

ARTICULO ORIGINAL

DIVERSITY AND DISTRIBUTION OF THE LARGE-SIZE FRACTION OF MESOZOOPLANKTON ACROSS COASTAL HABITATS IN THREE GULFS OF CUBAN ARCHIPELAGO (CARIBBEAN SEA)

Diversidad y distribución de la fracción de gran tamaño del mesozooplankton en hábitats costeros de tres golfos del Archipiélago cubano (Mar Caribe)

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ABSTRACT

Cuban archipelago harbors a large fraction of regional diversity but lacks recent studies about diversity and distribution of mesozooplankton. We aimed to characterize the large-size fraction (> 500 µm) of the mesozooplankton across four coastal habitats (mangrove, seagrass bed, unvegetated bottom, and coral reef) in three basins (or gulfs: Ana María, Batabanó, and Guanahacabibes). Furthermore, we tested the hypothesis that gulf and habitat type have a significant effect on mesozooplankton structure in relation with dispersal and selection respectively. The sampling included 71 plankton tows in 28 sites with a conical net of 500 µm mesh size. In total, 41049 organisms of 30 major taxonomic groups were identified; while 3551 chaetognaths belonging to eight species were reported. The mesozooplankton community structure was typical of tropical regions with large diversity, low abundance and dominance of Copepoda and Chaetognatha. Larvae and eggs accounted for a large proportion of total abundance suggesting the importance of coastal mesozooplankton for life cycles of many species and supporting the role of coral reefs as spawning areas. Most of the mesozooplankton taxa had broad distribution across gulfs and habitats likely associated with a complex oceanographic regime. The factor gulf had significant effects on mesozooplankton structure compared to the habitat type, highlighting the influential role of barriers to dispersal among basins and a weak selection by the coastal habitat type. Eight chaetognath species were recorded with *Parasagitta megalophthalma* and *Sagitta helenae* being new records for Cuban archipelago. The weak relationship between chaetognaths and habitat type likely reflected the broad ecological tolerance of coastal species.

KEY WORDS: mesozooplankton, Chaetognatha, coastal habitat, diversity, distribution, tropical.

RESUMEN

El Archipiélago Cubano contiene una gran fracción de la diversidad regional pero no existen estudios recientes sobre el mesozooplankton. Nuestro objetivo fue caracterizar la fracción de tamaño grande ($> 500 \mu\text{m}$) del mesozooplankton a través de cuatro hábitats costeros (manglar, pasto marino, fondo sin vegetación y arrecife de coral) en tres cuencas (o golfos: Ana María, Batabanó y Guanahacabibes). Además, probar la hipótesis de que el golfo y el tipo de hábitat tienen un efecto significativo sobre la estructura del mesozooplankton en relación con la dispersión y la selección respectivamente. El muestreo incluyó 71 arrastres de plancton en 28 sitios con una red cónica de $500 \mu\text{m}$ de apertura de malla. En total, se identificaron 41049 organismos de 30 grupos taxonómicos y 3551 quetognatos de ocho especies. La estructura de la comunidad del mesozooplankton fue típica de regiones tropicales con diversidad alta, abundancia baja y dominancia de Copepoda y Chaetognatha. Larvas y huevos contribuyeron en gran proporción a la abundancia sugiriendo la importancia del mesozooplankton costero para los ciclos de vida de muchas especies y reafirmando la función de los arrecifes de coral como áreas de desove. La mayoría de los taxa del mesozooplankton tuvieron amplia distribución a través de los golfos y los hábitats probablemente asociado a un régimen oceanográfico complejo. El factor golfo tuvo efectos significativos sobre la estructura del mesozooplankton comparado con el tipo de hábitat, indicando la importante función de las barreras a la dispersión entre golfos y una selección débil por parte del tipo de hábitat costero. Se registraron ocho especies de quetognatos, con Parasagitta megalophthalma y Sagitta helenae siendo nuevos registros para el Archipiélago cubano. La relación débil entre los quetognatos y el tipo de hábitat probablemente reflejó la tolerancia ecológica amplia de las especies costeras.

PALABRAS CLAVE: mesozooplankton, Chaetognatha, hábitat costero, diversidad, distribución, tropical.

INTRODUCTION

The zooplankton constitute a diverse and functionally important component of coastal marine ecosystems; but, still exists gaps in the knowledge of their community structure (Batchelder *et al.*, 2013; Nakajima *et al.*, 2017). Four processes determine the diversity and abundance of biological communities (Vellend, 2010): dispersal, selection, drift, and speciation. Within this conceptual framework, dispersal and selection play fundamental roles in determining the community structure of plankton at ecological scales. Circulation-driven dispersal of eggs, larvae and adults has been widely recognized as a critical process affecting the zooplankton distribution and abundance (Palumbi & Pinsky, 2014). Habitat selection as applied to plankton, which drift with the currents, is not straightforward to test and have been poorly explored in the literature. However, habitat selection may play an important role on zooplankton in coastal environments because the physical structure given by foundation species (e.g. stony corals, mangrove's roots) and the strong environmental gradients at local scales (e.g. salinity, temperature) (Robertson *et al.*, 1988; Boström *et al.*, 2010). These processes shaping the plankton communities are scale-dependent and we expect that dispersal plays a more important role at large spatial scale (*i.e.* 100s km) meanwhile habitat type affects at local scale where adjacency of habitats exists (*i.e.* 10s km). In our contribution, we addressed the effects of dispersal and habitat type using a nested design with four distinctive habitat types (mangrove, seagrass bed, unvegetated muddy bottom, and coral reef) located within three basins (hereafter "gulfs") in the north and south coasts of Cuba archipelago.

We also explored the influences of abiotic factors (e.g. salinity, temperature) on mesozooplankton community structure.

Cuban archipelago harbors an important fraction of the Caribbean marine biodiversity due to their large extension, variety of habitats, and intermediate location among Atlantic Ocean, Gulf of Mexico and Caribbean Sea (Miloslavich *et al.*, 2010). However, diversity of zooplanktonic communities in the Cuban archipelago is largely unknown with previous studies dating from more than 30 years ago (e.g. Fabré, 1976; Campos, 1981; Blanco & Alfonso, 1983; Popowski & Campos, 1987). Most of these surveys quantified the plankton to high taxonomic levels (e.g. copepods, ctenophores) and focused on local- or mid-scale distribution. Caribbean Sea is also understudied, although two studies on coastal zooplankton communities have been made using light traps (Andradi-Brown *et al.*, 2017) and tows in coral reefs (Carrillo-Baltodano and Morales-Ramírez, 2016). Gather new data about the diversity of zooplankton and its variation is critical to set an environmental baseline in the region in the face of global stressors such as contamination, habitat loss, and ocean warming (Chiba *et al.*, 2018).

Zooplankton community structure is coupled with benthic communities and affects processes of transference of nutrients and organic matter between water column and bottom (Griffiths *et al.*, 2017). Particularly in coastal ecosystems, macrobenthos may be correlated with plankton variables through complex and temporally variable links (Covazzi Harriague *et al.*, 2007). As part of a larger research program, our mesozooplankton study was also coupled with a study of macrobenthic diversity in the same sites (Armenteros *et*

al., 2018). Therefore, we explored also the potential link between macrobenthic and zooplanktonic communities from the same sites through correlative measures across the three studied gulfs.

The huge diversity of zooplankton usually conveys to the record of hundreds of species and more than 25 phyla which in turn poses a taxonomic challenge. Therefore, an operational solution is targeting a well-known taxon and describe it to species-level resolution. In our contribution, we chose to describe the structure of chaetognatha assemblages. The phylum Chaetognatha constitutes a major group of zooplankton in terms of abundance and biomass (Hernández-Flores *et al.*, 2009). Chaetognaths have been able to colonize all the marine pelagic and neritic environments but with relative low diversity (Pierrot-Bults & Nair, 1991). In Cuban waters there are only few studies about the diversity of the group: Suárez-Caabro (1955), Koliesnikov and Alfonso (1964), Campos (1981), and Fabré *et al.* (1986). Until now have been reported only nine species of Chaetognatha in Cuban waters (Suárez-Caabro, 1955): *Ferosagitta hispida* (Conant, 1895); *Flaccisagitta enflata* (Grassi, 1881); *Flaccisagitta hexaptera* (d'Orbigny, 1836); *Krohnitta pacifica* (Aida, 1897); *Krohnitta subtilis* (Grassi, 1881); *Parasagitta tenuis* (Conant, 1896); *Pterosagitta draco* (Krohn, 1853); *Sagitta bipunctata* Quoy & Gaimard, 1827; and *Serratosagitta serratodentata* (Krohn, 1853).

The aims of present contribution were: (1) characterize the abundance and composition of mesozooplankton across four coastal habitats in three gulfs of Cuban archipelago; and (2) test the hypotheses that gulf and habitat type have significant

effects, which in turn suggest the importance of the dispersal and selection respectively on (2a) mesozooplankton community structure; and (2b) Chaetognatha assemblage structure.

