuals/10 cm², with a mean value over

all samples of 58 ± 58 individuals/10 cm^2. There were significant differences in density of individuals (transformed as logarithm) among habitats (ANOVA, $F_{3, 12}$= 9, p= 0.001) with a strong average effect size of the habitat (114 individuals/10 cm^2). The highest value was in the unconsolidated bottoms (seagrass bed and sand flat) with 98 ± 61 individuals/10 cm^2 and the lowest in the hard substrates (dead coral and hard bottom) with 19 ± 5 individuals/10 cm^2 (Figure 5B).

The cumulative curves of species richness based on individuals suggested marked differences in the inventory diversity (α-diversity) among habitats (Figure 5C).The best estimates of observed species richness for the habitats (*i.e.* the four replicates combined) were 78 species in seagrass beds, 48 species in sand flats, 43 species in dead coral and 63 species in hard bottoms. For an abundance value of 200 individuals, the species richness per habitat could be ordered (from lowest to highest): dead coral, hard bottom, sand flat, and seagrass bed. The abundance per se could not be compared among habitats due to the curves were based on number of individuals collected with different devices; *i.e.* the number of nematodes recorded per habitat was very different due to the different area sampled.

The diversity variation (or β-diversity) between pairs of habitats was in whole high (75% ± 14%) indicating clear heterogeneity in the species identity. There were significant differences in diversity variation (ANOVA, $F_{5, 90}$= 18, p< 0.001) but only the pair dead coral - hard bottom had a significant lower va-

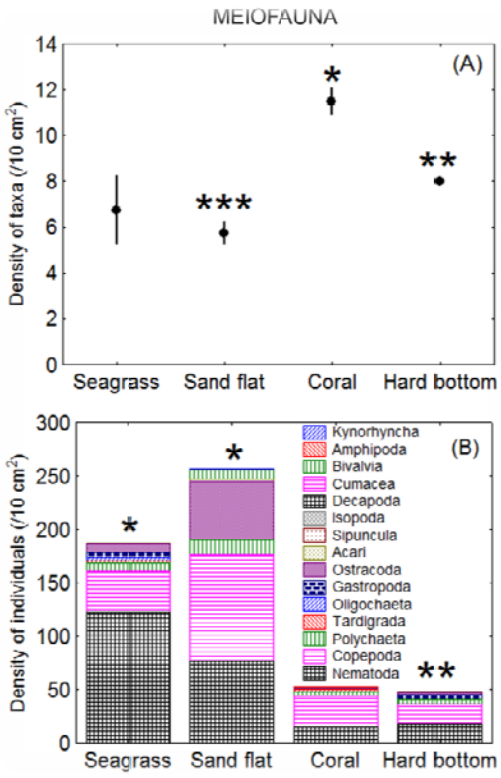

Figure 4. Meiofauna assemblage structure. (A) Mean and standard deviation of density of taxa, (B) Mean stacked density of individuals and taxonomic composition. * indicates significant differences after SNK test.

