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Changes in the crustacean community of a tropical rocky intertidal shore: is there a pattern?

Cambios en la comunidad tropical de crustáceos en la zona rocosa intermareal: ¿hay un patrón?

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ABSTRACT

A tropical rocky intertidal community in Montepio, southern Veracruz, Mexico, was sampled throughout a year to determine the extent of the changes in species composition and abundance. The study focused on the crustacean community, of which 49 species were identified. The community was characterized by a high species replacement rate, with 38.7% of the species appearing only once, 10% appeared twice, 16.3% were present in three different samples, and the remaining 34.7% were collected in 4 or more monthly samplings. Species diversity (H') varied constantly, while evenness remained relatively high and constant. An ordination analysis indicates that the crustacean community was dominated by the occurrence of rare species (47%). A cluster analysis, based on the Bray-Curtis similarity coefficient, shows that only a maximum of two consecutive samplings can have more than 50% similarity, reflecting the constant changes that occur in this community. When compared to the other numerically important phyla in the community, crustacean densities ranked third after annelids and mollusks. With such highly variable species composition and the absence of defined seasonal patterns, we propose that non-local processes, such as the strong winter winds ("northers") and a long season of tropical storms, are acting upon the community preventing the establishment of species for long periods of time and maintaining the biodiversity.

Key words: Rocky intertidal shore, community, Crustacea, species replacement, Gulf of Mexico.

RESUMEN

La comunidad de la zona intermareal rocosa tropical de Montepío, al sur de Veracruz, México, se muestreó por un año para determinar los cambios en la composición de especies y su abundancia. El estudio se enfocó a la comunidad de crustáceos, de la cual se identificaron 49 especies, ésta se caracterizó por un alto reemplazo de especies, con 38.7% de las especies que sólo se presentaron una vez, 10% presentes dos veces, 16.3% se capturaron en tres muestreos y el restante 34.7% fue recolectado en cuatro o más meses. La diversidad de especies (H') varió constantemente, mientras que la equitatividad se mantuvo con valores relativamente altos y constantes. Un análisis de ordenación indicó que la comunidad de crustáceos fue dominada por la presencia de especies raras (47%). El análisis de agrupamiento, basado en el coeficiente de similitud de Bray-Curtis, mostró que sólo un máximo de dos muestreos consecutivos pueden tener más del 50% de similitud, reflejando los constantes cambios que existen en esta comunidad. Cuando se comparó con otros phyla numéricamente importantes en la comunidad, la densidad de crustáceos se ubicó en tercer sitio, después de los anélidos y moluscos. Con una composición de especies tan variable y la ausencia de patrones estacionales definidos, se propone que procesos no locales, como los nortes y una larga temporada de tormentas tropicales, actúan sobre la comunidad evitando el establecimiento de especies por períodos largos de tiempo y manteniendo la diversidad.

Palabras clave: Zona intermareal rocosa, comunidad, Crustacea, reemplazo de especies, Golfo de México.

INTRODUCTION

Rocky intertidal communities have been intensely studied for a long time due to their accessibility and richness of natural resources. However, in spite of the long history of ecological studies conducted in this ecosystem, many questions related to the spatio-temporal structuring of the communities remain unexplored. Recent studies have identified important gaps in our knowledge about this ecosystem, including the use and relative importance of specific microhabitats (McKindsey & Bourget, 2001; Thompson *et al.*, 2002), methodological approaches to categorize species richness at a regional scale (Benkendorff & Davies, 2002), and the importance of short term temporal variation (Olabarria & Chapman, 2002).

The number of species and variability in occurrence of this fauna is determined by their ability to colonize and withstand the changing conditions of this habitat at a local scale and their capacity to maintain interspecific interactions (Lewis, 1964; Connell, 1972; Stephenson & Stephenson, 1972; Little & Kitching, 1996; Raffaelli & Hawkins, 1996). In many cases, rocky intertidal habitats are affected by the prevailing hydrographic conditions, specially in areas influenced by upwellings (Menge *et al.*, 1997; Menge, 2000).

