



The role of habitat selection on the diversity of macrobenthic communities in three gulfs of the Cuban Archipelago

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ABSTRACT.—Diversity and faunal composition of macrobenthic communities remain poorly known in the Caribbean Sea. Here, we explore the diversity and abundance of marine macrobenthos across three gulfs of the Cuban Archipelago and examine the role of habitat type in determining faunal composition and function. Samples collected from 32 soft-bottom sites across four habitat types (mangroves, seagrass beds, unvegetated mud bottoms, and coral reefs) yielded 4231 individuals representing 22 higher macrobenthic taxa. The most abundant taxa were polychaetes, nematodes, crustaceans, and mollusks. Mollusk fauna was particularly diverse (105 species and 74 genera) despite being dominated by two taxa: a bivalve (*Parvilucina* sp.) and gastropods (*Caecum* spp). Habitat type was weakly interrelated with the faunal composition of the entire macrobenthos and its molluscan component (<20% of explained variance, in both cases). This weak correlation might reflect the influence of within-habitat heterogeneity, ecological drift, or dispersal barriers. Functional traits differed among habitats, with infaunal mollusks typically found in mud bottom and carnivores more abundant in mangroves. The regional mollusk species richness (105 species) exceeded the richness observed within individual gulfs (39, 40, and 59 species), highlighting high regional diversity. Anthropogenic factors could also be at play. The results suggest, tentatively, that fisheries might have affected the functional and taxonomic structuring of the sampled macrobenthic communities. This initial survey suggests that habitat selection does not exert a strong effect on the macrobenthos (or its molluscan component), and other assembly processes such as drift, dispersal, and human impacts may be important.

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Macrobenthos, defined as metazoans with a proximate body size ranging from 0.5 to 5 cm, constitute a diverse and functionally important component of marine ecosystems (Gray and Elliot 2009). Four processes have been postulated to influence the diversity and abundance of macrobenthic communities (Vellend 2010): selection, drift, speciation, and dispersal. Within this conceptual framework, selection plays a fundamental role in determining the structure of macrobenthic communities. Assembly of these communities may be driven by ecological gradients defined by one or more environmental drivers (e.g., salinity, water depth, pollutant concentration; Peeters et al. 2000, Mucha et al. 2003). However, abiotic heterogeneity and biotic interactions within habitats can also play a major role (Kraft et al. 2015). Habitat selection can be the result of a complex set of physical, chemical, and biological factors that jointly determine macrobenthic community structure (e.g., Dolbeth et al. 2014, Donadi et al. 2015). In addition, examining macrobenthic assemblages across habitats can help derive more predictable, generalizable rules for studying marine benthic ecosystems (Ferraro and Cole 2007, Ferraro 2013). Finally, factors determining spatial diversity patterns are scale-dependent (Gaston and Spicer 2004, Magurran 2004): dispersal and environmental selection can be increasingly important at regional scales, whereas species interactions can play more prominent roles at local scales (Biswas et al. 2016). Consequently, analyses at multiple spatial scales can be informative when examining the effects of habitat selection on macrobenthic communities.

Studies aimed at documenting the distribution and composition of macrobenthic assemblages typically face challenges posed by high species diversity and the presence of numerous higher taxa, usually spanning 15–25 phyla (Gray and Elliot 2009). Consequently, solid taxonomic knowledge of multiple phyla is required for species identification. To circumvent this challenge, two strategies may be implemented: (1) restrict data to some well-known taxa and/or (2) classify organisms into functional groups by using approaches such as biological trait analysis (BTA; Bremner et al. 2006). The first strategy is supported by the central role of species as units of evolution, and also as key units for quantifying biodiversity patterns (Magurran 2004). Consequently, the use of species-level identification is critical for macrobenthic studies, though it is usually possible only for the few taxa for which identification keys and regional taxonomic synopses are available (e.g., mollusks).

Mollusks are among the most common macrobenthic groups and are typically dominated by two classes: Gastropoda and Bivalvia (Jones et al. 1990, Josefson and Hansen 2004). On tropical and subtropical shelves, mollusks may represent up to 38% of the invertebrate fauna, and in some regions they can represent the bulk of benthic biomass (Longhurst and Pauly 1987). Studies dealing with the ecology of mollusk assemblages in tropical soft bottoms are relatively few (e.g., Jackson 1972, 1973, Jones et al. 1990, Guerra-García and García-Gómez 2004), but additional studies have been conducted in the near subtropical habitats around the southern coast of Florida (e.g., Mikkelsen and Bieler 2007, Montagna et al. 2008). In addition, mollusk data are often aggregated with other taxa such as polychaetes and crustaceans (e.g., Munari and Mistri 2008, Kedra et al. 2010, Hidalgo et al. 2015), hampering the analyses of their distribution patterns.

The second approach includes the use of BTA and describes the contribution of a suite of ecological characteristics to species abundance patterns. BTA considers a range of features across the entire assemblage and is based on the relationships

between species characteristics and habitat constraints (Southwood 1977). BTA has the potential for describing linkages between functional diversity in marine systems and ecosystem processes (Coleman and Williams 2002) and has been increasingly used in biodiversity studies (e.g., Bremner et al. 2006, Paganelli et al. 2012). For mollusks, the most explored biological traits are mobility, burrowing activity, feeding habits, and body size (Boström et al. 2010, Aarnio et al. 2011).

In the Caribbean region, macrobenthic studies have been relatively scarce (e.g., Murina et al. 1966, Gómez et al. 1980, Armenteros et al. 2007, Arias-Schreiber et al. 2008, Hidalgo et al. 2015) and often focused on specific taxa such as Polychaeta (e.g., Ibarzábal 1985, Helguera et al. 2011) and Mollusca (Hoskins 1964, Capetillo-Piñar et al. 2015). However, previous mollusk studies in Cuba focused primarily on systematics, whereas quantitative ecological studies on biodiversity and distribution are lacking.

The present survey documents species richness, compositional variation, and biological trait distribution of macrobenthic mollusks and the selective effects of four habitat types in three regions of the Cuban shelf. We analyzed the biodiversity components of species richness and compositional variation at two spatial scales (local and regional), allowing us to compare the effects of habitat selection vs the effects of spatial scale (Gray 2000). We use the term *variation* (instead of *turnover*) as a type of β -diversity because of the absence of a clear environmental gradient in the studied systems (Anderson et al. 2011).

