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DISTRIBUTION AND SEASONAL VARIATION OF INTERTIDAL BIVALVES ON A SANDY BEACH AT CAIMARE CHICO, VENEZUELA

JOSÉ G. DELGADO[2], YINETT M. REVEROL[1], ANTONIO R. GODOY, AND HÉCTOR J. SEVEREYN

Laboratorio de Sistemática de Invertebrados Acuáticos, Departamento de Biología, Facultad Experimental de Ciencias, la Universidad del Zulia, Apdo. 526, Maracaibo 4011, Venezuela

[1]Laboratorio de Cultivo de Invertebrados Acuáticos, Departamento de Biología, Facultad Experimental de Ciencias, la Universidad del Zulia, Apdo. 526, Maracaibo 4011, Venezuela

[2]Present address: Laboratorio de Evaluación de Recursos Pesqueros, Estación Local El Lago, Instituto Nacional de Investigaciones Agrícolas (INIA), Maracaibo, Estado Zulia, Venezuela. Telefax: (58) (261) 7642324. jdelgado@inia.gob.ve

Abstract. We studied distribution and seasonal variation of intertidal bivalves on a sandy beach at Caimare Chico, Zulia State, Venezuela, from December 1995 to August 1996, during rainy and dry seasons. Samples were collected at lowest tide in water depths from 0.0 to 0.5 m, by using an Ekman dredge (0.022 m^2). Twenty-four species, in 18 genera and 12 families were collected. The Shannon-Weaver Index (H´) of species diversity varied from 0.24 to 1.50, evenness between 0.10 and 0.53, and Margalef´s species richness (Dmg) from 1.34 to 2.89. The intertidal area was divided into three different zones according to species distribution and abundance. The first zone was characterized by *Donax striatus, Tivela mactroides*, *Donax denticulatus*, *Strigilla pisiformis* and *Pteria colymbus*, the second zone by *Chione cancellata*, *Crassinella lunulata*, *Pitar dione*, *Macoma breviformis* and *Codakia orbicularis*, and the third zone by *Anadara braziliana* and *Macoma* sp. The structure of this distribution occurred throughout the sampling period. Total rainy season abundance was lower than that recorded in the dry season.

Key words: Benthos, bivalves, distribution, intertidal, mollusks, sandy beach, Venezuela, zonation.

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DISTRIBUCIÓN Y VARIACIÓN ESTACIONAL DE LOS BIVALVOS INTERMAREALES DE LA PLAYA ARENOSA DE CAIMARE CHICO, VENEZUELA

Resumen. Se determinó la distribución y variación estacional de los bivalvos macrobentónicos intermareales de la playa arenosa abierta de Caimare Chico, Estado Zulia, Venezuela, entre diciembre de 1995 y agosto de 1996. Las muestras de bivalvos se recolectaron en la superficie (0,0–0,50 m de profundidad) y en marea baja, tanto en la época de sequía como de lluvia, usando una draga Ekman (0,022 m^2). Se identificaron 24 especies, agrupadas en 18 géneros y 12 familias. La diversidad de Shannon-Weaver osciló entre 0,24 y 1,50, la equidad de 0,10 a 0,53 y la riqueza de especies de Margalef entre 1,34 y 2,89. Se identificaron tres zonas intermareales caracterizadas por la abundancia y la distribución de las especies. La primera zona fue caracterizada por la presencia de *Donax striatus*, *Tivela mactroides*, *Donax denticulatus*, *Strigilla pisiformis* and *Pteria colymbus*; la segunda zona por *Chione cancellata*, *Crassinella lunulata*, *Pitar dione*, *Macoma breviformis* y *Codakia orbicularis*, y la tercera zona por *Anadara braziliana* y *Macoma* sp. Este patrón de distribución no varió durante el período de estudio. Se observó una marcada disminución de la abundancia total en la estación de lluvia en comparación con la de sequía.

Palabras clave: Bentos, bivalvos, intermareal, molusco, playa arenosa, Venezuela, zonación.