MATERIAL AND METHODS

STUDY SITES

The study covered 28 sites (*i.e.* stations) sampled in four field expeditions to the gulfs of Batabanó (February 2013, April 2015), Ana María (October 2013), and Guanahacabibes (June 2014) (Fig. 1 and Table 1). The gulfs constitute independent basins separate each other by mainland mass (*i.e.* Cuba Island) and oceanic waters; hereafter, the terms gulf and basin are used in an interchangeable way. The three separate basins give the basis for the analyses of potential mesozooplankton dispersal among them.

The Gulf of Ana María (GAM) is a large inner lagoon in southeastern Cuban

archipelago with an area of *ca.* 9398 km². The mean depth is around 15 m and there are large extensions of unvegetated soft bottoms where shrimp fisheries take place. The gulf is bordered with the extensive coral reef system “Jardines de la Reina” mostly included in a National Marine Park. The Gulf of Batabanó (GB) is a lagoon in southwestern Cuban archipelago with an area of *ca.* 21305 km² and mean depth of 5 m. The gulf is subjected to lobster and finfish fisheries in the central and western portions. The Gulf of Guanahacabibes is located in northwestern Cuba with an area of *ca.* 1400 km² and mean depth of 5 m (Ionin *et al.*, 1977).

The sampling sites were classified into one type of coastal habitat (mangrove, seagrass bed, muddy unvegetated bottom, and coral reef) based on the foundation species that constituted the physical matrix. Mangroves were dominated by red mangrove and the tows were made along the

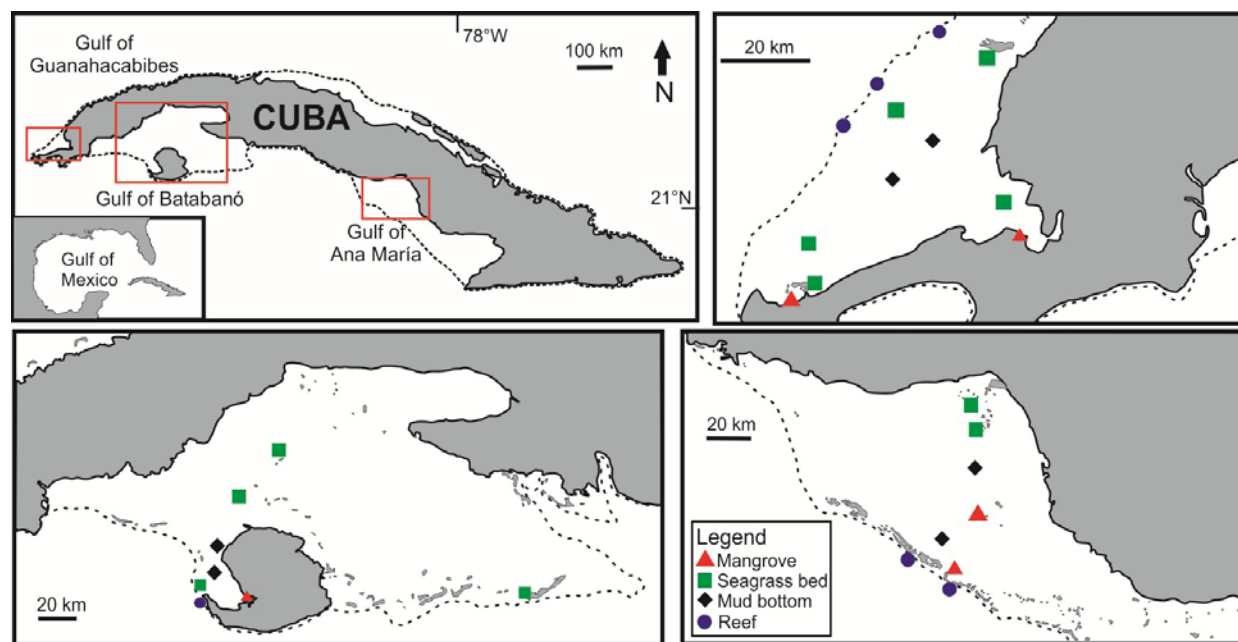


Fig. 1. Map of the three gulfs in the Cuban archipelago with the location of the sampling sites coded by habitat type.

Table 1. Sampling sites in the three gulfs with the number of replicates, sampling date, geographical location and the type of sampled habitat. GAM: Gulf of Ana María, GB: Gulf of Batabanó and GG: Gulf of Guanahacabibes. N = number of replicates.

Gulf	Site	N	Sampling date	Latitude (North)	Longitude (West)	Habitat type
Ana María	GAM1	2	11/10/2013	21°22.880	78°49.415	Seagrass bed
	GAM2	1	11/10/2013	21°28.830	78°49.970	Seagrass bed
	GAM3	2	13/10/2013	20°49.627	78°58.715	Coral reef
	GAM5	3	14/10/2013	20°46.397	78°54.930	Coral reef
	GAM6	3	14/10/2013	20°49.705	78°55.710	Mangrove
	GAM7	3	15/10/2013	20°56.513	78°55.473	Unvegetated muddy
	GAM9	2	18/10/2013	21°06.130	78°43.608	Mangrove
	GAM10	2	18/10/2013	21°14.880	78°47.142	Unvegetated muddy
Batabanó	GB2	3	11/02/2013	22°03.499	83°02.964	Seagrass bed
	GB3	2	11/02/2013	21°51.754	83°06.343	Unvegetated muddy
	GB4	3	12/02/2013	21°40.756	83°08.036	Unvegetated muddy
	GB5	3	12/02/2013	21°38.868	83°11.580	Seagrass bed
	GB6	3	15/02/2013	21°36.183	82°57.288	Mangrove
	GB7	3	17/02/2013	21°36.183	83°10.596	Coral reef
	GB8	1	18/02/2013	22°17.604	82°48.009	Seagrass bed
	GB10	2	02/04/2015	21°36.527	81°34.959	Seagrass bed
Guanahacabibes	GG1	3	30/05/2014	22°14.397	84°43.933	Coral reef
	GG2	2	31/05/2014	22°25.818	84°32.303	Coral reef
	GG4	3	03/06/2014	22°18.404	84°40.360	Coral reef
	GG5	3	06/06/2014	21°55.556	84°48.483	Seagrass bed
	GG6	3	07/06/2014	22°22.792	84°26.019	Seagrass bed
	GG8	2	09/06/2014	22°01.297	84°21.282	Mangrove
	GG9	3	08/06/2014	22°05.030	84°24.206	Seagrass bed
	GG11	3	08/06/2014	22°12.477	84°32.737	Unvegetated muddy
	GG12	3	08/06/2014	22°16.449	84°37.488	Seagrass bed
	GG13	3	09/06/2014	22°08.178	84°37.904	Unvegetated muddy
	GG14	2	10/06/2014	22°00.582	84°48.783	Seagrass bed
	GG15	3	10/06/2014	21°53.399	84°51.397	Mangrove
Total	28	71				

red mangrove (*Rhizophora mangle* L.) fringe. Seagrass beds were extensive areas of muddy-sandy bottoms covered by the turtle grass *Thalassia testudinum* K. D. Koenig, 1805; there were some interspersed patches of other seagrasses such as *Halophila* spp. and *Halodule wrightii* Ascherson, 1868. The muddy bottoms were characterized by fine sediment without vegetation

and relatively scarce faunal structures (e.g. polychaetes mounds). The coral reefs were characterized by high substrate heterogeneity and variable cover of stony corals, sponges, and octocorals.

SAMPLING AND SAMPLE PROCESSING

The collections were made during daylight (between 9:00–16:00), with horizontal

sub-surface tows (around 1–2 m below of surface), and by 3 minutes at 1-knot speed. The tows were made with a conical plankton net of 50 cm of aperture and 500 μm of mesh size. The relatively large mesh size implied that only the large fraction ($> 500 \mu\text{m}$) of the mesozooplankton could be sampled effectively and the small fraction ($\sim 300\text{--}500 \mu\text{m}$) was missed. The volume of filtered water was measured with a mechanical flow meter General Oceanics coupled to the aperture of the net. The retained material in the net was carefully poured into 1 l jars and preserved with 70% ethanol. Each tow was considered as a replicate, and we took three replicates in most of the sites (Table 1).

The identification and quantification of all the mesozooplankton organisms was made with a stereomicroscope Olympus CSZ7 with 115x of maximum magnification. We used the identification guides by Boltovskoy (1981) and Suthers *et al.* (2009) for the identification of mesozooplankton to higher taxa (*e.g.* copepods, ctenophores). The Chaetognatha were identified to genus/species level using the literature by Suárez-Caabro (1955), Michel and Foyo (1984), and McLelland (1989). The nomenclature of the species was updated from the World Register of Marine Species (www.marinespecies.org). The abundance of mesozooplankton per replicate was calculated dividing the counted organisms by the volume of filtered water and expressed as individuals m^{-3} (Ind. m^{-3}).

