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Polychaete diversity in the estuarine habitats of Términos Lagoon, southern Gulf of Mexico

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Abstract

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In order to establish the status of the biodiversity of the polychaete fauna inhabiting the soft bottoms in the largest lagoon-estuarine system from the southern end of the Gulf of Mexico, Términos Lagoon, we collected and identified 3,398 specimens belonging to 119 species and 33 families of polychaetes. The soft bottom fauna was then compared with records of polychaetes collected in other habitats in the lagoon such as seagrass beds and mangroves. In all, 190 species from 34 families of polychaetes previously recorded there were taken into account. The families Nereididae (20 spp.), Spionidae (15 spp.) and Syllidae (14 spp.) were the most diverse. The soft bottom habitat has by far the largest number of species (119) followed by the seagrass beds and mangroves with 75 and 42 species respectively. Large spatial heterogeneity in polychaete composition was observed, as only 5% of the species (*Melinna maculata, Capitella* sp., *Mediomastus californiensis, Schistomeringos rudolphii, Marphysa sanguinea, Alitta succinea, Diopatra cuprea, Scoloplos treadwelli, Prionospio heterobranchia* and *Scolelepis squamata*) were widely distributed in the lagoon. The polychaete fauna living in the mangroves is quite similar to that from seagrasses and soft bottoms ($R_{(ANOSIM)} = 0.247$ and 0.3 respectively), but the polychaetes in the seagrasses and soft bottoms are clearly different from each other ($R_{(ANOSIM)} = 0.622$). The 119 polychaete species identified in this study represent a significant increase in the records of biodiversity recorded so far in Términos Lagoon, while the total of 190 species recorded for the whole lagoon represents a larger number than any other recorded for an American tropical estuary.

Keywords Polychaeta, soft bottoms, seagrass beds, mangroves, distribution, Mexico

Introduction

The lagoon-estuarine environments are one of the most productive aquatic systems on earth and constitute important refuges, breeding and feeding grounds for marine and freshwater organisms that commonly live there or visit them, either occasionally or seasonally. These environments play a prominent role for man, due to their biological diversity and the fishing activities that are usually associated. However, the continuing increase of the human populations around these grounds has taken its toll and the negative effects are evident on the flora and fauna of the region (Lotze et al., 2006; Orth et al., 2006). Particularly, Términos Lagoon, one of the largest lagoons of Mexico, has been drastically impacted by human pressure during the last decades, mainly due to shrimp fisheries, urbanization of Carmen Island and deforestation of riverine vegetation for intensive agriculture (Villéger et al., 2010).

Coastal lagoons and estuaries are usually sites with low diversity but high faunal abundance due to their special environmental conditions (Constable, 1999). This is associated with the "minimum species" concept expressed by Remane (1934) to explain that the large variations of environmental factors in those brackish waters exclude many species and thus, the transitional marine-freshwater zones are typically species poor communities. In these water bodies the biota is characterized by a high level of adaptive evolution to stress and to those environmental variations that distinguish those aquatic systems, especially salinity variations. That is why the implementation of studies dedicated to the knowledge of the biodiversity of these lagoon-estuarine systems is fundamental to create monitoring programs that can help mitigate and control the anthropic effects on that biota.

In Mexico, even if coastal lagoons cover approximately 30-35% of its almost 11,000 km of littorals (Contreras, 1985), their study has not been a priority for benthic specialists. In these systems, polychaetes are typically the main component of the macrofaunal communities (Hutchings, 1998), and they frequently represent more than half the number of species and organisms present in any sample (Blake, 1994; Hutchings, 1998; Olsgard et al., 2003). So, it can be assumed that their abundance and diversity patterns are the most important for understanding the functioning of these systems and are crucial to define the structure, production and general dynamics and health of their benthic communities. The biological processes observed in this group alone, could in fact reflect those of the whole benthos in general (Mackie et al., 1997; Glasby and Read, 1998; Olsgard and Somerfield, 2000).

Even if in the southern Gulf of Mexico those systems are widely represented (623,600 ha) and the polychaetes are recognized as one of their most important benthic components (Hernández-Alcántara and Solís-Weiss, 1991, 1995), so far their presence has only been recorded in eleven, including Términos Lagoon, from the 174 lagoon-estuarine systems recorded in that region. That is why the objective of this study is to establish the biodiversity recorded in the polychaetes of the soft bottoms of one of the largest coastal lagoons of the Gulf of Mexico, Términos Lagoon, and to compare it to the variety of species so far recorded there in seagrasses and mangroves, as a departure point for future monitoring programs of the regional benthic fauna.