INTRODUCTION

High-energy sandy beaches provide a stressful and dynamic environment for intertidal marine fauna (Shelton and Robertson 1981, Leber 1982, Delgado 1997). As a result of this “pressure”, few macroinvertebrate species inhabit the intertidal zone of open beaches compared to those living in more stable subtidal areas. Even though bivalve mollusks are one of the most abundant invertebrate taxa inhabiting these zones, few studies of their communities are available (*e.g.*, Ansell *et al.* 1972, Shelton and Robertson 1981, Leber 1982, Bally 1983, Gianuca 1983, 1985, Mikkelsen *et al*. 1995, Souza and Gianuca 1995, Delgado 1997).

Dansereau (1947) studied zonation and succession of sandy beach communities in South Restinga, Rio de Janeiro, Brazil. Souza and Gianuca (1995) studied the intertidal macrofauna on the exposed sandy beach at Barrancos, Paraná, Brazil, where they characterized zonation, community structure and seasonal variation. Gianuca (1983, 1985) studied intertidal structure of macrofauna, production and life history of the main intertidal species and some supra and infralittoral species. Amaral *et al*. (1990) characterized species distribution on protected sandy beaches in São Paulo State, Brazil.

Escofet *et al*. (1979) included the southern Brazilian sandy beaches in a zonation scheme for the southeastern Atlantic coast, and Shelton and Robertson (1981) investigated the community structure of intertidal macrofauna on two surf-exposed beaches in Texas, USA, in terms of species composition, diversity, abundance, biomass, zonation and seasonal changes. In Venezuela, De Mahieu and Gamba (1980) studied the littoral zonation in some communities of sandy beaches in Golfo Triste, and Delgado (1997) studied macrobenthic communities of two sandy beaches north of Maracaibo, to determine and compare diversity, seasonal changes, abundance, distribution and species composition. The purpose of this study is to characterize the distribution, community structure and seasonal variation of intertidal bivalves on a sandy beach in Zulia State, Venezuela.

MATERIALS AND METHODS

STUDY AREA

We studied a high-energy beach (called Caimare Chico) on the southwestern coast of the Gulf of Venezuela, 80 km north of Maracaibo, in Zulia State, Venezuela (11° 10' 33.3" N, 71° 50' 4.4" W)(Fig. 1). The beach consists mostly of well-sorted, from fine to very fine sand grains (75–425 µm), and dead clam shell (*Donax striatus*) remains (Rodríguez 1973, Delgado 1997).

DATA COLLECTION

We sampled benthic bivalves monthly, from December 1995 to August 1996, during both rainy and dry seasons, using a systematic design similar to that of Leber (1982). Sampling was done at lowest tide (0.0–0.50 m depth) using an Ekman dredge ($0.022m^2$). One 50-m transect with three replicates was made perpendicular to the coastline, and each transect was divided into ten sampling quadrates (equal to area of dredge). Each transect replicate was separated by 2 m and quadrates within each transect were separated by 5 m. Samples were sieved (850 µm mesh) in the laboratory and preserved in 10% formalin and seawater. One day later, organisms were sorted, preserved in 70% ethanol, identified and counted.