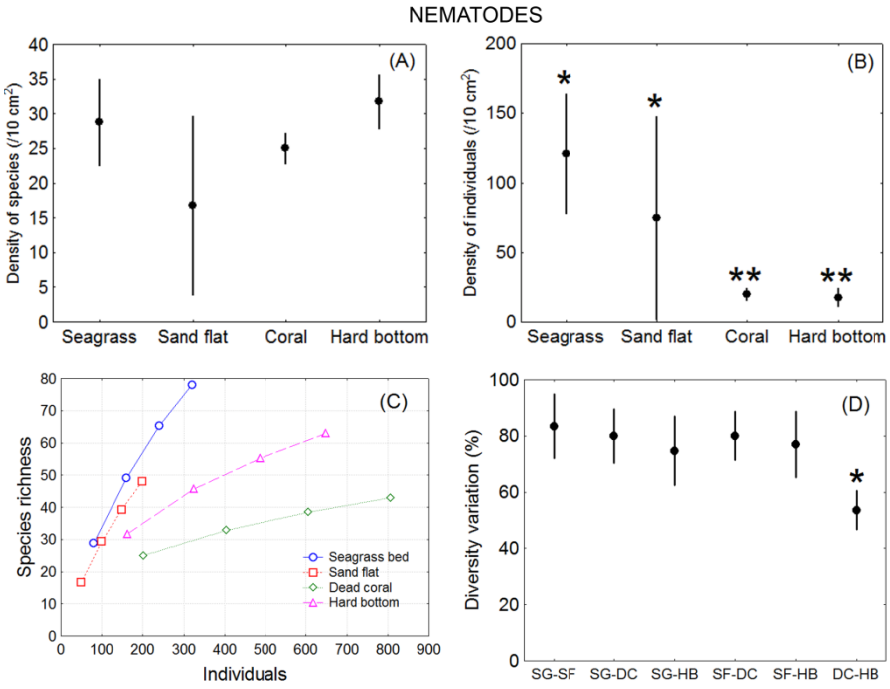

Figure 5. Nematode assemblage structure and diversity. Mean and standard deviation are shown. (A) Species richness, (B) Density, (C) Cumulative curves of species richness (Mau-Tau function), notice that abundance is not strictly comparable among habitats due to the differences in the sampled area (*i.e.* different sampling devices), (D) Diversity variation (β-diversity) measured as Sorensen dissimilarity index. Labels of habitats: SG = Seagrass bed, SF = Sand flat, DC = Dead coral, HB = hard bottom. * indicates significant differences after SNK test.

riation (53% ± 7%) compared with the other five pairs (average: 79% ± 11%). This suggests that hard substrate habitats are more homogeneous each other in species composition than soft bottoms (Figure 5D).

The trophic composition suggests changes related to the type of substrate, with higher relative contribution of epigrowth feeders (group 2A) in hard bottom and dead coral compared to the other habitats. Conversely, a relative higher contribution of deposit feeding nematodes (selective and non selective, groups 1A and 1B) occurred in the unconsolidated sediments compared to hard substrate habitats (Figure 6A).

The wet biomass per nematode ranged from 0.068 to 104.73 µg, with a mean value over all samples of 2.65 ± 4.75 µg. The biomass per nematode was significantly different among habitats (ANOVA, F3, 1880= 25, p< 0.001, data transformed as logarithm) with a strong average effect size of the habitat (2.6 µg). The biomass was highest in sand flat and seagrass bed (4.30 ± 8.16 µg), in second place dead coral habitat (2.16 ± 1.96 µg) and the lowest biomass was in hard bottom (2.02 ± 3.00 µg) (Figure 6B).

The de Man´s ratio *a* (length/width), as a measure of body shape, ranged from 6.8 to 203.6 with a mean value over all samples of 30.0 ± 16.0. There were significant differences among habitats in the ratio *a* (ANOVA, $F_{3, 1880}$= 148, p< 0.001) with a strong average effect size of the habitat (21.3). Nematodes in the seagrass beds and sand flats had the highest length/width ratio (42.3 ± 23.8), *i.e.* slender body, compared with those in dead coral and hard bottom (26.0 ± 9.6) (Figure 6C).

The multivariate structure of nematode assemblages changed significantly among habitats (ANOSIM, R= 0.74, p< 0.001). The assemblages living in the seagrass beds and sand flats had a large variability in the species composition and abundance, while nematodes living on hard substrates (dead coral and hard bottom) had a quite homogeneous assemblage structure (Figure 3C). The SIMPER procedure highlighted the species more contribute to the similarity among replicates within a group, *i.e.* those nematode species characteristic of a particular habitat. The results suggest that each habitat had a different set of species, although there were also widespread species in the reef (Table 1)