The present study represents the first effort to disentangle the role of habitat selection on Caribbean macrobenthic communities at regional scale using species level data. The new diversity data represent an important quantitative bio-inventory of regional mollusk assemblages. Here, we explore the selective effects of four different habitat types (mangroves, seagrass beds, unvegetated bottoms, and coral reefs) on the diversity and distribution of marine macrobenthos of the Cuban Archipelago at both local (within gulfs) and regional (between gulfs) scales. Our specific aims were to investigate the role of habitat selection on the higher-taxon diversity and distribution of macrobenthos, and on the species richness, variation, and functional diversity of mollusks.

MATERIALS AND METHODS

STUDY SITES AND HABITATS.—Our study was conducted in three inner seas (hereafter gulfs) of the Cuban Archipelago that vary in terms of geographic extent, depth, and oceanographic regime (Fig. 1). Guanahacabibes is located in the northwestern region of the Cuban Archipelago, facing the Gulf of Mexico, whereas Batabanó and Ana María are located in the southwest and south-central regions, respectively. The Ana María gulf has been subjected to commercial fishing for shrimp (*Farfantepenaeus* and *Litopenaeus*), whereas Batabanó has been affected by fishing for spiny lobsters, *Panulirus argus* (Latreille, 1804).

Sediment samples were collected from four distinct soft-bottom habitat types observed within the gulfs. The habitat types, as presented in Figure 2, include the following:

1. Mangroves: shoreline habitats covered mostly by the red mangrove, *Rhizophora mangle* L. The bottom was covered with variable quantities of mangrove litter.

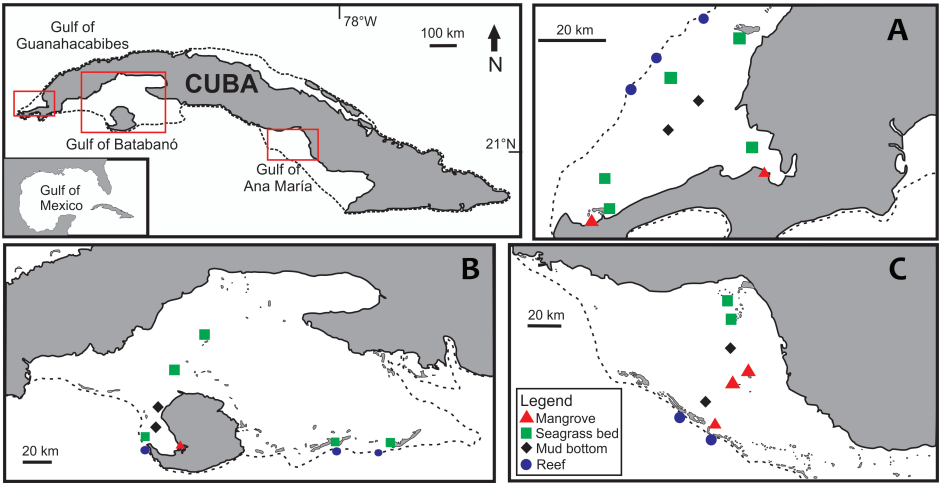


Figure 1. Map of the study region with the sampling sites indicated by habitat symbols within the three gulfs. Dashed lines indicate the border of the shelf (approximately 200 m depth). (A) Gulf of Guanahacabibes, (B) Gulf of Batabanó, (C) Gulf of Ana María.

At some sites, patches of the seagrass, *Thalassia testudinum* K. D. Koenig, were observed. Samples were taken in the subtidal sediment near prop roots.

2. Seagrass beds: subtidal mud-sand flats covered by variable amounts of *T. testudinum*. At some sites, *Halophila* spp., *Halodule wrightii* Ascherson, and macroalgae were also present. Samples were taken from unvegetated sediments in close proximity to seagrass beds.
3. Mud bottoms: areas at depth range of 10–20 m characterized by fine-sediment substrates devoid of marine macrophytes.
4. Coral reefs: heterogeneous habitats with abundant biogenic structures such as stony corals, sponges, and gorgonians. All samples were collected from sandy areas located in the fore reef. Sampling specifically targeted spur-and-groove structures (depth range: 7–18 m), where sediments dominated by medium-size sand occurred in seafloor depressions.

COLLECTION AND PROCESSING OF SAMPLES.—Thirty-two sites were sampled in February 2013 (Batabanó), October 2013 (Ana María), and June 2014 (Guanahacabibes) (Table 1, Online Appendix S1). Three replicates for macrobenthos were taken at each site and pooled prior to computing site-level biodiversity estimates. Each site belonged to one of the four types of targeted habitats. Depth was measured with a dive computer. Temperature, salinity, and dissolved oxygen (DO) were measured in situ at approximately 10 cm from the bottom using an oceanographic Hydrolab multi-probe 4a instrument. Salinity in Guanahacabibes could not be measured because the sensor was damaged in the first deployment. Two samples of the uppermost 3-cm layer of surficial sediments were taken at each site with a 250-ml propylene container for the measurement of total organic matter (TOM) and the percentage of silt/clay of sediments (D). D was determined by wet sieving through a 63- μm sieve. TOM was determined by the Walkley-Black method (UNEP 1995) using exothermic heating and oxidation with $\text{K}_2\text{Cr}_2\text{O}_7$ and H_2SO_4 .