Methods

Study area

Términos Lagoon is located at the southern end of the Gulf of Mexico (18° 38'N; 91° 34'W); it is about 70 km long and 30 km wide, including two small tributary lagoons and swamp areas (fig. 1). It was declared "Protected Area of Flora and Fauna of Términos Lagoon" (APFFLT for its initials in Spanish) in 1994, and a Ramsar site in 2004. Depth in the Lagoon averages 3.5 m. Two inlets connect it to the Gulf of Mexico (fig. 1), and the winds, coupled with the prevailing currents, force the seawater inflow through the Puerto Real Inlet (to the east), while the lagoon waters outflow through the Carmen Inlet (to the west) (Yáñez-Arancibia and Day, 2005). Soft bottoms devoid of vegetation are the dominant habitat in the lagoon and cover most of the approximately 2500 km² of its total surface while mangroves, dominated by Rhizophora mangle (Linnaeus, 1753) are present around most of its edges; dense and extensive prairies of seagrass beds dominated by Thalassia testudinum Banks ex König, 1805, are also present in the lagoon, although they are restricted to the south and southeast

of the Carmen Island and the southeastern end of the lagoon (fig. 1).

Data analysis

The faunal information presented here is primarily based on the specimens collected in soft bottoms in Términos Lagoon as part of the multidisciplinary project "Joint Environmental Study of Términos Lagoon (JEST)", carried out during 2008-2009 by the "Institut de Recherche pour le développement » (IRD) from France, the Universidad Autónoma Metropolitana-Iztapalapa México and the Universidad Nacional Autónoma de México. The objective of the general project was to compare scientific results obtained some 20 years ago, with new data, and thus establish, the present environmental status and biogeochemical functioning of the Lagoon. To this aim, the faunal data in this study were combined with information about the polychaete species previously reported in seagrasses (Ibañez-Aguirre and Solís-Weiss, 1986; Cruz-Ábrego et al., 1994) and mangroves of the Lagoon (Hernández-Alcántara and Solís-Weiss, 1991, 1995).

The biological samples for this study were taken with a Van Veen (0.06 m^2) or Ekman (0.053 m^2) grab at 24 stations distributed evenly over the soft bottoms of the Lagoon. The faunal information for the seagrass and mangrove areas was taken from published sources and made with a quadrat (0.06 m^2) at 22 stations for the seagrasses and five stations with a corer (25 cm inner diameter, 20 cm penetration in the sediment) for the mangroves. All samples collected in each habitat were washed through a 0.5 mm mesh, to separate the macrofauna and fixed in 4% formalin to be later preserved in 70% alcohol.

The comparison of the information resulting from this study with that coming from the literature was complicated by the different sampling procedures used in each case, so that for comparison purposes, the distribution of species in the three studied habitats was analyzed only as presence/absence information. The faunal list presented here is made using the current names of species as well as the names under which they were reported initially (in parentheses), so that they are readily traceable in the original source. Most species names were verified with the World Polychaeta database (Read and Fauchald, 2013), accessed through the World Register of Marine Species (WoRMS, 2013). Before data processing, the original list was filtered to remove all doubtful records, i.e. those attributed to species whose known world distribution does not correspond to the marine region studied here, or species whose identification was incorrect.

The differences among the polychaete species in the three habitats were evaluated with ANOSIM (analysis of similarity). ANOSIM tests the hypothesis that there are no differences between habitats in the composition of species, by calculating the test statistic R which varies from R = 0 (groups indistinguishable from one another) to R = 1 (no similarity between groups) (Clarke, 1993). By resampling the data, a probability level can be associated with R; in this case p < 1% was used to distinguish the different habitats. The ANOSIM test was performed using the Plymouth Routines in Multi-Variate Ecological Research (PRIMER v6) software (Clarke and Gorley, 2006).

Table 1. Distribution of the polychaete species collected in the three habitats of Términos Lagoon (SB: soft bottoms; SG: seagrass beds; M: mangroves).

