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Polychaeta Diversity in the Continental Shelf Off the Orinoco River Delta, Venezuela

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1. Introduction

Coastal waters are mainly influenced by two large spatial scale processes: upwellings and river inputs (Mann & Lazier, 2006). Rivers are the main conduits of water, dissolved and particulate organic matter, salt, and other organic materials from the continents to the sea (Alongi, 1998). In Venezuela, the largest watercourse is the Orinoco River, covering a total basin of 106 km² and discharging an average of 1,080 km³/yr of water, and 150x 106 tons³/yr of sediment to the Atlantic Ocean, representing the fourth largest river of the world in terms of discharge (Alongi, 1998). Several authors have shown that the Orinoco's river plume can extend up to 100 km from the coast line, during the rainy season, influencing the salinity patterns, coastal currents, suspended materials and nutrient concentrations in the Venezuelan Atlantic coast and the Caribbean Sea (Muller-Karger et al., 1989; Penchaszadeh et al., 2000). The dispersion of the riverine front follows a northwest direction due to the influence of the northeasterly trade winds and the Guayana current flow. The surface plume is well-mixed inshore but it is stratified on the outer shelf, creating unique environmental conditions that greatly modify the marine waters and sediments.

Very scarce information was available for this Atlantic area until recent years, as the Venezuelan government has undergone offshore gas exploration activities in the continental shelf off the Orinoco River delta (Gomez et al., 2005, Martín & Bone, 2007). This effort has allowed the scientific community to conduct large multidisciplinary base line studies for this Atlantic region, characterized by a large continental shelf, partly influenced by the Orinoco's continental waters, with salinity values ranging from 0.25 to 36.92‰ (Martín & Bone, 2007), and a steep slope, reaching more than 2,500 m deep. These studies have included the characterization of the environmental and biological settings of the area, including the benthic component. The benthic community has been recently reported in terms of the main groups inhabiting these large soft-bottom areas (Bone et al., 2007), where polychaetes represented the most important one, achieving more than 64% of the total macrofaunal abundance.

The biodiversity knowledge of the polychaeta fauna in Venezuela has been traditionally focused on shallow water areas. Previous studies have revealed a total of 40 families, 138 genera and 206 species for the Caribbean coast (Bone & Liñero, 2003), but there is no previous information for the Atlantic region or deep waters. In the course of this study we

report for the first time the biodiversity of the polychaete community inhabiting the Venezuelan Atlantic front. The area is described in terms of its environmental settings, and the role of the abiotic conditions in shaping the polychaete community is assessed.

2. Methodology

This study was conducted in the Venezuelan Atlantic coast, south-east from Trinidad & Tobago, and north-east offshore the Orinoco's River delta, between 10°16′ - 8°55′ N and 61°05′ - 58°49′W (Figure 1). The study area was subdivided into three depth zones: a shallow continental shelf zone (from 10 - 60 m), with vertically mixed waters under the Orinoco's direct influence (1), a continental shelf zone (from 60-200 m), with no vertical mixing (2), and a deep slope zone, > 200 m (3). A total of 82 stations were sampled during November-December 2005 (rainy season): 17 in zone 1, 50 in zone 2, and 13 in zone 3 (Figure 1). Baseline studies (Gomez et al., 2005; Martín & Bone, 2007) provided sea bottom environmental data -depth, salinity, water temperature, sediment texture and organic content of the sediments- for these and other sampling stations. Samples of the benthic fauna were taken using a Van Veen dredge of 0.20 m² surface area. Sediment samples were hand-sieved by means of 0.5 mm sieve. All fauna was removed and polychaetes were identified down to species level when possible.

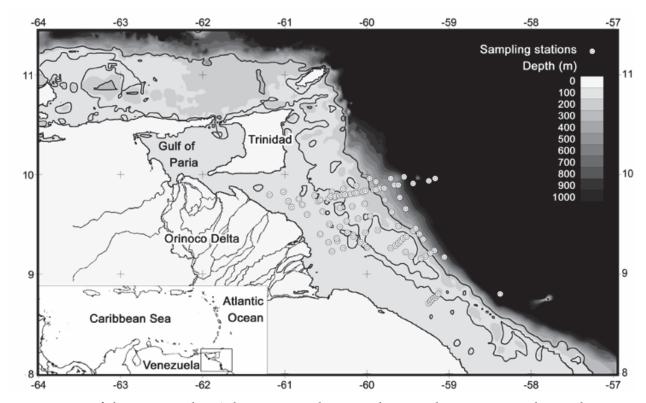


Fig. 1. Map of the Venezuelan Atlantic coast showing the sampling stations. The study area was divided in three bathymetric zones, delimited in the map by thick lines at the 60 m and 200 m isobaths.