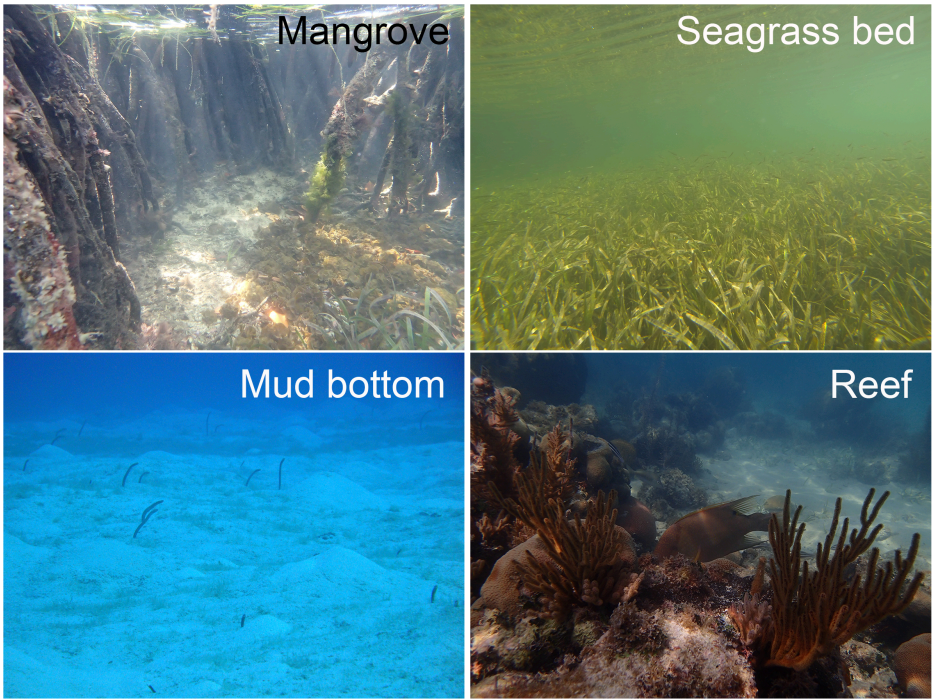


Figure 2. Photographs of the four habitat types: mangrove, seagrass bed, mud bottom, and coral reef.

Table 1. Summary of sampling sites and diversity. N_{total} = abundance of macrobenthos, S_{taxa} = number of higher taxa, $N_{mollusks}$ = abundance of mollusks, SR_{obs} = observed species richness of mollusks. Numbers are summed over the sites.

Gulf/habitat	Sites	N_{total}	S_{taxa}	$N_{mollusks}$	SR_{obs}
Ana María					
Mangrove	3	221	9	39	18
Seagrass bed	2	99	16	39	17
Muddy bottom	2	92	13	26	9
Reef	2	507	17	28	10
Batabanó					
Mangrove	1	63	11	5	5
Seagrass bed	5	460	18	46	21
Muddy bottom	2	243	12	10	6
Reef	3	540	19	37	14
Guanahacabibes					
Mangrove	2	591	16	30	18
Seagrass bed	5	780	20	79	25
Muddy bottom	2	229	16	14	9
Reef	3	406	18	28	14
Total	32	4,231	22	381	105

Sediment samples for macrobenthos were collected by scuba divers using a box core with an effective sampling area of 100 cm² (approximately 1000 cm³ of sediment) and immediately sieved with filtered seawater through a 500- μ m mesh sieve and preserved in 70% ethanol. The samples were transported to the laboratory, where macrobenthic organisms were sorted, identified to higher taxa (e.g., class or order), and counted under a stereomicroscope Olympus SZX. Mollusks were identified to species level using taxonomic literature (Morris 1973, Abbott 1974, Tunnell et al. 2010, Espinosa et al. 2012). Only live specimens were included in our study. Empty shells and other skeletal remains devoid of soft tissue were not counted.

BIOLOGICAL TRAITS.—Six biological traits reflecting morphological and ecological characteristics of bivalves and gastropods were compiled for each species: organism/substrate relationship (or tiering), mobility, attachment, feeding type, adult length, and shell shape (Online Appendix S2). Information about biological traits was obtained from Redfern (2001) and online sources (<http://porites.geology.uiowa.edu> and <http://www.marinespecies.org>). When a species exhibited more than one category within a given biological trait, it was assigned to the most frequently documented category. When information on a particular trait could not be obtained, species trait was assigned based on the trait state observed in the nearest living relative.

DATA ANALYSIS.—Multivariate and univariate techniques were applied to data using the software PRIMER 6.0.2 (Clarke and Gorley 2006) and STATISTICA 6.0 from StatSoft. All statistical techniques were non-parametric. Medians were used as measure of central tendency and Kruskal-Wallis tests (K-W) were used to test differences among groups. Density was calculated by dividing the counts by the sampling area and expressed as the number of individuals per 0.01 m². Diversity measures were computed using the software Estimate 9.0.1 (Colwell 2013). Species richness (SR) of mollusk assemblages was compared among habitats and among gulfs by rarefaction to the lowest number of individuals. Rarefaction standardizes the sample size, allowing for a direct comparison of SR estimates across samples (Magurran 2004). Confidence intervals (CIs) around sample-standardized species richness estimates were generated using the maximum number of possible permutations (Colwell 2013). Overlapping of CIs with observed values was used as the criterion for non-significant differences in SR among habitats or among gulfs.

Variation in mollusk assemblages between pairs of sites was calculated using the Bray-Curtis (B-C) dissimilarity index (Anderson et al. 2011). To visualize similarity of samples in terms of species composition and abundance, we derived a nonmetric multidimensional scaling (NMDS) ordination in two dimensions using 1000 random starting configurations (Clarke and Warwick 2001). Data were square root transformed to reduce the effects of numerical dominance by a few species, and a dummy variable with value 1 was added to accommodate the ordination of samples with very low abundance (Clarke et al. 2006). We used the routine SIMPER to identify the species that contributed most significantly to the similarity of a given habitat or gulf (Clarke and Warwick 2001). The contribution of each species to the dissimilarity was ordered and sequentially summed to yield its cumulative percentage. Only species that cumulatively contributed 90% of the total were reported.

A permutational analysis of variance (PERMANOVA) (Anderson et al. 2008) was used to assess the statistical significance and amount of variance explained by two design factors: gulf, and habitat nested within gulf. Estimated component of variation