Rocky shores are nursery and feeding areas for a number of species of crustaceans, fishes, and other vertebrates, which are interconnected with adjacent terrestrial and marine ecosystems (Rangeley & Kramer, 1995; Bradshaw *et al.*, 1999; Burrows *et al.*, 1999; Thompson *et al.*, 2000). The populations inhabiting the rocky intertidal have been considered as open due to larval transport and recruitment from separate populations (Gaines & Roughgarden, 1985; Underwood & Fairweather, 1989; Menge, 1991; Small & Goslling, 2001). This "openness" produces a variable recruitment which combined with diverse abiotic factors create a spatio-temporal mosaic from the local to the regional scale (Lewis, 1976; Bowman & Lewis, 1977; Underwood *et al.*, 1983; Hartnoll & Hawkins, 1985; Johnson *et al.*, 1998; Underwood, 1999; Jenkins *et al.*, 2001). The variability found in populations inhabiting the rocky intertidal may be due to different abiotic factors such as tidal regime, temperature, red tides, changes in sea level, storms, wave action, and fisheries (Crisp, 1964; Southgate *et al.*, 1984; Underwood & Fairweather, 1989; Bustamante & Branch, 1996; Denny & Paine, 1998).

In the Mexican portion of the Gulf of Mexico, rocky intertidal communities are spatially limited, occurring mainly as: a) limestone formations, in the northwestern section of the Yucatan Peninsula; b) coral reefs, in Isla Lobos, the Port of Veracruz, Antón Lizardo, and Cayo Arcas; c) lava flows, present in Los Tuxtlas region; and d) man-made structures, ever more prominent such as docks, jetties and oil rigs (Britton & Morton, 1988; Hernández, 2002). The rest of the coastline (>80%), mainly formed by sand bars, is under the influence of enormous sediment loads, discharged by a number of important rivers. Under these circumstances, the remaining rocky intertidal habitat is both spatially restricted and always influenced to some extent by freshwater, nutrients and sediments from the coastal runoff.

The present study examines the variation in the intertidal community composition in Montepio, southern Veracruz, Mexico, established along an ancient lava flow that extends 60 m from the shore to a depth of 1.5 m. This study represents the first report on the composition and dynamics of the crustacean assemblage inhabiting a rocky intertidal shore in the southwestern Gulf of Mexico. A monthly sampling program was designed to survey the community at a short temporal scale. We hypothesized that strong changes in the community composition would be detected since the region is constantly under the influence of extreme weather conditions, namely: the intense winter winds ("northers") from November to February, high temperatures and risk of desiccation at low tide during the dry season from March to May, and the tropical storms typical of the rainy season from June to October. We analyzed the community focusing on the crustacean species, but considered other abundant groups (mollusks, annelids, sipunculids, and echinoderms) for a general comparison.

MATERIALS AND METHODS

Eleven monthly samplings were conducted on the lava flow at Montepio, from February 1996 to February 1997. No samples were obtained in October and December due to bad weather caused by the "northers". Water temperature and salinity were recorded in every sampling. The sampling procedure consisted in obtaining pieces of rubble formed by encrusting, tubiculous, and coral forming organisms. Three replicates were obtained at depths ranging between 0.5 and 1 m, and placed in bags individually underwater to minimize the loss of organisms. The rocks were weighed and their volume estimated in a graduated bucket. Each rock was fragmented until all the organisms present were obtained. Crustaceans, mollusks, echinoderms, and sponges were preserved in 70% Ethanol (EtOH), while polychaetes were preserved in 4% formalin. In a previous sampling, 10 rock samples weighing between 1.6 and 6.7 kg were analyzed to determine the optimum sample size. The maximum number of crustacean species (18) was obtained in rocks weighing between 3.5 and 4.1 kg, a weight that was adopted for the whole sampling program (Hernández, 2002). It was further estimated that 4 kg rocks had a volume of 1.2 to 2.2 liters.

All crustaceans were identified to species using appropriate keys for each group as follows: for amphipods, Barnard (1969), Bousfield (1973), Barnard & Barnard (1983); for isopods, Menzies & Kruczynski (1983) and Kensley & Schotte (1989); and for decapods, Rathbun (1930), Provenzano (1959), Gosner (1971), Chace (1972), Gore & Abele (1976), Dardeau (1984), Williams (1984), and Abele & Kim (1986). Abundance, density (number of organisms/liter of sample, org/L), and biomass (grams of wet weight/liter of sample, g/L), were obtained for all species. All organisms were deposited in the National Crustacean Collection, Instituto de Biología, UNAM. Non-crustaceans were classified to phylum, and their densities and biomasses obtained.