Principal Component Analysis was applied to the environmental data in order to explore the structure of the dataset and detect any possible difference between depth zones. Univariate differences in the environmental variables according to the bathymetric zones were tested using parametric ANOVA, followed by a Fisher LSD test. Cluster analysis was used to study species distribution patterns along the depth gradient. Non-parametric ANOVA's (Kruskal-Wallis) were used to determine statistical differences in density and richness values between depth zones, due to the high variability between the benthic samples. The relationship between polychaete density and the environmental variables (depth zone, salinity, sand, clay, and organic content of the sediment) was explored within a piecewise regression approach to account for the non-linear relationship between the response and explanatory variables. As samples were grouped according to depth in shallow (0-60 m), intermediate (60-200 m) and deep areas (>200 m), depth was treated then as a nominal variable with three levels. After a preliminary data exploration, the redundant response variable family richness (related to density, R=0.9) and the explanatory variables temperature (explained by depth, R=-0.8) and lime (related to clay, R=-0.9 and organic content, R=0.6) were excluded from the analysis. Also, two outliers with density values higher than average+3sd (86.7 ind/m²) were excluded from the analysis.

3. Results

3.1 Environmental variables

The characteristics of the depth zones in terms of their main environmental parameters are presented in Table 1. As expected, temperature responds to the depth gradient (R=-0.87), with the deepest zone showing the lowest values (ANOVA test, p < 0.001, Fisher LSD test, p < 0.001). The behavior of the other environmental variables seems to respond to the influence of the Orinoco River, such as salinity, where the shallowest zone, near the Orinoco delta, has the lowest salinity and highest variability (ANOVA test, p < 0.001, Fisher LSD test, p < 0.001). Sediment textural analyses show that sand and silt have an opposite relationship (R=-0.92), but silt and organic content are positively correlated (R=0.65). Closest to the river influence, the shallowest zone has highest silt and organic content. The drop-off of the continental shelf is characterized by a sudden decrease of these fine components and an increase of sand, whereas in the deep waters these variables have intermediate values.

	Zone 1 (0-60m)	Zone 2 (60-200m)	Zone 3 (>200m)
Temperature (°C)	26.86 ± 1.29 (37)	22.97 ± 3.36(37)	6.24 ± 3.86 (40)
Salinity (‰)	26.12 ± 13.82 (28)	36.57 ± 0.35 (24)	$35.02 \pm 0.42 (35)$
%Sand	14.55 ± 21.62(38)	63.55 ± 23.42 (60)	30.78 ± 21.20 (17)
%Silt	73.30 ± 24.66 (38)	25.15 ± 16.92 (60)	49.58 ± 19.80 (17)
%Clay	12.16 ± 11.67 (38)	11.27 ± 9.52 (60)	19.64 ± 12.67 (17)
%Organic content	0.96 ± 0.28 (38)	0.51 ± 0.38(60)	0.61 ± 0.35 (17)

Table 1. Average and standard deviation (number of samples) for sea bottom environmental variables measured in each bathymetric zone. Highest values in bold letters, lowest values in gray. The differences between the zones are significant for all variables (ANOVA test, p<0.05). Groups in different colors according to post hoc comparisons (Fisher LSD test, p<0.05).

The Principal Component Analysis of the environmental variables restates the clear separation between the three bathymetric zones (Figure 2). Factor 1 accumulates 41% of the

total variance. This factor includes information concerning the sediment variables: salinity (-0.57), percentage of silt (0.83), organic content (0.83) and percentage of sand (-0.72). Factor 2 (28% of the explained variance) is represented by the variables depth (-0.75), temperature (0.69) and percentage of sand (0.63).

