

Research Article

Benthic Macrofauna Associated with Submerged Bottoms of a Tectonic Estuary in Tropical Eastern Pacific

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The composition and distribution of the main associations of submerged macrobenthos of *Bahía Málaga* (Colombian pacific coast), were studied in relation to the distribution of hard and soft substrates and some abiotic factors. Eight localities were sampled during six months: three in the external border of the estuary and five in the inner part. In total, 728 organisms were registered, belonging to 207 species, 132 genera, 86 families, and 14 orders of six invertebrate groups (Porifera, Cnidaria, Polychaeta, Mollusca, Crustacea, and Echinodermata). The submerged bottoms presented soft and hard substrates, with rocks and thick sand in five sites, soft bottoms with fine sand in one, and soft bottoms with slime and clay in two. The temperature and salinity values were higher in the external localities, while dissolved oxygen and pH were higher in the internal localities. The localities with hard substrates presented the highest richness of species while the soft substrates, were characterized by a paucity of species and individuals. The similarity classification analyses showed two groups: one characterized by having 61 species in common and high richness with 113 exclusive species. The other group with low diversity and richness values, 37 species in common and 23 exclusive species.

1. Introduction

Four main estuarine types are recognized: drowned river valleys (coastal plain estuaries), lagoons (sand bar or barrier island estuaries), fjords (glaciers originated estuaries), and tectonic estuaries [1, 2]. The latter is caused by tectonic processes such as faulting, gravels formation, landslide, volcanic eruption, and marine erosion. Drowned river valleys and lagoons are characterized by soft substrates, mud or sand bottoms, while tectonic estuaries present higher diversity of substrates, including rocky shores, and cliffs, and consequently more coastal ecosystems. These ecosystems are comprised of a high variety of habitats with different types of substrate, bottom topography and sediment types, presence of vegetation cover and biogenic structures, resulting from erosion processes, river fluxes, and mangrove leaves decomposition.

As a result of the habitat diversity and its interaction with the environment, benthic (epi- and endobenthic) communities differ in taxonomic composition, specific abundance and functional role of organisms [3, 4]. Knowledge of the abundance patterns and taxonomic composition of the benthic communities and their trophic relationships is important to reveal their functional role [5]. The main factors that influence the composition of the benthic communities are amount and size of substrate particles, sedimentation rate, amount of organic matter, and upwelling currents. In the coastal zones, variations of salinity, temperature, and dissolved oxygen in the water-sediment interface are also important.

Benthic organisms are used as indicators of oceanographic conditions and abnormal deposits, as well as of natural and/or anthropogenic disruptions and are occasionally used to monitor and evaluate conservation programs in some

parts of the world [6–8]. In the eastern tropical Pacific, these communities have mainly been studied in Costa Rica [9, 10], Perú [11, 12], and Chile [7, 13, 14].

Despite the importance of benthic communities, and the high diversity of habitats available for them in tectonic estuaries, macrobenthic assemblages associated to this type of estuary have received less attention, compared with other estuaries such as fjords and coastal plains or other coastal ecosystems such as rocky shores or coral reefs. There are few exceptions, for example, San Francisco Bay (USA) where benthic communities have been studied intensively in relation to pollution [15–18]). In tropical zones, the only tectonic estuary relatively well studied for benthic assemblages is the Gulf of Nicoya in Costa Rica [9, 10, 19, 20].

In the Tropical Eastern Pacific estuaries and the Colombian Pacific coast, most of the studies on distribution patterns and abundance of species have been focused on mangrove benthic communities and other intertidal ecosystems such as sandy beaches, muddy flats, mangroves, and rocky cliffs and shores [8, 21–26].

For submerged bottom communities, the few studies performed have been carried out in the coastal plain estuary of *Buenaventura* [8, 27] and submerged bottoms of sand, mud, rocks, and coral reefs of *Gorgona Island* [28]. Little is known about the macrobenthic fauna of tectonic estuaries and even less is known about the sublittoral fauna. The main purpose of this investigation was to determine the taxonomic composition, distribution, and abundance patterns of the species inhabiting a tectonic estuary in relation to other types of estuaries. The questions examined were (1) what is the assemblage structure of the submerged hard and soft bottom macrofauna in Bahía Málaga, an important tectonic [29] estuary of the Pacific coast of Colombia? (2) Are these assemblages different from the benthic macrofauna of other tectonic estuaries or from other types of estuaries of the Tropical Eastern Pacific? (3) How do the assemblages vary in relation to the differences in substrates and water environmental variables, following the estuarine gradients? (4) How are benthic assemblages of Málaga Bay compared with other estuaries of the world?

2. Materials and Methods

2.1. Study Area. This research was conducted in *Bahía Málaga* (4°05' N and 77°16' W), a tectonic estuary located on the Pacific coast of Colombia (Figure 1). The bay has a length of approximately 25 km and an area of 136 km² and is surrounded by rocky cliffs. The tidal current flux is ca. 20 000 m³s⁻¹ between the bay and the open ocean [30]. The north border is marked by a geological fault (Málaga Fault) and the southern border is limited by the uplifting of Pichidó Isthmus. At present, there are important erosive processes along all borders of the bay. These processes are mainly cliff erosion in the internal border of the bay with the fall of rocks caused by hydraulic action, wave pounding, bioerosión, and beach erosion in the external border by wave action.

The external border is composed of shallow sandy zones and rocky islands. The internal region has shallow bottoms

and rocky islands surrounded by muddy flats. The bay has two channels, one with hard substrate and average depths of around 15 m (maximum approximately 40 m), and the other with soft sediments and depths near 5 m. These channels converge in the narrow part of the bay, increasing the speed of the tidal current, which reaches up to 2.0 m s⁻¹ [30–32]. Water temperatures range from 24 to 30°C. The bay is subjected to a relatively large semidiurnal tidal range (macrotidal, ca. 4 m) which affects both salinity and depth [33, 34]. Despite the high rainfall (*Bahía Málaga* is located near to one of the most humid low land places in the world), there are few rivers, and consequently, the fresh water input is low compared to most estuaries of the Pacific coast of Colombia. Climatic conditions vary from less humid (dry) in June–July and December–January to more humid (rainy) in February–May and from September to November [35].