Family - Species		Habitat		Family - Species		Habitat	
	SB	SG	М		SB	SG	М
Acoetidae				Opheliidae			
Polyodontes lupinus (Stimpson, 1856)	+			Armandia agilis (Andrews, 1891)	+		
Ampharetidae				Armandia cirrhosa Filippi, 1861		+	
Melinnopsis sp. 1	+			Armandia maculata (Webster, 1884)	+	+	
Isolda bipinnata Fauchald, 1977	+	+		Armandia bioculata Hartman, 1938		+	
Melinna maculata Webster, 1879	+	+	+	Orbiniidae			
Melinna palmata Grube, 1870		+		<i>Leitoscoloplos foliosus</i> (Hartman, 1951) (as <i>Haloscoloplos foliosus</i> (Hartman, 1951))	+		+
Amphinomidae				<i>Leitoscoloplos fragilis</i> (Verrill, 1873) (as <i>Haloscoloplos fragilis</i> (Verrill, 1873))		+	+
Hipponoe sp.		+		<i>Leodamas rubra</i> (Webster, 1879) (as <i>Scoloplos (Leodamas) rubra</i> (Webster, 1879))	+	+	
Linopherus ambigua (Monro, 1933)			+	Nainereis sp.			+
Arenicolidae				Naineris setosa (Verril, 1900)		+	+
Arenicola cristata Stimpson, 1856		+		Protoaricia oerstedii (Claparède, 1864)		+	
Capitellidae				Scoloplos robustus Rullier, 1964 (as Leitoscoloplos robustus (Verrill, 1873))	+	+	
<i>Capitella</i> sp. (as <i>Capitella capitata</i> (Fabricius, 1780))	+	+	+	Scoloplos texana (Maciolek and Holland, 1978)	+		
Capitomastus sp.		+		Scoloplos treadwelli Eising, 1914	+	+	+
Mediomastus californiensis Hartman, 1944	+	+	+	Owenidae			
Notomastus hemipodus Hartman, 1945 (as Notomastus luridus Verrill, 1873		+		Galathowenia oculata (Zach, 1923)	+		
Notomastus sp.		+		Owenia fusiformis Delle Chiaje, 1844		+	
Rasghua sp.	+			Owenia sp.	+		
Cirratulidae				Paraonidae			
Aphelochaeta sp.	+			<i>Aricidea (Acmira) hirsuta</i> Arriaga- Hernández, Hernández-Alcántara and Solís-Weiss, 2013	+		
Caulleriella alata (Southern, 1914)			+	Aricidea (Strelzovia) suecica Eliason, 1920 (as Aricidea suecica Eliason, 1920)		+	+
Caulleriella bioculata(Keferstein, 1862)		+		Cirrophorus armatus (Glèmarec, 1966)		+	
<i>Timarete filigera</i> (Delle-Chiaje, 1828) (as <i>Cirriformia filigera</i> (Delle-Chiaje, 1828))		+		Paraonides lyra (Southern, 1914) = Paradoneis carmelitensis Arriaga- Hernández, Hernández-Alcántara and Solís-Weiss, 2013	+		+
<i>Timarete tentaculata</i> (Montangu, 1808) (as <i>Cirriformia tentaculata</i> (Montagu,1808))		+		Pectinariidae			
Monticellina dorsobranchialis (Kirkegaard, 1959)	+			Pectinaria meredithi Long, 1973	+		