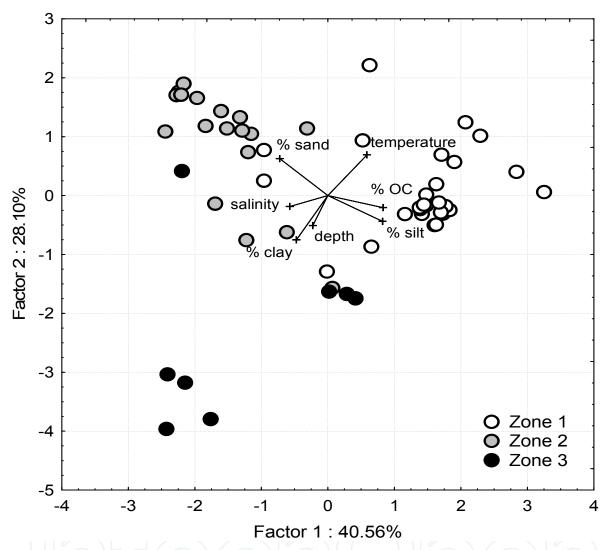


Fig. 2. Principal Component Analysis plot of site scores on the first two principal components derived from the environmental variables for sampling sites at the Venezuelan Atlantic coast according to the bathymetric zones.

3.2 Polychaete fauna

A total of 2,452 ind were collected, representing 43 families, showing a very high biodiversity for this region. None of the families were dominant, but Spionidae (13.1%), Pilargidae (11.5%) and Paraonidae (10.72%) were the most abundant ones; the rest represented less than 7% of the total abundance. At a species level, we identified 81 species for the area: 19 species in zone 1, 68 in zone 2, and 23 in zone 3 (Table 2).

We identified 19 families in the first zone, with Spionidae (19.81%), Paraonidae (14.32%), Magelonidae (11.79%) and Capitellidae (10.98%) as the most abundant. From the 19 species recorded here, 4 of them represented 53.38% of the total number of individuals: *Dipolydora*

Curaina	Zone 1 (0-60m)	Zone 2 (60-200m)	Zone 3 (>200m)	C	Zone 1 (0-60m)	Zone 2	Zone 3 (>200m)
Species	(U-6UM)	(60-200m)	(>200m)	Species	(U-6UM)	(60-200m)	(>200m)
Paramphinome besnardi				Scoloplos rubra			
Isolda pulchella				Scoloplos texana			
Lysippe annectens				Cirrophorus lyra			
Melinna cristata				Aricidea (acmira) cf. finitima			
Mediomastus californiensis				Aricidea (acmira) simplex			
Scyphoproctus platyproctus				Aricidea (allia) suecica			
Notomastus hemipodus	-	•		Aricidea (aricidea) fragilis			
Notomastus lineatus				Cirrophorus branchiatus			
Notomastus americanus				Levinsenia gracilis			
Notomastus angelicae			110	Paraonella nordica		\\\°_	\neg
Notomastus tenuis				Sigambra tentaculata	1-1/-		
Chaetozone cf. setosa		\top		Ancistrosyllis jonesi) 		
Monticellina dorsobranchialis				Sigambra wassi	/ / 		
Tharyx cf. setigera				Pilargis berkeleyae			
Cossura delta				Poecillochaetus johnsoni			
Schistomeringos pectinata				Eteone lactea			
Protodorvillea kefersteini				Lygdamis indicus			
Eunice filamentosa				Prionospio multibranchiata			
Eunice websteri				Prionospio delta			
Eunice vittata		-		Dipolydora socialis		•	
Marphysa sanguinea				Paraprionospio cf. tamaii			
Diplocirrus capensis		_		Aurospio dibranchiata			
Goniada maculata						·	
Glycinde normanni				Spiophanes duplex			
Glycera papillosa		_		Laonice cirrata			
Gyptis brevipalpa				Spio pettiboneae			
Heterospio cf. longissima	_	ı		Spiophanes wigleyi			
Scolotema verrilli				Sternapsis scutata			
Lumbrinereis jonesi				Sphaerosyllis parabulbosa			
Magelona cf. berkeleyi				Exogone (Exogone) naidina			
Asychis elongata				Exogone (Exogone) lourei			
Aglaophamus verrilli				Exogone (Parexogone) campo		-	
Nephtys squamosa				Exogone (Parexogone) cariber	nsis		
Nephtys incisa		-		Haplosyllis spongicola			
Nereis falsa				Pionosyllis weissmanni			
Ceratocephala oculata				Sphaerosyllis magnidentata			
Kimbergonuphis ceproensis				Syllis (Typosyllis) ortizi			
Kimbergonuphis tenuis				Streblosoma hartmanae			
Diopatra cuprea				Terebellides stroemi			
Diopatra tridentata							
Armandia agilis							
Ophelina cylindriculata							
Ophelina acuminata							

