

Composition of decapod crustacean assemblages in beds of *Pinctada imbricata* and *Arca zebra* (Mollusca: Bivalvia) in Cubagua Island, Venezuela: Effect of bed density

IVÁN HERNÁNDEZ-ÁVILA^{1,2}, ALEJANDRO TAGLIAFICO³, NÉSTOR RAGO⁴
and JESÚS MARCANO⁵

¹Departamento de Ciencias, Unidad de Cursos Básicos, Núcleo de Nueva Esparta, Universidad de Oriente, Venezuela.
E-mail: ivanhernavila@yahoo.com

²Grupo de Investigación en Carcinología, Universidad de Oriente, Venezuela.

³Escuela de Ciencias Aplicadas del Mar, Núcleo de Nueva Esparta, Universidad de Oriente, Venezuela.

⁴Maestría en Ciencias Marinas y Costeras, Universidad Nacional de Costa Rica.

⁵Instituto Nacional de Investigaciones Agrícolas, Venezuela.

SUMMARY: Beds of the Atlantic pearl oyster (*Pinctada imbricata*) and the turkey wing (*Arca zebra*) of contrasting population densities were evaluated to determine the occurrence of associated decapod crustaceans. In these beds at Cubagua Island, Venezuela, we recorded 40 decapod species belonging to 18 families. *Mithraculus forceps* (Majidae), *Pilumnus caribaeus* (Pilumnidae), *Cuapetes americanus* (Palaemonidae) and *Petrolisthes galathinus* (Porcellanidae) were the most common species found in these assemblages. The medium- and high-density bivalve beds exhibited more species and a greater abundance of associated decapods than the low-density bivalve beds, and more taxonomic distinctness. Multivariate analysis detected different groups of decapods in the low-density beds and the medium- to high-density beds. Additionally, similarities were found in the communities of crustaceans in the beds of Atlantic pearl oysters and turkey wing, demonstrating that bed density is important for the composition of associated fauna.

Keywords: Decapoda, benthos, bivalve beds, complexity, Caribbean, richness.

RESUMEN: COMPOSICIÓN DE ENSAMBLES DE CRUSTÁCEOS DE CÁPODOS EN BANCOS DE *PINCTADA IMBRICATA* Y *ARCA ZEBRA* (MOLLUSCA: BIVALVIA) EN LA ISLA DE CUBAGUA, VENEZUELA: EFECTO DE LA DENSIDAD DEL BANCO. – Bancos de la ostra perla del Atlántico (*P. imbricata*) y de la pepitona (*A. zebra*) de densidades poblacionales contrastantes fueron evaluados para determinar la ocurrencia de crustáceos decápodos asociados. En estos bancos en la isla de Cubagua, Venezuela, fueron colectadas 40 especies de decápodos, pertenecientes a 18 familias. *Mithraculus forceps* (Majidae), *Pilumnus caribaeus* (Pilumnidae), *Cuapetes americanus* (Palaemonidae) y *Petrolisthes galathinus* (Porcellanidae) fueron las especies más comunes en estos ensambles. Los bancos de densidad media y alta mostraron mayor riqueza de especies y abundancia que los de baja densidad de bivalvos, así como mayor distinción taxonómica. Análisis multivariados detectaron diferentes grupos de decápodos en los bancos de baja densidad en relación a los de densidad media y alta. Adicionalmente, la fauna encontrada en bancos de ostra perla y pepitona no mostró diferencias, demostrando que la densidad es importante para la composición de la fauna asociada.

Palabras clave: Decapoda, bentos, bancos de bivalvos, complejidad, Caribe, riqueza.

INTRODUCTION

Bivalve aggregations constitute a microhabitat for a wide variety of organisms in intertidal, subtidal

and deep-water marine benthic habitats (Tsuchiya and Nishihira 1985, 1986, Thiel and Ulrich 2002, Turnipseed *et al.* 2004, Galkin and Goroslavka 2008). The aggregations increase the spatial heterogeneity

of the benthic environment and provide shelter and food for a diverse assemblage of organisms (Jacobi 1987, Jones *et al.* 1997, Seed 1996). Local diversity, population dynamics, food webs and nutrient cycling could be affected by the presence of bivalve beds, thus increasing the abundance and diversity of associated fauna (Tsuchiya and Nishihira 1985, Thiel and Ulrich 2002, Gutiérrez *et al.* 2003, Carranza *et al.* 2008, 2009).

In the southeastern Caribbean, conspicuous beds of the turkey wing (*Arca zebra*) and the Atlantic pearl oyster (*Pinctada imbricata*) are present in shallow-water marine environments. The Atlantic pearl oyster has been exploited for pearl production since the 15th century (Mackenzie *et al.* 2003), and it supports a small artisanal fishery mainly for local food consumption. However, the turkey wing supports a locally important artisanal fishery with a volume ranging from 35000 to 40000 t m yr⁻¹, depending on the demands of the canning industry (Arias *et al.* 2002). Both species have a wide distribution and form beds with associated benthic fauna (Prieto *et al.* 2001b, Díaz and Liñero 2003, Liset *et al.* 2009).

The fauna associated with beds of different bivalve species has been studied over a large spatial gradient (Thiel and Ulrich 2002), comparing different sizes of aggregations of bivalves (Tsuchiya and Nishihira 1985), incorporating other factors such as age, size and density of patches (Tsuchiya and Nishihira 1986, Borthagaray and Carranza 2007), and comparing different beds of different bivalve species in different locations (Turnipseed *et al.* 2004) and at different depths (Van Dover and Trask 2000). However, studies of the differences between assemblages associated with patches of different bivalve species in the same area are scarce and generally deal with temperate waters. The role of bivalve aggregations in tropical benthic ecosystems is poorly understood.

