

The soft-bottom macrofauna of Sacrificios reef lagoon, SW Gulf of Mexico

La macrofauna de fondos blandos de la laguna arrecifal de Sacrificios, SO del Golfo de México

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ABSTRACT

The aim of the present work was to give a first approach on the composition, abundance and distribution of the soft-bottom macrofauna of Sacrificios reef lagoon (Veracruz Reef System: VRS); highlighting its function as part of a species macrofaunal reef corridor through the Gulf of Mexico and its relevance as a biodiversity bridge among coral reefs. This reef is part of an important protected area, however, the soft-bottom macrofauna is poorly known despite its species richness and biodiversity potential, considering the high biodiversity present in coral reefs and the variety of habitats they host. Sampling was carried out in four shallow soft sediment regions of the reef lagoon, considering three microhabitats. In all, 2211 individuals were collected and 137 species were identified. Polychaetes were the dominant group in abundance and diversity. East (windward) and West (leeward) regions were established based on the environmental analysis. These regions coincided with those proposed in coral reef studies. Nevertheless the community structure suggests the presence of a third zone (North). The seagrass and patch reef microhabitats had the highest diversity and species richness and their species turnover, or beta diversity, was high between them supporting the presence of a different community. The faunistic changes among regions were more evident than those among microhabitats.

Key words: Beta diversity, reef system, soft bottom macrofauna, SW Gulf of Mexico, tropical reef lagoon, Veracruz.

RESUMEN

El objetivo del presente trabajo fue dar una primera aproximación acerca de la composición, estructura, abundancia y distribución de la macrofauna de fondos blandos de la laguna arrecifal de Sacrificios (Sistema Arrecifal Veracruzano: SAV), resaltando su importancia como parte de un corredor de especies de la macrofauna a través del Golfo de México y su relevancia como un puente de biodiversidad entre los arrecifes coralinos. Este arrecife forma parte de una importante área natural protegida; sin embargo, la macrofauna de fondos blandos es poco conocida a pesar de su riqueza de especies y biodiversidad potencial, si se considera la elevada biodiversidad presente en los arrecifes coralinos y la variedad de hábitats que albergan. El muestreo se llevó a cabo en cuatro regiones someras de sedimentos blandos de la laguna arrecifal, considerando tres microhábitats. En total, se recolectaron 2211 individuos y se identificaron 137 especies. Los poliquetos fueron el grupo dominante en abundancia y diversidad. Se establecieron las regiones Este (barlovento) y Oeste (sotavento) con base en los análisis de parámetros ambientales. Estas regiones coincidieron con las propuestas para zonas arrecifales. Sin embargo, la estructura comunitaria sugiere la presencia de una tercera región (Norte). Los microhábitats de pastos marinos y parches de coral presentaron los valores más elevados de diversidad y riqueza específica y, su recambio de especies o diversidad beta, fue más elevada entre estos ambientes por lo que se presenta una comunidad diferente. Los cambios entre regiones fueron más evidentes que los cambios faunísticos entre microhábitats.

Palabras clave: Diversidad beta, laguna arrecifal tropical, macrofauna de fondos blandos, Sistema Arrecifal Veracruzano, SO Golfo de México.

INTRODUCTION

Coral reefs have a considerable structural diversity with a great variety of interactions (Spalding *et al.*, 2001). Among the reef areas of Mexico, the "Sistema Arrecifal Veracruzano" (here called VRS for Veracruz Reef System) is located in the southwestern region of the Gulf of Mexico. The VRS is a marine protected area that includes 23 reef structures located in the SW Gulf of Mexico (Fig. 1). It is an important system for the conservation and maintenance of marine biodiversity in the Gulf (Granados-Barba *et al.*, 2007). It also serves as a corridor for coral reef species within the Gulf of Mexico (Ortiz-Lozano *et al.*, 2013). It was declared a Mexican National Park in 1994 (DOF, 1994), a world RAMSAR site (2004), and a Biosphere Reserve (UNESCO, 2006). Coral reefs are complex systems that represent three dimensional environments which have different macrobenthic communities across the reef. The structure of a reef can be modeled among other variables by environmental factors that influence the type of associations according to light intensity and energy gradients. The persistence of those gradients through time can stimulate the interspecific competence, as well as, contribute to the biodiversity increase and the creation of reef habitats (Chávez *et al.*, 1985). The platform reefs of the southern Gulf of Mexico have a characteristic wide reef lagoon, which is formed by the consolidation and infilling of the reef rock (Chávez *et al.*, 2010). Small sandy islands or cays may then be formed by the accumulation of sand and coral rubble during storms, which is the case of the Sacrificios reef. The Sacrificios reef, as other reefs of the VRS, has a central island surrounded by a shallow reef lagoon (0.5 – 4 m depth) delimited by a reef crest (1000 m long, 500 m wide) (Chávez *et al.*, 2010; Tunnell, 2010). The low depth causes, in some areas of the lagoon, limited water circulation, significant water temperature fluctuations due to evaporation, and the occasional exposure of the coral structures during the lowest tides. There may be areas where the nutrients and sediments build up and the bright calm waters can provide ideal conditions for many macrobenthic species (Tunnell, 2010). The bottoms of the lagoon vary from hard substrates to coarse and fine sediments, which have benthic microhabitats that represent many developmental stages: bare sand, reef patches, reef algal patches, calcareous green algae or seagrass meadows of *Thalassia testudinum* Banks ex König (Chávez *et al.*, 2010). This microhabitats host a diverse benthic macrofauna permanently inhabiting the reef lagoon (Spalding *et al.*, 2001). Seagrass communities include elevated primary and secondary productivity and species abundance and diversity when compared to adjacent unvegetated sites. High macroinvertebrate diversity in seagrass results from complex biotic and abiotic interactions (Orth, 1992; De Troch *et al.*, 1996; Gilli *et al.*, 2014). Their presence represents an abundant food source for small fishes that use the reef lagoons as nursery (Arrivillaga y Baltz, 1999).