The community analysis consisted in estimating species richness by taxonomic group and season and Shannon-Wiener's diversity index (H') and Pielou's evenness (J), to analyze temporal variation in species composition. A one way analysis of variance and Tukey's HSD tests were used to test, among the monthly samples, for significant differences in species richness, density, and biomass of crustaceans. The Olsmtead-Tukey ordination technique was used to obtain the relative importance with respect to abundance of each species in the community. This analysis was performed with the total sample density values (Steele & Torrie, 1992). A cluster analysis based on the Bray-Curtis similarity coefficient was performed; square root-transformed abundance data were used.

RESULTS

Throughout the sampling period water temperature varied between 22 and 36ºC ($\overline{x}$ = 27.1ºC) in February and July, respectively, and salinity between 30 and 38 ($\overline{x}$ = 34.4) in July and April, respectively.

The whole invertebrate community at Montepio changed considerably at the phylum level. The five more abundant phyla were Annelida, Mollusca, Crustacea, Sipunculida, and Echinodermata. Three distinct density peaks were recorded: the first one occurred in April, with a major contribution of annelids with 149 org/L; the second peak appeared in July, with the mollusks contributing with 147 org/L; and the third peak, recorded in September, had two main contributions by the mollusks and annelids with 156 and 206 org/L, respectively (Fig. 1). A significant feature of this pattern is that the maximum crustacean density, obtained in June with 109 org/L, does not represent a density maximum for the whole community. The density for the whole community, considering these five phyla, ranged from a minimum of 111 org/L in February to a maximum of 482 org/L in September.

Species richness

The total sample was composed of 3657 crustaceans with a biomass of 677.7 g, representing 4 orders, 16 families, 31 genera, and 49 species (Table 1). The shape of the cumulative species richness curve suggests that still more species can be found in this microhabitat (Fig. 2). The families with more species in the total sample were: Porcellanidae (7), Alpheidae (7), Gammaridae (6), Hyalidae (5), Menippidae (4), and Corophiidae (4). The 10 remaining families contributed with three or less species each (Table 1). Species richness varied significantly throughout the study, from an average of 3 species in March to 15 in September (Anova, F = 3.34, P = 0.0087) (Fig. 3). A multiple comparison indicates that September is significantly different from the two months poorest in species March and May (Tukey HSD, P = 0.008 and P = 0.043, respectively; Fig. 3).

Diversity

Species diversity (H') varied constantly, with a tendency to increase, from 0.4 in February 1996 to 1.1 in January 1997 (Fig. 4). Evenness remained relatively high and constant, except for two periods, February and June 1996. In February 1996 only 9 species were collected, with the hermit crab *Clibanarius antillensis* Stimpson, 1862, numerically dominating the community (n = 244). Interestingly, this is the highest number of specimens collected for any individual species in one monthly sample. However, *C. antillensis* was only present in this period, disappearing for the rest of the year. In June 1996, an undescribed species of amphipod, *Elasmopus* sp 1, and the anomuran crab *Neopisosoma angustifrons* (Benedict, 1901), were the most abundant with 113 and 109 individuals, respectively; while the remaining 17 species present in this sample had an average of 12 individuals.

The species turnover pattern shows that a maximum of 58% of the total species present in two consecutive samplings are shared (January-February), while the two most dissimilar consecutive samplings (February-March) only shared 27% of the species. From another angle, 19 (38.7%) of the 49 species recorded were collected only once, five (10.2%) species appeared twice, eight (16.3%) species were present in three different samples, and the remaining 17 (34.7%) species were collected in 4 or more monthly samplings. Only two species, the menippid crab *Eriphia gonagra* (Fabricius, 1781) and the grapsid *Pachygrapsus transversus* (Gibbes, 1850) were present in all the samples.

Density

Regarding monthly crustacean density, although it varied considerably among samples, from a minimum average of 25 org/L

Table 1. Crustacean species collected in Montepio, Veracruz, Mexico, throughout the study, with their classification according to the Olsmtead-Tukey ordination technique (D = dominant, R = rare, I = indicator, C = common).