Many publications have shown the importance of topographical complexity in the structure of benthic fauna (Bourget *et al.* 1994, Chapman and Underwood 1994, Pech *et al.* 2001). Richness, abundance, and diversity in benthic communities are positively related to complexity (Archambault and Bourget 1996). In bivalve beds the increase in density or size is positively correlated with topographical complexity (Gutiérrez *et al.* 2003, Borthagaray and Carranza 2007). Increase in density of bivalve beds could offer more crevices and substratum for the associated fauna, diminishing inter- and intraspecific competition for space and bearing a positive relationship with abundance, species number and diversity. In the present study, we tested the hypothesis that abundance, diversity and structure of decapod crustacean aggregations living in a bivalve bed are associated with the density of the bed, by comparing different densities of beds of two species of bivalves at a single tropical locality (Cubagua Island, Venezuela).

MATERIALS AND METHODS

Area of Study

Cubagua is a semi-arid island of 22 km² situated in eastern Venezuela (10°47'-10°51'N; 64°8'-64°14'W). It is strongly influenced by coastal upwelling and is characterized by a shallow continental shelf with sandy bottoms of mainly coarse sediments (Cervigón 2005). The upwelling process occurs mainly during the first months of the year (January-May) and consists of the seasonal intrusion of water with low temperatures and oxygen levels, and high nutrient concentrations. The surface water temperature ranges between 22°C and 26°C and exhibits continuous high productivity (Gómez 1996). The Cubagua littoral zone is composed mainly of shallow waters (0-10 m deep) occupied by marginal reefs, rocky shore, *Thalassia testudinum* beds, *Arca zebra* and *Pinctada imbricata* beds and sandy areas. In the southeastern region of the island, patches of *A. zebra* and *P. imbricata* are found 200 to 500 m from the coast. Previous studies on the decapod fauna of Cubagua Island have focused on an inventory of the species and their taxonomic aspects (see Hernández-Ávila *et al.* 2007).

Sampling and data analysis

Decapod crustacean assemblages were compared between different bivalve beds and between the different densities of each bed. Bivalve beds were evaluated at two levels (*P. imbricata* and *A. zebra* bed), and density was considered at three discrete levels of bivalve abundance composing the bed (1, 60-100; 2, 100-200; 3, >200 ind m⁻²), corresponding to a two-way factorial design with seven replicates for each combination. Samples were collected between September 2005 and May 2006 during periods of non-upwelling (Sep-Nov) and upwelling (Dec-May). Due to logistics, it was not possible to evaluate temporal variation as an additional factor. To exclude potential seasonal effects in this design, randomizing the replicates between the periods was considered. Although randomization could generate additional patterns in experimental design (Hurlbert 1984), there was no pattern detected between collection periods (χ^2 rxc test =9.17, df=5, $P=0.12$).

Samples were collected within a 0.5×0.5 m plot by scuba diving at depths of 5 to 12 m. The plots were covered with the mouth of a plastic bag and removed from the bottom into the plastic bag avoiding escape of motile fauna. All benthic components associated with bivalve beds (including the bivalves) were collected for evaluation in the laboratory. The bivalves forming the bed were counted to determine their density and the dominance of the species forming the bed. Because there were few cases with low density, plots characterized by mixed beds (with a similar ratio of *P. imbricata* and *A. zebra*) were omitted. Decapod crustaceans were separated and fixed for later counting and identifica-

TABLE 1. – Mean abundance (ind 0.25 m⁻²) of decapod crustaceans collected in oyster beds and turkey wing beds at three densities.

Family	Species Density ind m ⁻²	Oyster bed (<i>P. imbricata</i>)			Turkey wing bed (<i>A. zebra</i>)		
		60-100	100-200	>200	60-100	100-200	>200
Sicyoniidae	<i>Sicyonia laevigata</i> Stimpson, 1871		0.57				0.14
Stenopidae	<i>Stenopus scutellatus</i> Rankin, 1898					0.14	0.14
Alpheidae	<i>Alpheus armillatus</i> H. Milne Edwards, 1837					0.14	
	<i>Alpheus beani</i> Verrill, 1922				0.29		
	<i>Alpheus normanni</i> Kingsley, 1878	0.14					
	<i>Alpheus</i> sp.						0.57
Palaemonidae	<i>Synalpheus</i> cf. <i>minus</i> (Say, 1818)					0.14	0.43
	<i>Cuapetes americanus</i> (Kingsley, 1878)	0.86	0.71	1.29		0.43	
Hippolytidae	<i>Periclimenes iridiscens</i> Lebour, 1949					0.14	
	no id		0.14			1.00	
Processidae	<i>Thor manningi</i> Chace, 1972					0.29	
	<i>Processa bermudensis</i> (Rankin, 1900)		0.14				
no id.	Caridea no id.			0.14			
Diogenidae	<i>Clibanarius antillensis</i> Stimpson, 1859	0.29	0.14		0.29	0.142	0.29
Paguridae	<i>Pagurus brevidactylus</i> (Stimpson, 1859)	0.29					
Porcellanidae	<i>Petrolisthes armatus</i> (Gibbes, 1850)		0.14			0.29	
	<i>Petrolisthes galathinus</i> (Bosc, 1801)		0.14	1.00	0.29	1.14	
Inachidae	<i>Stenorhynchus seticornis</i> (Herbst, 1788)			0.29	0.14		
Majidae	<i>Hemus cristulipes</i> A. Milne Edwards, 1875	0.14	0.14				0.71
	<i>Macrocoeloma trispinosum</i> (Latreille, 1825)		0.29	0.29			
	<i>Microphrys bicornutus</i> (Latreille, 1825)		0.86		0.14		
	<i>Mithraculus forceps</i> A. Milne Edwards, 1875	3.00	3.86	13.57	2.71	9.86	8.57
Epiplatidae	<i>Mithrax</i> sp.						0.29
	<i>Mithrax verrucosus</i> H. Milne Edwards, 1832		0.57	0.14			
	<i>Stenocionops coelatus</i> (A. Milne-Edwards, 1878)						0.14
	<i>Pitho lherminieri</i> (Desbone and Schramm, 1867)	0.14	0.14	0.43	0.14	0.29	
Portunidae	<i>Tyche emarginata</i> White, 1847					0.14	
Xanthidae	<i>Portunus ordwayi</i> (Stimpson, 1860)		0.14				
	<i>Cataleptodius floridanus</i> (Gibbes, 1850)	0.43					
Panopeidae	<i>Micropanope</i> sp.	0.71					0.43
	<i>Panopeus herbstii</i> H. Milne Edwards, 1834	0.14	0.29	0.14		1.71	
Pilumnidae	<i>Panopeus</i> sp.				0.14		
	<i>Pilumnus caribaeus</i> Desbonne and Schramm, 1867	0.57	1.57	0.86	0.43	1.29	0.57
Pinnotheridae	<i>Pilumnus dasypodus</i> Kingsley, 1879			0.29		0.29	
	<i>Calyptraeotheres hernandezii</i> Hernández-Ávila and Campos, 2006			0.57			