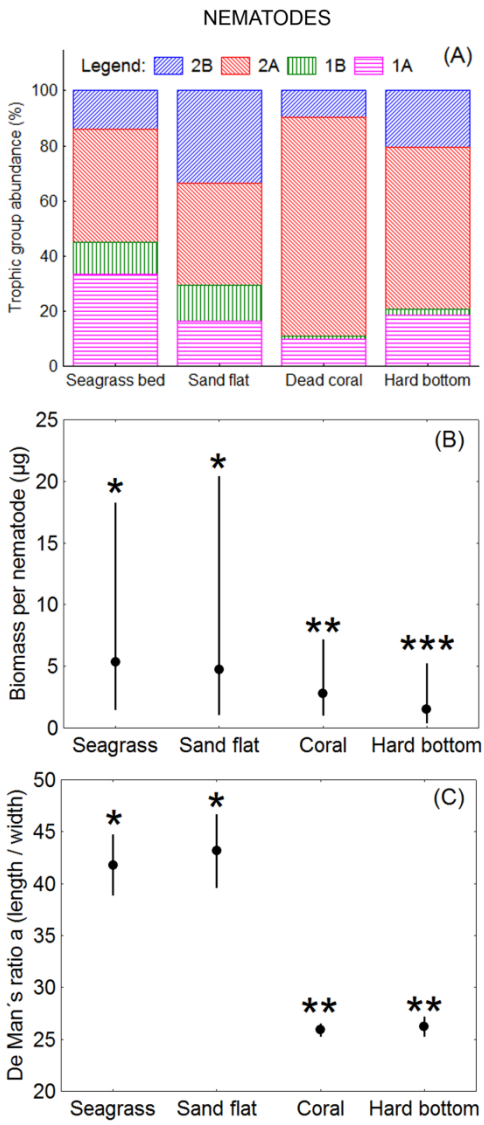

Figure 6. Nematode morphological and functional traits. Mean and standard deviation are shown. (A) Trophic composition, (B) Wet biomass, (C) De Man ratio a (length/width). 1A: selective deposit feeders, 1B: non selective deposit feeders, 2A: epigrowth feeders, 2B: predators/omnivores. * indicates significant differences after SNK test.

DISCUSSION

The integration of the results indicates that the ecological structure of small-sized animal assemblages is strongly affected by the type of habitat in Punta Francés coral reef. The evidence supports our *a priori* hypothesis about the important effects of the habitat architecture on macro- and meiofauna assemblages. However, the spatial distribution and influence of the habitat could not be estimated with the same accuracy for macro- and meiofauna.

The differences among the four habitats within the reef can be outlined on basis of empiric information (Table 2).Seagrass beds offer three types of spatial niches: (i) interstitial within the sediment, (ii) epibenthic for organisms living in the interface and (iii) epiphytic for those living on the blades. The hard substrates have a more restricted three dimensional niche with organisms living mostly on the surface of algal turf or rock. The hydrodynamic regime in the coral reefs is strong compared to other ecosystems; however the irrigation of the benthic space in very variable within the reef and dependent of the habitat architecture and the exposition to the

Table 1. Nematode species with highest contribution to the similarity among replicates within the habitat (*i.e.* characteristic species of that habitat). Only those species which contribute up to the 60 % of the cumulative similarity are shown.

Nematode species	Seagrass bed	Sand flat	Dead coral	Hard bottom
Zalonema ditlevseni	X			X
Eubostrichus parasitiferus	X			
Marilynnia eratos	X			
Dorylaimopsis punctata	X			
Chromaspirina inaurita	X			
Laxus sp.	X			
Spilophorella candida	X			
Enoploides longispiculosus		X		
Viscosia abyssorum		X		
Odontophora sp.		X		
Leptonemella sp.		X		
Euchromadora vulgaris			X	X
Euchromadora atypica			X	
Acanthopharynx denticulatus				X
Desmodora pontica				X
Epsilonema sp.				X

water currents (Gray and Elliot, 2009). Seagrass shoots and blades decrease the speed of currents within the canopy and then reduce the irrigation of sediments beneath. In contrast the flat habitats (sand and hard bottom) suffer a direct influence of the waving and currents causing the suspension of small resident fauna (De Troch *et al.*, 2001). Pieces of dead coral often are clustered in valleys over the reef and they should represent sheltered spaces for small fauna living within the interstices.