Recently, the scientific interest on the VRS has increased suggested by the increased number of papers published on the area (Aké-Castillo, 2011; Aké-Castillo *et al.*, 2010 planktonic algal blooms; Godínez-Ortega *et al.*, 2009 benthic flora; Granados-Barba *et al.*, 2007 researches in the VRS; Okolodkov, 2008, 2010; Okolodkov *et al.*, 2007; 2011 plankton, benthic and epiphytic dinoflagellates; Ortiz-Lozano *et al.*, 2009; 2012; 2013 management and conservation; Parra-Toriz *et al.*, 2010 dinoflagellates; Salas-Pérez & Granados-Barba, 2008; Pérez-España *et al.*, 2012 oceanographic characterization; Salas-Pérez *et al.*, 2007; 2012 physical oceanography; Salas-Monreal *et al.*, 2009; Chacón-Gómez *et al.*, 2013 currents; Taylor & Akins, 2007 new species of Gobiidae; Winfield *et al.*, 2007; 2009; 2010 crustaceans). Nevertheless, faunal studies of

its soft-bottom habitats are scarce (Jiménez-Hernández *et al.*, 2007). There are also many studies on coastal and estuarine ecosystems in tropical and subtropical regions (Valencia & Santos, 2012); though they are key to understand the overall coastal ecosystem (Gray, 2002; Veríssimo *et al.*, 2012) their absence on the VRS needs to be solved. The macrofauna in the benthic community function is important because it occupies different levels in the trophic web, as predators, grazers or detritivores, and it is also part of the recycling and reworking processes in sediments (Hutchings, 1998). In fact, benthic macrofauna reflects the recent history of the environmental conditions, and serves as an indicator of these conditions due to its strong dependence on the substrate (Pearson & Rosenberg, 1978; Soares-Gomes *et al.*, 2002; Zenetos & Bogdanos, 1987).

Most worldwide reef areas have undergone considerable changes and deterioration in recent decades (Nystrom & Folke, 2001; Orth *et al.*, 2006; Van Tussenbroek, 2011) and the VRS is not the exception. Sacrificios island and surrounding reef lagoon (Fig. 1) were closed to the public three decades ago, due to the severe damage to corals caused by some past tourist activities. To further protect the VRS, it is important to know what is happening with the soft-bottom macrofauna, a neglected component in terms of composition, abundance and diversity. This is a base line study to determine and analyze the spatial distribution and community structure of the benthic soft-bottom macrofauna around Sacrificios reef lagoon. We want to know if there are some differences in community structure and spatial distribution around the reef lagoon considering the leeward, windward and north sides of the reef, and if the presence of three soft-bottom microhabitats (bare sand, seagrass meadows and patch reef area) represent a difference on the species composition and beta diversity. This study will contribute to the knowledge of the macrobenthic components of VRS natural protected area and also to the knowledge of the species composition and biodiversity of the reefs within the Gulf of Mexico ecological corridor.

MATERIALS AND METHODS

Study site. Sacrificios reef is a small elliptical shaped reef located in front of the city and port of Veracruz (Fig. 1). It consists of an island (351 m x 197 m) in the middle of a shallow lagoon surrounded by the crest of the reef. The lagoon size is 750 m x 450 m in its widest part, with its largest axis oriented NW-SE (Ibarra-Morales & Abarca-Arenas, 2007; Lara *et al.*, 1992).

Sampling. According to the studies based on coral reef species and its structure in VRS reefs there are three main environments: leeward, reef lagoon and windward. This zoning is based mainly on the energy (surf intensity) and light intensity (depth) (Chávez *et al.*, 1985; Tunnell *et al.*, 2010). The water current during this season goes from south to north (Salas-Pérez *et al.*, 2008). Then, sampling was carried out considering four transects around the island in order to cover the geographic regions of the reef: W, N and E (south was not sampled because there is no soft substrate there). North was sampled as NE and NW to find the differences between leeward and windward sides of the lagoon. In total, 12 stations were sampled: three stations were sampled with no replicate per transect (Fig. 1) covering the three types of sand bottom microhabitats on the VRS reefs (Lara *et al.*, 1992; Terrados *et al.*, 2008; Chávez *et al.*, 2010). Starting from the shore of the island the microhabitats are: 1) bare sands (S) with occasional dead coral rocks (uns-