tion. Additional qualitative samples were collected in both types of bed by scuba diving to collect species that were not sampled by the quantitative sampling techniques.

Decapod crustaceans were identified to species level and counted. Total abundance, species number (S), evenness (J') (Pielou 1975), Shannon diversity (H') (Shannon 1948), taxonomic diversity (Δ), and taxonomic distinctness (Δ^*) (Warwick and Clarke 1995) were estimated as univariate descriptors of each sample. With respect to taxonomic diversity and distinctness, six levels of taxonomic hierarchy were considered: suborder, infraorder, superfamily, family, genus, and species. Classification from order to genus followed De Grave *et al.* (2009).

These indicators were contrasted using a two-way orthogonal permutational analysis of variance (PERMANOVA) (Anderson 2001, McArdle and Anderson 2001) to test the null hypothesis of no differences in univariate descriptors (total abundance, species number, evenness, Shannon diversity, taxonomic diversity and taxonomic distinctness in each case) associated with the factors "density", "bivalve bed", and of their interaction. The pair-wise *t* statistic was used as a posteriori analysis for detecting groups between levels of densities.

To test the null hypothesis of no differences in structure of decapod assemblages in the study design described above, a similarity matrix was constructed using the Bray-Curtis coefficient and tested with a PERMANOVA. A dummy species was added to each sample to avoid indeterminacy of the Bray-Curtis values between two samples without species (Clarke *et al.* 2006). The number of permutations of residuals used to determine the statistical significance of each term was 999 under a reduced model (Anderson 2001). A multivariate dispersion test (PERMDISP) was used to determine whether a significant source of variation was related to difference in multivariate dispersions or difference in centroid position. A SIMPER analysis was performed to identify species associated with differences between densities (Clarke 1993).

RESULTS

In the quantitative samples, 35 species belonging to 18 families (Table 1) were identified; two species could not be identified because the specimens were damaged (one hippolytid and one caridean, family not identifiable). The families represented by the largest number of species were Majidae (8 species) and Alpheidae (five species), whereas other families were represented

TABLE 2. – PERMANOVA for richness (A), abundance (B), Shannon diversity (C), evenness (D), taxonomic diversity (E), and taxonomic distinctness (F) of decapod crustaceans related to bivalve bed and density. Italics denote significant differences.

Source of variation	df	Sum Square	Mean Square	Pseudo-F	p	Perms
(A)						
Bivalve bed	1	1.17	1.17	0.188	0.645	990
<i>Density</i>	2	<i>46.71</i>	<i>23.35</i>	<i>3.76</i>	<i>0.035</i>	<i>998</i>
B. bed × dens	2	0.333	0.166	0.026	0.979	998
Residual	36	223.43	6.21			
Total	41	271.64				
(B)						
Bivalve bed	1	0.857	0.857	0.009	0.922	996
<i>Density</i>	2	<i>757.0</i>	<i>378.5</i>	<i>4.41</i>	<i>0.015</i>	<i>998</i>
B. bed × dens	2	340.43	170.21	1.98	0.142	999
Residual	36	3090.00	85.83			
Total	41	4188.30				
(C)						
Bivalve bed	1	0.274	0.274	0.660	0.402	996
<i>Density</i>	2	<i>2.56</i>	<i>1.28</i>	<i>3.08</i>	<i>0.073</i>	<i>999</i>
B. bed × dens	2	0.314	0.157	0.378	0.692	998
Residual	36	14.96	0.416			
Total	41	18.11				
(D)						
Bivalve bed	1	0.208	0.208	1.29	0.277	997
<i>Density</i>	2	<i>0.675</i>	<i>0.337</i>	<i>2.09</i>	<i>0.140</i>	<i>999</i>
B. bed × dens	2	0.119	0.059	0.367	0.678	999
Residual	36	5.81	0.161			
Total	41	6.81				
(E)						
Bivalve bed	1	640.21	640.21	0.886	0.373	997
<i>Density</i>	2	<i>3276.70</i>	<i>1638.40</i>	<i>2.28</i>	<i>0.119</i>	<i>997</i>
B. bed × dens	2	767.30	383.65	0.531	0.557	999
Residual	36	26017.0	722.7			
Total	41	30701.0				
(F)						
Bivalve bed	1	831.29	831.29	0.705	0.388	996
<i>Density</i>	2	<i>7870.5</i>	<i>3935.3</i>	<i>3.34</i>	<i>0.034</i>	<i>999</i>
B. bed × dens	2	63.19	31.59	0.027	0.976	999
Residual	36	42435.0	1178.7			
Total	41	51200.0				