#	Order	Family	Species	Classification
1	Sessilia	Tetraclitidae	*Tetraclita floridana*	D
2	Amphipoda	Ampithoidae	*Ampithoe tuberculatum*	R
3		Corophiidae	*Corophium tuberculatum*	R
4			*Corophium* sp 1	D
5			*Erichthonius* sp 1	R
6			*Lembos* sp 1	R
7		Gammaridae	*Elasmopus* sp 1	D
8			*Elasmopus* sp 2	I
9			*Elasmopus pectenicrus*	R
10			*Elasmopus spinidactilus*	I
11			*Maera inaequipes*	D
12			*Maera* sp 1	C
13		Hyalidae	*Allorchestes* sp 1	I
14			*Hyale plumulosa*	I
15			*Hyale* sp 1	D
16			*Hyale* sp 2	D
17			*Hyale* sp 3	R
18		Ischyroceridae	*Ischyrocerus* sp 1	I
19		Podoceridae	*Podocerus* sp 1	R
20	Isopoda	Cirolanidae	*Cirolana parva*	D
21			*Colopisthus parvus*	D
22		Corallanidae	*Excorallana sexticornis*	R
23			*Excorallana* sp 1	I
24			*Excorallana tricornis*	R
25		Sphaeromatidae	*Ischromene barnardi*	R
26			*Paradella quadripunctata*	D
27	Decapoda	Alpheidae	*Alpheus bouvieri*	D
28			*Alpheus malleator*	R
29			*Alpheus nuttingi*	R
30			*Synalpheus brevicarpus*	R
31			*Synalpheus curacaoensis*	R
32			*Synalpheus fritzmuelleri*	R
33			*Synalpheus scaphoceris*	R
34		Diogenidae	*Calcinus tibicen*	I
35			*Clibanarius antillensis*	I
36		Porcellanidae	*Clastotoechus nodosus*	D
37			*Megalobrachium soriatum*	R
38			*Neopisosoma angustifrons*	D
39			*Pachycheles rugimanus*	R
40			*Petrolisthes armatus*	C
41			*Petrolisthes jugosus*	R
42			*Petrolisthes marginatus*	R
43		Portunidae	*Callinectes sapidus*	R
44		Menippidae	*Eriphia gonagra*	D
45			*Menippe mercenaria*	D
46			*Menippe nodiffrons*	R
47			*Ozius reticulatus*	D
48		Grapsidae	*Pachygrapsus transversus*	D
49			*Plagusia depressa*	R

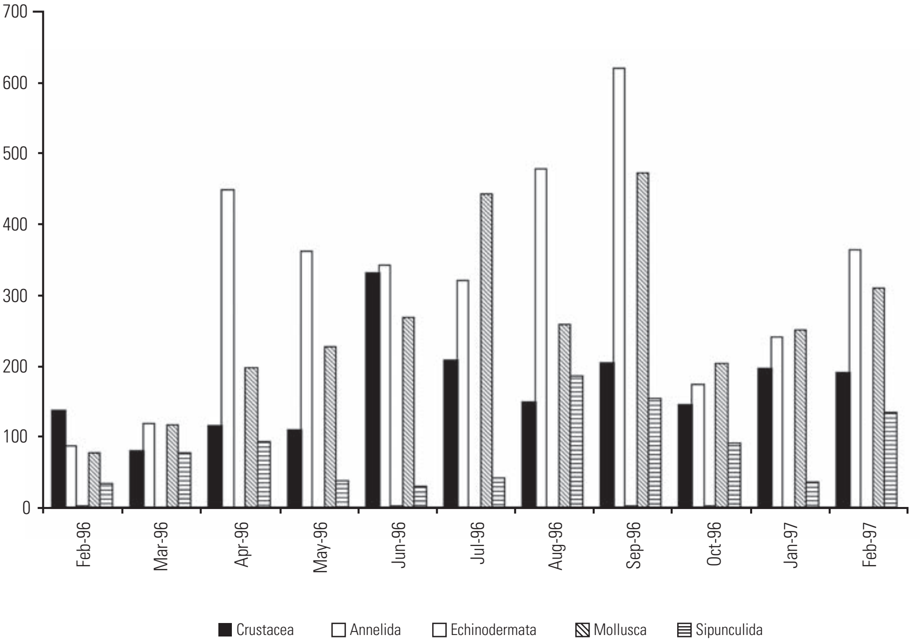

Figure 1. Variation in density (org/L) of the five more abundant phyla collected in Montepio, Veracruz, Mexico: Crustacea, Annelida, Echinodermata, Sipunculida, and Mollusca.