Table 2. Spatial distribution of polychaete species along the bathymetric gradient.

socialis (16.76%), Mediomastus californiensis (13.77%), Cossura delta (12.19%) and Prionospio delta (10.66%). In zone 2 only Spionidae (10.92%) and Pilargidae (10.03%) were important, with *P. delta* (9.86%) and *Aglaophamus verilli* (9.2%) as the dominant species. Zone 3 exhibited 4 main families: Pilargidae (19.41%), Spionidae (15.16%), Paraonidae (14.84%) and Cirratulidae (9.13%), with *P. delta* (13.54%), Levinsenia gracilis and Tharyx setigera (11.28% each), and Cirrophorus lyra (9.03%) as the most abundant species. We found that only 5 species (6.17%) were common to all zones along the depth gradient: *T. setigera*, *A. verrilli*, Sigambra tentaculata, *P. delta* and Spiophanes duplex, suggesting a certain degree of specificity in the spatial distribution of most species. Eight species were common to zones 1 and 2, one species was common between 1 and 3, and 10 were common to 2 and 3. The cluster analysis indicates that the shallowest, river influenced area, has a particular polychaete assemblage and that deeper areas are more similar (Figure 3).

3.3 Patterns of association between variables

Polychaete density was related to the environmental variables in a nonlinear fashion (piecewise regression, r= 0.94 percentage of variance explained: 87.82%, Figure 4).

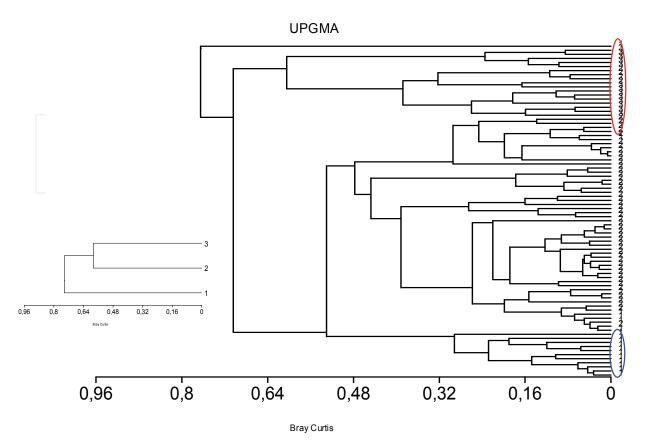


Fig. 3. Dendrogram comparing the species composition in the three depth zones.

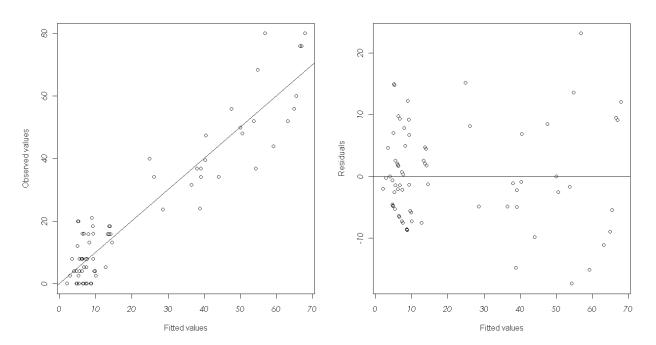


Fig. 4. Fitted values vs observed values (left) and residuals (right) for the piecewise regression applied to polychaete density data.

The river influence is determinant of the abundance patterns when densities are low (<21.19 ind/m²). However, when density is higher, depth zone, clay and organic content are the best variables explaining these patterns (Table 3).

	Intercept	Zone	Salinity	Sand	Clay	OC
M1 (density < breakpoint)	7.65	-2.97	0.22	-0.06	-0.02	1.77
p value		0.19	0.06 *	0.44	0.94	0.54
M2 (density> breakpoint)	-73.05	13.16	3.52	-0.05	-0.90	-27.32
p value		0.06*	0.12	0.36	0.03**	0.01**

Table 3. Parameter estimates and significance values of the two regression lines fitted using piecewise regression, estimated breakpoint=21.19 ind/m².