by three or fewer species. According to their frequency of occurrence and abundance, the species that characterized the study site were *Mithraculus forceps* (Majidae), *Pilumnus caribaeus* (Pilumnidae), *Panopeus herbstii* (Panopeidae), *Pitho lherminieri* (Epialtidae) and *Petrolisthes galathinus* (Porcellanidae). Additionally, species with few published records in Venezuelan waters, such as *Tyche emarginata* (Epialtidae), *Hemus cristulipes* (Majidae) and *Calyptraeotheres hernandezii* (Pinnotheridae), were present in the beds. Qualitative sampling from both beds recorded five additional species that were not collected in our quantitative sampling: *Periclimenes yucatanicus* (Ives, 1891) (Palaeomonidae), *Petrochirus diogenes* (Linnaeus, 1758) (Diogenidae), *Moreiradromia antillensis* (Stimpson, 1858) (Dromiidae), *Podochela riseii* Stimpson, 1860 (Inachidae), and *Platipodiella spectabilis* (Herbst, 1794) (Xanthidae).

Differences in univariate descriptors of decapod assemblages associated with the species of each bed were not detected. Richness, abundance and taxonomic distinctness exhibited significant differences related to bivalve density. However, differences associated with bivalve density were not detected for Shannon diversity, evenness, or taxonomic diversity (Table 2), which showed low values (mean ± se $H' = 1.08 \pm 0.15$,

TABLE 3. – Pairwise test for level of bed density. Levels of density are denoted by 1, low density; 2, medium density; 3, high density. Italics denote significant differences.

Groups	t	p	perms
Richness			
1, 2	2.48	<i>0.018</i>	984
1, 3	1.46	0.158	989
2, 3	1.47	0.151	994
Abundance			
1, 2	2.73	<i>0.016</i>	989
1, 3	2.92	<i>0.006</i>	994
2, 3	0.399	0.683	993
Taxonomic distinctness			
1, 2	2.24	<i>0.032</i>	999
1, 3	2.10	<i>0.050</i>	997
2, 3	0.27	0.778	999

$J' = 0.50 \pm 0.06$, $\Delta = 29.89 \pm 4.22$) because of the large ratio of *M. forceps* in most of the samples and the low frequency of many species.

For species number, abundance, and taxonomic distinctness, the *t* pairwise test between level of densities detected two groups. The low-density beds (60-100 ind m⁻²) were different ($P < 0.05$) from the medium- and high-density beds (the last two comprising a single group) (Table 3). The medium- and high-density beds had more species ($S = 3.96 \pm 0.50$) and a higher

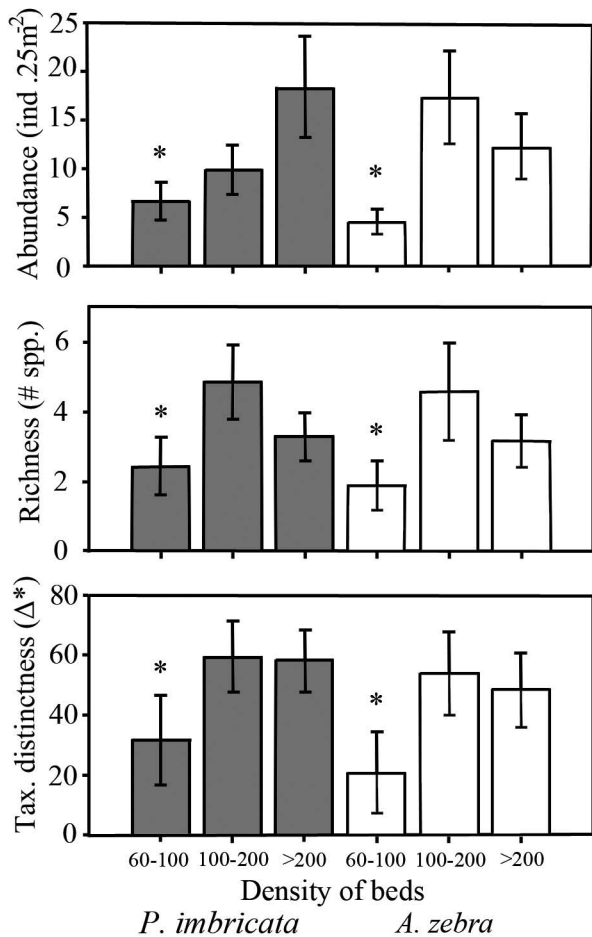


FIG. 1. – Abundance, richness and taxonomic distinctness of decapod crustaceans in beds of oyster (*Pinctada imbricata*) and turkey wing (*Arca zebra*) at different densities.

abundance of associated decapods ($N=14.54\pm 2.06$ ind 0.25 m^{-2}) than the low-density beds ($S=2.14\pm 0.52$; $N=5.64\pm 1.17$ ind 0.25 m^{-2}) (Fig. 1). Additionally, the differences detected in taxonomic distinctness indicate that decapods in the medium- and high-density beds included species of a higher taxonomic level (infraorder to family level, e.g. majid, xanthid, and porcellanid crabs; alpheid and palaemonid shrimps) ($\Delta^*=55.15\pm 5.80$) than the low-density beds, consisting of a few majid and xanthid species in most samples ($\Delta^*=26.25\pm 9.36$).