Bahía Málaga contains many of the habitats and marine life zones of the Pacific coast of Colombia [8] (Figure 1). The western external zone of the bay is surrounded by sandy beaches (*Juanchaco* and *Ladrilleros*) formed by the accumulation of sand of continental origin that is transported by rivers and marine hydrodynamic processes. The southern and central regions have borders constituted by consolidated sediments (mudstones, siltstones) of Tertiary origin, giving the bay a rocky appearance, with dense forests and large trees. The rocky coasts generally form high cliffs, sometimes separated by the sea, or by rocky, sandy, or muddy beaches between tides. Inside the bay, several small rocky islands are found, which were separated from the mainland by erosion (e.g., *Isla Palma*, *Los Monos*, and *Curichichi*) and by emersion (*La Plata*) [29].

2.2. Sampling and Data Analysis. Sampling was conducted for 14 months, in the following localities: *Los Negritos* (St. 1), *Isla Palma* (St. 2), and *La Barra* (St. 3) in the external part of the bay; *Los Negros* (St. 4), *Los Monos* (St. 5), *Curichichi* island (St. 6), *Mayordomo* (St. 7), and *La Plata* island (St. 8) in the internal part (Table 1). All samples, from hard and soft bottoms, were taken from depths between 2 and 10 m (Figure 1).

Due to some of the features of the bay (e.g., high sedimentation, mixed bottoms of hard and soft substrates, and turbid waters) and the paucity of benthic species which are distributed in patches, it is very difficult to use only one sampling method (transects in scuba diving or dredges) to obtain a global and true vision of the biodiversity of the zone. Hence, it was necessary to combine several sampling techniques. Some localities (Sts. 1, 2, 5, 6, 7, 8) were sampled using transects (30 m length) surveyed by snorkeling and scuba diving. The transects were marked by a line and the sampling was conducted on both sides, surveying two meters to each side. Along each transect (30 × 4 m), all organisms were collected. All transects had two replicates. Others (Sts. 3 and 4) were sampled with a “change” (artisanal bottom trawling net used by local fishermen). Since the net was damaged by the rugged bottom, it was possible to take only a few samples. Additionally, we used a Petersen dredge of 0.05 m² (2500 mL) for sampling the sediments and endobenthic

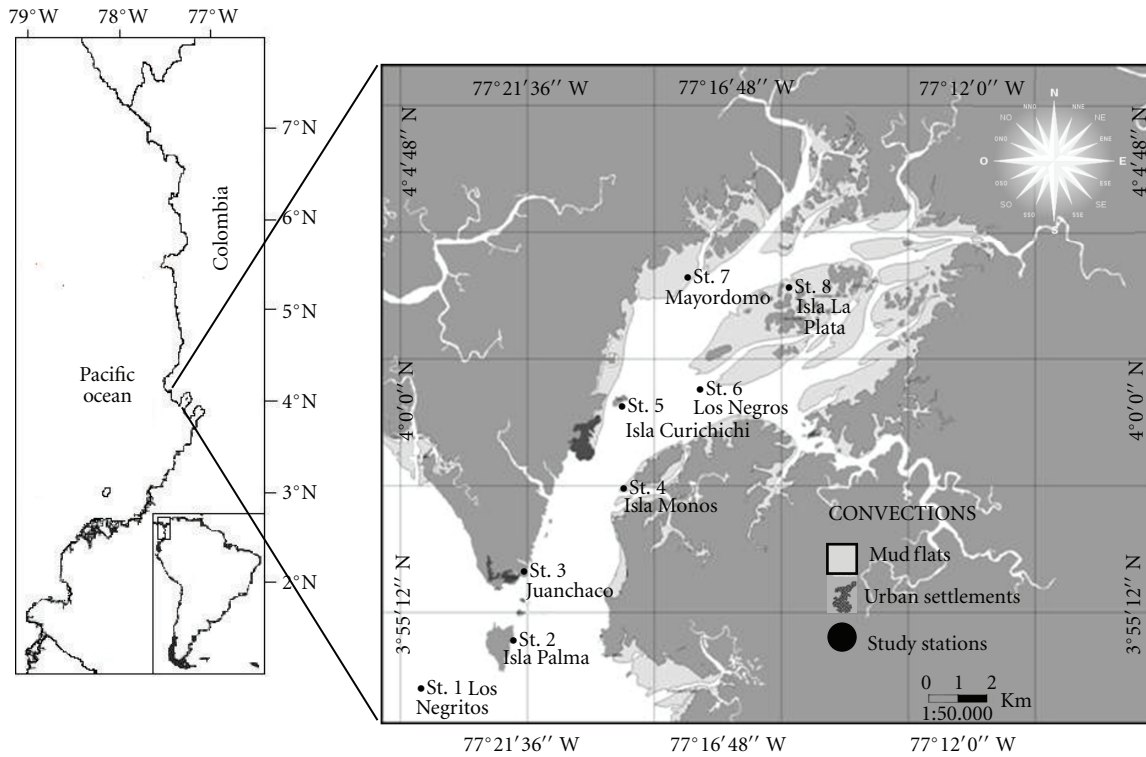


FIGURE 1: Study area: Bahia Málaga, Pacific coast of Colombia, the black dots correspond to the sampling stations.

TABLE 1: Geographical localization, abbreviations, and average depth of studied stations.

ID	Locality	Abbreviation	Depth (m)	Latitude N	Longitude W
St. 1	Los Negritos	LNE	3.5	3°53'	77°24'
St. 2	Isla Palma-Morro Chiquito	IPM	3.7	3°54'	77°21'
St. 3	La Barra-Juanchaco	BJL	3.4	4°01'	77°28'
St. 4	Isla Monos	MON	8.7	3°58'	77°28'
St. 5	Los Negros	LNG	2.7	3°59'	77°17'
St. 6	Isla Curichichi	CHI	2.8	3°59'	77°19'
St. 7	Mayordomo	MAY	3.2	4°01'	77°18'
St. 8	Isla La Plata—Isla Grande	ARP	2.9	4°03'	77°15'

fauna of soft bottoms. For the different sampling gear used in the study, we will use the term assemblages when referring to our study.