Canonical Correspondance Analysis (CCA) relating the environmental data and density of the polychaete species showed a strong association between *C. delta, M. californiensis, D. socialis, S. verrilli, S. platypatus* and salinity values (Figure 5). This result is reinforced by a significant positive correlation between salinity and total density along the depth gradient (Spearman, r: 0.36, p= 0.04), suggesting that this variable is one of the main ecological variables determining their distribution. Other environmental variables were also important in defining the spatial distribution patterns, like sediment silt content and deep water temperature, contributing to mark clear differences between zones.

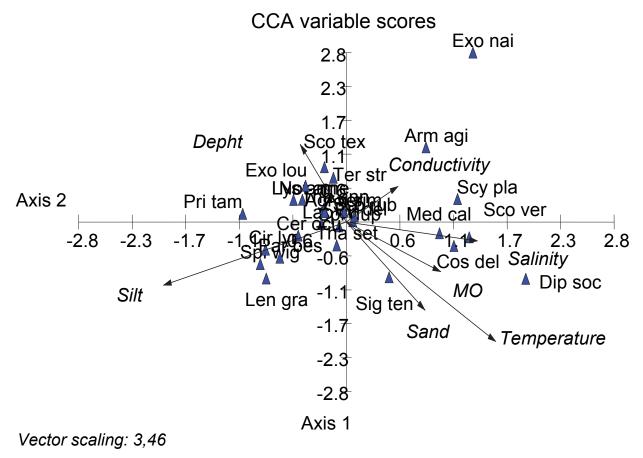


Fig. 5. Canonical Correspondance Analysis relating the environmental data and density values for the dominant polychaete species.

4. Discussion

This study represents the first contribution to the knowledge of polychaetes biodiversity from deep-sea waters in the south Caribbean, particularly for Venezuela, where such studies are very scarce. Previous research carried out at the Orinoco's river delta and its continental shelf (Bone et al., 2004, 2007) have established that polychaete communities associated to soft bottoms of this region, are characterized by high species richness but low organisms density in relation to coastal marine environments. These are expected characteristics in deep water benthic communities (Grassle & Macioleck, 1992; Nybakken, 1997; Sanders & Hessler, 1969). The presence of 43 families and 81 species of polychaetes demonstrate this high diversity. Nonetheless, the richness is lower than what has been reported for the Venezuelan coastal waters (Bone & Liñero, 2003), where over 200 species have been found. The most important polychaete families in the study site were Spionidae, Pilargidae and Paraonidae, while the rest of them presented relative abundances lower than 7%. Glover et al. (2001) and Pérez et al. (2003) pointed out that Spionidae, Cirratulidae and Paraonidae families represent between 50-60% of the total abundance in deep water areas, in the Atlantic and Pacific, independently of the sediment organic content. The authors explained that this can relate to a very similar functional structure between these communities, dominated by detritivorous polychaetes; being also present predator habits families, mainly syllids and lumbrinerids, but in a lower proportion. Probert et al. (2001) report the importance of Spionidae family for the west coast of New Zeland (48,7%), especially in shallow waters (depths < 100m), where there is a vast fresh water discharge and terrestrial sediment drag towards the marine receptor waters.

The polychaete species composition, richness and abundance found show the presence of a very marked spatial pattern. The highest average density and species number were observed at depths greater than 60 m, at zones called 2 and 3, the ones that are farther from the coastline, the Orinoco river influence and the Guayana current. At the shallowest zone (1), there is lower richness, and only some polychaete species increased their densities as in the particular case of the individuals from Spionidae (*Dipolydora. socialis*) and Capitellidae (*Mediomastus californiensis* and *Scyphoproctus platyproctus*), whose densities decreased towards the zones 2 and 3 (Balthis et al., 2006). In general, these species are opportunistic, have short reproductive and recruitment cycles (MacCord & Amaral, 2007); and are deposited organic matter consumers, taking advantage of the productivity peaks; which lets them inhabit highly disturbed systems (Méndez, 2002; Santos, 1994). Likewise, in this zone, a higher estuarine species relative abundance was observed with broad range of saline tolerance, like the case of species from Cossuridae (*Cossura delta*) and Spionidae (*Prionospio delta*) families.