The multivariate analysis (PERMANOVA) showed differences between the species composition of decapod crustaceans related to bed density, but no differ-

ences between bivalve beds of different species (Table 4). The differences detected were not associated with differences in multivariate dispersion (PERMDISP, $F=0.132$, $P=0.936$). The assemblages in beds with medium and high density were distinct from those in the lower density beds ($t=2.76$, $P=0.016$; and $t=2.92$, $P=0.006$ respectively) (Fig. 2A). According to the SIMPER analysis, the species most related to the differences between groups were *Mithraculus forceps* (mean contribution of dissimilarity 47.6%), *Pilumnus caribaeus* (8.55%), *Cuapetes americanus* (6.67%), and *Petrolisthes galathinus* (5.24%); the mean individual contributions of the other species of the dissimilarity were less than 5%. The abundance of the former species increased in the assemblages on beds with medium and high density (Fig. 2B-E).

DISCUSSION

We found similarities in decapod crustacean assemblages between beds of *A. zebra* and *P. imbricata*, which could be serving as alternative habitats. Most of the common decapod crustacean species associated with bivalves have been reported from other habitats in the region. *M. forceps* has a wide distribution in the Caribbean and is frequent in most of the shallow-water substrates of northeastern Venezuela (Rodríguez 1980, Hernández *et al.* 2000, Hernández-Reyes *et al.* 2001, Hernández-Ávila *et al.* 2007). Additionally, *P. caribaeus*, *P. herbstii*, *P. lherminieri*, *P. galathinus* and *C. americanus* have been reported from various locations in Venezuela and are associated with coral, rubble and *Thalassia* beds (Rodríguez 1980, Carmona-Suárez and Conde 1996, Hernández-Ávila *et al.* 2007). Some infrequent species have recently been reported in the region (Hernández-Ávila 2004, Hernández-Ávila and Campos 2006, Hernández-Ávila *et al.* 2007). Thus, these bivalve aggregations represent a potential habitat for some common shallow-water decapod crustaceans and for some uncommon species. However, no species have been detected living in exclusive association with beds of *A. zebra* or *P. imbricata*, respectively. At Cubagua Island, 60% of the decapod species found in bivalve beds have also been collected in subtidal rocky biotopes, 42.9% in coral patches and 28.6% in *Thalassia* beds.

Various publications have identified the role of oyster reefs as a potential habitat or as a refuge for decapods (Ruiz *et al.* 1993, Dittel *et al.* 1995, Eggleston *et al.* 1998, Posey *et al.* 1999). The physical structure of oyster reefs serves as substratum for the recruitment

TABLE 4. – PERMANOVA of decapod assemblages related to species bed and density. Italics denote significant differences.

Source of variation	df	Sum square	Mean square	Pseudo-F	<i>P</i>	Perms
Bivalve bed	1	2662.5	2662.5	1.281	0.249	999
<i>Density</i>	2	9217.5	4608.8	2.217	<i>0.016</i>	998
B. bed × dens	2	4778.3	2389.1	1.149	0.293	999
Res	36	74829	2078.6			
Total	41	91487				