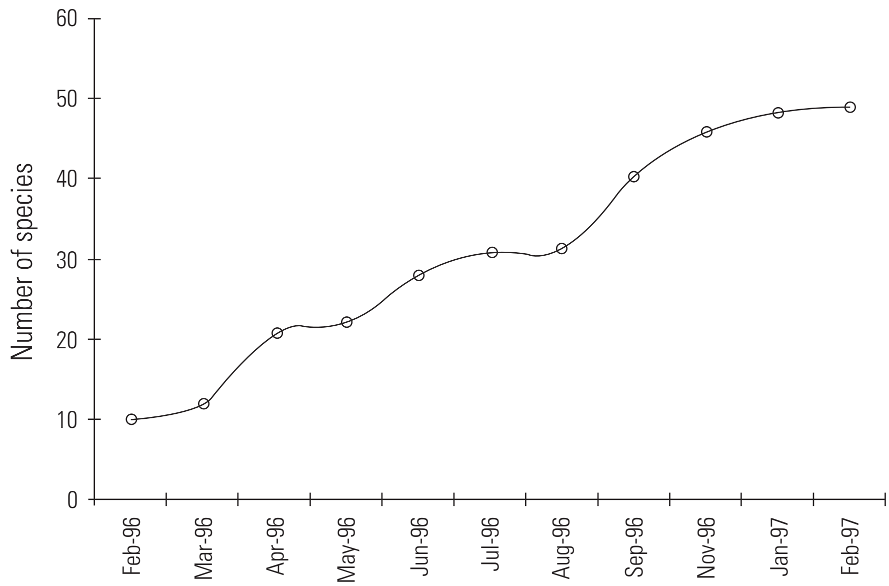

Figure 2. Cumulative species richness curve for crustaceans in Montepio, Veracruz, Mexico.

in March to 109 org/L in June, no significant differences were detected (Fig. 5). Mean density values are low from February to May, peaking in June, and remaining above 50 org/L the rest of the period. Although the biomass increases considerably from February (5 g/L) to July (80 g/L), decreasing seven months later to comparable initial levels (February, 9 g/L), no significant differences were obtained either (Fig. 6). The biomass peak obtained in July is due to the presence of the barnacle *Tetraclita floridana* Pilsbry, 1916, and the crabs *N. angustifrons* and *P. transversus*, which appeared in large numbers, besides being relatively large organisms.

Community analysis

The Olmstead-Tukey association technique shows that, for the complete study period, 47% of the species were rare, 33% dominant, 16% indicator, and 4% common in terms of density (Table 1). Considerable variation, not presented here, was observed as to what species were in each of the four categories every month. This result is consistent with the high species turnover rate that characterizes this community.