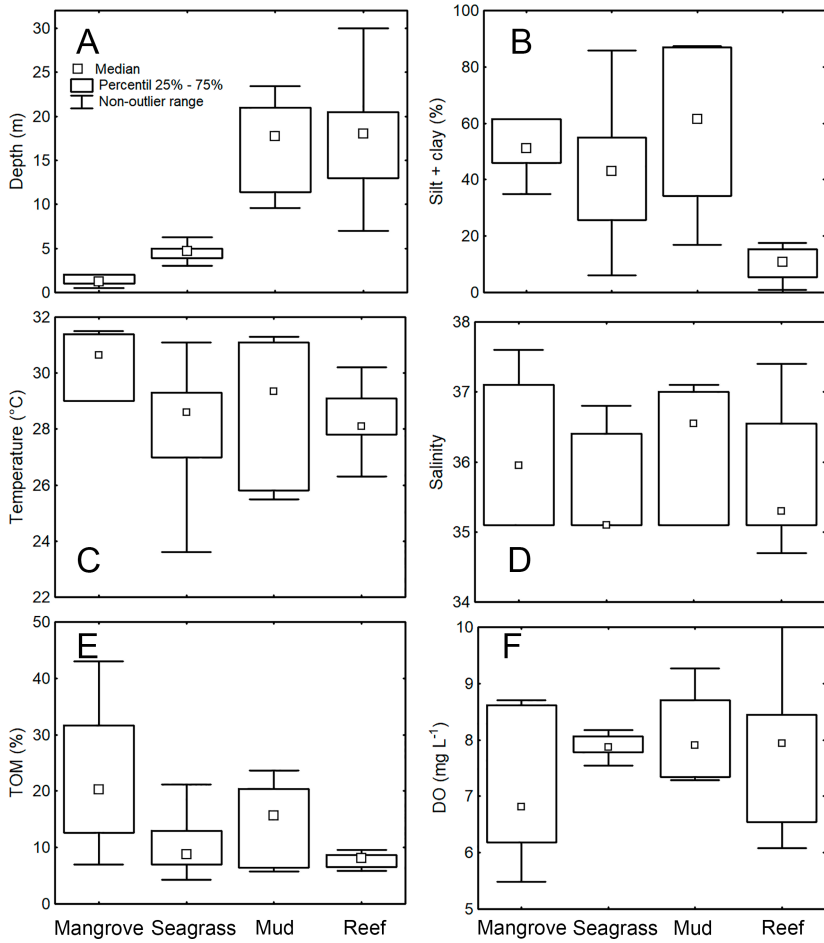


Figure 3. Abiotic factors measured in the four habitats of the Cuban Archipelago. (A) Depth, (B) percentage of fine sediment (<63 μm), (C) temperature, (D) salinity, (E) content of total organic matter (TOM), (F) dissolved oxygen (DO). All samples are pooled by habitat across the three gulfs.

(ECV) in the analysis of variance was used as an indicator of the magnitude of effects associated with each factor (Anderson et al. 2008). The PERMANOVA procedure was based on 9999 permutations under a reduced model to generate the sampling distribution. The measure of resemblance was Euclidean distance for density and species richness data, and Bray-Curtis measure of similarity for species composition data.

Spearman rank correlation coefficients (all samples pooled) were calculated between each pair of values of abiotic (depth, grain size, salinity, temperature, total organic matter, and dissolved oxygen) and biotic (abundance of macrobenthos, number of macrobenthic higher taxa, mollusk abundance, and mollusk species richness) variables.

RESULTS

ABIOTIC DATA.—The four habitats varied in water depth: mangroves and seagrass sites were shallower than 6 m, whereas mud bottom and reef sites were deeper than 10 m (K-W test: $P < 0.001$) (Fig. 3A). The percentage of fine sediment ($<63 \mu\text{m}$) ranged widely for mangroves, seagrass beds, and mud bottoms. Reef habitats had a significantly lower content of fine sediment (K-W test: $P = 0.01$) (Fig. 3B). No differences in temperature reflected sampling months (K-W test: $P = 0.11$) (Fig. 3C). Salinity did not vary significantly across the four habitats (Fig. 3D) in the two gulfs where we were able to measure it (K-W test: $P = 0.50$). Median values of TOM varied marginally among habitat types (K-W test: $P = 0.055$), with highest TOM in mangroves and lowest in reef (Fig. 3E). Dissolved oxygen content was relatively high and did not vary significantly across habitat types (K-W test: $P = 0.55$) (Fig. 3F). The full data set of abiotic variables is given in the Online Appendix S1.

MACROBENTHIC COMMUNITIES.—In total, 4231 macrobenthic animals belonging to 22 higher taxa were recovered from samples (Online Appendix S3). Seven higher taxa constituted 80% of total abundance: Polychaeta (20%), Nematoda (19%), Ostracoda (11%), Bivalvia (9%), Amphipoda (8%), Oligochaeta (8%), and Gastropoda (5%). Seagrass beds and coral reefs were the habitats with the highest diversity of higher taxa across the three gulfs (Table 1). Total abundance of macrobenthos (all taxa and habitats pooled) varied significantly across gulfs (K-W test: $P = 0.032$); it was lowest in Ana María (median of 20 ind 0.01 m^{-2}) and highest in Batabanó and Guanahacabibes (both with 34 ind 0.01 m^{-2}). The median density of higher taxa varied across habitats and gulfs, but a clear pattern was not evident. Nevertheless, nematodes were abundant in the reefs of Ana María (median of 39 ind 0.01 m^{-2}) and Batabanó (median of 15 ind 0.01 m^{-2}) compared to other habitats (Fig. 4A).

Multivariate ordination indicated that neither habitat type nor gulf played a major role in determining the faunal composition of macrobenthic associations. In the NDMS coordinate system, samples did not form distinct groups based on either region or habitat type (Fig. 4B, C). The analysis of components of variance broadly supports the NMDS results—at most there were significant but weak effects of habitat type and gulf on density and faunal composition of macrobenthos (Table 2). Habitat type exerted a somewhat stronger effect compared with gulf, but most variance was unexplained (71% and 78%, Table 2). The density and number of higher taxa of macrobenthos were significantly correlated with sedimentary variables: grain size (proportion of silt and clay) and organic content, as measured by TOM (Table 3).

SPECIES RICHNESS OF MOLLUSK ASSEMBLAGES.—Mollusks were represented by 381 specimens belonging to 74 genera and 105 species. They constituted approximately 14% of total macrobenthic abundance (Table 1, Online Appendix S4). Mollusk samples were dominated by a few taxa, with only five species belonging to two genera accounting for 34% of all collected mollusks: the bivalve, *Parvilucina* sp., and the gastropods, *Caecum regulare* Carpenter, 1858, *Caecum antillarum* Carpenter, 1858, *Caecum* sp., and *Caecum imbricatum* Carpenter, 1858. There were 56 mollusk species represented by one specimen and 16 by two specimens.