The abiotic factors were measured *in situ* using an oceanographic probe YSI 83 at mid-water column level: depth, temperature, salinity, and dissolved oxygen. Benthic data from the same sites have been published in Armenteros *et al.* (2018) and were used for investigate relationships between mesozooplankton and macrobenthos.

DATA ANALYSES

Nonparametric statistical techniques were preferred due to the nature of the data. Medians and observations were showed in scatterplot graphs because the large variance, asymmetry, and relatively few observations per group. Excel spreadsheets were used for built the graphs (Weissgerber *et al.*, 2015). Statistical significance (cut-off p-value: 0.05) were tested with permutational analysis of variance (PERMANOVA) (Anderson *et al.*, 2008) in the software PRIMER 6.1.15 (Clarke & Gorley, 2006). The statistical design was a bifactorial with habitat type nested within gulf. Euclidian distance was the resemblance measure for univariate biotic variables; meanwhile Bray-Curtis (B-C) similarity index was used for multivariate data (*i.e.* community composition). For chaetognatha assemblage, B-C index based on presence-absence equaled to Sorensen index. Bivariate correlations were calculated using the Spearman rank coefficient (S_R).

RESULTS

ABIOTIC VARIABLES

Depth ranged from 0.5 to 23.4 m (median: 5.9 m, $N = 28$) across all the sites. Deepest habitats were the muddy bottoms and the coral reefs with most of the sites having depth > 12 m. Meanwhile, mangroves and seagrass beds were shallower with depth < 6 m (Fig. 2A). Temperature varied from 24 to 32 $^{\circ}\text{C}$ (median: 29 $^{\circ}\text{C}$, $N = 28$) across all the sites. Ana María had the highest temperature (median: 31 $^{\circ}\text{C}$) followed by Guanahacabibes (median: 30 $^{\circ}\text{C}$) and Batabanó (median: 26 $^{\circ}\text{C}$) (Fig. 2B). Variations of temperature were largely due to sampling in different seasons (*i.e.* Batabanó in winter, and Guanahacabibes in summer). Salinity varied from 34.7

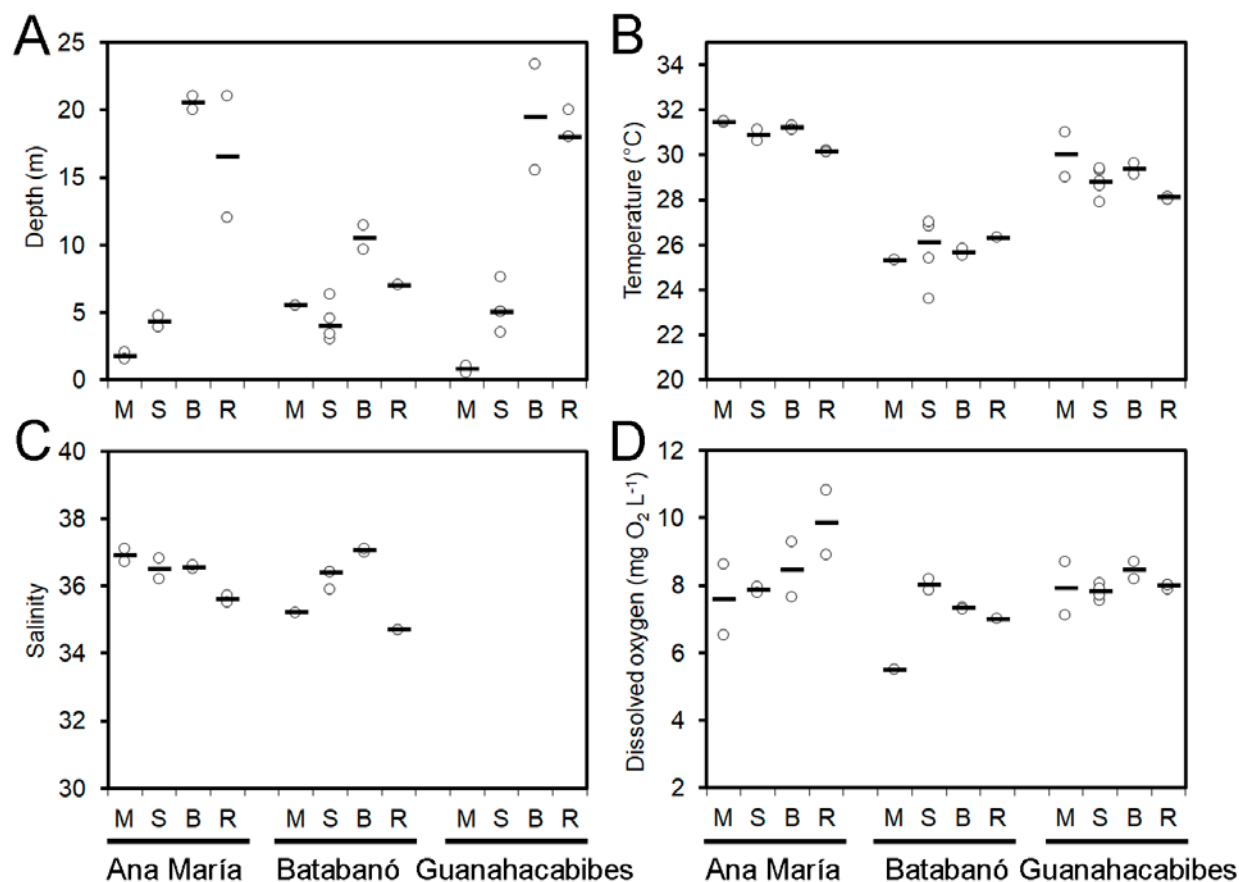


Fig. 2. Abiotic factors measured in three gulfs and four coastal habitats. (A) Depth. (B) Temperature. (C) Salinity. (D) Dissolved oxygen. Open circles indicate the observations and horizontal bars the median per gulf-habitat combination. The codes for habitats: M = mangrove, S = seagrass bed, B = muddy bottom, and R = reef. Salinity was not measured in Guanahacabibes.

to 37.1 (median: 36.4, $N = 15$). Reefs had lower salinity (median: 35.5) than other habitats (median: 36.6) although paucity of observations made weak this finding (Fig. 2C). The concentration of dissolved oxygen ranged from 5.5 to 10.8 mg L⁻¹ (median: 7.9 mg L⁻¹, $N = 26$) (Fig. 2D).

MESOZOOPLANKTON

We identified 41049 organisms belonging to 30 major taxonomic groups. Primary data were given as supporting information (Supplementary data S1). The taxon

richness per sample varied between 2 and 18 taxa (median: 9 taxa; $N = 71$). There were significant differences among gulfs but not among habitat types (Table 2). Batabanó and Guanahacabibes had the highest taxon richness (medians: 10 and 9 taxa respectively) and Ana María the lowest richness (median: 6 taxa) (Fig. 3A). The abundance per sample varied between 1 and 92 ind. m⁻³ (median: 8 ind. m⁻³; $N = 71$) and no significant differences were detected among gulfs neither habitats (Table 2; fig. 3B).

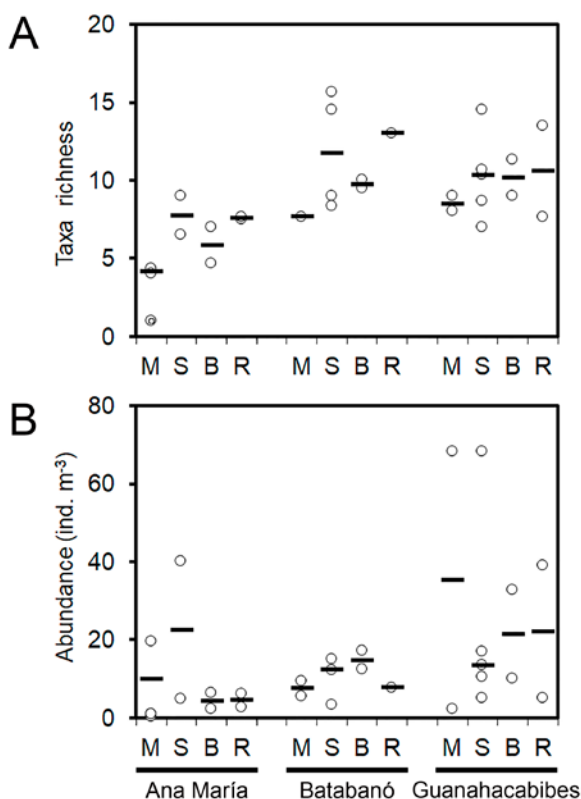


Fig. 3. Taxon richness and abundance of mesozooplankton in three gulfs and four coastal habitats. (A) Taxon richness. (B) Abundance. Open circles are the values of replicates (i.e. tows) and horizontal bars indicate the median per gulf-habitat combination. The codes for habitats: M = mangrove, S = seagrass bed, B = muddy bottom, and R = reef.