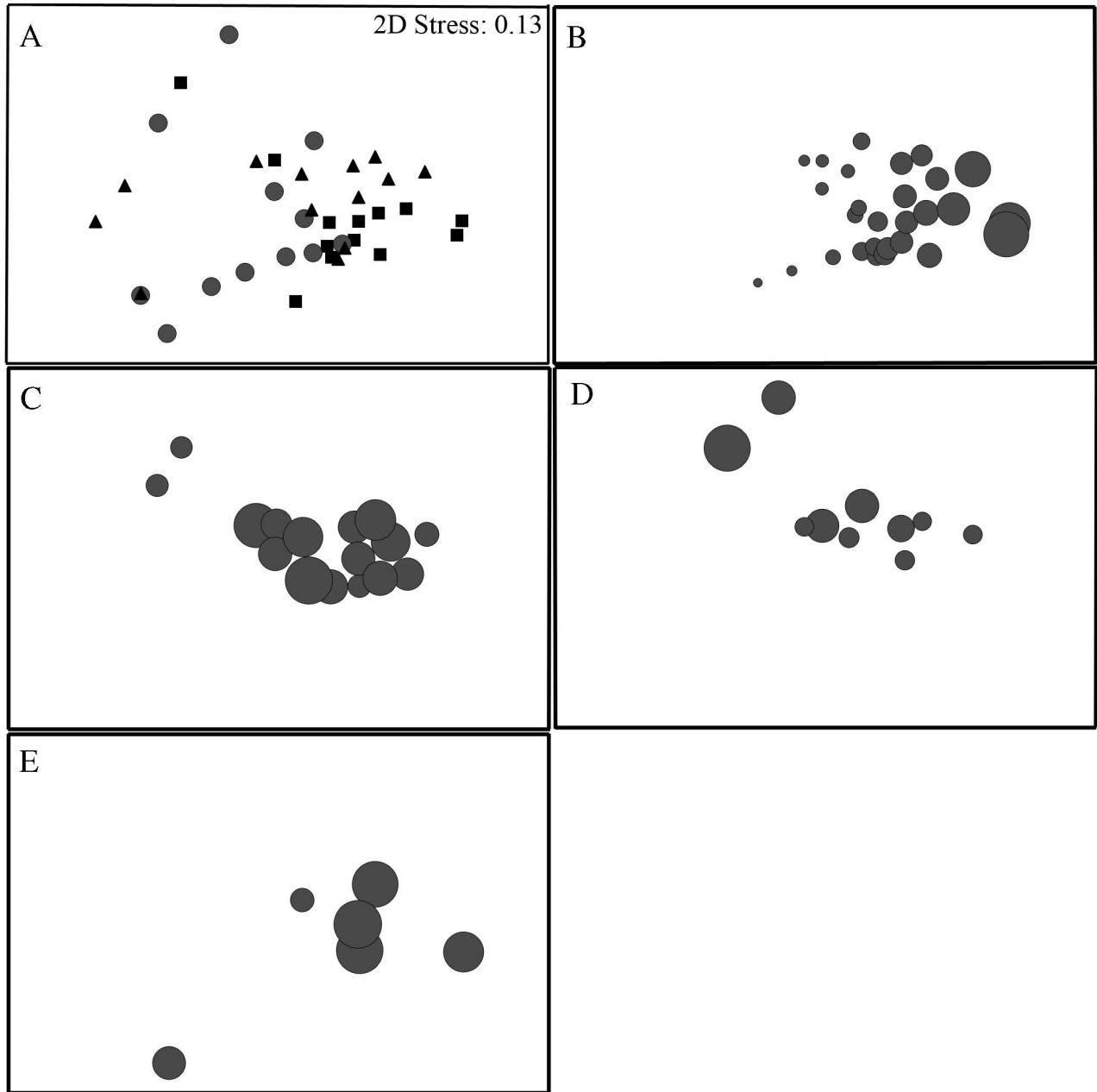


FIG. 2. – nMDS of decapod assemblage according to bed density. A, ● density 60-100 ind m⁻², ▲ density 100-200 ind m⁻², ■ density >200 ind m⁻². B-E, bubble plot with abundance of *Mithraculus forceps*, *Pilumnus caribaeus*, *Cuapetes americanus* and *Petrolisthes galathinus*, respectively.

of grass shrimps and blue crab megalopae in laboratory and field experiments (Eggleston *et al.* 1998, Welch *et al.* 1997). Laboratory habitat experiments suggest that shrimps actively select oyster habitats in response to the presence of fish predators (Posey *et al.* 1999). Our results suggest that bivalve aggregations at Cubagua Island provide an additional habitat for decapod crustaceans living in other shallow habitats such as *Thalassia* beds, corals, and rocky environments.

Different assemblages of decapod species were associated with beds with contrasting bivalve densities. Beds with a low density exhibited lower levels of rich-

ness, abundance and taxonomic distinctness of decapod crustaceans than beds with 100 or more ind m⁻². Since the relative importance of the common species of the assemblages was similar in beds with different levels of density, differences observed in decapod composition were due to the increased decapod abundance and to the incorporation of species that were not recorded in low-density beds. The bivalve aggregations in high-density beds generate a more complex topography. Spatially complex surfaces tend to support richer faunal communities, presumably because they provide a greater number of crevices (Abele 1974, Ricciardi *et*

al. 1997). Aggregated mussels have an abundance of interstitial spaces that may serve as a refuge from disturbances and predation in mobile macrofauna (Gosselin and Chia 1995, Borthagaray and Carranza 2007). The increase in the number of crevices in high-density beds could also decrease the competition for space between members of a decapod assemblage. Moreover, the increase in the surface for attachment and the control of transport of particles could be provided by bivalve aggregations and associated with bed density (Crooks and Khim 1999, Gutiérrez *et al.* 2003).

Hernández-Ávila *et al.* (2007) recorded 14 species of decapod crustaceans in aggregations of *Arca zebra* along the coastal margin of Cubagua Island, *M. forceps* being the most common species found. Only six species found in this previous study were collected in the present study. Differences between the coastal margin and the depth investigated in the previous study (0-100 m off the coast and at 2-5 m depth) and those investigated in the present study (300-500 m off the coast and at 5-12 m depth) could have been responsible for the differences in the species sampled. With respect to assemblages of decapods associated with *Pinctada imbricata*, only a few sporadic records of decapods associated with these beds exist. Spatial variation, patterns of aggregation of other taxa, and dynamics of both bivalve beds and associated fauna could provide a better understanding of this habitat.

Bivalve beds of *P. imbricata* and *A. zebra* are exploited by artisanal fisheries, though *A. zebra* is processed industrially and subjected to wider commercialization than *P. imbricata*. In the study of the biology of these two species a serious effort has been made to develop conditions for their culture and to regulate fisheries (Jiménez *et al.* 2000, Prieto *et al.* 2001a, Lodeiros *et al.* 2002, Marcano *et al.* 2005). The associated fauna reported previously for both species (Prieto *et al.* 2001b, Díaz and Liñero 2003, Liset *et al.* 2009) and the effect of bed density in decapod assemblages detected in the present study suggest the importance of controlling bivalve fisheries for the maintenance of benthic communities. The local bivalve fisheries operate with small trawls (about 0.9 m mouth width) that remove most of the benthic components from the beds. Although the large megafaunal bycatch is returned during fishing, decreasing density of beds could result in less abundance, richness and complexity of decapod crustacean assemblages associated with the beds.

ACKNOWLEDGEMENTS

H. Sanabria and M. Morales helped in the field collections. R. Parkinson and A. Guzmán reviewed the early drafts. Very constructive criticism was received from J.A. Baeza, G. Hendler, J. García Gómez and R. Bauer. Two anonymous referees provided valuable comments. This work was partially supported by grants from INIA and the Comisión de Investigación, Universidad de Oriente, Venezuela.