The response of polychaetes to steep salinity variations was reported in Venezuela for a few spionids (*Streblospio gynobranchiata* and the polydorids group) at coastal zones affected by intense rain events that cause salinity to decrease down to 5PSU (Chollet & Bone, 2007). Bone & Rodríguez (2004) also report the presence of only 9 polychaete families and 14 species, at the littoral zone of the Orinoco's river delta, where salinity values are close to 0PSU, and higher density and biodiversity at areas with greater marine influence during the dry season, when the river discharges are lower. The result showed no significant correlation with depth or other environmental variables, except salinity (Spearman, p<0.04), suggesting a clear influence of the Orinoco river in the spatial distribution pattern of polychaetes found in the shallow continental shelf zone.

Similar results were found by Yáñez-Arancibia & Day (1988), who report the presence of some species from Cossuridae and Spionidae families at Términos lagoon west area, Gulf of Mexico, where the higher fluvial discharge and lower salinity values are observed, indicating that distribution of organisms at the lagoon is determined by salinity. Gaston & Nasci (1988) report the capitellid *Mediomastus californiensis* dominance all year long, at the lower Calcasieu estuary, Louisiana, USA, with salinity fluctuations between 0-23PSU, showing its euryhaline condition. On the other hand, restricted spatial distribution was observed for some families like Eunicidae, Syllidae, Onuphidae, Nereididae, Amphinomidae, Ampharetidae, Glyceridae, Fauveliopsidae, Questidae and Sabellidae, limited to zones 2 and 3, with a marked richness reduction towards zone 3 (deepest one), suggesting that they can be less tolerant to marked salinity decreases.

Our results show that this low polychaete density at shallow bottoms off the northeast Venezuelan region can be related to the Orinoco's river discharge, and that this influence determines the existence of two zones in the region, not three. One shallow, conditioned by the river discharge, with low organic matter content in sediments (< 1%), high water turbidity and extreme salinity variations (0.25-23PSU); and a deeper, an oceanic influenced and oligotrophic zone, characterized by a steep depth gradient, low temperature and marine current influences (Martín & Bone, 2007). These environmental conditions contribute to define the polychaete community spatial distribution pattern, with low densities for the first one, and higher for the second one (Martín & Bone, 2007; Pérez et al., 2003). At the shallowest zone (< 60 m depth), there is active sedimentation, with high silt and organic content. This area is replaced by another one dominated by a higher sandy fraction content, where sedimentation is scarce, which reaches about 200 m depth. Thereafter, the behavior of the data is very variable towards deeper zones, and could be related to differential sedimentation and transportation processes, as it has been suggested by Martín & Bone (2007). Muller-Karger et al. (1989) have shown that this influence may extent over 100 km offshore, especially during the rainy season, when the water volume discharged into the marine environment is higher. Orinoco's river plume effect combines with the one from the Amazon river that skirts the east coast from the south, and together they extend to 18°N, specifically to La Mona island, between Puerto Rico and Dominican Republic, extending 300km over the Caribbean Sea (Cherubin & Robertson, 2007).

Conlan et al. (2008) found a positive correlation between macrofauna density and distance from the coast, at Beaufort, Canada, due to the Mackenzie's river influence, and a negative correlation with depth (between 10-400 m), where there is a salinity gradient from 16 to 30PSU at 75km from the coast, and a higher carbon and nitrogen concentration in sediment at the shallow area. Our results showed a different spatial pattern, where polychaete densities are related to environmental variables in a nonlinear fashion. The river influence is determinant of the abundance patterns where densities are low (<15 ind/m²). However, where density is higher, depth, clay and organic content are the best variables explaining these patterns. In this deeper zone, the highest biodiversity by station is also reported, particularly between 60-200 m deep. The polychaete average density at zones 2 and 3 was very similar (34 and 36ind/m² respectively), but with only 23% of family composition resemblance; with a clear depth effect. This oceanic zone, away from the coastline, corresponds to oligotrophic waters and low primary productivity, due to the influence of the Orinoco river and Guayana current, in consequence species richness is again reduced (Alongi, 1998).