Family - Species		Habitat		Family - Species		Habitat		
	SB	SG	М		SB	SG	Μ	
Moticellina sp.	+			Pectinaria sp.	+			
Aphelochaeta marioni (Saint-Joseph, 1894) (as Tharyx marioni (Saint-Joseph, 1894))			+	<i>Petta pellucida</i> (Ehlers, 1887) (as <i>Petta pusilla</i> Malmgren, 1866)		+		
<i>Aphelochaeta parva</i> (Berkeley, 1929) (as <i>Tharyx parvus</i> (Berkeley, 1929))		+	+	Petta tenuis Caullery, 1944			+	
Cossuridae				Petta sp.		+		
Cossura delta Reish, 1958	+		+	Phyllodocidae				
Dorvilleidae				Hypereteone heteropoda Hartman, 1951 (as Eteone heteropoda Hartman, 1951)	+			
Dorvillea rubra (Grube, 1856)	+			<i>Hypereteone foliosa</i> (Quatrefages, 1865) (as <i>Eteone foliosa</i> Quatrefages, 1866)	+			
Schistomeringos rudolphii(Delle-Chiaje, 1828)	+	+	+	<i>Hypereteone lactea</i> Claparède, 1868 (as <i>Eteone lactea</i> Claparède, 1868)	+			
Eunicidae				- Hypereteone sp. (as Eteone sp.)		+		
<i>Lysidice ninetta</i> Audouin and Milne- Edwards, 1833		+		Phyllodoce arenae Webster, 1879	+			
<i>Lysidice unicornis</i> (Grube, 1840) (as <i>Nematonereis unicornis</i> (Grube, 1840)	+			Pilargidae				
Marphysa aransensis Treadwell, 1939	+			Ancistrosyllis commensalis Gardiner, 1976	+			
Marphysa sanguinea (Montagu, 1815)	+	+	+	<i>Hermundura fauveli</i> (Berkeley and Berkeley, 1941) (as <i>Loandalia fauveli</i> (Berkeley and Berkeley, 1941))	+	+		
Flabelligeridae				<i>Hermundura vivianneae</i> (Salazar-Vallejo and Reyes-Berragán, 1990) (as <i>Parandalia</i> <i>vivianneae</i> Salazar-Vallejo and Reyes- Berragán, 1990)		+		
Piromis eruca (Claparède, 1869) (as Pherusa eruca (Claparède, 1869))		+		Hermundura sp. 1 (as Parandalia sp.)	+		+	
Piromis roberti (Hartman, 1951)	+			Sigambra bassi (Hartman, 1945)		+	+	
Glyceridae				- Sigambra grubii (Müller, 1858)	+			
Hemipodia sp. 1	+			Sigambra wassi Pettibone, 1966	+			
Goniadidae				Polynoidae				
<i>Glycinde multidens</i> Müller, 1858 (as <i>Glycinde solitaria</i> (Webster, 1879))	+		+	Antinoe microps Kinberg, 1856	+			
Goniada echinulata Grube, 1870	+			Antinoe uschakovi (Ibarzabal, 1988)	+			
Goniada maculata Oersted, 1843	+			Antinoe sp. 1	+			
Goniadides carolinae Day, 1973	+			Lepidonotus lacteus (Ehlers, 1887)	+			
<i>Ophiogoniada</i> sp. 1	+			Lepidonotus sublevis Verrill, 1873	+			
Hesionidae				Malmgreniella taylori Pettibone, 1993	+			
Gryptis arenicola glabra (Hartman, 1961)		+		Malmgreniella variegata (Treadwell, 1917)	+			
<i>Podarkeopsis brevipalpa</i> (Hartmann-Schröder, 1959) (as <i>Gyptis brevipalpa</i> (Hartman-Schroeder, 1959))	+	+		Malmgreniella sp. 1	+			

Polychaete diversity in the estuarine habitats of Términos Lagoon, Southern Gulf of Mexico.

Family - Species	Habitat			Family - Species	Habitat		
	SB	SG	Μ		SB	SG	М
Hesiocaeca sp.	+			Malmgreniella sp. 2	+		
Oxydromus sp.	+			Sabellidae			
Lumbrineridae				Branchioma sp.		+	
Lumbrineris impatiens Claparède, 1868			+	Megalomma bioculatum (Ehlers, 1887)	+		
Ninoe sp.	+			Parasabella lacunosa (Perkins, 1984)	+		
Scoletoma candida (Treadwell, 1921)	+			Demonax microphthalmus (Verrill, 1873) (as Sabella microphthalma (Verrill, 1873))		+	
Scoletoma elongata (Treadwell, 1931)	+			Sabella sp.		+	
Scoletoma ernesti (Perkins, 1979)	+			Serpulidae			
Scoletoma tenuis (Verrill, 1873) (as Lumbrineris tenius (Verrill, 1873))	+			Hydriodes parvus (Tradwell, 1902)		+	
Scoletoma treadwelli (Hartman, 1956)	+			Hydroides dianthus (Verrill, 1873)	+		
Scoletoma verrilli (Perkins, 1979)	+			Hydroides protulicola Benedict, 1887	+		
Scoletoma sp.	+			Sigalionidae			
Maldanidae				Sthenelais boa (Johnston, 1833)		+	
Sabaco elongatus (Verrill, 1873) (as Branchioasychis americana (Hartman, 1945))	+		+	Sthenelais helenae Kinberg, 1856		+	
Axiothella sp.			+	Sthenelais sp.	+		
Axiothella mucosa(Andrews, 1891)		+		Sthenolepis sp.	+		
Clymenella torquata (Leidy, 1855)	+			Spionidae			
<i>Clymenella</i> sp. 1	+			Dipolydora socialis (Schmarda, 1861) (as Polydora socialis (Schmarda, 1861))		+	
Clymenura sp. 1	+			Dipolydora sp.	+		
Isocirrus sp. 1	+			Malacoceros vanderhorsti (Augener, 1927)			+
Maldane sp. 1	+			Minuspio ca. cirrifera Wirén, 1883	+		
Nereididae				Paraprionospio alata (Moore, 1923) (as Prionospio (Paraprionospio) pinnata Ehlers, 1901 or Paraprionospio pinnata (Ehlers, 1901))	+		+
<i>Allitta succinea</i> (Frey and Leuckart, 1847) (as <i>Neanthes succinea</i> (Frey and Leuckhart, 1847))	+	+	+	Polydora cornuta Bosc, 1802 (as Polydora ligni (Webster, 1879))		+	+
Ceratonereis costae (Grube, 1840)		+		Polydora plenaBerkeley and Berkeley, 1936		+	
Ceratonereis irritabilis (Webster, 1879)	+			Prionospio ehlersi Fauvel, 1928		+	
Ceratonereis versipedata (Ehlers, 1887)		+		Prionospio heterobranquiaMoore, 1907	+	+	+
Ceratonereis sp.		+		Prionospio pygmaeus Hartman, 1961	+		
Dendronereis sp.		+		Prionospio sp.		+	
Laeonereis culveri (Webster, 1879)			+	Scolelepis ca. lighti Delgado-Blas, 2006	+		
Laeonereis sp.	+			Scolelepis squamata (O.F. Muller, 1806)	+	+	+
Leonnates sp. 1	+			Spiophanes sp.		+	