The taxon composition of mesozooplankton was (in alphabetical order): Amphipoda, Anomura, Bivalvia, Brachyura, Bryozoa, Chaetognata, Cirripedia, Copepoda, Cubozoa, Cumacea, Decapoda, Dendrobrachiata, Echinodermata, Euphausiacea, Gastropoda, Globigerínido, Hydrozoa, Isopoda, Mysidacea, Ostracoda, Pycnogonida, Actinopterygii, Polychaeta, Radiolaria, Scyphozoa, Siphonophorae, Stomatopoda, and Tunicata. We also included the category “eggs” that accounted for eggs with unknown taxonomic membership.

Table 2. Results of the PERMANOVA on the biotic (mesozooplankton and chaetognaths) variables. Fully nested design of habitat (fixed) within gulf (fixed). DF = degrees of freedom, ECV = estimated component of variation (expressed as square root).

Variable	Factor	DF	p-value	ECV*
Mesozooplankton taxon richness	Habitat (Gulf)	9	0.20	0.8
	Gulf	2	0.0004	2
	Residual	59		3
Mesozooplankton abundance	Habitat (Gulf)	9	0.71	0
	Gulf	2	0.32	2
	Residual	59		20
Mesozooplankton composition	Habitat (Gulf)	9	0.001	20
	Gulf	2	0.001	17
	Residual	59		42
Chaetognatha composition	Habitat (Gulf)	9	0.16	11
	Gulf	2	0.60	0
	Residual	48		42

* Negative ECV are expressed as zero

Only five taxa contributed to the 80% of the total abundance of mesozooplankton (in parentheses the relative contribution): Copepoda (24%), Chaetognata (19%), Dendrobrachiata (larvae) (16%), Brachyura (larvae) (15%), and Anomura (larvae) (6%). For the analyses of relative abundance per taxon, all the remaining taxa were grouped in the category “others”. The five most abundant taxa were broadly distributed across gulfs and habitats and no clear pattern of distribution emerged (Fig. 4A). Other taxa had a restricted distribution such as Scyphozoa (only in Batabanó) and Bryozoa (only in Guanahacabibes). Some taxa concentrated their abundance in one single gulf, for instance Brachyura occurred mostly in Ana María meanwhile Stomatopoda occurred fundamentally in Batabanó.

The analysis of the mesozooplankton composition by developmental stage indicated a large variability across gulfs

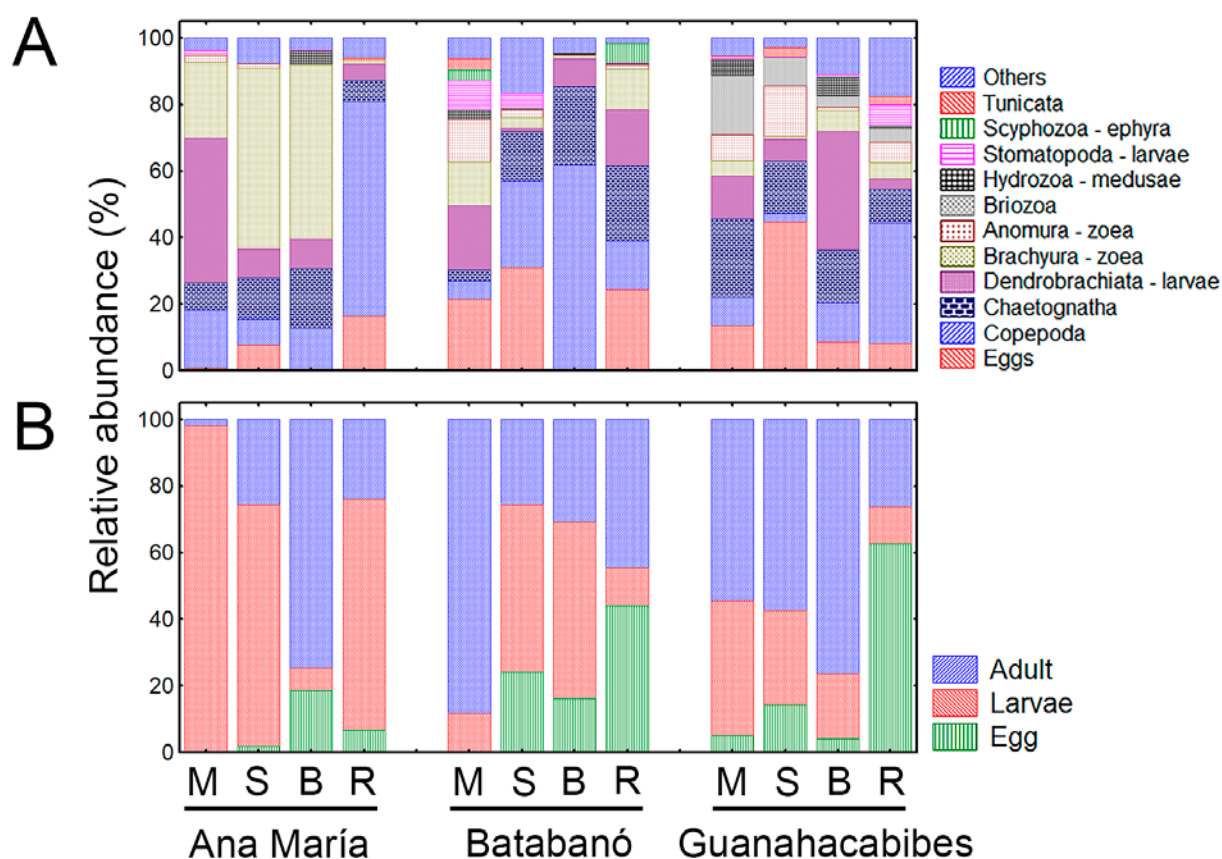


Fig. 4. Community composition based on relative abundance of mesozooplankton in three gulfs and four habitats. (A) Composition by taxon. (B) Composition by life stage. Bars are the average of replicates within each gulf-habitat combination. The codes for habitats: M = mangrove, S = seagrass bed, B = muddy bottom, and R = reef.

and habitats (Fig. 4B). In terms of relative abundance, adults (44%) slightly dominated over larvae (39%) and eggs (16%). The highest abundance of adults and eggs occurred in Guanahacabibes meanwhile the larvae were abundant in Ana María. The eggs tended to be more abundant in the reefs (except in Ana María) and did not occurred in mangroves (except in Guanahacabibes).

The taxon composition and abundance of mesozooplankton showed significant differences among habitats and among gulfs (Table 2). The pattern of similarity based on the composition was represented in a

numerical ordination by MDS without a clear pattern of clustering of the samples coded by gulf (Fig. 5A) neither habitat (Fig. 5B). Note that stress value was large suggesting a regular representation in the 2D ordination plot of the similarity patterns in the samples.

The taxon richness and abundance of mesozooplankton were significantly correlated (Table 3). However, no significant correlations were detected between mesozooplankton and abiotic variables. The correlation between temperature and abundance was an artifact because the sampling of each gulf occurred in different

Table 3. Spearman rank correlation coefficients between biotic mesozooplankton variables and abiotic and benthic variables. N = abundance, S = taxon richness, SR = species richness, Macro = macrobenthos, D = depth, T = temperature, Sal = salinity, DO = dissolved oxygen. Correlations based on 28 observations, except for salinity with 15 observations.

Variable	Mesozooplankton S	Chaetognatha N	Chaetognatha SR	D	T	Sal	DO	Macro N	Macro S
Mesozooplankton N	0.55	0.28	0.04	0.05	-0.13	-0.23	0.07	-0.11	0.02
Mesozooplankton S		0.35	0.22	0.08	-0.60	-0.29	0.09	0.23	0.33
Chaetognatha N			0.66	0.25	0.02	-0.11	-0.32	0.08	0.47
Chaetognatha SR				0.18	-0.17	-0.11	-0.26	0.01	0.49
Larvae	0.68	-0.03	-0.13	-0.09	-0.13	0.14	0.17	0.20	0.02
Eggs	0.39	0.31	0.01	0.30	-0.45	-0.14	0.03	0.09	0.29

seasons. Larvae and eggs were only significantly correlated with mesozooplankton richness.

CHAETOGNATHS

The analysis of chaetognatha assemblages allowed the identification to species level of 3551 specimens out of 6101. It meant that only the 58% of specimens were identifiable and further analysis of abundance would be biased. Therefore, we did not apply any formal statistical comparison of abundance. The analysis of species composition, based on presence/absence, did not detect significant differences among gulfs neither habitat types (Table 2). The chaetognatha assemblages were constituted by eight species. One species belonged to the family Pterosagittidae: *Pterosagitta draco*. Seven species belonged to the family Sagittidae: *Flaccisagitta enflata*; *Flaccisagitta hexaptera*; *Parasagitta megalophthalma* (Dallot & Ducret, 1969); *Parasagitta tenuis*; *Sagitta bipunctata*; *Sagitta helenae* Ritter-Záhony, 1911; and *Sagitta* sp. Two species constituted 79% of the total abundance of chaetognaths: *F. enflata* (36%) and

S. helenae (33%) and were well-represented in all the gulfs and habitats. Only the 10% of the individuals could not be identified to the species level and they were listed as *Sagitta* sp. The species *P. tenuis* and *P. draco* had intermediate abundance (9% and 8% respectively); meanwhile *F. hexaptera*, *S. bipunctata*, and *P. megalophthalma* had low abundance (3%, 1%, and 1% respectively) and occurred only in one or two gulfs (Fig. 6).