Salinity, dissolved oxygen, conductivity, temperature, and pH were used to evaluate the physicochemical parameters of the water column. For the sediment analysis, the procedure of sifting based on the Wentworth scale [36] was employed, in which the sediments were dried at air temperature. The results were shown in percentages for each particle size. The samples were then heated to 100°C to reach a constant weight for the calculation of organic matter.

The biological samples were fixed *in situ* with 10% neutralized formalin. Next, the macrobenthos was separated using a 0.5 mm mesh sieve [36, 37] identified, and the number of individuals in the total area was determined. Finally, the organisms were preserved in 70% alcohol or 10% buffered formalin (depending on the taxonomic group) and

placed in the reference collection of the *Universidad del Valle-CRBMUV* “Univalle,” the *Museo de Ciencias Naturales del Departamento del Valle-IMCN* “Inciva,” and the *Museo de Historia Natural Marina de Colombia-MHNMC* “Invemar.”

The obtained data were arranged in matrices of abundance for each species (individual numbers per sampled area, 0.10 m²) for each locality and then compared with the other localities. The spatial distribution pattern of the community was estimated according to presence-absence data of species (due to the high species richness, low species abundance, patchiness in the distribution, and different types of sampling). The relationship between localities was studied using a hierarchical agglomerate clustering technique (cluster analysis) and unweighted pair group average linking method (UPGMA) [38] using the Bray-Curtis similarity index [39]. Ordination using nonmetric multidimensional scaling analysis (nMDS) was performed to determine the variation of

species composition [40] and confirm the groups formed by the cluster. Then, a superimposed analysis was done using nMDS, to find the relationship within the group with the physicochemical parameters [41]. Finally, a modification of inverse analysis was utilized to find, by composition and relative frequency, the key species in each group and to determine which of these species were exclusive or generalist [42]. The results were analyzed including abiotic variables (sediments and water conditions) for each locality. Multivariate analysis was applied for the assemblage structure with PRIMER software (plymouth routines in multivariate ecological research).

3. Results

3.1. Environmental Variables

3.1.1. Physicochemical Parameters. The four physicochemical variables of the water column (temperature, salinity, pH, and dissolved oxygen) showed weak gradients along the bay. Highest average values of temperature and salinity were found at St. 1, showing the effects of tropical marine waters on the external zones. The lowest values for temperature and salinity were found at St. 7 and for pH and dissolved oxygen at St. 4 (Table 2). The average surface water temperature in all localities varied between 26.8 and 30.6°C. The average salinity is higher than 20 (in practical unities of salinity) along the bay at high tide as well as low tide, except in two stations of the inner part: St. 8 and St. 4. The low salinity at low tide is due to fresh water inputs by inner creeks in St. 8 and of the La Sierpe River in St. 4. The external part (St. 3) is also affected by fresh water inputs, at times when the San Juan River discharge arriving by the northern part causes important decreases in salinity. The highest values of dissolved oxygen were found at Sts. 2, 3, and 6 (>7.0 mg/L in high tide). In the other stations, values were uniform along the bay and throughout the time of study.

3.1.2. Sediment Composition. Submerged bottoms are very heterogeneous in *Bahía Málaga*; the external zone contains sandy substrates, enriched by muddy material or detritus originated from mangrove decomposition (St. 3) and rocky substrates forming islands or submerged reefs (Sts. 1, 2). The internal zone has mainly muddy substrate, with detritus coming from decomposition of continental mangroves (Sts. 7, 5) and submerged and intertidal rocks originated by erosion (Sts. 5, 6, 8) near to emerged islands and/or independent accumulation of rocks together with mud in the central part of the bay (St. 4, 5, 6) (Figure 2).

Sediment analysis showed that bottoms with coarse particles (gravel, coarse sand) are found mainly in St. 1, 2, 5, 6 and 8, soft bottoms with fine sands in St. 3 and 7 and slime and clays in St. 7 and 8 (Figure 3). Coarse sand is very abundant in St. 1, gravel in St. 6, fine sand in St. 3, and lime and clay in St. 4. Organic matter values of the sediments range between 0.2 and 4.4%, with the highest in St. 8 and lowest in St. 7. Selection factor of sediment particles are variable (Table 3).

TABLE 2: Physicochemical parameters for each locality in Bahía Málaga estuary from May 2006 to May 2007.

Station	Temperature (°C)	Salinity	Dissolved oxygen (mg/L)	pH
St. 1	29.7–31.5	25.0–28.0	6.6–7.2	8.3–8.4
St. 2	28.0–28.6	21.6–27.0	6.4–7.1	8.2–8.3
St. 3	27.2–28.2	15.3–23.4	6.3–7.5	8.1–8.1
St. 4	28.7–30.1	17.0–24.8	6.4–6.3	7.7–8.2
St. 5	28.7–29.1	21.6–25.8	6.3–6.7	8.0–8.3
St. 6	28.5–29.0	22.4–27.7	6.2–7.3	8.0–8.4
St. 7	26.8–28.5	20.6–22.1	6.5–6.6	8.0–8.2
St. 8	28.8–30.4	18.6–24.1	6.0–7.0	7.8–8.1

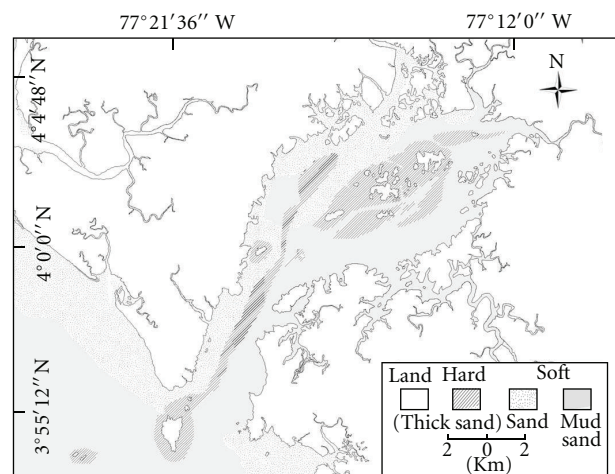


FIGURE 2: Distribution of substrate types in submerged bottoms of Bahía Málaga estuary.