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Family - Species		Habitat		Family - Species		Habitat	
	SB	SG	Μ		SB	SG	М
Leptonereis sp.			+	Streblospio benedicti (Webster, 1879)	+	-	+
Neanthes acuminata Ehlers, 1868	+			Sternaspidae			
Neanthes caudata (Delle-Chiaje, 1827)		+	+	Sternaspis sp. 1	+		
Nereis falsa Quatrefages, 1866		+		Sternaspis sp. 2	+		
Nereis grayi (Pettibone, 1956)		+		Syllidae			
Nereis micromma Harper, 1979	+			Exogone dispar (Webster, 1879)	+		
Nereis oligohalina (Rioja, 1946)		+		Exogone lourei Berkeley and Berkeley, 1938	+		
Nereis pelagica Linnaeus, 1758	+			Haplosyllis spongicola (Grube, 1855) (as Syllis spongicola (Grube, 1855))		+	
Nereis riisei Grube, 1857	+			Perkinsyllis spinisetosa (San Martín, 1990)	+		
Nicon sp.	+			Pionosyllis sp.	+		
Platynereis sp.			+	Prosphaerosyllis riseri (Perkins, 1980)	+		
Stenoninereis martini Wesenberg-Lund, 1958			+	Streptosyllis sp. 1	+		
Oenonidae				Syllis garciai (Campoy, 1932)	+		
Arabella iricolor (Montangu, 1804)		+	+	Syllis gracilis Grube, 1840	+		
Arabella sp.	+			Syllis mexicana (Rioja, 1960) (as Elhersia mexicana (Rioja, 1960))		+	+
Drilonereis longa Webster, 1879	+			Sylliis variegataGrube, 1860		+	
Onuphidae				- Syllis sp. (as Syllis (Typosyllis) sp.)		+	
Americonuphis magna(Andrews, 1891)		+		Syllis hyalina Grube, 1863		+	
Diopatra cuprea (Bosc, 1802)	+	+	+	<i>Syllis lagunae</i> Tovar-Hernández, Hernández- Alcántara and Solís-Weiss, 2008		+	+
Kinbergonuphis cedroensis (Fauchald, 1968)	+			Terebellidae			
Kinbergonuphis pulchra (Fauchald, 1980)	+			Loimia viridis Moore, 1903		+	
Kinbergonuphis rubrescens (Augener, 1906)	+			Polycirrus ca. haematodes (Claparède, 1864)	+		
<i>Kinbergonuphis simoni</i> (Santos, Day and Rice, 1981)	+			Scionides sp.		+	
Kinbergonuphis vermillionensis (Fauchald, 1968)	+			Terebella lapidaria Linnaeus, 1767		+	+
Kinbergonuphis sp.	+			<i>Terebella</i> sp.		+	
Kinbergonuphis sp. 1	+			Trichobranchidae			
Kinbergonuphis sp. 2	+			<i>Terebellides carmenensis</i> Solís-Weiss, Fauchald and Blankensteyn, 1991 (as <i>Terebellides stroemi</i> Sars, 1835)	+		+
Kinbergonuphis sp. 3	+			<i>Terebellides lanai</i> Solís-Weiss, Fauchald and Blankensteyn, 1991	+		
Onuphis eremita (Audowin and Milne- Edward, 1833)		+					



numpa

Figure 1. Location and distribution of habitats in Términos Lagoon, southern Gulf of México.