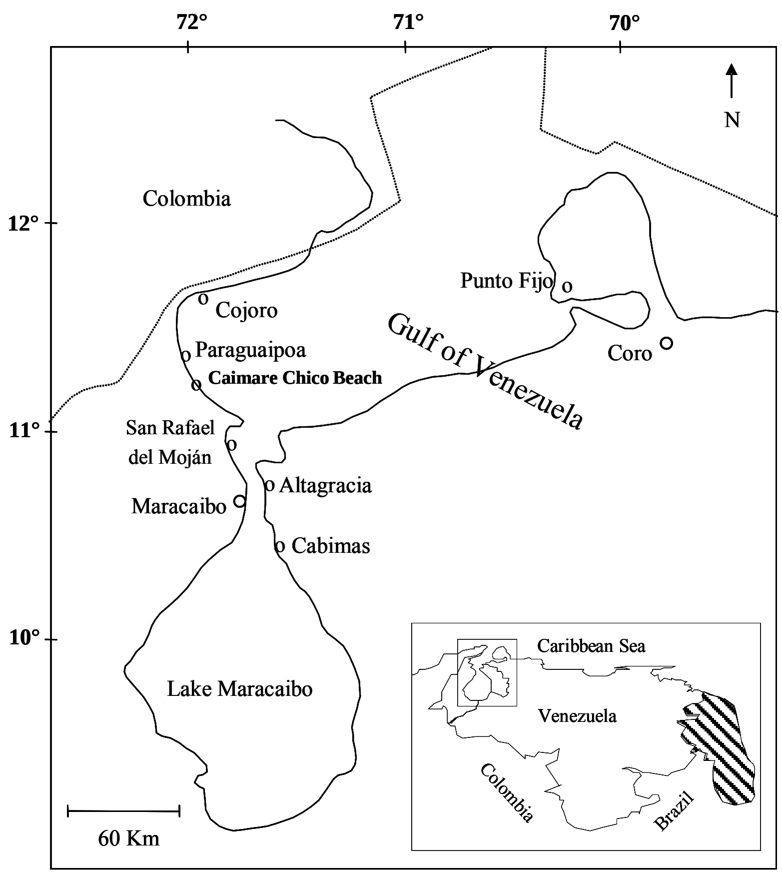

Figure 1. Location of Caimare Chico beach, on the southwestern coast of the Gulf of Venezuela.

Water temperature (mercury thermometer), salinity (American Optical refractometer 10419), pH (Piccolo pH meter) and dissolved oxygen (field oximeter YSI Model 51B) were measured in each sampling period. Substrate samples (~ 500 g) were taken to a depth of ten cm, using an Ekman dredge on the beach at low tide. Dried substrate (100 g) from each sample was sieved sequentially through 850, 710, 425, 250, 180, 150, and 75 μm meshes. Granulometric composition was determined by calculating the cumulative percent (by weight) for each fraction. Organic matter was quantified by separating heavy particulate organic matter (> 1 mm) from fine particulate organic matter (1 mm–0.45 μm).

DATA ANALYSIS

We used the Shannon-Weaver index (H′) (Shannon and Weaver 1963) to calculate species diversity, the Shannon evenness index to determine evenness, and the Margalef index (Dmg) to estimate species richness. Abundance was estimated as the number of individuals/m^2. The criterion used to establish distribution patterns was the distribution of bivalves along the beach and species abundance. Cluster analysis was used to aid in interpretation of distributional patterns. All density values were transformed to log (X + 1), and similarity values were calculated for months and species using Euclidean distances and the Pearson correlation coefficient (*r*) respectively. Cluster analysis was performed using average linkages with unweighted distances for species and complete linkages for months. STATISTICA 3.0 software was used for the analysis.

RESULTS

PHYSICAL AND CHEMICAL ASPECTS

Extension of the intertidal zone varied from 30 to 100 m. The beach showed a concave profile, with the slope decreasing toward the infralittoral (Fig. 2). Sediment grain size ranged from 75 to 425 μm, and 50 % was fine sand (125 μm). Sand was fine textured and soil was sand-franc. Mean organic matter in sediment was 143.3

g/m^2 (range = 104.0–190.2)(Fig. 3). Mean salinity was 26.3 ‰ (range = 17.2–34.0). Mean water temperature was 28.5 °C (range = 27–31), mean pH was 7.62 (range = 6.23–8.15), and mean dissolved oxygen was 3.93 mg/L (range = 3.00–6.13) (Table 1).

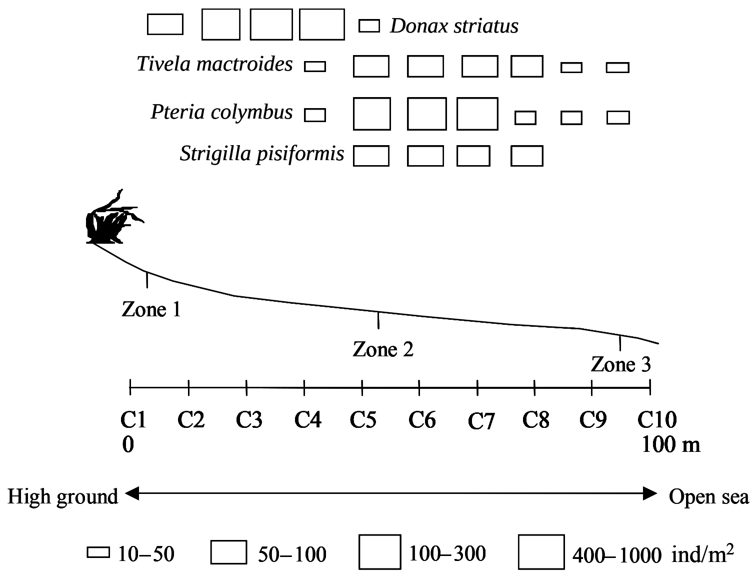

Figure 2. Intertidal distribution of the most abundant bivalves at Caimare Chico beach, Zulia State, Venezuela. The zones 1, 2 and 3, are the three intertidal zones located on the beach and C is the quadrate.