3.2. Assemblages Analysis

3.2.1. Taxonomic Characterization. A total of 728 individuals from 207 species, 132 genera, 86 families, and 14 orders of six taxa of invertebrates (Table 5) were obtained in both, soft and hard bottom samples (Table 4). Mollusca dominated in number of species comprising 66% (137 spp.) of the macrofauna, crustaceans constituted 19% (39 spp.), Echinodermata 9% (19 spp.), Polychaeta 3% (6 spp.), Porifera 2% (4 spp.), and Cnidaria 1% (2 spp.). The localities that presented the highest number of species were St. 1 (28% of the species), St. 4 (18%), St. 6 (13%), and St. 2 (15%). The low number of species and individual polychaetes in relation to mollusks could be explained by the presence of hard substrates of different sizes mixed with the mud and sand in this tectonic estuary. These hard substrates are suitable habitat for some species of gastropods.

In terms of relative specific abundance, the organisms were comprised of mollusks (56%, 407 individuals), crustaceans (15%, 109), echinoderms (13%), corals (9%), sponges (5%), and polychaetes (2%). The most abundant groups of species were: *Acanthais brevidentata*, *Cardita affinis*, *Crepidula aculeata*, *Natica unifasciata*, *Nemocardium* sp.,

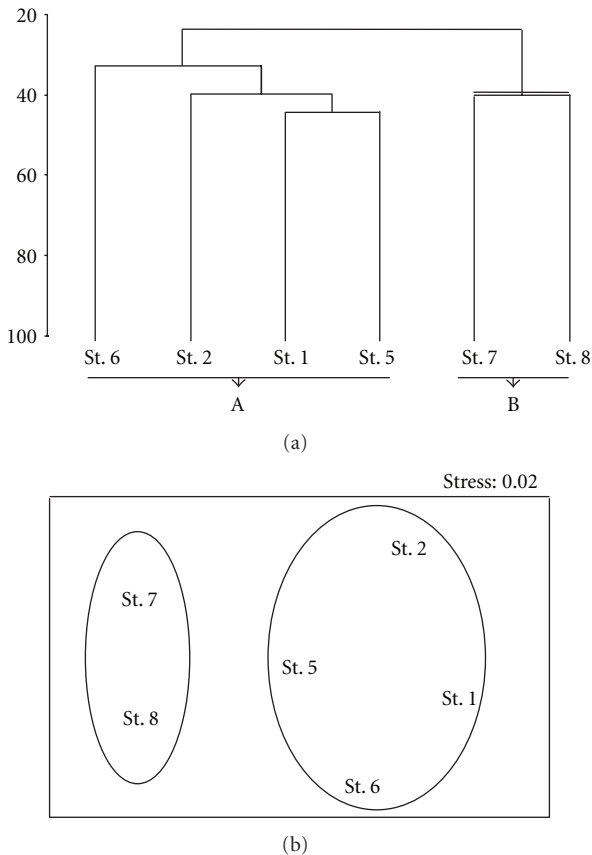


FIGURE 3: Classification and ordination analysis of studied stations made from absence-presence data of species matrix for the studied stations in Bahía Málaga estuary: (a) Bray-Curtis similarity dendrogram and (b) nMDS ordination (stress value <math>< 0.02</math>).

TABLE 3: Particle size distribution (%), organic matter (%), and particle selection factor of sediments of the stations of Bahía Málaga estuary.

Particle type	Station							
	St. 1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7	St. 8
Gravel	26.5	28.6	0	0.9	29.4	32.2	0	24.8
Very coarse sand	6.1	16.5	0	3.2	35.2	20.8	0	23.7
Coarse sand	40.6	24.1	0.8	5.0	25.5	29.5	6.0	32.0
Middle sand	19.0	18.7	26.4	6.3	4.6	12.9	3.9	9.2
Fine sand	7.5	6.8	72.5	62.7	4.0	1.5	79.2	6.6
Slime and clay	0.2	3.1	0.2	21.1	1.0	0.8	8.4	3.4
Organic Matter	3.8	3.2	1.4	1.9	3.4	4.3	0.2	4.4
Particle Selection	1.4	1.5	0.7	0.7	0.6	1.1	0.5	1.0

Nerita funiculata, *Petalocochus complicatus*, and *Zonaria robertsi*; (Mollusca); *Alpheus cylindricus*, *A. formosus*, *Hepatus kossmanni*, *Pachycheles panamensis*, *Petrolisthes edwardsii*, *P. galathinus*, and *P. haigae*; (Crustacea); *Echinometra vanbrunti*, *Hesperocidaris asteriscus*, *Holothuria impatiens*, *Ophiocoma aethiops*, *Ophioderma panamensis*, *Ophionereis*

annulata, *Ophiotrix spiculata*, *Pharia pyramidata*, and *Phartaria unifascialis* (Echinodermata); *Eunice* sp. and *Platynereis* sp. (Polychaeta); *Leptogorgia alba* and *Pacifigorgia eximia* (Cnidaria) and *Aplysina* (or *Verongia*) sp. (Porifera). The most common species (being present in 40% or more of the samples) were Mollusca: *Cardita affinis*, *Thais melones*, *Natica unifasciata*, and *Nerita funiculata*; Crustacea: *Alpheus wickstenae*, *Petrolisthes nobilii*, *P. armatus*, *Panopeus chilensis*, *Panopeus purpureus*, and *Clibanarius panamensis*; Cnidaria: *Leptogorgia alba* and *Pacifigorgia eximia*; and Porifera: *Aplysina* sp.