Species richness and abundance of chaetognatha were significantly correlated between them; but also both variables were correlated with macrobenthos taxon richness. No other significant correlations were detected between chaetognatha and abiotic variables (Table 3).

DISCUSSION

ABUNDANCE AND COMPOSITION OF MESOZOOPLANKTON

The mesozooplankton community was characterized by high diversity of taxa in agreement with reports from Cuban archipelago (e.g. Fabr , 1976; Blanco & Alfonso, 1983; Popowski & Campos, 1987).

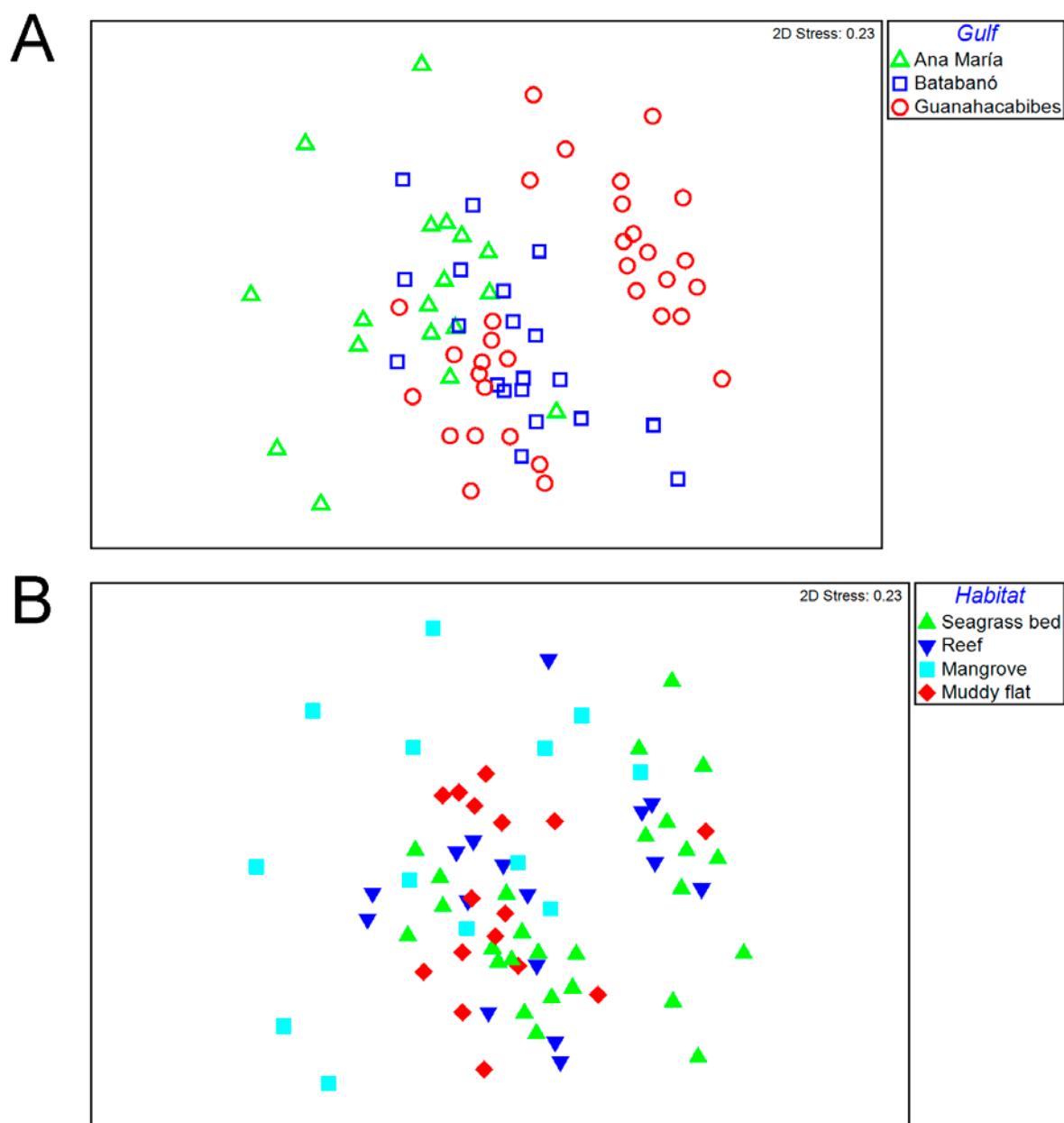


Fig. 5. Pattern of similarity among samples based on the mesozooplankton community structure. (A) Numerical ordination by MDS coded by gulf. (B) The same MDS but coded by habitats. Abundance transformed as square root and Bray-Curtis similarity index used as resemblance measure.

We reported low values of abundance that can be partially explained by the natural oligotrophic conditions of the water column in these tropical habitats. However, two biases likely caused an underestimation of mesozooplankton abundance. First,

the used mesh size (500 μm) did not catch the smaller fraction of the mesozooplankton, although the fraction of the macrozooplankton could be fairly assessed. This bias tends to be smaller in oligotrophic waters where small-sized copepods are the main

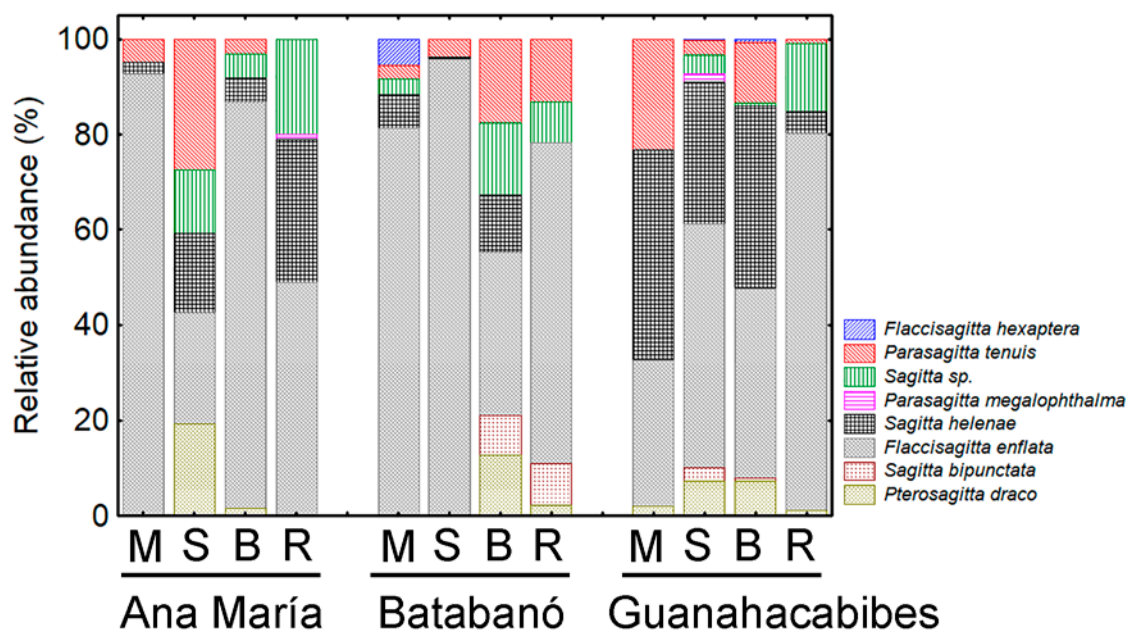


Fig. 6. Average relative abundance of chaetognath species in three gulfs and four habitats. The codes for habitats: M = mangrove, S = seagrass bed, B = muddy bottom, and R = reef.

group to be missed due to large mesh aperture (Miloslavic *et al.*, 2014). Second, tows were made only during daylight missing the component of demersal zooplankton that emerge into the water column only during the night (Melo *et al.*, 2010). However, the biases in abundance estimates due to large mesh size and diel patterns did not preclude the usefulness of our data for setting a regional baseline and for cross-habitat comparisons.

In a regional context, the mesozooplankton community structure was typical of tropical zones with large diversity, low abundance and dominance of copepods and chaetognathes. These features have been reported from sites in the Gulf of Mexico and the Caribbean Sea (*e.g.* Escamilla *et al.*, 2001; Márquez-Rojas *et al.*, 2011; Andradi-Brown *et al.*, 2017). Studies in Cuban waters have also reported similar characteristic of coastal zooplankton

(Campos, 1981; Blanco & Alfonso, 1983; Popowski & Campos, 1987).

Larvae and eggs constituted an important fraction of the mesozooplankton in Cuban waters (Reyes *et al.*, 2017) and for other regions of the Gulf of Mexico (*e.g.* Morales & Murillo, 1996). The eggs were the most important group (compared to larvae and adults) in the reefs similar to the results by Campos (1981). Our results support the role of coral reefs as spawning areas of coastal species since eggs likely were linked to demersal zooplanktonic stages in interaction with reef substrates (Lewis & Boers, 1991; Carrillo-Baltodano & Morales-Ramírez, 2016). However, no significant correlations were found between the abundance of larvae and eggs and macrobenthos suggesting a partial decoupling between larval supply and benthic settlement (Pineda *et al.*, 2010).