At the scale of individual gulfs, we compared diversity by habitat types using rarefaction to sample-standardize species richness (SR) down to 25 individuals (SR_{25}). When split by gulf, sites were represented by fewer than 25 individuals (Table 1) in

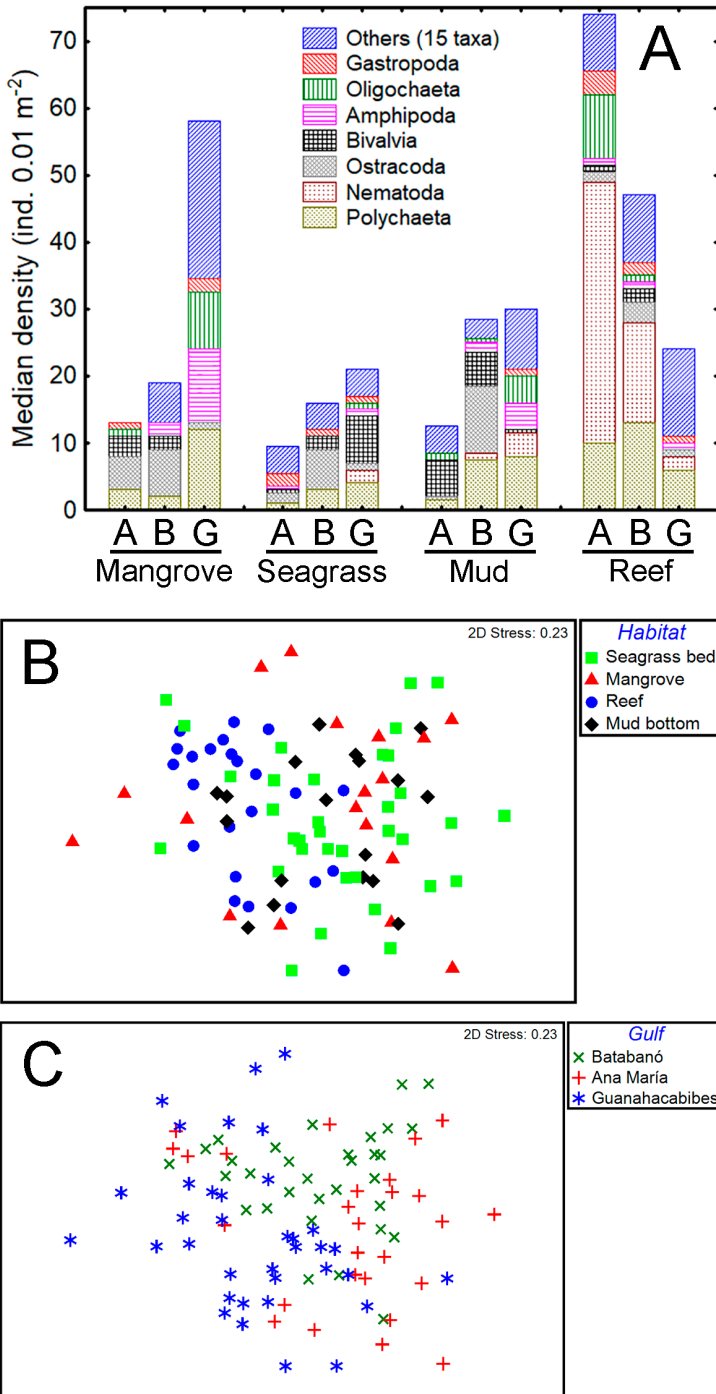


Figure 4. Macrobenthos density and faunal composition. (A) Median density of higher taxa of macrobenthos across habitats and gulfs. The three gulfs indicated as follows: A = Ana María, B = Batabanó, and G = Guanahacabibes. (B) Ordination of samples by NMDS based on abundance of macrobenthic taxa with sites coded by habitats. (C) The same ordination plot with sites coded by gulfs. M = mangrove, S = seagrass bed, MB = mud bottom, R = reef.

Table 2. The magnitude of the effects of habitat and gulf on the community structure of macrobenthos and mollusks. Effects assessed by the components of variation (ECV) associated to each factor using permutational analysis of variance (PERMANOVA). *P*-values associated to each test are given, * indicates significant differences at *P* < 0.05.

Variable/factor	ECV	ECV (%)	<i>P</i>
Macrobenthos			
Density			
Gulf	103.0	5	0.084
Habitat (gulf)	346.0	15	0.021*
Residual	1,793.0	78	
Taxon composition			
Gulf	309.0	10	0.001*
Habitat (gulf)	590.0	19	0.001*
Residual	2,230.0	71	
Mollusks			
Density			
Gulf	4.0	6	0.250
Habitat (gulf)	0.0	-	0.900
Residual	65.0	94	
Species richness			
Gulf	0.5	4	0.260
Habitat (gulf)	0.0	-	0.830
Residual	11.0	96	
Species composition			
Gulf	267.0	7	0.002*
Habitat (gulf)	610.0	17	<0.001*
Residual	2,730.0	76	

Nested bifactorial design: habitat (fixed) nested within gulf (fixed).
 Degrees of freedom of the factors: Gulf: 2, habitat (gulf): 9, residual: 83.
 Measures of distance: Euclidian distance for density, Bray-Curtis for multivariable.

three cases. Consequently, SR estimates were underestimated for these sites, and caution is needed when interpreting these results. The 95% confidence intervals of SR tended to overlap, indicating no significant differences in species richness among habitats within each of the three gulfs (Online Appendix S5A–C).

At the regional scale, we selected 100 individuals for rarefaction to compare the observed SR among the three gulfs. The SR₁₀₀ estimator of mollusk species richness was statistically indistinguishable among the three gulfs (Online Appendix S5D).

Table 3. Spearman rank correlation between the abiotic and biotic variables. N_{total} = abundance of macrobenthos, S_{taxa} = number of higher taxa, N_{mollusks} = abundance of mollusks, SR_{obs} = observed species richness of mollusks. *n* = 32 for all the variables (except salinity: *n* = 17). * indicates significant differences at *P* < 0.05.