REFERENCES

- Abele L. 1974. Species diversity of decapod crustaceans in marine habitats. *Ecology* 55: 156-161.
- Anderson M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26: 32-46.
- Archambault P., Bourget E. 1996. Scales of coastal heterogeneity and benthic intertidal richness, diversity and abundance. *Mar. Ecol. Prog. Ser.* 136: 111-121.
- Arias A., Guzmán R., Jiménez R., Molinet R. 2002. La pesquería de la pepitona, *Arca zebra*, en Chacopata, estado Sucre, Venezuela: Un análisis bioeconómico. *Zoot. Trop.* 20(1): 49-67.
- Borthagaray A.I., Carranza A. 2007. Mussels as ecosystem engineers: Their contribution to species richness in a rocky littoral community. *Acta Oecol.* 31: 243-250.
- Bourget E., De Guise J., Daigle G. 1994. Scales of substratum heterogeneity, structural complexity, and early establishment of a marine epibenthic community. *J. Exp. Mar. Biol. Ecol.* 181: 31-51.
- Carmona-Suárez C., Conde J. 1996. Littoral brachyuran crabs (Crustacea: Decapoda) from Falcon, Venezuela, with biogeographical remarks. *Rev. Bras. Biol.* 56(4): 725-747.
- Carranza A., Defeo O., Beck M. 2008. Diversity, conservation status and threats to native oysters (Ostreidae) around the Atlantic and Caribbean coasts of South America. *Aquat. Conserv.* 19(3): 344-353.
- Carranza A., Deffeo O., Beck M., Castilla J.C. 2009. Linking fisheries management and conservation in bioengineering species: the case of South American mussels (Mytilidae). *Rev. Fish Biol. Fisher.* 19(3): 349-366.
- Cervigón F. 2005. *Estudio bionómico de la isla de Cubagua*. Technical Report FONACIT. 550 pp.
- Chapman M.G., Underwood A.J. 1994. Dispersal of the intertidal snail, *Nodolittorina pyramidalis*, in response to the topographic complexity of the substratum. *J. Exp. Mar. Biol. Ecol.* 179: 145-169.
- Clarke K.R. 1993. Non-parametric multivariate analyses of changes in community structure. *Austral. J. Ecol.* 18: 117-143.
- Clarke K.R., Somerfield P.J., Chapman M.G. 2006. On resemblance measures for ecological studies, including taxonomic dissimilarities and a zero-adjusted Bray-Curtis coefficient for denuded assemblages. *J. Exp. Mar. Biol. Ecol.* 330: 55-80.
- Crooks J.A., Khim H.S. 1999. Architectural vs. biological effects of a habitat altering, exotic mussel, *Musculista senhousia*. *J. Exp. Mar. Biol. Ecol.* 240: 53-75.
- De Grave S., Pentcheff N.D., Ah Yong S.T., Chan T., Crandall K.A., Dworschak P.C., Felder D.L., Feldmann R.M., Franssen C.H., Goulding L.Y., Lemaitre R., Low M.E., Martin J.W., Ng P.K., Schweitzer C.E., Tan S.H., Tshudy D., Wetzer R. 2009. A classification of living and fossil genera of decapod crustaceans. *Raffles Bull. Zool.*, Suppl. 21: 1-109.
- Díaz O., Liñero I. 2003. Poliquetos epibiontes de *Pinctada imbricata* Röding, 1798 (Bivalvia: Pteridae) en el golfo de Cariaco, Venezuela. *Interciencia* 28(5): 298-301.
- Dittel A., Hines A., Ruiz G., Ruffin K. 1995. Effects of shallow-water refuge on behavior and density-dependent mortality of juvenile blue crabs in Chesapeake Bay. *Bull. Mar. Sci.* 57: 902-916.
- Eggleston D., Etherington L., Elis W. 1998. Organism response to habitat patchiness: species and habitat-dependent recruitment of decapod crustaceans. *J. Exp. Mar. Biol. Ecol.* 223 (1): 111-132.
- Galkin S.V., Goroslavskaya E.I. 2008. Bottom fauna associated with mussel beds and alvinellid communities in the hydrothermal field at 9°N of the East Pacific Rise. *Oceanology* 48(4): 509-516.
- Gómez A. 1996. Causas de la fertilidad marina en el nororiente de Venezuela. *Interciencia*, 21(3): 140-146.
- Gosselin L.A., Chia F.S. 1995. Distribution and dispersal of early juvenile snails: effectiveness of intertidal microhabitats as refuges and food sources. *Mar. Ecol. Prog. Ser.* 128: 213-223.
- Gutiérrez J.L., Jones C.G., Strayer D.L., Iribarne O. 2003. Mollusks as ecosystem engineers: the role of the shell production in aquatic environments. *Oikos* 101: 79-90.
- Hernández G., Lares L., Bolaños J. 2000. Crustáceos decápodos bentónicos del monumento natural de la Laguna de las Marites, Isla de Margarita, Venezuela. *Bol. Inst. Oceanogr. Vzla.* 38(2): 25-32.