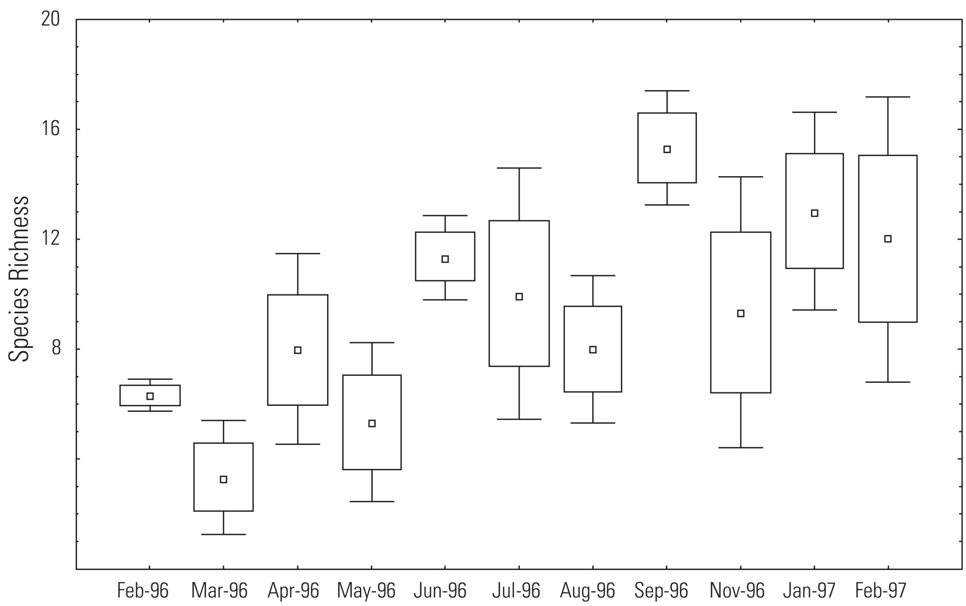

Figure 3. Species richness variation for crustaceans over the study period in Montepio, Veracruz, Mexico (circle = mean, box = ± 1 standard error, horizontal marker = ± 1 standard deviation).

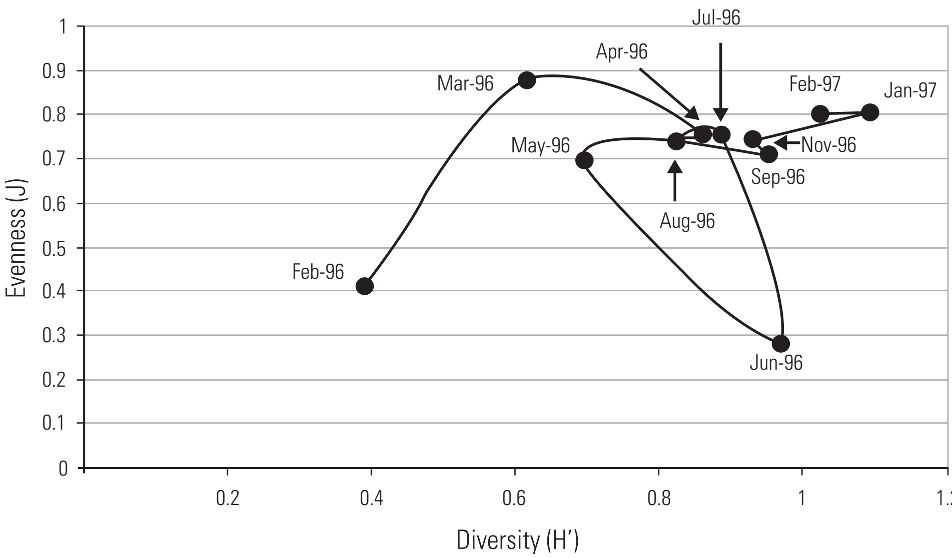

Figure 4. Relationship between evenness (J) and diversity (H') for crustacean species throughout the course of the study in Montepio, Veracruz, Mexico.