Three different primary producers are contributing to the production of organic matter in the studied habitats: seagrasses (*Thalassia testudinum*), macroalgae turf and microphytobenthos (Moriarty *et al.*, 1985; Alongi, 1989). All of these producers have remarkable rates of primary production but we were not able to quantify the differences among them neither among habitats. Deposition and burial of the vegetal debris strongly depends of the hydrodynamic regime thus seagrass beds and in lesser extension sand flats should have the higher content of particulate organic matter compared to more exposed habitats. The organic content is closely linked to the vertical gradients of oxygen and hydrogen sulfide in benthic habitats (Johnstone *et al.*, 1990); it can explain the existence of a deeper redox-cline in sand flats compared to seagrass beds.

The signal/noise ratio in the distribution data related to the effect of habitat was strong enough to show different macrofaunal assemblages living in each type of substrate (*i.e.* hard vs. unconsolidated). The recorded taxa included most of the main taxa included in the macrofauna (Riddle, 1988; Frouin and Hutchings, 2001), but the small sizes of the used sampling units were not adequate to represent accurately the spatial patterns of distribution of macrofauna. Although sampling devices to sample macrofauna can be suitable to sample meiofauna (Somerfield *et al.*, 2005), the converse is not true and we encourage the use of different devices to sample each type of assemblages in coral reefs.

The assemblage structure for meiofauna and nematodes showed a sharp difference between unconsolidated and hard substrates. Our findings reinforce the very fundamental effect of the type of habitat on the assemblage structure of coral reef meiofauna (Netto *et al.*, 1999b; Raes *et al.*, 2007). Within the unconsolidated habitats (*i.e.* seagrass bed and sand flat) there were also large differences in the meiofauna assemblage structure probably due to differences in the milieu such as productivity, macrophyte biomass and granulometric composition (Table 2) (Boucher, 1997). Meiofauna living in hard bottom (*i.e.* algal turf) showed larger variability in the assemblage structure than those living in dead coral maybe suggesting a higher disturbance by both the reef grazers and the hydrodynamic forces (Logan *et al.*, 2008).

The taxonomic resolution used for meiofauna analysis (*i.e.* main taxa) hampers the interpretation of the spatial patterns across habitats. Nevertheless, the higher taxonomic resolution used for nematodes (*i.e.* species) and the high diversity of this group offered a robust tool to disentangle distribution patterns. In addition, individual-level response to the habitat could be inferred from the analysis of biomass and body shape of nematodes.

The density of nematodes, like meiofauna density,

Table 2. Summary of the abiotic and biotic milieu in the four habitats studied in Punta Francés coral reef.

Habitat	Seagrass bed	Sand flat	Dead coral	Hard bottom
Spatial niche	Interstitial + epibenthic + epiphytic	Interstitial + epibenthic	Epibenthic	Epibenthic
Influence of hydrodynamic regime and interstitial irrigation	Weakened by canopy, poor irrigation within sediment	Strong influence due to exposition, good irrigation	Dependent of coral fragment configuration, good irrigation	Strong influence due to exposition, good irrigation
Productivity and organic content accumulation	High rate of primary production (*Thalassia*) + accumulation	High/intermediate rate? (microphytobenthos) + weak accumulation	High/intermediate rate? (microphytobenthos)	High rate of primary production (turf macroalgae)
Oxygen availability	Steeper vertical gradient	Smoother vertical gradient	High	High