An additional source of uncertainty in regards to life stages, productivity, and benthic-planktonic coupling could be the seasonal fluctuations of plankton communities. Unfortunately, the relatively large spatial coverage of the study (i.e. three basins) created logistic impediments to replicate the sampling across seasons (i.e. wet and dry). Even more, the design of studies addressing temporal dynamics of zooplankton communities in tropical regions is not straightforward. For instance, extreme events such as cold fronts (in winter) and hurricanes (in summer) may dramatically change the water column properties in scale of few days adding further variability to seasonal patterns.

The species of chaetognaths found in our study have been also reported for the Caribbean region and the Gulf of Mexico (Gasca *et al.*, 1996; Mille-Pagaza & Carrillo-Laguna, 1999; Álvarez-Cadena *et al.*, 2008). The genus *Sagitta* has been reported as the most abundant worldwide (McLelland, 1989), in the Caribbean Sea (Álvarez-Cadena *et al.*, 2008; Suárez-Morales *et al.*, 2009), and in Cuba (Suárez-Caabro, 1955; Koliesnikov & Alfonso, 1964; Campos, 1981; Fabré *et al.*, 1986). The species *S. helenae* and *P. megalophthalma* constituted new reports of Chaetognatha for Cuban waters. The species *F. enflata* and *S. helenae* were dominant and broadly distributed in the three gulfs as they are typical of coastal waters (Boltovskoy, 1981). The species *F. hexaptera*, *S. bipunctata*, and *P. megalophthalma* were rare in the samples because they inhabit oceanic waters (McLelland, 1989). Despite of ca. 3500 specimens identified, we reported only eight species that constitute one third of the 25 species reported for the Caribbean Sea (Suárez-Morales *et*

al., 2009). This suggested a less evolutionary success of most of the chaetognatha species in coastal waters when compared with oceanic waters.

EFFECTS OF GULF AND HABITAT TYPE ON MESOZOOPLANKTON

Our data did not support the hypothesis that habitat type had a significant effect on the mesozooplankton community structure. The relatively small amount of explained variance by the habitat type and the non-significant correlations between mesozooplankton and abiotic variables supported latter statement. Habitat types were defined mostly by benthic foundation species (e.g. stony corals, seagrasses, and mangrove trees) that likely affected very little the overlying mesozooplankton community. The relatively low depth of these coastal habitats and the well-mixed waters probably determined a transient mesozooplankton community largely transported by currents and weakly linked to benthic communities and habitats. The low habitat-specificity of mesozooplankton have been also reported elsewhere in mangroves, seagrass meadows, and coral reefs (Melo *et al.*, 2010; Reyes *et al.*, 2017). Indeed, the degree of habitat fragmentation, more than habitat type itself, may have more important effects on planktonic larvae (Boström *et al.*, 2010). This highlights the influential role in our study of the dispersal (and barriers) as ecological driver of mesozooplankton when compared with the habitat selection.

Basins (i.e. gulfs) had significant effects on the mesozooplankton community structure suggesting that geographical setting may affect the dispersal and distribution of taxa. The relatively large distances among the three basins and the

separation by oceanic waters may have acted as effective barriers to the dispersal. Hydrodynamics and water exchange with adjacent ocean are different among the three gulfs as result of differences in bottom topography, configuration of coastal line, and natural obstacles such as keys and reefs (Arriaza *et al.*, 2008a; 2008b). The system of currents in the oceanic waters surrounding Cuban archipelago is complex (Gallegos *et al.*, 1998) and constitute a determining factor in the transport, dispersion and maintenance of plankton (Paris *et al.*, 2005). Currents and local hydrographic conditions have been also reported as ecological drivers of zooplankton community structure in neritic waters (López-Salgado *et al.*, 2000; Gómez-Gutiérrez *et al.*, 2017). For instance, the lowest diversity in Ana María Gulf may be explained by limited exchange with open waters due to an extensive barrier constituted by Jardines de la Reina archipelago (Emilsson & Tápanes, 1971) and eddies causing retention of waters (Arriaza *et al.*, 2008a).

At species level, the lack of relationship between chaetognaths and habitat type likely reflected the wide ecological tolerance of the coastal species (Suarez-Caabro, 1955; McLelland, 1989). However, chaetognaths were significantly correlated with macrobenthos abundance and richness maybe indicating a selective predation by chaetognaths of benthic resting stages (Boero and Bonsdorff, 2007; Covazzi Harriague *et al.*, 2007).

In summary, mesozooplankton had a typical structure of tropical zones with large diversity (30 major groups), low abundance, and dominance of copepods and chaetognaths. The high proportion

of larvae (39%) and eggs (16%) supported the key role of coastal mesozooplankton for the life cycles of many species and the importance of coral reefs as spawning areas. The high variability of mesozooplankton structure indicated a broad distribution across habitats and gulfs likely associated with a complex oceanographic regime. The factor basin (gulf) had significant effects on mesozooplankton compared to the habitat type, highlighting the influential role of barriers to dispersal among basins and low habitat-specificity. Eight chaetognath species, typical of the Caribbean region, were recorded with *P. megalophthalma* and *S. helenae* being new records for the Cuban archipelago. Macrobenthos was weakly correlated with mesozooplankton indicating likely complex mechanisms of benthic-planktonic coupling. The lack of relationship between chaetognaths and the habitat type likely reflected the broad ecological tolerance of the coastal species.

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ANEXO

Supplementary data. Counts of mesozooplankton.

Taxon	Group	GAM1R1	GAM1R2	GAM2R2	GAM3R1	GAM3R3	GAM4R1	GAM4R2	GAM4R3	GAM5R1	GAM5R2	GAM5R3
Huevos	Zooplankton	0	0	28	0	20	91	105	29	10	11	11
Copepoda	Copepoda	23	15	276	13	51	36	1	12	4	2	6
Chaetognata	Chaetognata	12	25	21	2	14	51	5	12	41	22	1
Dendrobrachiata - larva	Crustacea	37	135	392	14	2	45	4	29	34	6	1
Brachyura - zoea	Crustacea	24	27	398	66	194	84	66	47	57	35	69
Anomura - zoea	Crustacea	0	0	79	0	5	0	1	0	5	0	2
Bryozoa	Bryozoa	0	0	0	0	0	0	0	0	0	0	0
Hydrozoa - medusa	Cnidaria	0	0	0	0	0	0	0	0	0	0	0
Stomatopoda - larva	Crustacea	3	2	3	0	0	0	0	1	0	0	0
Scyphozoa - éfira	Cnidaria	0	0	0	0	0	0	0	0	0	0	0
Tunicata	Tunicata	0	0	0	0	0	0	0	0	0	0	0
Radiolaria	Radiolaria	3	16	1	2	0	2	0	0	1	1	17
Siphonophorae	Cnidaria	0	0	0	0	0	0	0	0	0	0	0
Echinodermata - pluteus	Echinodermata	0	0	0	14	0	0	0	0	0	0	0
Cirripedia - larva	Crustacea	0	0	0	0	0	0	0	0	0	0	0
Pisces - larva	Pisces	0	0	1	0	2	0	1	2	2	1	0
Mysidacea	Crustacea	0	0	0	0	0	3	0	0	0	0	0
Scyphozoa	Cnidaria	0	0	0	0	0	0	0	0	0	0	0
Amphipoda	Crustacea	0	0	0	1	0	0	0	0	0	0	0
Bivalvia	Mollusca	0	0	0	0	0	0	0	0	0	0	0
Bryozoa - larva	Bryozoa	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Annelida	1	0	0	0	0	1	0	0	0	0	0
Decapoda - phyllosoma	Crustacea	0	0	0	0	0	0	0	0	0	0	0
Ostracoda	Crustacea	0	0	0	0	0	0	0	0	0	0	0
Cubozoa	Cnidaria	0	0	0	0	0	0	0	0	0	0	0
Picnogonida	Chelicerata	0	0	0	0	0	0	0	0	0	0	0
Euphausiacea	Crustacea	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	Mollusca	0	0	0	2	0	0	0	0	0	1	0
Cumacea	Crustacea	0	0	0	0	0	0	0	0	0	0	0
Isopoda	Crustacea	0	0	0	0	0	0	0	0	0	0	0
Globigerinido	Alveolata	0	0	0	0	0	0	0	0	0	0	0
Volume (m ³)		37,77	31,28	29,96	30,42	33,64	34,53	35,30	37,51	46,87	38,42	40,17