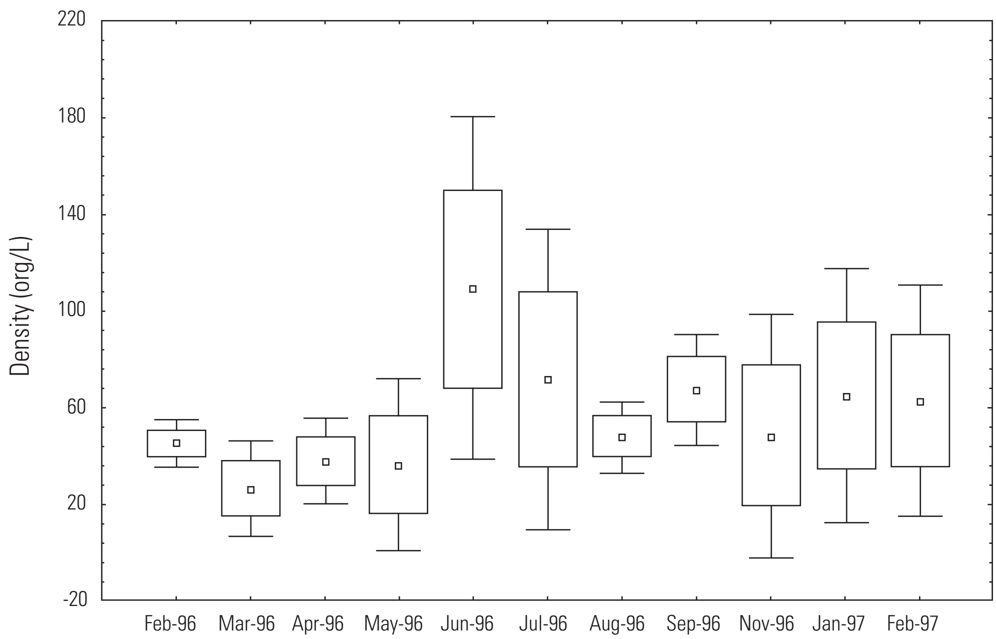

Figure 5. Variation in density (org/L) for crustaceans over the study period in Montepio, Veracruz, Mexico (circle = mean, box = ± 1 standard error, horizontal marker = ± 1 standard deviation).

The cluster analysis shows that the monthly samples cannot be associated in any defined general pattern (Fig. 7). Since the Bray-Curtis similarity coefficient considers the abundance of each species in relation to the total sample, it reflects up to some extent changes in community composition. In that sense, the abrupt changes in species composition from one sample to the next one produces in Montepio a different number of groups depending on the level of similarity. Between 60 and 80% similarity only four groups consisting of two months each can be recognized: April and May, characterized by low densities; January and February 1997, with high species richness and intermediate densities; July and August share intermediate values for both species richness and density; and June and September combine intermediate to high species richness and density.

DISCUSSION

A clear controversy emerges between those studies that find that non-local processes, such as changing environmental

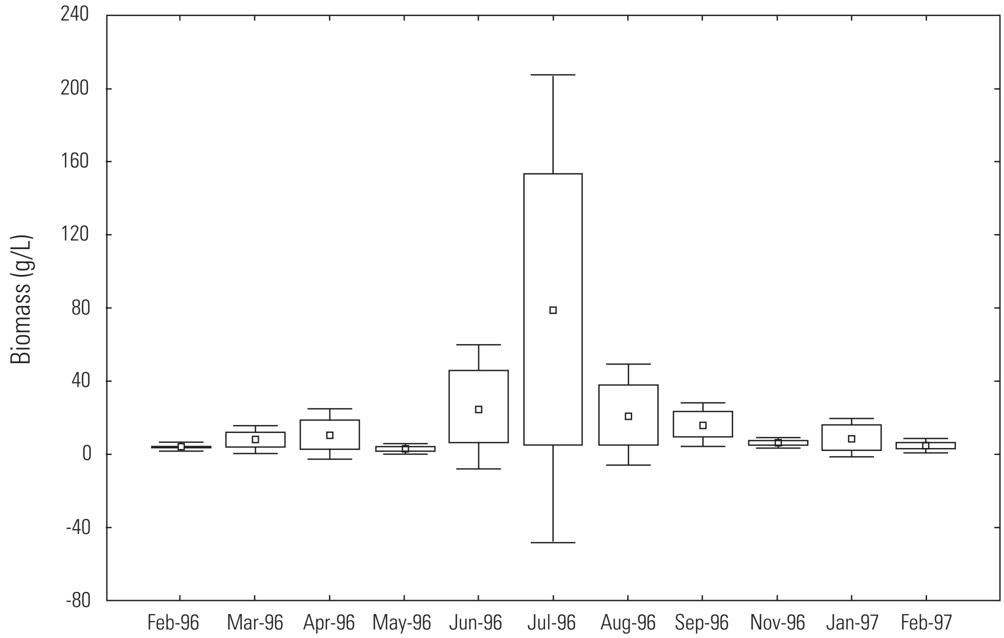

Figure 6. Variation in biomass (g/L) for crustaceans over the study period in Montepio, Veracruz, Mexico (circle = mean, box = ± 1 standard error, horizontal marker = ± 1 standard deviation).

conditions and recruitment intensity (Roughgarden *et al*., 1988; Hutchinson & Williams, 2001), rather than local processes or within the community interactions, such as competition for microhabitats (Minton & Gochfeld, 2001; Neil, 2001), are the main factors structuring intertidal communities and maintaining biodiversity. In this study, the very high species replacement rate (Gore *et al*., 1978; Domínguez, 2006), which may be preventing the establishment of long-term interspecific interactions, suggests that non-local processes such as storm mediated stress and stochastic recruitment of species, are key factors shaping the community. Similarly, Bertness & Leonard (1997) have already summarized these ideas for intertidal communities recognizing that at low levels of physical stress predation pressure may be high, becoming rare at high levels of physical stress.