was higher in unconsolidated substrates probably due to larger spatial niche, less exposition to physical reworking and more resource availability (Raes *et al.*, 2007).The variance in density of species and individuals was also larger in unconsolidated habitats suggesting stronger patchiness in the distribution of nematodes as response to the environmental heterogeneity (Tietjen, 1991). Nematode species richness, as a measure of α-diversity, followed the same tendency of abundance being the most diverse habitats the sand flats and the seagrass beds. However, other meiofauna taxa can show different habitat preference, for instance after Gheerardyn *et al.* (2008) harpacticoid copepods are more diverse on coral fragments. Nematode diversity variation, as a measure of β-diversity, was in general high suggesting a high level of heterogeneity in species composition and very high species diversity in the whole coral reef with a total number of 135 species. The hard bottoms, *i.e.* dead coral and hard bottom, were more similar each other in the species composition suggesting more similar environment compared to unconsolidated habitats. These hard bottom habitats possibly are ephemeral for nematodes due to the frequent events of suspension and recruitment imposed by the hydrodynamic regime.

Seagrass beds and sand flats were dominated by large burrower nematode species with high length/width ratios suitable for cuticle exchange (*e.g. Phanoderma unica*, *Enoploides longispiculosus, Enoploides* sp. 1). Nematodes belonging to the subfamily Stilbonematinae bearing ectosymbiotic chemoautotrophic bacteria are typical from tropical coralline sediments (Ott *et al.*, 1991; Ott, 1996). They were dominant in seagrass beds and sand flats, with at least five sympatric species: *Catanema porosum, Eubostrichus parasitiferus, Laxus sp, Leptonemella granulosa and Leptonemella* sp. 1. Despite of these morphological and taxonomic similarities of nematodes living in the unconsolidated habitats the quantitative assemblage structure was quite different and variable between seagrass beds and sand flats (Raes *et al.*, 2007).

The organismal traits of nematodes living in dead coral and hard bottom constituted adaptations to these environments where hydrodynamic regime is intense and most of food is as biofilm or macroalgae turf (Gobin, 2007; Raes *et al.*, 2007). Dominant species were “hard-body” nematodes able to withstand physical stress thanks to morphological adaptations such as stouter body shape, ornamented cuticle, cephalic capsule, somatic setae and developed spinneret + caudal glands (*e.g. Desmodora pontica*, *Euchromadora atypica, Euchromadora vulgaris* and *Acanthopharynx denticulatus*) (Jesús-Navarrete, 2007). Epigrowth feeding nematodes (group 2A) had a higher contribution to the trophic composition possibly because they have advantages over deposit feeders (groups 1A and 1B) in these hard bottom habitats where most of food resources occurred as biofilm (Tietjen, 1991; Raes *et al.*, 2007).

Biotic interactions are hard to envisage in these

assemblages compose by minute animals and experimental approaches have to be applied to disentangle them (*e.g.* Postma-Blaauw *et al.*, 2005; Read *et al.*, 2006). For instance, the percentage of predator/omnivore nematodes did not show a clear tendency across habitats but the Wieser´s classification we used could be a poor predictor of the real trophic relationships among species (Moens and Vincx, 1997; Moens *et al.*, 2004). We suggest that the predation by macrofauna and fishes and the competition should be more important ecological drivers in the physically more stable unconsolidated habitats than in hard substrate habitats (Alongi, 1986; Tietjen, 1991).

In summary, the spatial patterns of distribution of macrofauna, meiofauna and nematodes were strongly influenced by the habitat heterogeneity in the coral reef of Punta Francés. Signal/noise ratio in the distribution data of macrofauna was enough strong to detect changes across habitats but the sampled area was not adequate to represent accurately the distribution patterns. Meiofauna showed distinctive patterns of distribution drove by the type of substrate (unconsolidated versus hard bottoms) and probably this was related to the hydrodynamic regime. Free-living nematodes showed clear-cut spatial patterns of density, diversity and organismal traits with evidence of adaptative strategies to the coral reef environment. The species diversity of nematodes was high at the scale of the whole coral reef both in terms of α- and β-diversity.

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Recibido: 05/03/2012
Aceptado: 09/05/2012