Results

18° 40

Pom

For this study, 3,398 specimens (33 families and 119 species) were collected and identified in the soft bottoms of Términos Lagoon. Combining these results with the published information in its seagrasses and mangroves, we found that, so far, 190 species from 34 families have been recorded there (Table 1). The most diverse families were Nereididae (20 spp.), Spionidae (15 spp.) and Syllidae (14 spp.), although we note that their presence in the different habitats under study is highly variable. On the other hand, 68% of the families collected for this study were represented by only five or fewer species (fig. 2).

Palizad

The distribution of the polychaete fauna in the Lagoon shows that soft bottoms constitute the more diversified habitat (119 species in 33 families), followed by the seagrasses with 75 species in 26 families, while the mangroves' environment has the least diverse fauna, with 42 species in 21 families. Although some caution is advisable when comparing the number of species of soft bottoms with literature records, mainly because the methodology and sampling effort are different, we observed that the faunal differences between habitats are more pronounced among families with the highest number of species: in the soft bottoms, six families are represented by eight species or more, but in the seagrasses only the nereidids and spionids (eight species) were similarly represented, and in the mangroves only these same families (Nereidae and Spionidae) were found with a maximum of six species (fig. 2).

Grass beds Mangroves

Oyster banks

Swamps

In the soft bottoms, the highest number of species was found in the families Onuphidae (10 spp.), Nereididae and Polynoidae (both with 9 species), and Lumbrineridae, Syllidae and Spionidae (8 species). Although the nereidids and spionids were also diversified taxa in the seagrasses (both with 8 species) and mangroves (both with 6 species), the high diversity of onuphids, lumbrinerids and polynoids seems to be exclusive of the soft bottoms (fig. 2). Besides the polynoids, the families Acoetidae, Glyceridae and Sternaspidae have been only recorded in soft bottoms, while the Amphinomidae is the only one which has not been collected in that habitat. The family Syllidae occurs preferably in soft bottoms and seagrass beds, while the Maldanidae and Cossuridae are mainly found in soft bottoms and mangroves.

The distribution of the polychaetes in the three habitats shows that most species are not widely distributed: most of them, 154 species (81% of the total species), have been recorded in only one habitat, and only 5% of the polychaetes (10 species) are able to spread out to the different habitats of



Figure 2. Number of species by family at each habitat in Términos Lagoon.



Figure 3. Distribution of the number of species by habitat in Términos Lagoon. (SB: soft bottoms; SG: seagrass beds; M: mangroves).

the lagoon (Table 1). Most of the species (7) distributed in all habitats have limited motility, and belong mainly either to Spionidae (*Scoloplos treadwelli* (Eising, 1941), *Prionospio heterobranchia* Moore, 1907 and *Scolelepis squamata* (O.F. Müller, 1806) or Capitellidae (*Capitella* sp. and *Mediomastus californiensis* (Hartman, 1944)). On the other hand, 26 species were found in two of the habitats, but the number of motile species clearly increased and more than 40% (11 species) can be classified as motile polychaetes (Table 1, fig. 3): six species are common to soft bottoms and seagrasses, nine species occur simultaneously in soft bottoms and mangroves.

The biotic heterogeneity in the habitats of Términos Lagoon, evaluated by the ANOSIM test, shows that the global value of R = 0.51 is clearly much larger than any of the 999 permuted values (p = 0.1%), rejecting the null hypothesis that there are no differences in the polychaetes' composition of the three environments. However, these faunal differences are not equal in each combination of groups, since pairwise tests show that the main separation of habitats, based on their species composition, is between the soft bottoms and seagrass beds (R = 0.622, p < 0.1%). On the other hand, the polychaete species in the soft bottoms and mangroves (R = 0.3, p = 1.1%), and in the seagrasses and mangrove environments (R = 0.247, p = 5.5%) are very similar, and their faunal differences are not significant.