Variable	N _{total}	S _{taxa}	N _{mollusks}	SR _{obs}
Depth	0.15	0.44*	-0.10	-0.14
Silt + clay	-0.54*	-0.63*	<0.01	0.03
Temperature	-0.15	-0.18	0.44*	0.47*
Salinity	-0.02	-0.20	-0.04	0.01
Total organic matter	-0.52*	-0.71*	0.10	-0.01
Dissolved oxygen	0.14	0.07	0.01	0.01

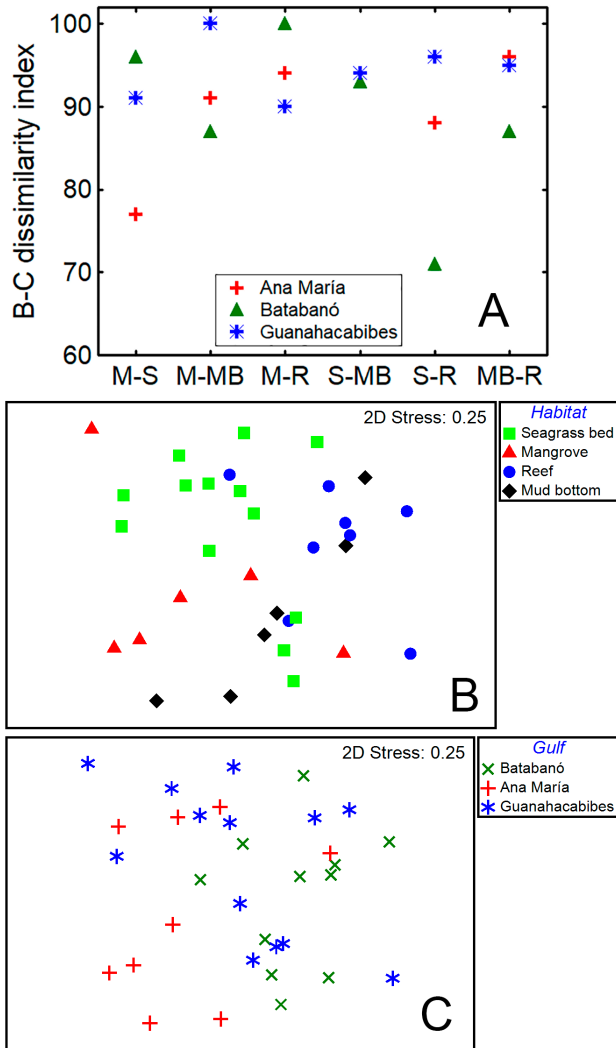


Figure 5. β -diversity (variation) of mollusk assemblages. (A) Pairwise dissimilarities between habitats for the three gulfs as measured by Bray-Curtis (B-C) dissimilarity index. (B) Ordination of samples by NMDS based on square-root transformed abundance of mollusk species with sites coded by habitats. (C) The same ordination used above but with sites coded by gulfs. M = mangrove, S = seagrass bed, MB = mud bottom, R = reef.

PERMANOVA results indicated at most weak and non-significant effects of habitat type and gulf on the density and species richness of mollusks as measured by components of variance (Table 2). Abundance and species richness of mollusks were only weakly correlated with temperature ($R = 0.44$ and 0.47 , respectively; Table 3).

COMPOSITIONAL VARIATION OF MOLLUSK ASSEMBLAGES.—For all three gulfs, sites from different habitat types differed statistically in faunal composition with B-C dissimilarity values exceeding 70% for all cross-habitat pairwise comparisons (Table 2, Fig. 5A). Sixteen species contributed to similarity within habitats at the

Table 4. Mollusk species characteristic of each habitat type measured as those that contributed most to the within-habitat Bray-Curtis similarity at a cut-off level of 90%. Data reported separately for each of the three gulfs. Symbols: M = mangrove, S = seagrass bed, MB = muddy bottom, R = reef.

Species	Ana María				Batabanó				Guanahacabibes			
	M	S	MB	R	M	S	MB	R	M	S	MB	R
<i>Bulla occidentalis</i>	X											
<i>Caecum antillarum</i>												X
<i>Caecum imbricatum</i>				X				X				
<i>Caecum regulare</i>								X				
<i>Caryocorbula swiftiana</i> (C. B. Adams, 1852)			X									
<i>Codakia orbicularis</i>										X		
<i>Cylindrobulla beauii</i> P. Fischer, 1857						X						
<i>Eulithidium thalassicolum</i>										X		
<i>Gemma gemma</i> (Totten, 1834)			X									
<i>Haminoea petiti</i>	X											
<i>Murchisonella spectrum</i> (Mörch, 1875)										X		
<i>Nucula</i> sp.	X											
<i>Parvilucina</i> sp.		X				X				X		
<i>Saccula acuta</i> (Conrad, 1831)			X									
<i>Solemya occidentalis</i> Deshayes, 1857			X							X		
<i>Tampaella mera</i> (Say, 1838)	X											

cut-off level of 90% (Table 4). There were a few abundant species that were diagnostic of a particular habitat. *Parvilucina* sp. was characteristic of seagrass beds, as was the genus *Caecum* in reef habitats. In general, each habitat harbored a unique set of species. For example, the gastropods, *Bulla occidentalis* A. Adams, 1850 and *Haminoea petiti* (d'Orbigny, 1841), and the bivalve, *Nucula* sp., were recovered only from mangroves of Ana María, whereas the gastropod, *Eulithidium thalassicolum* (Robertson, 1958), and the bivalve, *Codakia orbicularis* (Linnaeus, 1758), were observed only in seagrass beds of Guanahacabibes. Only two species were common in all three gulfs: the gastropod, *C. regulare*, and the bivalve, *Parvilucina* sp. (Table 5).

Mollusk density data were characterized by many species represented by one or two specimens. In addition, several sites yielded samples with few specimens. The high dispersion of samples in the NMDS ordination and lack of clustering by habitat type indicate high within-habitat variability in faunal composition (Fig. 5B). In other words, no distinct mollusk assemblage that was characteristic of a given habitat type could be identified. Similarly, the high dispersion of samples from single gulfs suggested that no distinct gulf-specific faunal-assemblage types could be delineated (Fig. 5C). Component variance supports the finding reported above of relatively larger effects of habitat type on species composition when compared to regional effects (gulf), but both factors explained little overall variance (7% for gulf and 17% for habitat, Table 2).