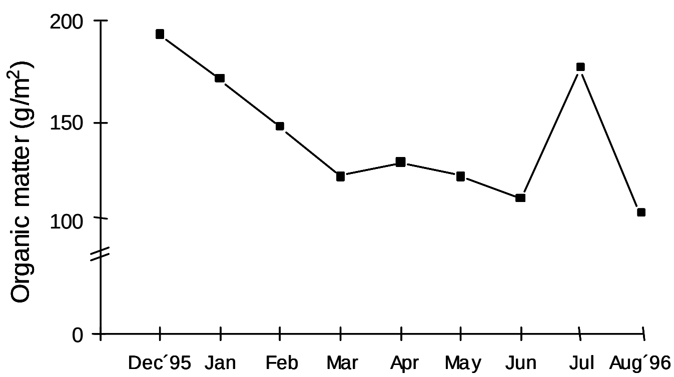

Figure 3. Monthly variation (December 1995 to August 1996) of organic matter in sediment at Caimare Chico beach, Zulia State, Venezuela.

Table 1. Seasonal variation in physical and chemical water quality parameters measured at Caimare Chico beach, Zulia State Venezuela.

Sampling Date	Temperature (°C)	Salinity (‰)	pH	Dissolved O_2 (mg/L)
Dec 1995	29.0	17.2	7.87	3.60
Jan 1996	27.0	22.0	7.08	5.21
Feb 1996	27.0	25.0	7.74	2.96
Mar 1996	27.0	28.5	6.23	4.00
Apr 1996	28.0	34.0	7.93	6.13
May 1996	31.0	27.0	7.99	3.60
Jun 1996	31.0	25.2	8.15	3.00
Jul 1996	28.0	29.0	7.72	3.13
Aug 1996	28.5	28.5	7.91	3.70
Mean	28.5	26.3	7.62	3.93

COMMUNITY COMPOSITION AND DISTRIBUTION

Descriptive measures of community structure and seasonal differences in species diversity, evenness, species richness and abundance are summarized in Table 2. Twenty-four macrobenthic bivalve species in 18 genera and 12 families were collected. A maximum of four species per family was identified for Veneridae and Tellinidae, and a minimum of one species was identified for the Pteriidae, Petricolidae, Pholadidae and Diplodontidae. Diversity ranged from 0.24 to 1.50, evenness from 0.10 to 0.53 and species richness from 1.34 to 2.89. Relatively low H´ values were due to dominance of *Donax striatus* in all samples. Total monthly abundance ranged from 42 to 1,031 ind/m^2 (Table 2). *D. striatus* was the most abundant bivalve, comprising 86.3% of the total fauna, and occurring in all samples; its mean density was 298.7 ind/m^2. *D. striatus*, along with *Tivela mactroides* (5.0%), *Strigilla pisiformis* (1.4%), *Pteria colymbus* (1.3%), *Donax denticulatus* (1.0%) and *Tellina sendix* (1.0%) comprised 96.1% of the total fauna.

Cluster analysis, according to total monthly abundance, revealed the formation of four groups. The first group constituted March, February and December (dry season months); the second

Table 2. Descriptive measures of community structure and seasonal differences in species diversity, evenness, species richness and abundance of macrobenthic bivalves on Caimare Chico beach, Venezuela. Values are the total number of individuals collected during a given sampling period.