3.2.2. *Spatial Distribution Patterns.* The two localities sampled with fishing nets (Sts. 3 and 4) were neither included in the nMDS analysis nor in the cluster analysis because of differences in the sampled areas, capture time, frequency of sampling, and bottom composition (fine sand and/or slime and clays in Sts. 3 and 4 versus gravel and coarse sand in other localities). After the cluster analysis, the other six localities can be separated into two groups (Figure 3): *Group A* contains four localities with more than 40% similarity, two located outside the bay (Sts. 1 and 2) and two on the inside with little more than 40% similarity (Sts. 5 and 6), with high richness (between 45 and 92 species); the four stations shared 61 species; *Group B* containing two localities with 40% similarity (Sts. 7 and 8), in inner parts of the bay, these stations were characterized by low richness (between 23 and 57 species) and they shared 37 species. The inverse analysis (Table 5) presents 113 exclusive species for Group A, 23 species for Group B, and 41 frequent species. The most frequent species were *Bursa corrugata*, *Cantharus ringens*, *Zonaria robertsi*, and *Macrocypraea cervinetta* in Group A; *Corbula biradiata* in Group B.

3.3. *Relation between the Assemblages and Environmental Variables.* The environmental variables superimposed on the nMDS revealed that the sediment characteristics are the most important parameters determining assemblage structure of macrobenthos of Bahía Málaga. Group A (Sts. 1, 2, 5, 6) displays high values for hard or thick sediments (gravel and coarse sand), while Group B displays mixed soft bottoms: fine sand, slime and clay in St. 7 and slime and clay mixed with gravel in St. 8. In addition, Group A shows high values for organic matter and the particle selection coefficient with respect to the other localities (Table 2). The physicochemical parameters of water (temperature, dissolved oxygen, and pH) do not have a strong influence on the groups, although the values of salinity for Group A are slightly greater than those for Group B (Figure 4).

4. Discussion

This study evaluates the invertebrate (macrofauna) assemblage structure of the submerged bottoms of a tectonic estuary: Bahía Málaga in relation to several physicochemical characteristics. Since this is a macrotidal estuary, intertidal areas are wide, and they have been well studied. The first observation about this estuary is the unusually high species

TABLE 4: Number of species and families (parenthesis) of taxonomic groups in the sampled localities of *Bahía Málaga* estuary.

Taxa	St.1	St. 2	St. 3	St. 4	St. 5	St. 6	St. 7	St. 8
Crustacea	13(9)	19(14)	8(7)	2(2)	6(6)	10(8)	3(3)	4(2)
Mollusca	40(28)	20(13)	13(12)	11(10)	23(13)	28(23)	39(23)	3(2)
Polychaeta	4(4)	1	0	1	0	5(5)	3(3)	0
Echinodermata	10(8)	3(3)	1	1	4(4)	2(2)	2(2)	1
Cnidaria	2(2)	1	2(2)	0	1	1	1	0
Porifera	0	1	0	0	2(2)	1	1	0

richness compared to the coastal plain estuaries of this area (625 species of macroinvertebrates [31], 207 present in submerged substrates) in relation to 126 in the estuary of Buenaventura Bay [27], 78 in the Dagua River estuary [26] and 36 in the San Juan river [43], which are located near *Bahía Málaga*. As was shown by Gray [44] worldwide, by Guzmán-Alvis et al. [45] for the Caribbean coast of Colombia and by Cortés [25] and Cantera [8] for other zones of the Pacific coast of Colombia, the most important factors determining the structure of these tropical benthic assemblages are sedimentological variables. The particularly high species richness of the submerged bottoms of this estuary can be explained by two factors: (1) the predominance of hard substrates such as rocks, gravel and coarse sand, where there are 151 species, of which 113 are exclusive (70 molluscs, 24 crustaceans 14 echinoderms, 4 polychaetes and 1 sponge); (2) the relatively high salinity. Both conditions are not common in Tropical Pacific estuaries. Species richness is lower in areas with predominance of soft bottoms (fine sand, slime, and clays) and low salinities, where only 57 species were found, of which 23 were unique (20 mollusks, 2 crustaceans, and 1 soft coral). Both conditions (hard substrate and high salinity) are infrequent in most estuaries of the Pacific coast of Colombia and other regions of the Tropical Eastern Pacific, because the high precipitation in the zone (more of 6000 mm yr⁻¹) causes high sedimentation and lower salinity.

The localities in *Bahía Málaga* with a greater percentage of soft bottoms are structurally more homogeneous and contain less diversity, while the ones with greater variety in the size of the sediment particles have a structurally heterogeneous habitat and therefore more diversity. The composition and selection of bay sediments are related to the patterns of current circulation. In the internal region of *Bahía Málaga*, high percentages of fine sand, slime, and clay are accumulated due to weaker tidal currents, at the same time the effect of freshwater is greater. In the external localities of the bay (and in the islands located in the Central channel), there are hard bottoms with abundant boulders, gravel, and coarse sand. Fine sediments are absent mainly due to the influence of tidal currents and stronger swells. The values of organic matter in the sediments are similar to previous studies in these zones [8] and to previously reported values in tropical zones [46]; nevertheless, the high levels found in this study in some areas can be explained by the sediments contributed by the micro-upwellings in the estuary [21] and by areas adjacent to river discharge [47].

Variables of sea water, usually very important in estuarine environments especially in coastal plain estuaries, have minor importance in the distribution of macrobenthic assemblages of the tectonic estuary of *Bahía Málaga*. Some of these conditions (e.g., temperature, dissolved oxygen, and pH) are strongly variable due to tidal changes, high turbidity, high organic decomposition, and freshwater input as is the case in the majority of the Pacific estuaries of Colombia, in which differences in processes and conditions exist in different times during the day or in different seasons, allowing a wide range of physiologically adaptive macrofaunal species to live there [21]. In this way, the distribution of benthic assemblages is influenced only by salinity where substrate conditions are very similar (e.g., organisms highly dependent on seawater, such as echinoderms and gorgonians, are more abundant in St. 1, with salinity between 25 and 28 than in St. 5, with salinity between 21 and 25). These groups are completely absent in stations with salinity values lower than 20 (Sts. 7 and 8) in the daily variations and high sedimentation rate. As the bay is a complex estuary, with inputs of freshwater in different parts, not only in the inner regions, the parameters are not of equal magnitude in the different sectors of the bay, and therefore, fluctuations over short periods of time affect the spatial distribution of organisms in patches; that is why they do not follow the classic gradient found in other types of estuaries with marine fauna in the external parts of the bay and freshwater fauna in the inner zones [48]. In a few particular cases, some of the variables become significant; for instance, the high temperature (nearly 29°C) and the low oxygen concentration (less of 4 mg L⁻¹) reached at the surface of muddy plains during low tides in shallow zones, can be related to the very low diversity and abundance of species in the internal localities of the estuary. The shape and bathymetry of the bay also cause fluctuations in the sediment structure, because there are different velocities of currents, with some zones exposed to strong currents in two channels at both sides of the bay, causing erosion, and some sedimentation zones with low currents in the central area of the bay and at the border where mangroves are abundant. These fluctuations have been observed also in other estuaries of the world, for example, in the Sao Sebastian Chanel in Brazil, San Francisco Bay where the variation in the types of sediment determines changes in the physical-chemical variables of the zones, giving important and indirect causes in the patterns of community establishment [47].