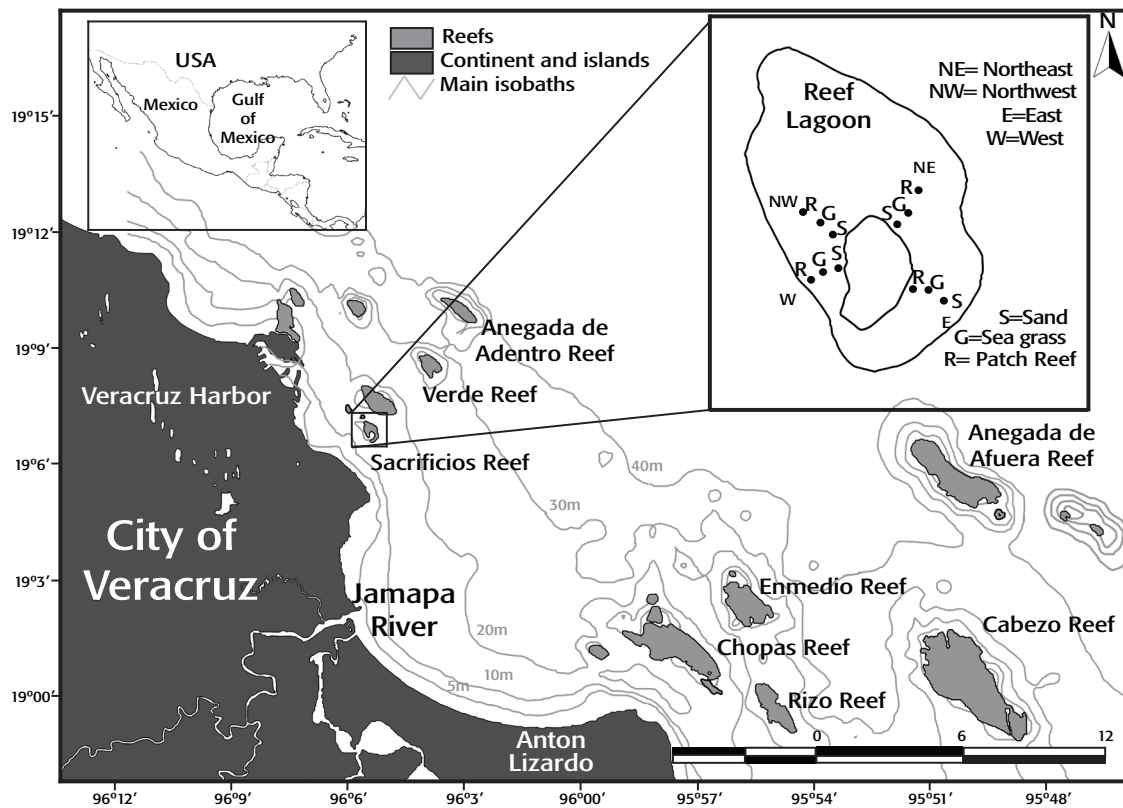


Figure 1. Study area. Veracruz Reef System with Sacrificios reef and the sampling stations. Transects NE= northeast, NW= northwest, W= west and E= east. Microhabitats sampled: S= bare sand, G= seagrass meadows and R= coral reef patches.

structured habitat), characterized by very shallow water (0.5 m), located close to the island coast line and subjected to tidal effect and surf; 2) seagrass meadows (G), consisting of *Thalassia testudinum* mixed with macroalgae (structured habitat), characterized by depths around 1 m with less surf effect and 3) live patch reef (R) surrounded by sand (unstructured habitat), characterized by deeper waters (2 to 4 m) and without influence of tides and surf at this season. A fourth habitat present on this lagoon is the live coral reef (only hard substrate) that was therefore not sampled. Sampling took place from June 3 to 13, 2004 (rainy season), from 8:00 am to 3:00 pm, to sample within the high tide period.

In each station single samples of sediment were manually collected with a 5 cm diameter-10 cm depth core for granulometric analysis (Folk, 1969). The macrofauna was collected with a suction device core (0.20 m²; 29.45 dm³), operated by compressed air from a SCUBA tank (Bone, 1991) with a 0.5 mm mesh at its top. Suction was applied until the core area was suctioned to 15 cm depth and directly sieved through the 0.5 mm mesh. The suction method is among the most effective sampling techniques for seagrass and patch reef benthos because it collects epifauna and infauna working over many surfaces, and collects quantitative benthos samples. It also collects the organisms with little damage and their identification to species level is in most cases possible (Brook, 1979; Heck & Wilson, 1900). The samples were then processed by standardized methods (Holme & McIntyre, 1984; Solís-Weiss *et al.*, 2000), fixed in formalin (at 4%), sorted, preserved in alcohol at 70% and identified.

Analysis of the data. The affinities of the sampling stations according to their grain size and depth were established by means of a non-metric multidimensional scaling analysis (NMDS). The data were normalized (to have an average value of 0 and a variance of 1) and the similarities were measured using the Euclidean distance with the Primer v. 6 routines. The community structure was analyzed in terms of density, species richness and diversity (Shannon-Wiener Diversity Index) (Margalef, 1958). Species accumulation test were made with the indexes Chao 1 and bootstrap. Dominance was calculated with the Biological Index (BI) (Sanders, 1960). Beta diversity was used to determine the replacement rate or turnover of the individual species between habitats (Wilson & Schmida, 1984) and to find out if there were differences in community composition among the microhabitats analyzed. The beta diversity was measured within each region (transects) between each microhabitat. The diversity values were calculated only between contiguous stations.

To establish faunal affinities among stations and microhabitats, a non-metric multidimensional scaling analysis (NMDS) was performed using the Bray-Curtis (1957) similarity index, and data transformation to the fourth root (Clarke & Gorley, 2001). The beta diversity results were compared to the groups found through the NMDS.

RESULTS

Moderately sorted coarse grain sands dominated the sediments (Table 1) in all habitats on E, NW and NE regions. On the W region the grain size and sorting decreased (0.4 to 1.22 Phi) from the sand to the patch

reef. On E and NE seagrass stations the sorting was poor, as well as on the NW patch reef. Depth varied from 0.22 to 4 m, the patch reef stations were the deepest ones, while the bare sand stations were the shallowest. On the NW region deeper stations (3.9 m) were found than in the rest of the lagoon; while, on the NW region the shallowest stations (0.35 m) were registered. On the NMDS based on the grain size and depth (Fig. 2) it can be observed a split between the East and West regions (windward and leeward sides), with a good stress value (0.06). Stations were distributed by decreasing depth from the lower left to the upper right; while the grain size decreased from right to left (Fig. 2). Based on these data, the reef lagoon was characterized by an East

(windward) side protected by the reef crest, shallow water and smaller grain sizes, while the west (leeward) was characterized by a reduced reef crest, deeper waters and bigger grain sizes. The distance among all north stations can be observed due to their differences in grain sizes. The station WS was included in the eastern stations due to their similar grain size composition and low depth.

Community structure. Altogether, 2211 individuals from the four major taxa of benthic macrofauna (polychaetes, mollusks, crustaceans and echinoderms) were collected and 119 species identified (Table 2). Of these, 81 had not been previously recorded for the VRS and 14 (all an-

Table 1. Environmental and faunistical data showing the grain size and its skewness, kurtosis, corresponding texture and sorting. Depth (m), species richness (ind), diversity and density (ind/m3) for each sampling station.