Species	Sampling Period									Mean
	1995	1996								
	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	
Donax striatus	990	194	640	259	110	167	30	114	184	298.7
Donax denticulatus	4	4	8	7	2	2	2	2	1	3.6
Pteria colymbus	15	16	3	1	0	1	1	2	2	4.6
Tivela mactroides	6	97	8	5	6	3	2	2	1	14.4
Chione cancellata	1	2	3	3	3	0	1	0	6	2.1
Pitar dione	0	0	0	0	1	0	0	0	0	0.1
Mulinia lateralis	1	6	4	2	3	1	1	1	7	2.9
Macoma sp.	0	0	0	0	3	2	1	0	5	1.2
Macoma breviformis	0	0	0	0	0	2	0	1	0	0.3
Strigilla pisiformis	8	7	5	3	3	0	1	3	11	4.6
Anadara sp.	1	5	1	0	1	0	0	0	0	0.9
Anadara floridana	1	1	1	2	0	0	1	0	6	1.3
Anadara braziliana	0	0	0	1	0	0	0	0	1	0.2
Tellina sendix	2	7	4	1	2	0	1	2	13	3.6

Table 2. - Cont.

Species	Sampling Period									Mean
	1995	1996								
	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	
Codakia pectinella	1	0	0	0	0	0	0	0	0	0.1
Codakia orbicularis	0	0	0	0	0	0	0	1	0	0.1
Mytilus sp.	1	0	1	1	2	1	1	0	5	1.3
Crassinella sp.	0	1	1	1	2	0	0	0	1	0.7
Crassinella lunulata	0	4	1	0	0	0	0	0	6	1.2
Petricola pholadiformis	0	0	0	0	4	0	0	0	1	0.6
Transenella cubaniana	0	0	0	0	1	0	0	0	0	0.1
Brachidontes sp.	0	0	0	0	0	0	0	1	0	0.1
Diplodonta sp.	0	0	0	0	0	0	0	0	1	0.1
Pholas campechiensis	0	0	0	0	0	0	0	0	1	0.1
Total abundance (ind/m^2)	1,031	344	680	286	143	179	42	129	252	342.9
Mean monthly abundance	85.9	28.7	52.3	23.8	10.2	22.4	3.8	12.9	14.8	-
Number of species	12	12	13	12	14	8	11	10	17	12.1
Evenness	0.10	0.52	0.14	0.21	0.42	0.18	0.51	0.26	0.53	0.31
Shannon Diversity Index (H')	0.24	1.28	0.35	0.51	1.10	0.37	1.24	0.60	1.50	0.80
Margalef Richness Index (Dmg)	1.58	1.88	1.83	1.94	2.61	1.34	2.67	1.85	2.89	2.06

group constituted April, May and July (rainy months); whereas January (dry month) and August (rainy month) were distinguished separately (Fig. 4).

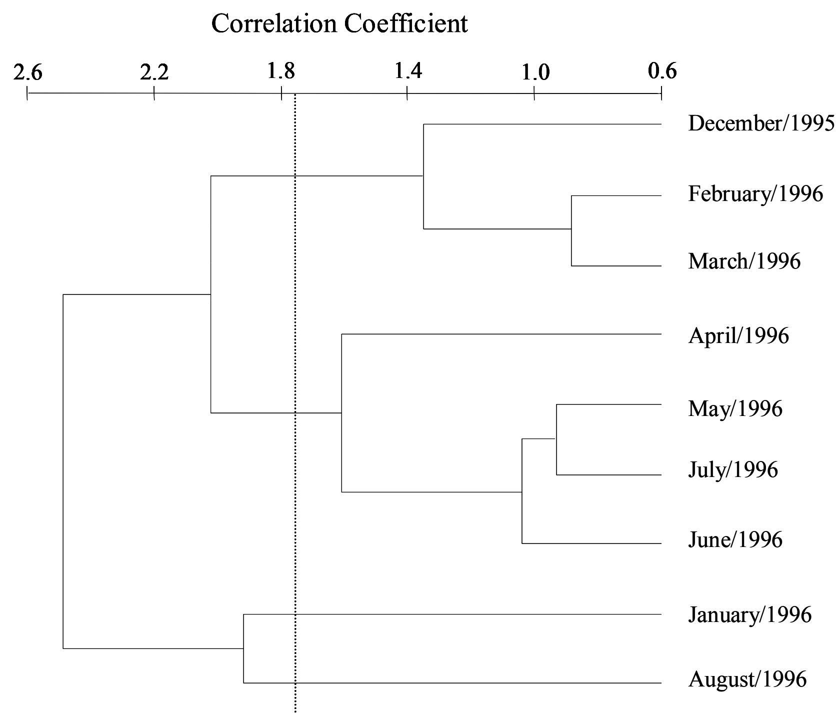

Figure 4. Dendrogram showing relative similarities of sample groups produced by complete linkage agglomerative cluster analysis, at Caimare Chico beach, Venezuela.