TABLE 5: *Exclusive species of Group A. **Exclusive species of Group B. ***Frequent species of Groups A-B.

Localities/species	LNE	LNG	CHI	MAY	MON	IPM	BJL	ARP
PORIFERA								
<i>Placospongia carinata</i> *	1	1	1					
<i>Verongia</i> sp.***		1	1	1				1
CNIDARIA								
<i>Leptogorgia alba</i> ***	1	1	1	1		1		1
<i>Pacifigorgia eximia</i> ***	1	1	1	1				
<i>Tubastrea coccinea</i>							1	
<i>Renilla</i> sp.**				1			1	
POLYCHAETA								
<i>Eunice</i> sp.***			1	1				
<i>Platynereis</i> sp.***			1	1				
<i>Sabella</i> sp.*			1					
<i>Notomastus</i> sp.*			1					
<i>Megalomma</i> sp.*			1					
<i>Palolo</i> sp.*						1		
MOLLUSCA								
<i>Acirsa murrha</i> *		1						
<i>Acanthais brevidentata</i> ***	1		1				1	1
<i>Acteocina</i> sp.					1			
<i>Anachis</i> sp.*						1		
<i>Anachis pygmaea</i> *			1					
<i>Anadara Formosa</i>							1	
<i>Arca mutabilis</i> *	1							
<i>Barbatia reevana</i> *		1	1					
<i>Bulla gouldiana</i> *	1		1					
<i>Bulla punctulata</i> *			1					
<i>Bursa corrugata</i> *	1	1	1			1	1	
<i>Bursa nana</i>							1	
<i>Caecum undatum</i> *	1							
<i>Caecum</i> sp.***			1	1				
<i>Cantharus</i> sp.**				1				
<i>Cantharus elegans</i> *						1		
<i>Cantharus ringens</i> *	1	1	1			1	1	
<i>Cantharus sanguinolentus</i> *	1					1		
<i>Cardita affinis</i> ***		1	1	1		1	1	
<i>Cardita spurca beebei</i> **				1				
<i>Cardita radiata</i> *		1	1				1	
<i>Cardita</i> sp.					1			
<i>Cassis centiquadrata</i> *	1							
<i>Cheilea cepacea</i> ***			1	1				
<i>Cheilea corrugata</i> **				1				
<i>Chione amathusia</i> *			1				1	
<i>Chione compta</i> *	1							
<i>Chione gnidia</i> *		1						
<i>Chione subimbricata</i> *		1				1		
<i>Chione subrugosa</i> ***			1	1				1
<i>Cerithium adustum</i> *	1							
<i>Clementia solida</i> **					1			1
<i>Crepidula aculeata</i> ***			1	1			1	1
<i>Crepidula striolata</i> **				1				
<i>Crucibulum scutellatum</i> *	1	1						
<i>Crucibulum spinosum</i> ***			1	1		1		

TABLE 5: Continued.

Localities/species	LNE	LNG	CHI	MAY	MON	IPM	BJL	ARP
<i>Crucibulum personatum</i> ***			1	1				
<i>Columbella strombiformis</i> *	1					1		
<i>Conus patricius</i>							1	
<i>Corbula biradiata</i> **				1				1
<i>Corbula</i> sp.					1			
<i>Cyclinella sacata</i>					1			
<i>Cymatium vestitum</i>							1	
<i>Cypraea arabicula</i> *	1		1					
<i>Diodora inaequalis</i> *			1					
<i>Diodora pica</i> *	1							
<i>Donax carinatus</i> ***			1	1				
<i>Dosinia</i> sp.*			1					
<i>Ficus ventricosa</i>							1	
<i>Fissurella</i> sp.*		1						
<i>Fissurella</i> sp. 2*			1					
<i>Fissurella longifissa</i> **				1				
<i>Fissurella virescens</i> *	1		1			1	1	
<i>Fissurella microtrema</i> *	1		1					
<i>Florimetis cognata</i> **				1				
<i>Florimetis dombeyi</i> **				1				
<i>Glycymeris</i> sp.**				1				
<i>Grandiarca grandis</i> *		1			1			
<i>Hindsiclava resina</i> **				1				
<i>Hipponix grayanus</i> *	1							
<i>Hipponix panamensis</i> *	1		1					
<i>Isognomon recognitus</i> *						1		
<i>Latirus concentricus</i> *	1							
<i>Latirus hemphilli</i> *		1						
<i>Latirus mediamericus</i> *	1	1	1					
<i>Leptopecten tumbezensis</i> *						1		
<i>Lithophaga plumula</i>							1	
<i>Macrocallista</i> sp.***		1		1		1		
<i>Malea ringens</i> *			1				1	
<i>Megacypraea cervinetta</i> *	1	1	1			1		
<i>Megatella</i> sp.**				1				
<i>Melongena patula</i> *	1						1	
<i>Mitra</i> sp.*			1					
<i>Mitra lens</i> *	1							
<i>Modulus disculus</i> *			1					
<i>Muricanthu stradix</i> ***		1	1	1	1			
<i>Muricopsis zeteki</i> *	1	1				1		
<i>Nassarius angulicostis</i> *			1					
<i>Nassarius shaskyi</i>					1			
<i>Natica broderipiana</i>					1		1	
<i>Natica chemnitzii</i>					1		1	
<i>Natica unifasciata</i> ***		1	1	1	1		1	1
<i>Nemocardium</i> sp.*		1						
<i>Nerita funiculata</i> ***	1	1	1	1	1		1	1
<i>Northia pristis</i>							1	
<i>Notoacmaea</i> sp.*	1						1	
<i>Oliva spendidula</i> *	1							
<i>Opeatostoma pseudodon</i> *	1							
<i>Papyridea aspersa</i> *	1					1		

TABLE 5: Continued.