Stations	Grain size f	Skwness	Kurtosis	Texture	Sorting	Depth	Species richness	Diversity	Density (ind/dm3)
ES	0.28	-0.08	1.11	Coarse sand	Moderately sorted	0.75	41	4.33	26.7
EG	0.26	-0.01	0.99	Coarse sand	Poorly sorted	0.64	35	4.06	27.8
ER	0.27	-0.01	1.07	Coarse sand	Moderately sorted	0.77	22	3.38	9.2
WS	0.4	-0.06	1.07	Coarse sand	Moderately sorted	1.2	20	3.63	4.3
WG	1.22	-0.04	1.07	Medium sand	Moderately sorted	2	20	2.57	15.8
WR	0.89	0	1	Coarse sand	Good sorted	4	13	3.16	6.8
NWS	0.42	-0.02	0.96	Coarse sand	Moderately sorted	3.9	20	3.01	13.9
NWG	0.5	0.03	1.01	Coarse sand	Moderately sorted	3.8	30	3.17	91.5
NWR	0.68	0.02	1	Coarse sand	Poorly sorted	3.9	29	3.78	74.4
NES	-0.05	-0.1	1.13	Very coarse sand	Moderately sorted	0.22	22	2.52	91.6
NEG	0.16	0.19	1.17	Coarse sand	Poorly sorted	0.47	19	2.6	23.0
NER	0.2	-0.01	1.08	Coarse sand	Moderately sorted	0.3	21	2.96	66.7

NE (Northeast), NW (Northwest), E (East), W (West), S (Sand), G (Grass), R (Reef)

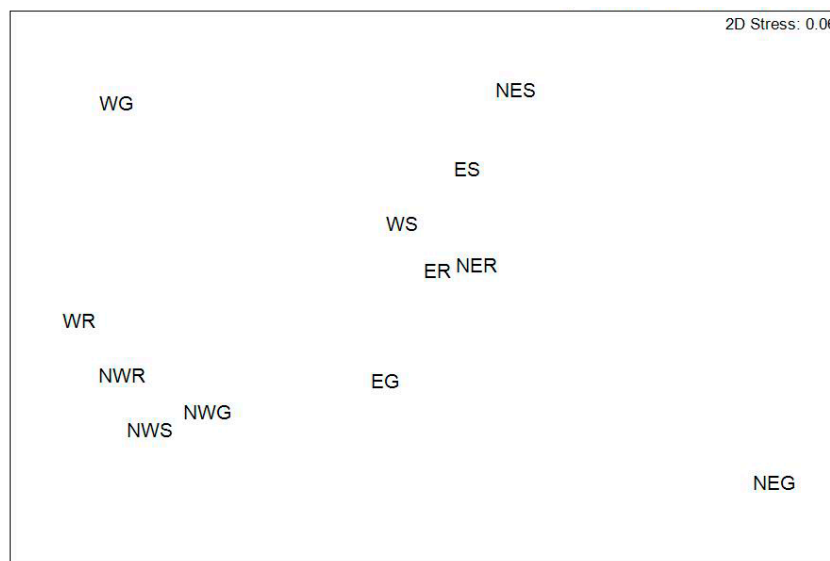


Figure 2. Multidimensional non-metric scaling of the stations based on grain size (Phi) and depth (m). Stations: NW, NE, W or E= northwest, northeast, west and east + S, G or R= bare sand, seagrass and patch reef.

nelid polychaetes) are potentially new to science (Table 2). The species accumulation index Chao 1 estimated a grand total of 177 species in the VRS of which 119 were observed; that is, the 67% of the species present in the reef lagoon were represented in the sampling.

The polychaetes were the dominant group (372.15 ind. dm⁻³, 82.5% of the total fauna collected). They were distributed with high values in all the microhabitats studied, especially along the NW and NE regions (310

ind. dm⁻³). Crustaceans (62.3 ind. dm⁻³, 13.8%) were also present in all habitats, but with lower densities; their highest values were recorded in the patch reef (29.8 ind. dm⁻³) on the NW region, as well as on the W region in the seagrass meadows. Mollusks (11.87 ind. dm⁻³, 2.6%) were distributed predominantly in the seagrass meadows (NW, 3.63 ind. dm⁻³) and patch reef (NW 2.65 ind. dm⁻³), but were notably few or absent in bare sands. Echinoderms (4.83 ind. dm⁻³, 1%) were very scarce in the study area; with their highest values on the E region (4.49 ind. dm⁻³).

Table 2. Species list for the Sacrificios reef lagoon. * Species potentially new to science, the ones named A, B, C are included in Uebelacker & Johnson (1984). ** New records of species for the Sacrificios reef lagoon. Habitat: S (Sand), G (Seagrass), R (Patch reef zone). Zone: N (North), NE (Northeast), NW (Northwest), E (East), W (West) and All (the species occur in the three reef soft bottom zones studied: N, E, W

Species	Habitat	Zone	Density (ind/dm ³)
CRUSTACEA			
<i>Amphitoe longimana</i> Smith, 1873	G, R	NW	21.63
** <i>Ampithoe valida</i> Smith, 1873	S	E	0.09
<i>Ampelisca verrilli</i> Mills, 1967	G	NW	0.23
** <i>Cataleptodius floridanus</i> (Gibbes, 1850)	S, G	W, NW	0.38
<i>Elasmopus</i> sp.	S	E	0.26
<i>Gammaropsis</i> sp.	S, G, R	E, W	0.43
<i>Grandidierella bonnieroides</i> Stephensen, 1948	S, G, R	All	9.82
** <i>Hargeria rapax</i> (Menzies & Glynn, 1968)	S, G, R	All	3.81
** <i>Harpinia propinqua</i> Sars, 1895	R	NE	0.57
** <i>Lembos</i> spp.	R	NW	0.76
<i>Lysianopsis alba</i> Holmes, 1903	S, G, R	All	10.34
** <i>Lyssianassa</i> sp.	R	NE	0.28
** <i>Microdeutopus</i> spp.	S, G	E, W	8.48
** <i>Monoculodes</i> sp.	S	E	0.17
** <i>Neogonodactylus bredini</i> (Manning, 1969)	S	W	0.08
<i>Paraphoxus spinosus</i> Holmes, 1905	G	W	0.23
** <i>Pinnixa floridana</i> Rathburn, 1918	S	NW	0.11
** <i>Pinnixa sayana</i> Stimpson, 1860	S, R	NW, NE	0.4
** <i>Portunus gibbesii</i> (Stimpson, 1859)	S	NE	0.16
<i>Portunus ordwayi</i> (Stimpson, 1860)	S, R	NE, NW	0.68
** <i>Rhepoxynius epsitonus</i> Shoemaker, 1938	G, R	W, NW, NE	3.4
** <i>Sychelidium americanum</i> Bousfield, 1973	R	NE	0.28
<i>Trichopoxus epistomus</i> Sheider & Harrington, 1981	G	E	0.11
MOLLUSCA			
<i>Alaba incerta</i> (d'Orbigny, 1842)	G	NE	0.14
<i>Bulla striata</i> Bruguière, 1792	G, R	E, NE, NW	5.21
** <i>Cancellaria</i> sp.	R	W	0.14
<i>Cerithium (Thericium) atratum</i> (Born, 1778)	G, R	E, W, NW	1.63
<i>Cochliolepsis</i> sp.	S, G, R	E, W, NW	0.63
<i>Collisella</i> sp.	S	E	0.11
** <i>Diodora aspera</i> (Rathke, 1833)	R	NW	0.38
<i>Diodora cayensis</i> (Lamarck, 1822)	G	E	0.68