- Hernández-Ávila I. 2004. Primer reporte de *Tyche emarginata* White, 1847 (Crustacea: Decapoda: Tychidae) para Venezuela. *Bol. Inst. Oceanogr. Vzla.* 43(1-2): 37-40.
- Hernández-Ávila I., Campos E. 2006. *Calyptraeothers hernandezii* n. sp. (Crustacea: Brachyura: Pinnotheridae), a new crab symbiont of the West Indian cup-and-saucer *Crucibulum auricula* (Gmelin) (Mollusca: Gastropoda: Calyptraeidae) off Cubagua Island, Venezuela. *Proc. Biol. Soc. Wash.* 119(1): 43-48.
- Hernández-Ávila I., Gómez A., Lira C., Galindo L. 2007. Benthic decapod crustaceans (Crustacea: Decapoda) from Cubagua Island, Venezuela. *Zootaxa* 1557: 33-45.
- Hernández-Reyes I.M., Palazón-Fernández J.L., Bolaños J., Hernández J. 2001. Aspectos reproductivos de *Mithrax forseps* (A. Milne Edwards, 1875) (Crustacea: Decapoda: Majidae). *Cienc. Mar.* 27(1): 21-34.
- Hurlbert S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* 54(2): 187-211
- Jacobi C.M. 1987. The invertebrate fauna associated with intertidal beds of the brown mussel *Perna perna* (L.) from Santos, Brazil. *Stud. Neotrop. Fauna & Environm.* 22: 37-72.
- Jiménez M., Lodeiros C., Márquez B. 2000. Captación de juveniles de la Madre Perla *Pinctada imbricata* (Röding, 1798) con colectores artificiales en el Golfo de Cariaco, Venezuela. *Caribb. J. Sci.* 36(3-4): 221-226.
- Jones C.G., Lawton J.H., Shachak M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946-1957.
- Liset B., Acosta V., Prieto A., García N. 2009. Contribución al conocimiento de los macromoluscos asociados a la Pepitona, *Arca zebra* (Swainson, 1833), en el banco natural de Chacopata, Península de Araya, Venezuela. *Zoot. Trop.* 27(2): 195-203.
- Lodeiros C., Pico D., Prieto A., Narváez N., Guerra A. 2002. Growth and survival of the pearl oyster *Pinctada imbricata* (Röding 1758) in suspended and bottom culture in the Golfo de Cariaco, Venezuela. *Aquacut. Int.* 10(4): 327-338.
- Mackenzie C., Troccoli L., León, L. 2003. History of the Atlantic Pearl-Oyster, *Pinctada imbricata*, industry in Venezuela and Colombia, with biological and ecological observations. *Mar. Fish. Rev.* 65(1): 1-20.
- Marcano J., Prieto A., Lárez A., Alió J., Sanabria H. 2005. Crecimiento y mortalidad de *Pinctada imbricata* (Mollusca: Pteridae) en Guamachito Península de Araya, Estado Sucre, Venezuela. *Cienc. Mar.* 31(2): 387-397.
- McArdle B.H., Anderson M.J. 2001. Fitting multivariate models to community data: a comment on distance based redundancy analysis. *Ecology* 82: 290-297.
- Pech D., Ardisson P.L., Bourget E. 2001. Settlement of a tropical marine epibenthic assemblage on artificial panels: Influence of substratum heterogeneity and complexity scales. *Est. Coast. Shelf Sci.* 55(5): 743-750.
- Pielou E.C. 1975. *Ecological diversity*. Wiley, New York.
- Posey M., Powel C., Alphin T., Townsend E. 1999. Oyster reefs as habitats for fish and decapods. In: Luckenbach, M. (ed.), *Oyster Reef Habitat Restoration: A Synopsis and Synthesis of Approaches*, Maryland Sea Grant Press.
- Prieto A., Ramos O., Arrieche D., Villalba J., Lodeiros C. 2001a. Producción secundaria e índice de condición en *Arca zebra* (Mollusca: Bivalvia) del Golfo de Cariaco, Venezuela. *Rev. Biol. Trop.* 49(2): 599-608.
- Prieto A., Ruíz L., García N., Álvarez M. 2001b. Diversidad malacológica en una comunidad de *Arca zebra* (Mollusca: Bivalvia) en Chacopata, Estado Sucre, Venezuela. *Rev. Biol. Trop.* 49(2): 591-598.
- Ricciardi A., Whoriskey F., Rasmussen J. 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. *Can. J. Fish. Aquat. Sci.* 54: 2596-2608.
- Rodríguez G. 1980. *Crustáceos decápodos de Venezuela*. IVIC. 494 pp.
- Ruiz G., Hines A., Posey M. 1993. Shallow water as a refuge habitat for fish and crustaceans in non-vegetated estuaries: An example from Chesapeake Bay. *Mar. Ecol. Prog. Ser.* 99: 1-16.
- Seed R. 1996. Patterns of biodiversity in the macroinvertebrate fauna associated with mussel patches on rocky shores. *J. Mar. Biol. Asso. U.K.* 76: 203-210.
- Shannon C.E. 1948. A mathematical theory of communication. *Bell System Tech. J.* 27: 379-423.
- Thiel M., Ulrich N. 2002. Hard rock versus soft bottom: the fauna associated with intertidal mussel beds on hard bottom along the coast of Chile, and considerations on the functional role of mussel beds. *Helgol. Mar. Res.* 56: 21-30.
- Tsuchiya M., Nishihira M. 1985. Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of island size on community structure. *Mar. Ecol. Prog. Ser.* 25: 71-81.
- Tsuchiya M., Nishihira M. 1986. Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of *Mytilus* age structure on the species composition of the associated fauna and community organization. *Mar. Ecol. Prog. Ser.* 31: 171-178.
- Turnipseed M., Kinck K.E., Lipsius R.N., Drejer J., Van Dover C.L. 2004. Diversity in mussel beds at deep-sea hydrothermal vents and cold seeps. *Ecol. Lett.* 6(6): 518-523.
- Van Dover C.L., Trask J. 2000. Diversity at deep-sea hydrothermal vent and intertidal mussel beds. *Mar. Ecol. Prog. Ser.* 195: 169-178.
- Warwick R.M., Clarke K.R. 1995. New biodiversity measures reveal a decrease in taxonomic distinctness with increasing stress. *Mar. Ecol. Prog. Ser.* 129: 301-305.
- Welch J.M., Rittschof D., Bullock T.M., Forward R.B. 1997. Effects of chemical cues on settlement behavior of blue crab *Callinectes sapidus* postlarvae. *Mar. Ecol. Prog. Ser.* 154: 143-153.

Scient. ed.: W.E. Arntz.

Received April 18, 2011. Accepted April 17, 2012.

Published online September 28, 2012.