In the literature, many diverse results exist for depth effects in benthic communities spatial patterns, like is pointed out by Allen et al. (2006) at a revision of 120 investigations within the Gulf of Mexico continental shelf and the Atlantic coast of the EEUU. Aller et al. (2002) explains that despite the fact of having a well-defined depth gradient at Cape Hatteras platform, in North Carolina, they found a very similar macrofauna density from the shallow area to 800 m deep, with a reduction towards 2000 m. These density variations in the depth gradient for the Tropical Atlantic, has been attributed to nutrient entry and flux reduction at greater distances from the coast (Cosson-Sarradin et al., 1998). Aller et al. (2002) and Juul-Pedersen et al. (2008) explain that organic matter entry to marine water masses, as phytoplankton, feces or particulate rests, contribute to the existence of a extremely active benthic community, with high abundance and biomass that inhabits these deep bottoms. But benthic communities from shallow areas receive a greater organic matter input and other sources of carbon from the nearby coastal platform, showing greatest organisms' density. At the Orinoco's delta region this does not seem to be the case, where we observed differences at the shallow area due to salinity reduction as a consequence of the river discharge. Aller et al. (2002), showed that this organic matter entry to the system does not have direct relation with depth patterns, due to the zone's topography, which can alter particles deposition. As well, Glover et al. (2001) pointed out after evaluating this relationship at abyssal bottoms, that species diversity and polychaete density do not depend in a linear way on the water column productivity, but can be affected by local factors like depth, fluvial discharges and hydrodynamic patterns, suggesting that the oligotrophic condition does not limit diversity in a given zone.

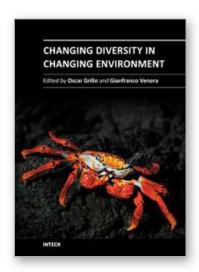
The response to variation in organism density and species richness in the case of the Orinoco's delta could be adjusted to the model proposed by Alongi (1998) to explain infauna spatial distribution patterns associated to soft-bottoms areas affected by river and delta discharges. Following this model, the most influenced area by an important river discharge is the shallow one, affected by a great nutrient and sediments deposition, but does not allow the establishment of a high diverse community, like the case of our zone 1. At the shallowest zone, salinity can be reduced, and only a few polychaete species, considered as opportunistic, can increase their density with these environmental changes, being this condition adverse to many other species. This response can be favored by organic matter dragged by runoffs from the coast and nearby rivers, increasing the organic matter input, which can be a direct or indirect source of food to these organisms (Probert et al., 2001). As the distance progresses from this point of high discharge of the delta towards open sea, Alongi's model predicts reduced solid suspended amounts in the water column, which permits development of a higher primary productivity (more light penetration), this last one also favored by a higher water column mix and oxygenation, because depth is greater, which leads towards the development of a denser and more bio diverse benthic community. This situation could be present in our zone 2, which is farther away from the Orinoco's river discharges and the Guayana current effect, characterized by stable and higher salinity values and species richness. Our zone 3, the farthest one from coastline and Orinoco river influence, corresponds to an oligotrophic zone, with low primary productivity due to the lower nutrient input, so the species richness is again reduced. This deep zone is dominated by species from the Pilargidae, Spionidae, Paraonidae and Cirratulidae families, similar to Pérez et al. (2003) results from the Gulf of Mexico, who report the presence of these families at zones between 200-3800m depth. Therefore, in this work we stress the importance of studying large-scale biodiversity spatial and temporal patterns in marine environments

subjected to heavy continental influence, in order to contribute to reduce the existent gap of information, especially in tropical regions, where riverine inputs are determinant.

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Changing Diversity in Changing Environment

Edited by PhD. Oscar Grillo

ISBN 978-953-307-796-3 Hard cover, 392 pages **Publisher** InTech **Published online** 14, November, 2011

Published in print edition November, 2011

As everybody knows, the dynamic interactions between biotic and abiotic factors, as well as the anthropic ones, considerably affect global climate changes and consequently biology, ecology and distribution of life forms of our planet. These important natural events affect all ecosystems, causing important changes on biodiversity. Systematic and phylogenetic studies, biogeographic distribution analysis and evaluations of diversity richness are focal topics of this book written by international experts, some even considering economical effects and future perspectives on the managing and conservation plans.

How to reference

In order to correctly reference this scholarly work, feel free to copy and paste the following:

David Bone, Carmen Teresa Rodriguez and Iliana Chollett (2011). Polychaeta Diversity in the Continental Shelf Off the Orinoco River Delta, Venezuela, Changing Diversity in Changing Environment, PhD. Oscar Grillo (Ed.), ISBN: 978-953-307-796-3, InTech, Available from: http://www.intechopen.com/books/changing-diversity-in-changing-environment/polychaeta-diversity-in-the-continental-shelf-off-the-orinoco-river-delta-venezuela

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