Table 2. (Continuation)

<i>Modulus disculus</i> (Linnaeus, 1758)	G, R	All	1.78
** <i>Nuculana concentrica</i> (Say, 1824)	R	NW	0.49
<i>Patella</i> sp.			0.11
POLYCHAETA			
** <i>Aonides mayaguezensis</i> Foster, 1969	S	W	0.23
** <i>Aricidea (Acmira) finitima</i> Strelsov, 1973	G	NE	0.43
<i>Armandia maculata</i> (Webster, 1884)	R	NW	0.38
* <i>Axiiothella</i> sp.1	S	W, NE	1.00
<i>Capitella</i> sp.	G	NW	0.23
** <i>Caulleriella alata</i> (Southern, 1914)	S, G	E, W	0.49
** <i>Caulleriella</i> cf. <i>alata</i> (Southern, 1914)	S, R	E, NE	2.79
* <i>Caulleriella</i> sp. A Wolf, 1984	S	E	0.09
<i>Caulleriella</i> sp. B Wolf, 1984	S, R	NE	3.16
** <i>Caulleriella zetlandica</i> (McIntosh, 1911)	S, R	E, NE	9.53
* <i>Chaetozone</i> sp.D Wolf, 1984	S, R	E, W	0.51
<i>Chloeia viridis</i> Schmarda, 1861	R	E	0.08
** <i>Dasybranchus lumbricoides</i> Grube, 1850	R	W	0.14
** <i>Decamastus</i> cf. <i>gracilis</i> Hartman, 1963	S	NE	0.16
** <i>Decamastus gracilis</i> Hartman, 1963	S, G	E, NE	0.69
** <i>Dipolydora socialis</i> (Schmarda, 1861)	S, G	E	1.00
** <i>Drilonereis longa</i> Webster, 1879	G, R	N	0.66
* <i>Euclymene</i> sp. B Wolf, 1984	S	W	0.08
** <i>Exogone (Exogone) brevi antennata</i> Hartmann-Schroeder, 1959	S	W	0.08
** <i>Exogone (Exogone) dispar</i> (Webster, 1879)	S, G	NW	1.36
** <i>Exogone (Exogone) lourei</i> Berkeley & Berkeley, 1938	S, R	N	2.21
* <i>Exogone (Exogone)</i> sp. 1	R	E	0.08
** <i>Fabricinuda trilobata</i> (Fitzhugh, 1983)	S, G, R	E, W, NW	14.55
** <i>Glycera brevicirris</i> Grube, 1870	S, R	All	0.43
** <i>Isolda pulchella</i> O. F. Mueller, 1858	S	W	0.08
* <i>Lumbrineris</i> sp. 1	R	NW	1.13
<i>Magelona</i> sp. C Uebelacker & Jones, 1984	S	E	0.35
* <i>Magelona</i> sp. F Uebelacker & Jones, 1984	R	NW	0.38
** <i>Mediomastus californiensis</i> Hartman, 1944	S, G, R	All	20.98
** <i>Mooreonuphis dangrigae</i> (Fauchald, 1980)	S, G, R	E, N	5.86
** <i>Mooreonuphis stigmatis</i> (Treadwell, 1922)	S, G, R	All	3.08
** <i>Myrianida multidentaculata</i> (Westheide, 1974)	G	W	0.11
** <i>Naineris bicornis</i> Hartman, 1951	S, G	E	0.69
** <i>Naineris grubei</i> (Gravier, 1909)	R	NW	0.76
** <i>Nematonereis hebes</i> Verrill, 1990	S, G, R	E, W	0.54
** <i>Nereis falsa</i> Quatrefages, 1865	S, G	E, NE	0.34
** <i>Notomastus lobatus</i> Hartman, 1947	R	E	0.08
<i>Odontosyllis enopla</i> Verrill, 1900	R, G	E, NW	0.38
** <i>Paramphinome jeffreysii</i> (McIntosh, 1868)	S, G, R	All	109.14

Table 2. (Continuation)