Distribution of the four most abundant species is presented in Figure 2. Cluster analyses, based on species abundance, revealed the formation of three groups corresponding to three beach zones (Fig. 5). In general, the first zone experienced intermediate tide levels (depending on zone length), but in some cases the zone was intertidal. This zone was characterized by *D. striatus*, *T. mactroides*, *D. denticulatus*, *S. pisiformis*, *Pteria colymbus*, *T. sendix*, *Anadara* sp., *Mulinia lateralis*, *Codakia pectinella*, *Transenella cubaniana* and *Petricola pholadiformis*. The first zone exhibited the highest abundance, due principally to the high abundance of *Donax striatus*. *Donax* spp. are very common in low, deep waters of sandy beaches, where they feed on suspended particles (Gianuca 1985).

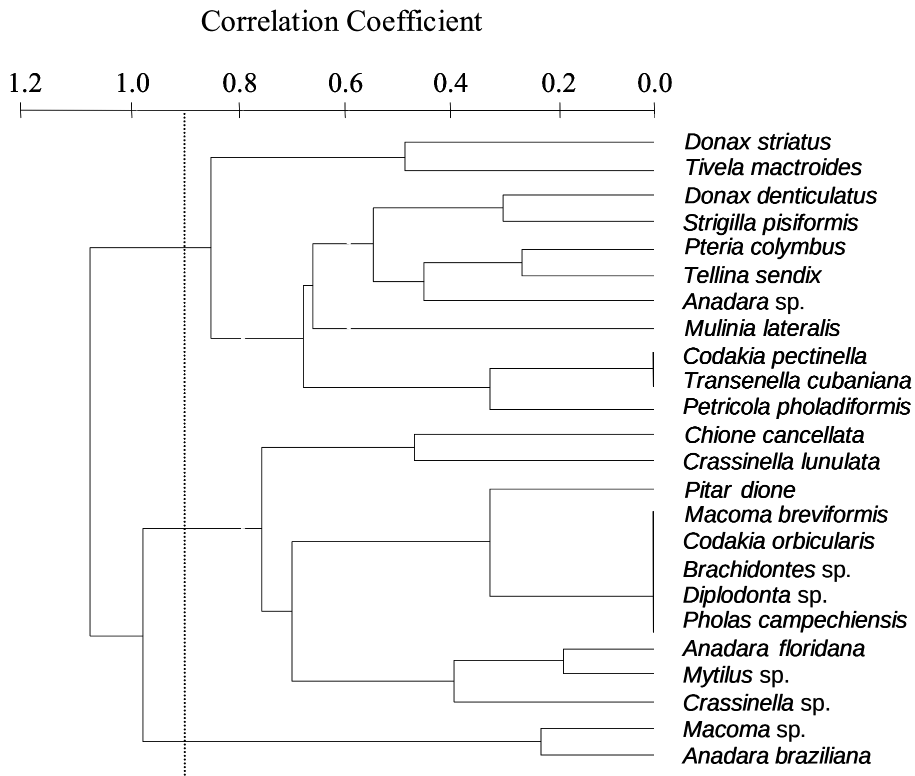

Figure 5. Dendrogram showing relative similarities of species groups produced by unweighted pair-group average agglomerative cluster analysis, at Caimare Chico beach, Venezuela.

The second zone represented the nearshore subtidal area, and was permanently covered by water. Species richness was high, but abundance was lower than in the first zone. This zone was characterized by *Chione cancellata*, *Crassinella lunulata*, *Pitar dione*, *Macoma breviformis*, *Codakia orbicularis*, *Brachidontes* sp., *Diplodonta* sp., *Pholas campechiensis*, *Anadara floridana*, *Mytilus* sp., and *Crassinella* sp. When currents are present in this zone, these resident bivalve species feed by filtering suspended material from the water column (Daver 1983, Souza and Gianuca 1995).

The third zone exhibited low species richness and abundance. *Anadara brasiliana* and *Macoma* sp. characterized the zone. These species feed on suspended materials, and are situated in the infralittoral part of the beach, below the detritivore zone. McLachlan (1990) defined them as surf zone species whose upper distributional limit is on the lower shore.