Taxon	Group	GAM6R1	GAM6R2	GAM6R3	GAM7R1	GAM7R2	GAM7R3	GAM9R1	GAM9R3	GAM10R2	GAM10R3
Huevos	Zooplankton	0	1	0	59	29	13	0	0	4	6
Copepoda	Copepoda	8	0	0	222	63	46	7	3	45	38
Chaetognata	Chaetognata	0	0	0	4	8	3	1	21	13	1
Dendrobrachiata - larva	Crustacea	2	33	6	3	4	1	1	0	4	8
Brachyura - zoea	Crustacea	893	1213	12	18	0	0	0	0	0	0
Anomura - zoea	Crustacea	1	0	0	0	0	0	0	0	0	0
Bryozoa	Bryozoa	0	0	0	0	0	0	0	0	0	0
Hydrozoa - medusa	Cnidaria	0	0	0	0	0	0	3	0	0	0
Stomatopoda - larva	Crustacea	0	1	0	0	0	0	0	0	0	0
Scyphozoa - éfira	Cnidaria	0	0	0	0	0	0	0	0	0	0
Tunicata	Tunicata	0	0	0	0	0	0	0	0	0	2
Radiolaria	Radiolaria	0	0	0	0	0	0	0	0	2	0
Siphonophorae	Cnidaria	0	0	0	0	0	0	0	0	0	0
Echinodermata - pluteus	Echinodermata	0	0	0	0	0	0	0	0	0	0
Cirripedia - larva	Crustacea	0	0	0	0	0	0	0	0	0	0
Pisces - larva	Pisces	0	0	0	0	0	1	0	0	3	1
Mysidacea	Crustacea	0	0	0	0	0	0	0	0	0	0
Scyphozoa	Cnidaria	0	0	0	0	0	0	0	0	9	6
Amphipoda	Crustacea	1	0	0	0	0	0	2	1	0	0
Bivalvia	Mollusca	0	0	0	0	0	0	0	0	0	0
Bryozoa - larva	Bryozoa	0	0	0	0	0	0	0	0	0	0
Polychaeta	Annelida	3	3	0	0	0	0	0	0	0	0
Decapoda - phyllosoma	Crustacea	0	0	0	0	0	0	0	0	0	0
Ostracoda	Crustacea	0	0	0	0	0	0	0	0	0	0
Cubozoa	Cnidaria	0	0	0	0	0	0	0	0	0	0
Picnogonida	Chelicerata	0	0	0	0	0	0	0	0	0	0
Euphausiacea	Crustacea	0	0	0	0	0	0	0	0	0	0
Gastropoda	Mollusca	0	0	0	0	0	0	0	0	0	0
Cumacea	Crustacea	0	0	0	0	0	0	0	0	0	0
Isopoda	Crustacea	0	0	0	0	0	0	0	0	0	0
Globigerínido	Alveolata	0	0	0	0	0	0	0	0	0	0
Volume (m ³)		49,70	31,60	30,36	24,18	26,35	28,94	45,21	58,15	31,47	31,88

Taxon	Group	GB1R1	GB1R2	GB1R3	GB2R1	GB2R2	GB2R3	GB3R1	GB3R2	GB4R1	GB4R2	GB4R3	GB5R1
Huevos	Zooplankton	39	40	16	17	2	6	286	0	107	0	175	308
Copepoda	Copepoda	77	112	9	0	12	2	88	73	24	7	261	7
Chaetognata	Chaetognata	48	47	43	0	0	0	11	37	3	179	424	3
Dendrobrachiata - larva	Crustacea	54	48	29	255	0	22	260	29	1	26	645	3
Brachyura - zoea	Crustacea	4	4	5	0	6	9	155	85	0	6	85	43
Anomura - zoea	Crustacea	0	15	2	0	342	6	1	3	1	9	11	8
Bryozoa	Bryozoa	0	1	0	0	0	0	0	0	0	0	0	4
Hydrozoa - medusa	Cnidaria	0	0	0	0	0	0	4	3	0	1	2	22
Stomatopoda - larva	Crustacea	0	0	0	2	6	2	2	0	0	1	1	199
Scyphozoa - éfira	Cnidaria	0	1	1	0	23	2	0	0	0	4	656	17
Tunicata	Tunicata	0	0	0	0	0	0	0	0	0	0	1	4
Radiolaria	Radiolaria	0	0	0	0	0	0	0	1	0	0	25	0
Siphonophorae	Cnidaria	0	0	0	0	0	0	0	0	0	4	0	0
Echinodermata - pluteus	Echinodermata	0	0	0	0	0	0	0	0	0	0	0	0
Cirripedia - larva	Crustacea	0	0	0	0	2	0	0	0	0	0	0	0
Pisces - larva	Pisces	1	2	2	6	6	4	0	1	0	0	6	0
Mysidacea	Crustacea	0	0	0	0	0	0	0	0	0	0	1	0
Scyphozoa	Cnidaria	2	1	1	0	0	0	0	0	0	2	11	0
Amphipoda	Crustacea	1	1	1	1	0	0	0	0	0	0	0	1
Bivalvia	Mollusca	0	0	0	0	1	0	0	0	0	0	0	0
Bryozoa - larva	Bryozoa	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Annelida	0	0	0	0	0	0	0	1	0	0	0	0
Decapoda - phyllosoma	Crustacea	0	0	0	0	0	0	0	0	0	0	0	0
Ostracoda	Crustacea	0	0	0	0	0	0	0	0	0	0	0	0
Cubozoa	Cnidaria	0	0	0	0	0	0	0	0	0	0	0	0
Picnogonida	Chelicerata	0	0	0	1	2	1	1	5	0	0	0	2
Euphausiacea	Crustacea	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	Mollusca	1	1	0	0	0	0	0	0	0	0	1	0
Cumacea	Crustacea	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda	Crustacea	0	0	0	0	0	0	0	0	0	0	0	0
Globigerinido	Alveolata	0	0	0	0	0	0	0	0	0	0	0	0
Volume (m ³)		34,68	37,71	34,36	44,04	44,76	39,65	43,08	40,21	47,37	53,91	52,11	43,95

Taxon	Group	GB5R2	GB5R3	GB6R1	GB6R2	GB6R3	GB7R1	GB7R2	GB7R3	GB8R3	GB10R1	GB10R3	GG1R1
Huevos	Zooplankton	129	176	0	1	0	573	14	67	46	76	229	182
Copepoda	Copepoda	21	21	121	733	68	296	18	96	16	76	109	0
Chaetognata	Chaetognata	11	1	125	175	11	38	19	73	0	50	163	15
Dendrobrachiata - larva	Crustacea	37	48	38	83	4	1	1	5	2	129	43	28
Brachyura - zoea	Crustacea	26	56	5	12	0	18	8	4	85	141	34	0
Anomura - zoea	Crustacea	43	33	0	8	0	5	7	0	3	0	2	109
Bryozoa	Bryozoa	0	0	0	0	0	0	0	0	0	0	0	4
Hydrozoa - medusa	Cnidaria	23	8	1	1	0	1	1	0	0	73	17	0
Stomatopoda - larva	Crustacea	19	224	0	0	0	25	11	4	2	2	2	0
Scyphozoa - éfira	Cnidaria	56	31	0	0	0	0	0	0	0	0	0	0
Tunicata	Tunicata	0	0	0	0	0	0	0	1	0	88	139	0
Radiolaria	Radiolaria	1	0	0	0	0	0	3	11	0	1	0	0
Siphonophorae	Cnidaria	2	1	0	0	0	1	1	21	0	7	102	1
Echinodermata - pluteus	Echinodermata	0	0	0	0	0	0	0	0	0	0	2	0
Cirripedia - larva	Crustacea	0	0	0	0	0	0	0	0	0	1	0	0
Pisces - larva	Pisces	4	6	5	7	0	3	3	0	2	2	4	0
Mysidacea	Crustacea	0	0	0	0	0	0	0	0	0	0	0	3
Scyphozoa	Cnidaria	74	0	2	0	1	4	0	0	0	0	0	0
Amphipoda	Crustacea	0	0	0	1	0	0	0	0	0	0	2	0
Bivalvia	Mollusca	3	0	2	0	0	0	0	0	0	0	0	0
Bryozoa - larva	Bryozoa	3	1	0	0	0	2	24	27	0	0	0	0
Polychaeta	Annelida	1	0	0	0	0	0	0	0	0	1	1	0
Decapoda - phyllosoma	Crustacea	0	0	0	0	0	0	0	0	0	0	0	0
Ostracoda	Crustacea	0	0	0	0	1	0	0	0	0	1	0	0
Cubozoa	Cnidaria	3	2	0	0	0	0	0	0	0	0	0	0
Picnogonida	Chelicerata	0	1	0	0	0	0	1	1	0	1	0	0
Euphausiacea	Crustacea	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	Mollusca	0	3	0	0	0	1	0	1	0	0	0	0
Cumacea	Crustacea	0	0	0	0	8	0	0	0	1	0	0	0
Isopoda	Crustacea	1	1	0	0	0	0	0	0	2	0	0	0
Globigerínido	Alveolata	0	0	0	0	0	2	0	0	0	0	0	0
Volume (m ³)		47,04	48,02	43,99	53,14	47,26	67,64	56,45	45,53	47,61	47,18	51,55	39,07