* <i>Paramphinome</i> sp. B Gathof, 1984	R	E	0.15
* <i>Phyllochaetopterus</i> sp. 1	G, R	E, NW	0.61
** <i>Perkinsyllis spinisetosa</i> (San Martín, 1990)	S, G, R	All	6.30
** <i>Podarkeopsis levifuscina</i> Perkins, 1984	S, G	W, NE	0.60
** <i>Potamilla torelli</i> Malmgren, 1865	G	NW	0.91
** <i>Prionospio (Minuspio) cf. multibranchiata</i> (Berkeley, 1927)	G	W	0.11
** <i>Prionospio (Minuspio) cirrifera</i> (Wirén, 1883)	S, G, R	E, NW	0.43
** <i>Prionospio (Minuspio) multibranchiata</i> (Berkeley, 1927)	G, R	N	0.90
<i>Procera cornuta</i> (Agassiz, 1862)	S	NE	0.16
* <i>Proscoloplos</i> sp. 1	S, G, R	All	32.61
* <i>Proscoloplos</i> sp. A Wolf, 1984	G	NW	0.45
<i>Protodorvillea kefersteini</i> (McIntosh, 1869)	S, G	E	0.64
* <i>Sabella</i> sp. 1	S, G, R	E, W	4.41
** <i>Salvatoria mediodentata</i> (Westheide, 1974)	S, G	W, N	0.73
** <i>Salvatoria rugulosa</i> (Verrill, 1900)	S	NE	0.16
** <i>Schistomeringos pectinata</i> Perkins, 1979	S, G, R	N	34.31
** <i>Scoletoma verrilli</i> (Perkins, 1979)	S, G, R	E, NW, NE	1.38
** <i>Scoloplos (Leodamas) rubra</i> (Webster, 1879)	S	W	0.15
<i>Shpaerosyllis piriferopsis</i> Perkins, 1981	S, G	NE	1.76
** <i>Spio pettiboneae</i> Foster, 1971	S, G, R	All	16.36
** <i>Spiophanes</i> spp.	R	NE	0.28
* <i>Sthenelais</i> sp. A Wolf, 1984	S, G	E, NE	0.34
** <i>Syllides cf. caribica</i> Licher, 1996	G	NW	0.23
** <i>Syllis armillaris</i> (O. F. Mueller, 1771)	G, R	E, NW	0.49
** <i>Syllis botosaneanui</i> Hartmann-Schroeder, 1973	S, G, R	All	72.26
** <i>Syllis cf. botosaneanui</i> Hartmann-Schroeder, 1973	G	NE	0.28
** <i>Syllis corallicola</i> Verrill, 1900	G	E	0.11
** <i>Syllis corallicoloides</i> Augener, 1922	G	W	0.11
** <i>Syllis garciai</i> (Campoy, 1982)	S	E, NE	0.41
** <i>Syllis maryae</i> (San Martín, 1992)	R	NW	0.38
** <i>Syllis prolifera</i> Krohn, 1852	R	E	0.08
** <i>Syllis vivipara</i> Krohn, 1869	S, G, R	All	8.70
** <i>Terebellides klemani</i> Kinberg, 1867	S	W	0.15
ECHINODERMATA			
<i>Amphipholis squamata</i> (Delle Chiaje, 1828)	S, G	E	0.20
<i>Amphipholis</i> sp.	S, G	E	0.80
<i>Amphiura</i> sp.	S	NW	0.11
<i>Epitomapta roseola</i> (Verrill, 1873)	S, G	E	0.40
<i>Ophiactis savignyi</i> (Mueller & Troschel, 1842)	S, G	E	1.41
<i>Ophiactis</i> sp.	R	E	0.08
<i>Ophilepis impressa</i> Luetken, 1859	S, G	E	0.20
<i>Ophiotrix orstedii</i> Luetken, 1856	G	W	0.23
** <i>Pseudothyone belli</i> (Ludgwig, 1887)	S, G	E	1.41

The highest macrobenthic densities were recorded in the seagrass meadows (158.04 ind dm⁻³) on the NW region and in bare sands on the NE (91.60 ind dm⁻³). The highest value of species richness (41 species) was recorded on the E region in sands, whereas the lowest (13 species) was recorded on the W in the patch reef (Table 3). Combining *a priori* the four transects, it turns out that the same number of species (105 species) was found in bare sands and seagrass meadows, while a lower number of species (86 species) was found in the patch reef. The diversity distribution pattern was similar to that of the species richness among the different microhabitats (Table 3) since the highest values were found on the E region in the bare sands (4.33) and seagrass meadows (4.06). The lowest values were found on the NE region (2.52 for bare sand, 2.60 for seagrass meadows, and 2.96 for patch reef). The dominant species were all polychaetes. *Mediomastus californiensis* (Hartman, 1944) (BI = 188 out of 240) was more abundant at the E and W, in the seagrass meadows and patch reef. *Spio pettiboneae* Foster, 1971 (BI = 151) occurred in bare sands along the W region and, with a lower density, on the E region. *Paramphinome jeffreysi* (McIntosh, 1868) (BI = 140), *Syllis botosaneanui* (Hartmann-Schröder, 1979) (BI = 180), *Syllis vivipara* (Krohn, 1852) (BI = 81), and *Perkinsyllis spinisetosa* (San Martin, 1990) (BI = 59) were mainly found along the N region. *Proscoloplos* sp.1 (BI = 151) was collected in all habitats and abundant in most stations, mainly along the E and NW regions.

Faunistic affinities around the lagoon and among the microhabitats. On the NMDS analysis three distinct groups of stations were shown (with a good stress value: 0.08) (Fig. 3): at the right side of the graph, group A, included the stations of the W region; group B at the center, includes the stations of the E region and to the left, group C contained the stations of the N (NW and NE) region, except for station NEG that belongs to group B. Stations with the highest density values were located to the left of the figure. The distribution of the stations in the analysis by regions showed that the species composition and spatial distribution were differential along an E and W line, while the NE and NW regions were grouped together. No grouping pattern was observed considering microhabitat distribution.

Beta diversity. The species turnover observed was consistent with the stations distance shown in the NMDS analysis, highlighting a difference in abundance and also in species composition among the microhabitats. This section is analyzed by region considering the species turnover among the microhabitats inside each region: In group A, the species turnover (Fig. 4) between the bare sand habitat (WS) and the seagrass meadows (WG) was 70% (beta diversity, 0.70; out of 34 species, six are common). Between the seagrass meadows (WG) and the patch reef (WR), the turnover was 82% (out of 30 species, three are common), and between sand (WS) and patch reef (WR) it was 70% (out of 28 species, four are common). In group B, the species turnover between ES and EG was 37% (out of 52 species, 24 are common), between EG and ER 75% (out of 49 species, seven are common), and between ES and ER 77% (out of 55 species, seven are common).