DISCUSSION

According to Short and Wright (1983) beaches can be classified into three types by wave and sediment characteristics: reflective, intermediate and dissipative. Dissipative beaches develop under conditions of fine sand (grain size < 2,000 µm) and heavy wave action, and are characterized by low gradients of the beach and surf zone. Caimare Chico beach is a dissipative beach, best explained by the continuous deposition of fine to very fine sand on the shore face, decreasing the surf zone gradient. This shows that other factors besides wave action may maintain the dissipative state of the beach (with fine sands and flat slope).

Dahl (1952) first proposed a distribution scheme for sandy beaches consisting of three zones, based on the distribution of crustaceans. Salvat (1964) divided the intertidal into four zones based on sediment moisture. In contrast, Souza and Gianuca (1995) divided the Barrancos beach, Brazil, into four intertidal zones, based on their macrofauna (dry sand, retention, resurgence and saturation zone). Various authors have used these schemes with different results (Jaramillo 1978, Escofet *et al.* 1979, Wendt and McLachlan 1985, McLachlan 1990), because they are not mutually exclusive and most animal distribution data could fit either scheme (Brown and McLachlan 1990).

We distinguished three zones across Caimare Chico beach, based on bivalve abundance. All three zones were evident and persistent throughout the study. The distributional scheme of Caimare Chico beach could fit into that of Salvat (1964) and Souza and Gianuca (1995). However, the first zone of Souza and Gianuca (dry sand zone) is not mentioned in this study, because pilot sampling indicated that the dry sandy zone on Caimare Chico beach lacked macrofauna. The distribution of *D. striatus* in the retention zone at Caimare Chico agrees with the occurrence of *Donax serra* in the retention zone of fine grain sediment beaches on the western coast of South Africa (Bally 1983).

Abundance and richness patterns on Caimare Chico beach are similar to sandy beaches in other areas of the world. The number of species and abundance increases from shore to high tidal depths, a known characteristic of this habitat (McLachlan 1977, Souza and Gianuca 1995). Seasonal changes in richness may also be due to species that appear sporadically on the beach, but do not persist through time. Boesch (1973) maintained that fluctuations at the community level were clearly influenced by population dynamics of the numerically abundant species. Sousa and Gianuca (1995) stated that seasonal changes in abundance on the sandy beach intertidal macrofauna of Barrancos are a product of recruitment.

Because the two dominant species, *D. striatus* and *T. mactroides*, are subject to considerable harvesting at Caimare Chico beach, it is possible that seasonal differences in abundance of bivalve communities are due mainly to the interaction of recruitment events and harvesting activity (Delgado 1997). Lewis (1978) mentioned that recruitment variability could help interpret abundance patterns of intertidal benthos, and Osman (1977) the community development.

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LITERATURE CITED

AMARAL, A. C., E. C. MORGADO, P. P. LOPES, L. F. BELÚCIO, F. P. LEITE, AND C. P. PEREIRA. 1990. Composition and distribution of the intertidal macrofauna of sandy beaches on São Paulo coast. ACIESP 71: 131−147.

ANSELL, A. D., P. SIVADAS, B. NARAYAHAN, V. N. SANKARANARAYANAN, AND A. TREVALLION. 1972. The ecology of two sandy beaches in south west India, I: Seasonal changes in physical and chemical factors, and in the macrofauna. Marine Biology 17: 38−62.

BALLY, R. 1983. Intertidal zonation on sandy beaches of the west coast of South Africa. Cah. Biol. Mar. 24: 85−103.

BOESCH, D. F. 1973. Classification and community structure of macrobenthos in Hampton Roads Area, Virginia. Marine Biology 21: 226−244.

BROWN, C., AND A. MCLACHLAN. 1990. Ecology of sandy shores. Elsevier, Amsterdam.

DAHL, E. 1952. Ecology and zonation of fauna of sandy beaches. Oikos 4: 1−27.

DANSEREAU, P. 1947. Zonation et succession sur la restinga de Rio de Janeiro, I: Halosere. Rev. Canadian Biol. 6: 448−447.

DAVER, D. M. 1983. Functional morphology and feeding behavior of *Scolelepis squamata* (Polychaeta: Spionidae). Marine Biology 77: 279−285.