Localities/species	LNE	LNG	CHI	MAY	MON	IPM	BJL	ARP
<i>Papyridea mantaensis</i> *	1							
<i>Pecten</i> sp.*			1					
<i>Pecten perulus</i> *		1						
<i>Pecten vogdesi</i> *		1						
<i>Petalocochus innumerabilis</i> **				1			1	
<i>Petalocochus complicatus</i> ***		1	1	1			1	
<i>Petricola exarata</i> ***			1	1				1
<i>Pholadidea esmeraldensis</i> *	1					1	1	
<i>Pinctada mazatlanica</i> ***		1			1			1
<i>Pitar aequinoctalis</i> *		1						
<i>Polinices uber</i> *			1					
<i>Polystira nobilis</i>							1	
<i>Protothaca ecuadoriana</i> *		1						
<i>Psammotreta mazatlanica</i>					1			
<i>Psammotreta viridotincta</i> ***			1	1				
<i>Pteria</i> sp.***		1			1			1
<i>Semele</i> sp.***			1	1				
<i>Scaphande cylindrellus</i> **				1				
<i>Strigilla disjuncta</i> **				1			1	
<i>Strigilla chroma</i> **				1			1	
<i>Strombus galeatus</i> *	1	1						
<i>Tagelus affinis</i> **				1	1			
<i>Tellina</i> sp.*			1				1	
<i>Tellina subtrigona</i>					1			
<i>Terebra robusta</i> **				1			1	
<i>Terebra glauca</i>					1		1	
<i>Thais biserialis</i> *	1		1				1	
<i>Thais melones</i> *	1		1				1	
<i>Thais speciosa</i> *	1							
<i>Trachycardium pistipleura</i> *	1		1					
<i>Trachycardium senticosum</i> ***		1	1	1				
<i>Trachycardium</i> sp.*		1						
<i>Trigoniocardia biangulata</i> **				1				
<i>Trigoniocardia guanacastensis</i> ***			1	1		1		
<i>Trigoniocardia granifera</i> *			1					
<i>Turbonilla</i> sp.**				1				
<i>Turritella anactor</i> *		1						
<i>Turritella leucostoma</i>					1			
<i>Tripsyca tulipa</i> *		1						
<i>Vermicularia pellucida</i> ***			1	1		1		1
<i>Zonaria robertsi</i> *	1	1	1			1	1	
CRUSTACEA								
<i>Alpheus</i> sp.*			1					
<i>Alpheus cylindricus</i> *	1							
<i>Alpheus formosus</i> *	1		1			1		
<i>Alpheus wickstenae</i> ***			1		1	1		1
<i>Ambidexter panamensis</i> ***		1		1				
<i>Aniculus elegans</i> *	1							
<i>Callinectes toxotes</i> *			1				1	
<i>Cleantioides vonprahli</i>							1	
<i>Clibanarius panamensis</i> ***			1	1	1	1	1	1
<i>Cycloxanthops vittatus</i> *	1		1			1		
<i>Daldorfia garthi</i> *	1							

TABLE 5: Continued.

Localities/species	LNE	LNG	CHI	MAY	MON	IPM	BJL	ARP
<i>Dardanus sinistripes</i>							1	
<i>Farfantepenaeus californiensis</i>					1			
<i>Gonodactylidae</i> sp.*			1					
<i>Hepatus kossmanni</i>							1	
<i>Menippe frontalis</i> *	1		1			1		
<i>Mithrax spinipes</i> *	1							
<i>Pachycheles panamensis</i> ***						1		1
<i>Panopeus chilensis</i> ***		1	1	1	1		1	1
<i>Panopeus purpureus</i> ***		1	1	1	1	1	1	1
<i>Panulirus gracilis</i> *	1	1	1				1	
<i>Petrolisthes armatus</i> ***		1	1	1	1		1	
<i>Petrolisthes nobilii</i> ***		1	1	1	1	1		1
<i>Petrolisthes edwardsii</i> ***	1		1	1		1		
<i>Petrolisthes galathinus</i>			1			1		
<i>Petrolisthes glasselli</i> *						1		
<i>Petrolisthes ortmanni</i> *	1		1			1		
<i>Petrolisthes vicarius</i> *						1		
<i>Petrolisthes haigae</i> *	1					1		
<i>Pilumnus</i> sp.*	1		1			1		
<i>Pilumnus limosus</i> *			1					
<i>Pilumnus nobili</i> *		1	1		1			
<i>Pilumnus townsendi</i> ***			1	1		1		
<i>Pinnotheres</i> sp.**				1				
<i>Pisidia magdalenensis</i> *	1		1			1		
<i>Podochela angulata</i> *			1					
<i>Squillaaculeataaculeata</i> ***			1	1			1	1
<i>Synalpheus nobilii</i> ***						1		1
<i>Synalpheu stownsendi peruvianus</i> ***	1			1				1
<i>Trizopagurus</i> sp.							1	
<i>Trizopagurus magnificus</i> *	1	1				1		
<i>Typton serratus</i> *		1	1					
<i>Upogebia thistle</i> *	1							
ECHINODERMATA								
<i>Diadema mexicanum</i> *	1							
<i>Echinometra vanbrunti</i> *	1	1				1	1	
<i>Encope</i> sp.**				1				
<i>Hesperocidaris asteriscus</i> *	1		1					
<i>Holothuria hilla</i> *	1	1	1					
<i>Holothuria impatiens</i> *	1							
<i>Holothuria inhabilis</i> *	1	1	1					
<i>Holothuria leucospilota</i> *	1	1	1					
<i>Isostichopus fuscus</i> *	1							
<i>Luidia superba</i>							1	
<i>Ophiocoma</i> sp.					1			
<i>Ophiocoma aethiops</i> *	1		1		1	1		
<i>Ophiocoma alexandri</i> *	1				1			
<i>Ophioderma panamensi</i> *	1		1					
<i>Ophionerei sannulata</i> *	1		1			1		
<i>Ophiotrix spiculata</i> ***	1		1	1		1		1
<i>Pharia pyramidata</i> *	1		1					
<i>Phataria unifascialis</i> *	1	1	1					