Discussion

The benthic macrofauna of tropical estuaries is commonly dominated by the Polychaetous annelids (Flint and Younk, 1983; Hernández-Alcántara and Solís-Weiss, 1995; Silva et al., 2011). This is due, among other things, to their highly diverse ethological habits which help them adapt to the (also) high environmental variability (Magalhaes and Barros, 2011). In this context, polychaetes are known for their tolerance of drastic environmental changes that make it possible for them to be well represented in lagoon-estuarine ecosystems (Gambi et al, 1997; Dittman, 2000; Rosa Filho et al., 2005). The "species minimum" concept indicates that the variable environmental features present in brackish systems, tend to exclude species (Remane, 1934). As a whole, the 190 species recorded in Términos Lagoon do not seem to represent outstanding diversity levels; this is especially true if they are compared to the 854 species of polychaetes recorded in the sublittoral soft bottoms of the Gulf of Mexico (Fauchald et al., 2009) even if, admittedly, the last are living in the more stable environment of the continental shelf. On the other hand, the comparison of biodiversity with other estuarine systems in the southern Gulf of Mexico is difficult, because knowledge of the polychaetes is very limited : only one species is known to have been collected in each of three estuaries, and a maximum of 70 species have been recorded in the other seven estuaries in this region. However, even considering that comparisons with other such studies in the region are to be taken with caution, due to the different sampling procedures used (Sicinski and Janowska, 1993; Gambi et al, 1997), the 190 species of polychaetes recorded in Términos Lagoon clearly represent a much higher biodiversity than that observed in many of the tropical estuarine systems of the American continent. Such is the case with the 83 taxa registered in an estuary of the Amazon (Silva et al., 2011), the 58 species of polychaetes recorded in an estuarine system in southern Brazil (Magalhaes and Barros, 2011), the 77 species registered in an impacted estuary of Rio de Janeiro, also in Brazil (Santi and Tavares, 2009), or the 120 species of polychaetes collected in an estuary in Costa Rica (Maurer and Vargas, 1984). Notwithstanding the relatively high diversity observed in Términos Lagoon, few families are diverse and widely distributed: of the 34 families recorded, 23 are represented by fewer than five species.

It is known that, along an estuary, the benthic communities vary widely in composition and are often associated with changes in salinity and type of sediment; in addition, the greater complexity of habitats, such as the presence of vegetation or heterogeneous substrates, could be accompanied by increased species richness (Castel et al., 1989; Junoy and Vieitez, 1990). In this sense, we noted that few species (5%) occur in the whole lagoon and therefore, the faunal composition is different from one habitat to the next. However, these differences are only significant between the soft bottoms and seagrass environments. Most of these widely distributed species are deposit feeders or detritivores, which have already been reported as dominant in the soft bottoms of the lagoon (Hernández-Alcántara, 1991). For their part, the motile species, like *Marphysa sanguinea* (Montagu, 1815), *Alitta succinea* (Frey and Leuckart, 1847) and *Diopatra cuprea* (Bosc, 1802) have been usually reported on seagrass beds (Ibañez-Aguirre, 1986; Cruz-Ábrego et al., 1994).

It is necessary to have a much better knowledge of the life histories and behavior of the benthic fauna in the estuarine systems to achieve an adequate analysis of the structure of the marine communities. However, the complexity of the habitat structure created by the aquatic vegetation is an important factor in determining the diversity and composition of the communities, since they provide feeding resources and refuges to many invertebrates. This, in turn, generates differences with the fauna in unstructured habitats, such as soft bottoms (Minello et al., 2003).

In the mangrove sediments, the number of species was the lowest and the polychaete species present were very similar to those recorded in soft bottoms or seagrasses. In this case, the sampling effort was lower than in the other habitats, which could lead to an underestimate of their real biodiversity. However, few species are limited to the mangroves and, for many this environment is an extension of their "normal" habitat (Hutchings and Recher, 1982; Hernández-Alcántara and Solís-Weiss, 1991). Anyhow, it is possible that in this lagoon, an active faunal exchange takes place between the mangroves and the other two habitats studied (Hernández-Alcántara and Solís-Weiss, 1991).