In group C, the species turnover between NWS and NWG was 49% (out of 44 species, 15 are common); between NWS and NWR 63% (out of 40 species, nine are common); between NWG and NWR 49% (out of 27 species, 16 are common); between NES and NEG 61% (out of 33 species, eight are common); between NEG and NER 75% (out of 35 species, five are common); and between NES and NER 58% (out of 34 species, nine are common). In general, in this group, the species turnover among microhabitats was lower than in the other groups.

DISCUSSION

The soft-bottom environments were separated into two main groups of stations according to the previous zonation proposed for the VRS reefs in leeward and windward sides (Tunnell *et al.*, 2010). Even though, the grain size was the same for almost all stations, there was a difference in size between leeward and windward sides (east and west groups), which can evidence the differences in the energy present in both sides of the reef lagoon. A similar East and West pattern was found in the benthic macrofauna, defining two faunistic assemblages; however, the fauna also discriminated a distinct assemblage for the northern region of the reef lagoon.

Heterogeneity of the habitats was suggested by the environmental analysis (NMDS) on the northern region; these was also observed by the community structure based on the beta diversity values, in the NE region with a species turnover rate among the microhabitats above 49%, while on the NW the turnover was above 52%. This means that more than 50% of the species changed among the microhabitats; nevertheless, further studies are needed to show if there is a difference between NE and NW regions in the leeward and windward sides as found on the eastern and western stations. This N region corresponds to the largest part of the reef lagoon protected by the reef crest; in general, there is little energy and less fluctuation at sea level due to the higher depths, but mainly at the NW. The dominance of some species such as *Paramphinome jeffreysi* (Amphinomidae) and *Syllis botosaneanui* (Syllidae) in this region caused low species richness and diversities. These dominances can be explained since they can feed on other polychaetes, corals, anemones or debris (Gray, 1981) typical of the extensive seagrass meadows and patch reef, living in sandy and coralline bottoms. Syllids have been recorded consistently as a diverse group on the continental shelf (Martins, 2013), the carbonate bottoms of the Caribbean Sea (Gobin, 2010), or the shelf reefs in the Philippines (Hildie *et al.*, 1997). The syllids are also dominant in coral and coarse sands mixed with coral and shell rubble on the Gulf of Mexico where the highest densities, species richness and diversity have been found on the VRS (Granados-Barba *et al.*, 2003). The species found as dominant in Granados-Barba *et al.* (2003) *S. botosaneanui*, was particularly abundant in the N region, perhaps because it gathers food among the seagrass meadows or the patch reef (it is an omnivore species feeds on seagrass or other invertebrates), or because it uses them as sites for reproduction (several individuals were found in a reproductive state). Further studies on this region could confirm the differences found here.

On the W region, the high species turnover evidenced the local habitat heterogeneity, finds support in the environmental NMDS. The heterogeneity is mainly due to the changes in depth, the patchy coralline structures, mostly hard substratum, even in the seagrass and bare sands habitats. The reduction of available soft substratum for the macrofauna in the west region is responsible of the lowest density and species richness in this part of the lagoon, where species were different in each habitat. The grain size, in the W region, was relatively smaller than in the other two, but moderately to good sorted. This is an unexpected result since this zone of the reef is exposed to the intensity of the surf and tides, expecting coarser and poorly sorted sediments (Syms & Jones, 2004). Nevertheless, the Jamapa river input increases during this rainy season, and as Sacrificios reef is near the river and the city discharges, it could be expected that terrigenous sediments with finer grain size influence the reef area. The reef has a narrow shelf and a depth change from 1 to 4 m, being similar to other elliptical platform reefs

Table 3. Density (ind.dm⁻³), species richness (# ind.), diversity and evenness values measured by station and habitat.

Density	East	West	Northwest	Northeast	Total
Sand	26.66	4.25	13.87	91.60	136.38
Grass	27.80	15.78	91.50	22.97	158.05
Patch reef	9.15	6.81	74.43	66.73	157.12
Species Richness					
Sand	41	20	20	24	105
Grass	35	20	31	19	105
Patch reef	23	13	29	21	86
Diversity					
Sand	4.33	3.63	3.01	2.52	
Seagrass	4.06	2.57	3.17	2.60	
Patch Reef	3.34	3.16	3.78	2.96	
Evenness					
Sand	0.81	0.84	0.70	0.55	
Grass	0.79	0.59	0.64	0.61	
Patch Reef	0.74	0.85	0.78	0.67	

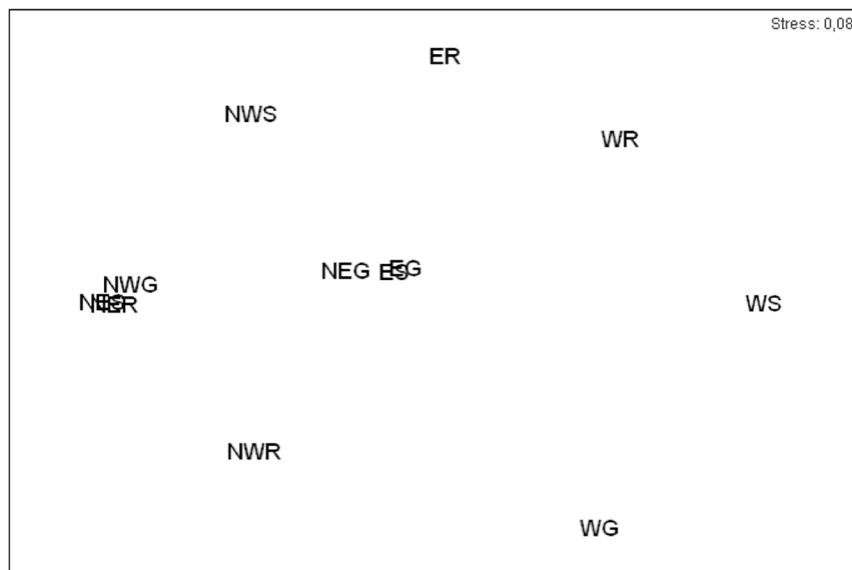


Figure 3. Multidimensional non-metric scaling of the stations along regions: W, NW, NE and E (west, northwest, northeast and east) with the macrofauna at the species level (S, bare sand; G, seagrass meadows; R, patch reef). A, B and C indicate the groups of stations found.

within the VRS. The similarity has been explained as a product of the wind and currents, with water flux directed towards the north during this season (Zavala-Hidalgo *et al.*, 2003; Salas-Monreal *et al.*, 2009; Chacón-Gómez *et al.*, 2013). The jet stream that flows south between Sacrificios and the coast line, and the anticyclonic eddy near the Jamapa river (Salas-Pérez & Granados-Barba, 2008), can possibly keep the fine terrigenous sediments out of Sacrificios reef lagoon, explaining the presence of relatively finer grain size but without the presence of clay.