Taxon	Group	GG1R2	GG1R3	GG2R2	GG2R3	GG4R1	GG4R2	GG4R3	GG5R1	GG5R2	GG5R3	GG6R1	GG6R2	GG6R3
Huevos	Zooplankton	35	2442	44	1004	40	374	1	5	0	17	128	3	105
Copepoda	Copepoda	0	24	23	196	0	20	0	43	0	0	0	1	75
Chaetognata	Chaetognata	15	9	525	31	26	13	5	73	19	5	12	72	13
Dendrobrachiata - larva	Crustacea	3	125	8	15	17	0	4	37	26	8	9	321	59
Brachyura - zoea	Crustacea	0	55	0	6	0	21	0	28	0	0	0	0	137
Anomura - zoea	Crustacea	46	0	166	0	24	0	2	0	16	11	65	146	1
Bryozoa	Bryozoa	5	0	147	0	35	0	4	0	195	67	5	27	0
Hydrozoa - medusa	Cnidaria	0	0	1	2	0	1	0	0	0	0	0	0	30
Stomatopoda - larva	Crustacea	0	10	0	0	0	0	0	6	0	0	0	0	26
Scyphozoa - éfira	Cnidaria	0	0	0	0	0	0	0	0	0	0	0	0	0
Tunicata	Tunicata	0	1	6	182	3	37	0	1	0	0	0	0	7
Radiolaria	Radiolaria	0	0	2	0	0	0	0	0	1	0	0	0	0
Siphonophorae	Cnidaria	0	0	0	108	0	0	0	0	0	0	0	0	28
Echinodermata - pluteus	Echinodermata	0	0	0	3	0	2	0	0	0	0	0	0	3
Cirripedia - larva	Crustacea	4	0	9	0	0	0	0	1	13	0	1	63	0
Pisces - larva	Pisces	0	5	0	11	0	1	0	6	0	0	2	0	7
Mysidacea	Crustacea	0	0	21	0	4	0	0	1	1	0	3	15	0
Scyphozoa	Cnidaria	0	0	0	0	0	0	0	0	0	0	0	0	0
Amphipoda	Crustacea	0	0	0	0	0	0	0	49	0	0	0	0	1
Bivalvia	Mollusca	0	0	1	0	1	0	0	0	0	0	0	0	0
Bryozoa - larva	Bryozoa	0	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Annelida	0	0	0	6	0	0	0	1	0	0	0	0	0
Decapoda - phyllosoma	Crustacea	0	1	3	0	3	2	0	0	0	0	0	0	0
Ostracoda	Crustacea	0	0	0	1	0	0	0	1	0	0	0	0	0
Cubozoa	Cnidaria	0	0	0	0	0	0	0	0	0	0	0	0	0
Picnogonida	Chelicerata	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausiacea	Crustacea	0	0	8	0	0	0	0	2	0	0	0	0	3
Gastropoda	Mollusca	0	0	1	0	0	0	0	0	0	0	0	1	0
Cumacea	Crustacea	0	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda	Crustacea	0	0	0	0	0	0	0	0	0	0	0	0	0
Globigerinido	Alveolata	0	0	0	0	0	0	0	0	0	0	0	0	0
Volume (m ³)		26,54	42,80	33,08	32,12	42,86	42,03	39,55	40,50	42,11	43,36	40,02	38,64	55,84

Taxon	Group	GG8R1	GG8R3	GG9R1	GG9R2	GG9R3	GG11R1	GG11R2	GG11R3	GG12R1	GG12R2	GG12R3	GG13R1
Huevos	Zooplankton	9	18	6	30	22	182	52	10	21	38	567	8
Copepoda	Copepoda	3	0	0	250	0	78	75	0	48	7	11	1336
Chaetognata	Chaetognata	2	3	384	62	285	99	96	63	179	6	149	40
Dendrobrachiata - larva	Crustacea	24	26	0	110	36	10	6	65	176	11	17	12
Brachyura - zoea	Crustacea	12	0	0	25	0	93	28	0	70	0	0	30
Anomura - zoea	Crustacea	0	0	0	0	9	0	0	197	0	148	15	0
Bryozoa	Bryozoa	0	0	0	0	84	0	0	133	0	256	351	0
Hydrozoa - medusa	Cnidaria	12	7	0	650	2	1	0	0	26	1	0	16
Stomatopoda - larva	Crustacea	4	0	0	8	0	8	134	0	8	0	0	32
Scyphozoa - éfira	Cnidaria	0	0	0	0	0	0	0	0	0	0	0	0
Tunicata	Tunicata	0	0	0	0	0	1	4	0	10	0	0	106
Radiolaria	Radiolaria	0	0	0	0	0	121	0	0	0	0	0	0
Siphonophorae	Cnidaria	0	1	0	0	0	8	0	0	2	0	0	0
Echinodermata - pluteus	Echinodermata	1	0	0	0	0	0	0	0	0	0	0	140
Cirripedia - larva	Crustacea	0	0	0	0	6	0	0	71	0	7	5	0
Pisces - larva	Pisces	2	0	0	1	1	0	1	0	9	4	0	6
Mysidacea	Crustacea	0	1	4	0	9	0	0	0	0	15	5	0
Scyphozoa	Cnidaria	0	0	0	0	0	0	0	0	0	0	0	0
Amphipoda	Crustacea	34	0	0	0	0	1	0	0	4	0	0	0
Bivalvia	Mollusca	0	0	0	0	0	0	0	1	0	0	0	0
Bryozoa - larva	Bryozoa	0	0	0	0	0	0	0	0	0	0	0	0
Polychaeta	Annelida	0	0	0	0	0	0	0	0	0	6	11	0
Decapoda - phylosoma	Crustacea	0	0	0	0	0	0	0	0	0	0	0	0
Ostracoda	Crustacea	3	0	0	0	11	0	0	1	0	0	0	0
Cubozoa	Cnidaria	0	0	0	0	0	0	0	0	0	1	0	0
Picnogonida	Chelicerata	1	0	0	0	0	0	0	0	0	0	0	0
Euphausiacea	Crustacea	0	0	0	0	0	0	0	0	0	0	0	0
Gastropoda	Mollusca	0	0	0	0	0	0	0	0	0	0	0	0
Cumacea	Crustacea	0	0	0	0	0	0	0	0	0	0	0	0
Isopoda	Crustacea	0	0	0	0	0	0	0	0	0	0	0	0
Globigerínido	Alveolata	0	0	0	0	0	0	0	0	0	0	0	0
Volume (m ³)		37,68	36,72	47,21	53,63	42,78	55,34	48,29	48,22	47,36	43,00	41,42	28,38

Taxon	Group	GG13R2	GG13R3	GG14R1	GG14R2	GG15R1	GG15R2	GG15R3
Huevos	Zooplankton	10	9	170	591	8	0	0
Copepoda	Copepoda	800	140	1140	22	240	0	0
Chaetognata	Chaetognata	31	17	364	1672	21	64	13
Dendrobrachiata - larva	Crustacea	13	2	130	950	36	27	62
Brachyura - zoea	Crustacea	20	18	220	0	87	0	0
Anomura - zoea	Crustacea	0	0	0	343	0	7	0
Bryozoa	Bryozoa	0	0	0	252	0	20	1
Hydrozoa - medusa	Cnidaria	6	4	14	0	17	0	0
Stomatopoda - larva	Crustacea	42	0	60	0	2	0	0
Scyphozoa - éfira	Cnidaria	0	0	0	0	0	0	0
Tunicata	Tunicata	56	4	0	2	0	0	0
Radiolaria	Radiolaria	0	182	0	1	0	0	0
Siphonophorae	Cnidaria	0	32	0	1	0	0	0
Echinodermata - pluteus	Echinodermata	68	21	6	0	4	0	0
Cirripedia - larva	Crustacea	0	0	0	12	0	4	1
Pisces - larva	Pisces	2	4	5	9	4	2	1
Mysidacea	Crustacea	0	0	0	35	0	2	1
Scyphozoa	Cnidaria	0	0	0	0	0	0	0
Amphipoda	Crustacea	2	1	6	0	0	0	0
Bivalvia	Mollusca	0	0	0	51	0	0	0
Bryozoa - larva	Bryozoa	0	0	0	0	0	0	0
Polychaeta	Annelida	0	0	0	3	0	0	0
Decapoda - phylosoma	Crustacea	0	0	1	9	1	0	0
Ostracoda	Crustacea	0	0	0	1	0	0	0
Cubozoa	Cnidaria	0	0	0	12	0	0	0
Picnogonida	Chelicerata	0	0	0	0	0	0	0
Euphausiacea	Crustacea	0	0	0	0	3	0	0
Gastropoda	Mollusca	0	0	0	0	0	0	0
Cumacea	Crustacea	0	0	0	2	0	0	0
Isopoda	Crustacea	2	0	0	0	0	0	0
Globigerínido	Alveolata	0	0	0	0	0	0	0
Volume (m ³)		39,81	39,32	47,27	43,24	52,25	41,55	36,51