BIOLOGICAL TRAITS OF MOLLUSK ASSEMBLAGES.—We explored the changes in abundance across the four habitat types and three gulfs for six biological traits: organism/substrate relationship (or tiering), mobility, attachment, feeding type, adult length, and shell shape. Only two traits (tiering and feeding type) were informative. The relative abundance of functional groups defined by tiering varied in a complex way across the gulfs within the same habitat (Fig. 6A). Nevertheless, a trend existed

Table 5. Mollusk species characteristic of each gulf (all habitats pooled) measured as those that contributed most to the within-gulf Bray-Curtis similarity at the cut off level of 90%.

Species	Ana María	Batabanó	Guanahacabibes
<i>Ameritella sybaritica</i> (Dall, 1881)			X
<i>Atys caribaeus</i> (d'Orbigny, 1841)	X		
<i>Bulla occidentalis</i>	X		
<i>Caecum antillarum</i>			X
<i>Caecum imbricatum</i>	X		
<i>Caecum regulare</i>	X	X	X
<i>Crassinella lunulata</i> (Conrad, 1834)	X		
<i>Cylichnella bidentata</i> (d'Orbigny, 1841)	X		
<i>Cylindrobulla beaulti</i>		X	
<i>Eoacmaea pustulata</i> (Helbling, 1779)	X		
<i>Eulithidium thalassicolum</i>			X
<i>Gemma gemma</i>	X		
<i>Haminoea petiti</i>	X		
<i>Nucula</i> sp.	X		
<i>Nuculana acuta</i>	X		
<i>Parvilucina</i> sp.	X	X	X
<i>Semelina nuculoides</i> (Conrad in Hodge, 1841)		X	
<i>Solemya occidentalis</i>	X		X
<i>Tampaella mera</i> (Say, 1838)	X		

related to habitat type. The largest contrast was observed between mud bottoms, which had a higher proportion of infaunal siphonate forms (38%–85%), and coral reefs, with a predominance of epifaunal species (range: 46%–93%). Mangrove and seagrass beds were characterized by a more even distribution of tiering modes, with all tiering strategies well represented.

The analysis of feeding types also suggests the presence of informative patterns across habitats (Fig. 6B). Coral reefs were characterized by the dominance of herbivorous mollusks. Mud bottoms harbored abundant deposit and suspension feeders as well as moderately abundant herbivores. In seagrass beds, all feeding types were represented. The mangroves were distinctive for the presence of carnivores.

DISCUSSION

Our study represents the first quantitative analysis of macrobenthic communities across iconic tropical marine habitats of the Cuban Archipelago on a regional-scale of 100s of kilometers. Most similar studies in the Caribbean region have focused on reef ecosystems; therefore, our work contributes to a fuller understanding of the benthos and its distribution across multiple marine habitat types. It should be noted that our method relies on a small sampling device, which could bias the analysis toward small-bodied mollusks. As a result, the recovered mollusk assemblages may not be fully representative of the larger or more mobile species, such as *Lobatus gigas* (Linnaeus, 1758), *Fasciolaria tulipa* (Linnaeus, 1758), and *Melongena melongena* (Linnaeus, 1758), which were not captured effectively by our sampling device (see also Hoskins 1964). The analysis is also limited by the relatively low number of live mollusks that were recovered in the samples. This limitation translates into

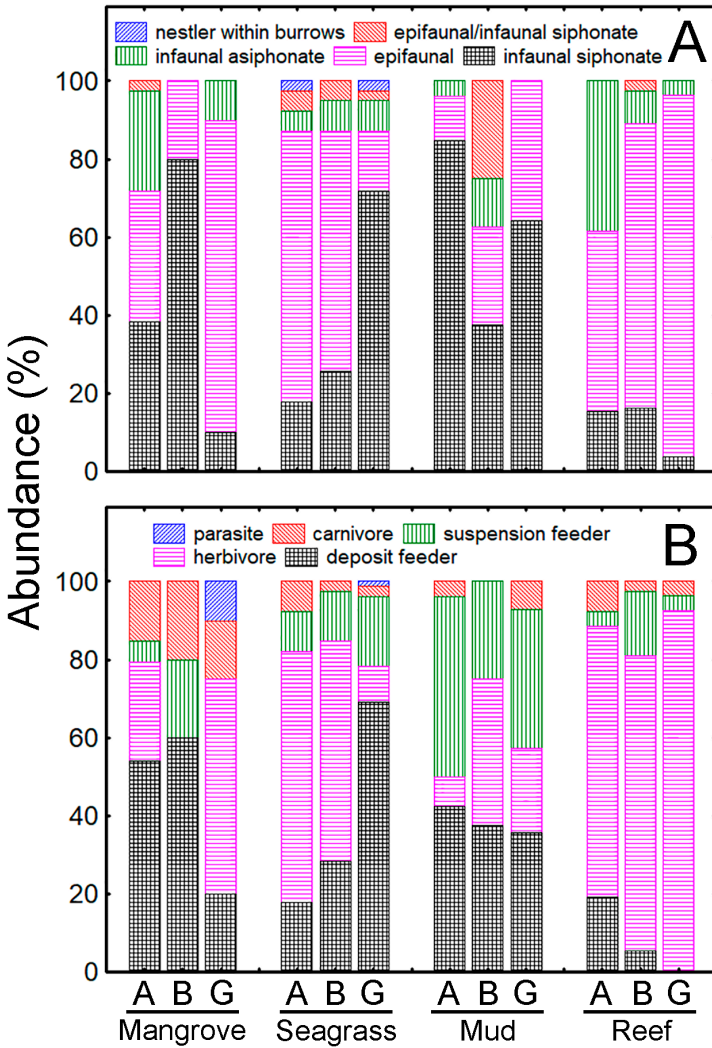


Figure 6. Relative abundance of functional groups of mollusks across habitats and gulfs. The species were grouped by two different trait types: (A) tiering (organism/substrate relationship) and (B) feeding type. The labels of the gulfs: A = Ana María, B = Batabanó, G = Guanahacabibes.

an elevated risk of underestimating the biodiversity of sites, habitats, and regions. However, the uniform sampling and processing procedures used in our study ensure its reproducibility and make the resulting database amenable to cross-study comparisons.