Differences in the structure of the habitats analyzed and the highly variable environmental changes, which characterize the lagoon-estuarine systems, determine the high number of species recorded exclusively in one habitat (154 species), but it may also provide a particular space for opportunistic species, like, in this instance, the spionid polychaetes. Spionids are one of the most diverse families in the lagoon and their characteristic species Scoloplos treadwelli, Prionospio heterobranchia and Scolelepis squamata, occur in the three habitats while Paraprionospio alata (Moore, 1923), Streblospio benedicti (Webster, 1879) and Polydora cornuta Bosc, 1802, have been collected in two habitats at the same time. Spionids are often abundant in fine sediments and they can show marked population fluctuations. Many are opportunistic, responding to enrichment and disturbance (Pearson and Rosenberg, 1978). Another species frequently recorded in the three habitats of the Términos Lagoon, Capitella sp. (Capitellidae), is closely related to Capitella capitata (Fabricius, 1780), which thrives in organic-rich environments and has been used as a biological indicator of organic pollution (Reish, 1959). The enrichment of the sediments in this lagoon could well cause the presence of these opportunistic polychaetes. However, this "species" is actually considered to include a group of unnamed sibling species with different life histories and reproductive attributes, but with only slight morphological differences between them (Grassle and Grassle, 1976). That is why, in this study, the analyzed individuals were left as *Capitella* sp., and the previous records of *C. capitata* in the lagoon, whose specimens were also revised, were all renamed *Capitella* sp., until their taxonomic status can be elucidated.

The presence of root structures in seagrass beds may reduce the water flow, increase the content of organic matter in that sediment and provide refuge from predation for benthic invertebrates (Orth et al., 1984), encouraging the presence of a rich benthic fauna. However, in Términos Lagoon, the number of species of polychaetes is clearly higher in soft bottoms than in seagrasses, which is probably the result of this being the largest habitat of the lagoon, but also of its large variation in environmental conditions, while the seagrass beds are mainly distributed in areas with strong marine influence from southern Del Carmen Island and patches of different size at the eastern end of the lagoon (both sides of Puerto Real inlet).

The faunal composition is related to habitat type in estuarine environments, and usually the number of species is higher in a structured habitat, such as the seagrasses, compared to soft bottoms devoid of vegetation (Ferraro and Cole, 2004; Hosack et al., 2006). However, the results obtained in this study do not support previous observations which suggest that complex habitat structure increases the presence of species (Hosack et al., 2006), and the faunal differences could be associated to other physical-chemical factors. Unfortunately, the scarce information available on the structural organization of the benthic communities, not only in Términos Lagoon, but in all the tropical estuarine systems of the Gulf of Mexico, makes it difficult to evaluate and verify these statements. Besides, from the 1980s, Términos Lagoon conditions have been changing constantly, with an increase of marine influence, more turbidity, a general decrease of depth, and even a decrease in the seagrass meadows, particularly around Ciudad del Carmen (the island city), associated with an increasingly fast urbanization (Villéger et al., 2010). This could modify the relationships between the species already settled, new settlements and their distributional patterns.

Anyway, the information about the biodiversity of the polychaetes from this study is important as a departure point for understanding the ecological mechanisms prevalent in this lagoon-estuarine system, since the polychaetes have been widely used as indicators of the general "health" in benthic communities, especially those under pollution impacts (Dean, 2008). Unfortunately, anthropogenic influence is increasing in those systems all along the southern region of the Gulf of Mexico, negatively affecting them. In 1971, the largest deposit of hydrocarbons in Mexico (Cantarell) and one of the largest in the world was discovered, precisely in front of Términos Lagoon on the continental shelf. Following this discovery the area became one of the most important economic zones of the country, but this development triggered the transformation of previously rural areas into urban zones quite rapidly (Soto-Galera et al., 2010).

This exceptional economic development and its many related activities (oil extraction and associated industry, fisheries, tourism, fast urbanization, etc.) has increased the exploitation and deterioration of the natural resources of the region, and its traditional activities which often collide with the modern and excessively fast development (Sánchez-Gil et al., 2004).

Finally, it is necessary to emphasize the fact that benthic communities are severely threatened by the worsening conditions of those habitats due to human activities (Snelgrove et al., 1997), and that only a small fraction of the species which live in the benthos in general have been described in tropical regions. So, there is a high probability that many of them will disappear even before they are known (Snelgrove, 1998, 1999), in particular, in the southern Gulf of Mexico, where oil extraction and processing of its derivates take place in the vicinity of these lagoon-estuarine systems. Even if the characterization of the polychaete fauna found in Términos Lagoon is still incomplete, the information generated by this type of biotic inventory, including spatial and seasonal variation, is key to understanding the functioning of these communities and will hopefully further stimulate the study of these environments in the southern region of the Gulf of Mexico. In turn, those studies will help to manage and protect these natural resources, while allowing the rational exploitation of the oil and fisheries industry.

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