The wave pattern is considered of low energy within the VRS explaining the presence of finer sediments in the surf area of the reef. The macrobenthos was representative of this type of sediment and showed a small shift in the sediment grain size with the presence of the dominant species on the W, *Spio pettiboneae*, and the surface deposit-feeders as spionid, capitellid and cirratulid polychaetes.

On the East zone, the bare sand and the seagrass habitats were similar because the turnover species was very low, which means that the

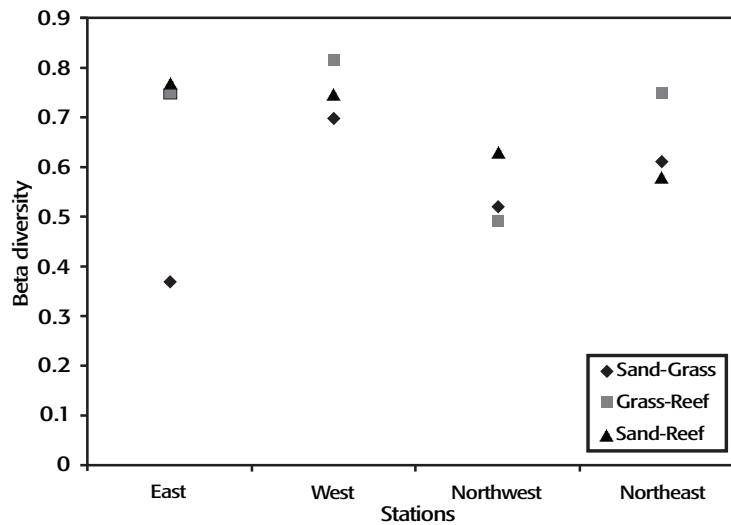


Figure 4. Beta diversity values between habitats within each region. W, NW, NE and E (west, northwest, northeast and east); S (bare sand); G, (seagrass); R (patch reef).

two environments have many species in common. In contrast, between seagrass meadows and patch reef, the species turnover was high, indicating that the two habitats differ and that there is little connection between them which was also found in the NMDS analysis. This is due to a strip of bare sand with dead coral rocks that divides them. This could be an adverse environment for some species and could also act as a barrier for the recruitment of macrofauna species between both habitats, even at the larval stage (Drew & Eggleston, 2006). To this respect, although the tidal effect in the reef has not been documented, it might as well be that its influence in the generation of currents is more important than that of the wind (Salas-Pérez & Granados-Barba, 2008; Salas-Pérez *et al.*, 2007; 2008). The eastern reef lagoon is the shallowest of the zones (0.6 m), and its extension (100 m from the island shore to the crest of the reef) is intermediate between those of the W and N zones. All this could determine the distribution of species in the lagoon as the tidal effect is more obvious in this region of the reef. Nevertheless, the faunistic pattern between seagrass and patch reef was not observed on the environmental analysis, where the grain size and depth were almost the same in the three stations, showing a homogeneous environment. This supports the hypothesis of the tidal effect as an important factor structuring the macrobenthic assemblages on this side of the reef. Another factor that could contribute to determine the community structure is the energy of that part of the reef, which has to be studied further, may be during the rainy season the energy will not be relevant; but during the northers season the increase of the wind intensity on the windward side would affect the reef lagoon, but the energy could be softened by the reef crest functioning as a protection to the reef itself and the fauna inhabiting it (Granados-Barba *et al.*, 2007). The coarser and poorly sorted sediment points to the increased energy on that side of the reef, or to the fact that this zone is more isolated from the surrounding water and then be less influenced by terrigenous sediments from the Jamapa river.

The dominant macrobenthic species, although abundant and frequent throughout the study area, were particularly so in specific zones. Here, the exception was *M. californiensis*, a polychaete which

was evenly distributed throughout the study area. It is found mainly in seagrass meadows, which are sites where nutrients and sediment are easily trapped. Also, like other capitellids, it has a preference for organic matter, albeit at low concentrations; it can be found in communities with complex trophic webs based on detritus (Hernández-Alcántara & Solís-Weiss, 1991). This is surprising whenever the dominant and keystone species along the Gulf of Mexico within the Campeche Bay is *Paraprionospio yokoyamai*, a spionid polychaete deposit-feeder that is widespread in a wide variety of environments (Dominguez-Castanedo *et al.*, 2007). It is also relevant that the species found in the reef lagoon are different from those on the surrounding environments; the faunistic assemblages found in the continental shelf soft bottoms adjacent to the VRS have some species in common, mainly those deposit-feeders (Álvarez-Aguilar, 2010); but this reef area has more common species (of syllids, amphinomid, maldanids and sabellids among others) with the southern VRS reefs and northern Lobos-Tuxpan coral reefs, as well as the Caribbean and Florida coral reefs. This highlights the importance of the VRS and Sacrificios reef as part of the ecological corridor to the biodiversity conservation. The presence of the three regions on the reef lagoon represents different environments with their own macrobenthic community, and the microhabitats add heterogeneity to those environments increasing the biodiversity. The 81 new records and the 14 potentially new species highlight the absence of knowledge about the macrofauna of soft bottoms of the Sacrificios reef and in the VRS.

This work represents a first approach to understand the soft bottom macrofauna of the reef in this protected area. It increases the number of species recorded for the reef zones of the Veracruz Reef System, particularly of the reef lagoons, thereby emphasizing the paucity of knowledge of its macrobenthos that has high biodiversity potential, since all groups of benthic invertebrates are represented in these habitats.

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