Unfortunately, we could not control for temporal variation in our sampling design because we were limited to a single expedition to each gulf. Seasonality is an ecological driver of the structure of soft-bottom tropical sites, but mainly in regions with monsoonal regimes (Alongi 1989). We assume that spatial patterns, if present, should have emerged even despite effects of seasonality. An instance of possible temporal spurious effects was the positive correlation of temperature with mollusk density and species richness: Guanahacabibes was sampled in summer, and Ana María and

Batabanó in winter, so, effects of temperature on diversity metrics are confounded with seasonal differences between sampling events.

Polychaetes are dominant in the Cuban macrobenthic communities sampled here, which is consistent with many studies from other regions (e.g., Fauchald and Jumars 1979). Nematodes ranked second in our study, mostly because of the abundance of large enoplid species typically associated with coralline sands (Ruiz-Abierno and Armenteros 2017). This finding is in contrast to other studies in the region that reported mollusks (Díaz Asencio et al. 2016) or crustaceans (Murina et al. 1966, Hidalgo et al. 2015) as the second most important taxon. Differences in the rank abundance of higher taxa can be explained by local environmental heterogeneity (e.g., hydrodynamics and grain size), but other factors related to ecological drift (e.g., random variation in larval supply and post-settlement survival) cannot be ruled out at this time.

Habitat explained <20% of variation in the macrobenthic data and we offer two possible explanations. First, patterns observed for higher taxa do not reflect species-level environmental responses (Bevilacqua et al. 2012). Second, habitat type, as defined in the present study, does not capture the real three-dimensional nature of the habitats, such as prop roots in mangroves, leaves in seagrass beds, and crevices in coral reefs. Sampling those microhabitats could add a considerable number of epiphytic and cryptic species and substantially increase habitat-level diversity estimates. The sampling of these associated structures should be accomplished with different devices according to the physical structure of the habitats.

Sediment variables, such as grain size and organic content, appear to be meaningful predictors of community structure and diversity of higher taxa. This outcome is not necessarily surprising given that these local environmental variables are correlate with pore-water chemistry (e.g., oxygen and sulfur) and physical setting (e.g., mobility and turbidity), factors that exert important effects on benthic organisms (Gray and Elliot 2009).

At the regional scale, such as among gulfs, some trends in total macrobenthic density emerge. Except on the reefs, the density of macrobenthos was lowest in Ana María and highest in Guanahacabibes. This density trend could reflect deleterious effects of historical fisheries. Soft bottoms in Ana María Gulf have been subjected to shrimp trawling, an activity that exerts strong physical influence on benthic communities found around shrimp grounds and adjacent habitats (Gray et al. 2006). Lobster fisheries in Batabanó could have also contributed to the depletion of macrobenthos in habitats of the inner shelf, such as mangroves, seagrass beds, and mud bottoms, due to the physical impact of fishing devices, such as artificial shelters or *casitas*, on the seafloor or historical overfishing that could have changed the structure of local benthic communities. Explicitly designed studies comparing fishing and no-fishing zones are needed to test the impact of bottom fisheries on the Ana María and Batabanó regions. In the three studied gulfs, the reefs were included within protected areas and avoided by commercial fishers, further supporting the notion that regional differences in non-reef habitats could be due to human activities.

Habitat type accounted for a minor component of variance (<20% of ECV) in diversity within and among gulfs. We postulate that high within-habitat heterogeneity, ecological drift, and dispersal may all be possible explanations for the negligible role of environmental variables in affecting the structure of faunal assemblages across habitats. In an extensive study of the Gulf of Batabanó, Hoskins (1964) indicated that

salinity, median grain size, and hydrodynamics were important drivers of mollusk assemblages. However, our study did not find evidence supporting the claim that salinity or grain size strongly influences present-day mollusk assemblages. Further studies assessing hydrodynamics at the regional scale are needed to address this issue more rigorously. Species composition appears to have shifted in the Gulf of Batabanó, with relatively few species observed both in the Hoskins' surveys (1956) and in our 2012–2014 surveys. Possible causes of these differences may be methodological, such as different seasons of sampling or processing protocols. However, historical data on mollusk diversity based on dated cores did not provide any compelling evidence for a historical decline in the regional diversity of mollusk communities (Armenteros et al. 2012).

Habitat selection played a more relevant role in the distribution of functional groups of mollusks. The low relative abundance of herbivorous and epifaunal forms in mud bottom habitats likely reflects the lack of vegetation and the presence of more homogeneous substrate, whereas the high proportion of carnivorous mollusks might reflect the abundance of sponges and other encrusting organisms that tend to live on mangrove prop roots.

Individual gulfs harbor some unique species and thus regional species diversity (105 species) is higher than the biodiversity of each gulf (Ana María: 39, Batabanó: 40, and Guanahacabibes: 59 species). This result may reflect undersampling of rare species, as suggested by the high number of species represented by only one or two specimens. The other plausible explanation for higher regional diversity is limited dispersal among gulfs because of substantial geographic distances and physical barriers, which include deep-water habitats that separate Ana María and Batabanó, and the Cuba mainland that separates Batabanó and Guanahacabibes (García-Machado et al. 2018). The postulated isolation of local species pools is further supported by our data, which indicate that only two out of 105 species were common to all three gulfs (*Parvilucina* sp. and *C. regulare*).

The three studied gulfs support diverse macrobenthic communities (22 higher taxa), display high within- and between-habitat variability, and may be affected by regional stressors such as fisheries. When compared to habitat type, environmental variables such as organic content and grain size appear to play more important roles in spatial structuring of the macrobenthos. The effects of habitat selection and measured environmental variables on mollusk assemblages were negligible, indicating that within-habitat heterogeneity, drift, and dispersal may be affecting those highly diverse assemblages (103 species in a data set of only 381 individuals).

Despite data limitations, the results provide useful, if tentative, assessments on the importance of habitat selection and allowed us to evaluate a regional-scale quantitative bio-inventory of macrobenthic communities with a focus on mollusks. This report represents a starting reference point for conducting future investigations in the region. Based on results presented here, we suggest three research directions for the future: (1) to explore the effects of fisheries on benthic communities at relevant spatial scales; (2) to describe species richness and variation of mollusk assemblages with a sample size of at least 100 individuals per site to tackle the high diversity and rarity of species; and (3) to improve sampling within habitats based on finer sub-habitat partitioning with an emphasis on structurally complex microhabitats, such as mangrove prop roots and seagrass leaves.

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