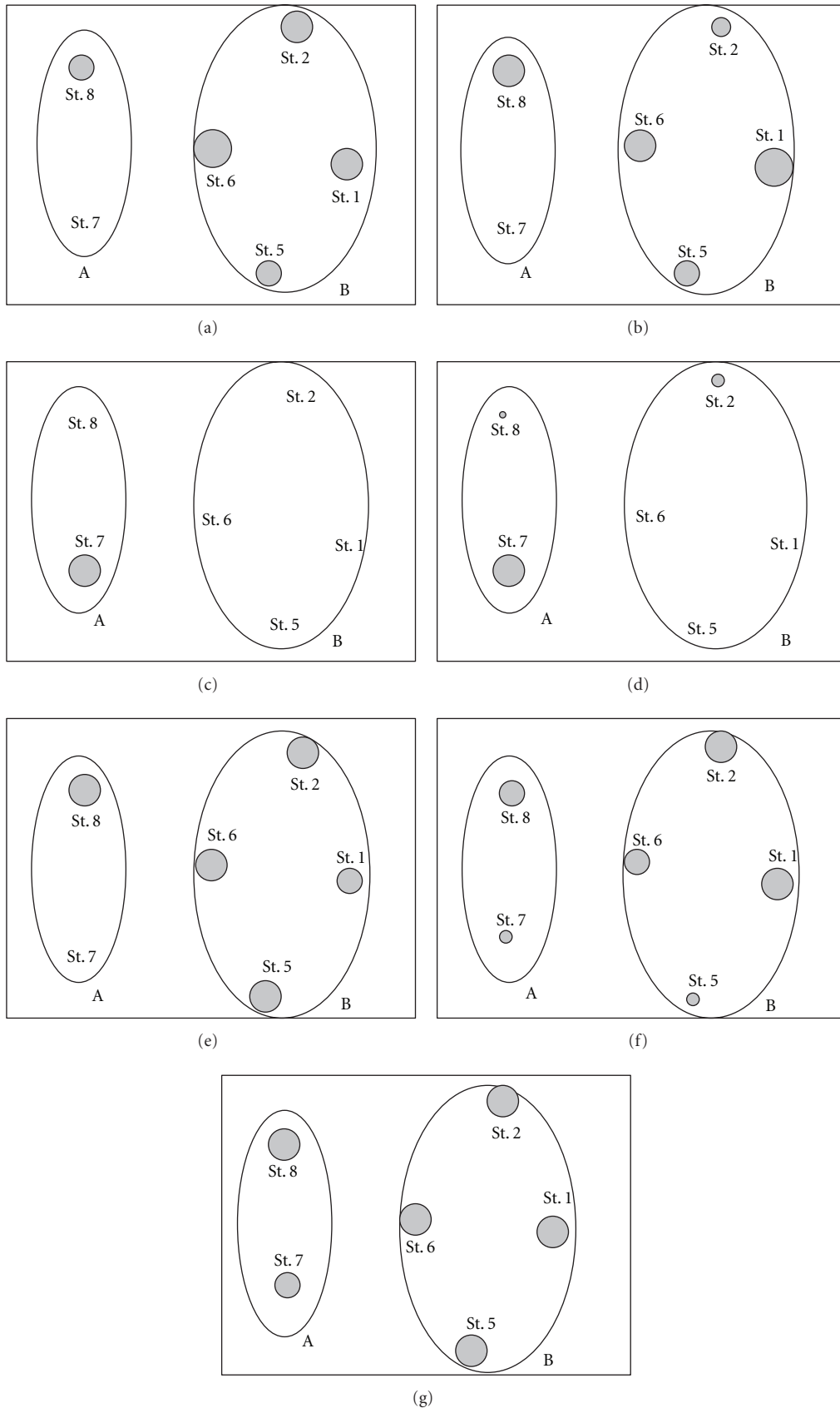


FIGURE 4: Environmental variables superimposed in each localities on frequency nMDS: (a) gravel, (b) coarse sand, (c) fine sand, (d) slimes and clays, (e) organic matter, (f) selection coefficient, and (g) salinity.

A final comparison with other tectonic estuaries (e.g., San Francisco Bay, USA or the Gulf of Nicoya, Costa Rica) shows that the benthic macrofauna is similar in their specific richness and composition although the differences in latitudinal location. A total of 537 species (taxa) have been cited for San Francisco Bay (USA) [49] and 205 (using a Smith and McIntyre bottom grab) from the Gulf of Nicoya, Costa Rica [19]. On the other hand, if we compare this tropical bay with other estuaries and coastal zones worldwide, we find a wide range in specific richness, but *Bahía Málaga* is consistently richer than others regions, for example, the coastal lagoon estuary of Jiaozhou Bay, Yellow sea, China, with 322 species [50], Sao Sebastian Channel, Brazil, 392 species [51], coastal zone of Peru, 175 species, [11, 12], coastal zone of Santa Marta, Colombia (232 genera), [45, 46], Gorgona island, Colombia, 200 species [25].

In summary, this research confirms certain hypotheses about the factors that determine the benthic macrofauna abundance and distribution patterns. First, the submerged bottoms of this tectonic estuary are essentially similar in species composition to other types of estuaries of the Tropical eastern Pacific; however, it has a higher number of species as a consequence of the higher number of habitats (substrate heterogeneity), in this way, marine-specific richness and biological diversity are related to a higher variety of habitats. Second, rocky habitats have a higher diversity of benthic fauna than mangrove and mudflat habitats in the same bay, the latter having few species as a consequence of temperature and salinity variations. Besides this condition, the most important factors controlling the macrofauna distribution are variables associated to diversity of habitats and characteristics of the sediments and substrate and not with the estuarine gradients of environmental variables of the water column.

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