DELGADO, J. G. 1997. Estudio comparativo de la biodiversidad y distribución de la fauna macrobentónica invertebrada presente en las playas arenosas de alta energía de Caño Sagua y Caimare Chico (Municipio Páez, Estado Zulia). Trabajo Especial de Grado, Departamento de Biología, Facultad Experimental de Ciencias, Universidad del Zulia, Maracaibo, Venezuela, 103 pp.

DE MAHIEU, G. C., AND A. L. GAMBA. 1980. Zonación litoral en algunas comunidades de sustrato arenoso del área de Golfo Triste, Venezuela. Primeras Jornadas Científicas de la Universidad Simón Bolívar, Caracas, Venezuela, pp. 77−114.

ESCOFET, A., N. M. GIANUCA, S. MAYTIA, AND V. SCARABINO. 1979. Playas arenosas del Atlántico Sudoccidental entre los 29 y 43 LS: consideraciones generales y esquema biocenológico. Memorias del seminario sobre ecología bentónica y sedimentación de la Plataforma Continental del Atlántico Sur. UNESCO, Montevideo, pp. 245−248.

GIANUCA, N. M. 1983. A preliminary account of the ecology of sandy beaches in southern Brazil. *In* A. McLachlan and T. Erasmus (eds.), Sandy beaches as ecosystems. W. Junk, The Hague, pp. 413−419.

GIANUCA, N. M. 1985. Zonação e produção nas praias arenosas do litoral sul e sudeste do Brasil: síntese dos conhecimentos. Simposio sobre Ecosistemas da costa sul e sudeste brasileira. Acad. Ciênc. São Paulo 54: 313−332.

JARAMILLO, E. 1978. Zonación y estructura de la comunidad macrofaunistica en playas de arena del sur de Chile (Mehuin, Valdivia). Studies on Neotropical Fauna and Environment 13:71−92.

LEBER, K. M. 1982. Seasonality of macroinvertebrates on a temperate, high wave energy sandy beach. Bull. Marine Science 32: 86−98.

MCLACHLAN, A. 1977. Composition, distribution, abundance and biomass of the macrofauna meiofauna of four sandy beaches. Zool. Afric. 12: 279−306.

MCLACHLAN, A. 1990. Dissipative beaches and macrofauna communities on exposed intertidal sands. J. Coast. Res. 6: 57−71.

MIKKELSEN, P. M., P. S. MIKKELSEN, AND D. J. KARLEN. 1995. Molluscan biodiversity in the Indian River Lagoon, Florida. Bull. Marine Science 57: 94−127.

LEWIS, J. R. 1978. The role of physical and biological factors in the distribution and stability of rocky shore communities. *In* B. F. Keegan, P. O´Ceidigh, P. J. S. Boaden (eds.), Biology of benthic organisms, Pergamon Press, Oxford, pp. 417−423.

OSMAN, R. W. 1977. The establishment and development of a marine epifaunal community. Ecological Monographs 47: 37−63.

RODRÍGUEZ, G. 1973. El Sistema de Maracaibo. Editorial San José, Caracas, pp. 21−49.

SALVAT, B. 1964. Les conditions hidrodynamiques interstitielles des sedimentes meubles intertidaux et la repartition verticale de la faune endogée. Cah. Rech. Acad. Sci. Paris 259: 1576−1579.

SHANNON, E. C., AND W. WEAVER. 1963. The mathematical theory of communication. Illinois Univ. Press, Urbana, Illinois, 119 pp.

SHELTON, CH. R., AND P. B. ROBERTSON. 1981. Community structure of intertidal macrofauna on two surf-exposed Texas sandy beaches. Bull. Marine Science 31: 833−842.

SHORT, A. D., AND L. D. WRIGHT. 1983. Physical variability of sandy beaches. *In* A. McLachlan and T. Erasmus (eds.), Sandy beaches as ecosystems. W. Junk, The Hague, pp. 133−144.

SOUZA, J. R., AND N. M. GIANUCA. 1995. Zonation and seasonal variation of the intertidal macrofauna on a sandy beach of Paraná State, Brazil. Scientia Marina 57: 94−127.

WENDT, G. E., AND A. MCLACHLAN. 1985. Zonation and biomass of the intertidal macrofauna along a South African sandy beach. Cah. Biol. Mar. 26: 1−14.