The discontinuous nature of the rocky intertidal habitat along the coast of the southwestern Gulf of Mexico may also be contributing to the high species replacement pattern observed. The recruitment of different species throughout the study may be reflecting the absence of large source populations for most species that could predictably produce propagules to recolonize disturbed areas. A likely explanation is that most of the recorded species follow a "fugitive species" strategy, settling in newly opened spaces, and growing and reproducing rapidly before the next disturbance modifies the abiotic conditions and they disappear from that rocky shore.

The analysis of the obtained results is based on species diversity, abundance and density of each species, and their patterns of occurrence. The percentage of rare species (47%), which were present in three or less samplings with very low densities, suggests that recruitment intensity is low for a high proportion of species in this group. In contrast however, six of the 19 species that occurred only once throughout the study, were present in large numbers most probably as a result of high recruitment rates (Robles, 1997). This ample variation in recruitment patterns may also be preventing the establishment of interspecific interactions such as competition and predation, precluding also the presence of a keystone predator (Robles *et al*., 1995; Robles, 1997).

Two crustacean species that were present in all samples and that could have been part of a significant community structuring interaction as predators, were the crabs *Eriphia gonagra* and *Pachygrapsus transversus*. Both have extensive geographical ranges and reproduce virtually all year-round, being the commonest species at every site where they are recorded (Williams, 1984; Cuesta & Schubart, 1998). Both species could be considered omnivorous, feeding on algae, or preying upon a wide variety of organisms (Gore *et al*., 1978). *Eriphia gonagra* had medium to low densities, being abundant only in March (26 org/L), the most species-poor month; whereas *P. transversus* was relatively abundant (25 – 37 org/L) from July to January, a period characterized by high species richness and variable densities. Thus, *P. transversus* could be a key species, with a significant role in the shaping of the community as the most important invertebrate predator.

The constant variation detected in species composition in this study contrasts with other results from rocky intertidal habi-

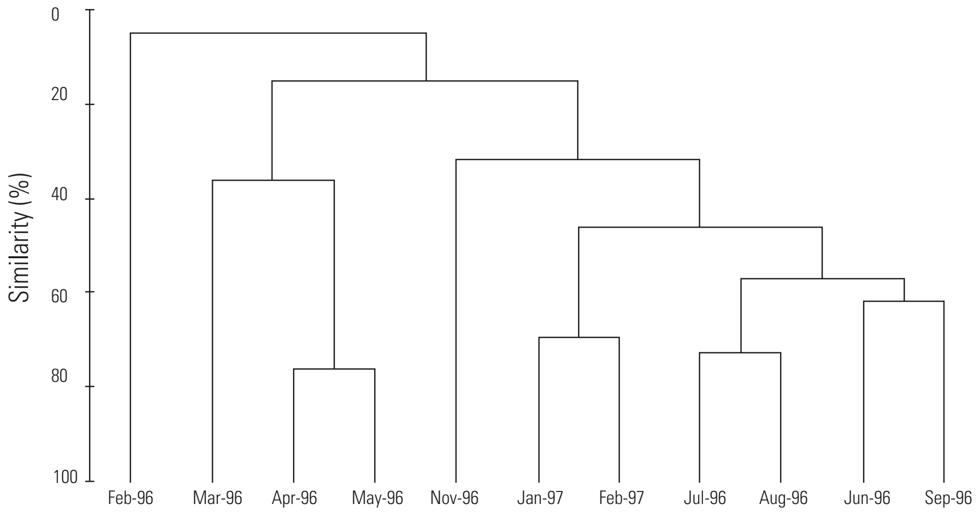

Figure 7. Dendrogram based on the Bray-Curtis similarity index for monthly crustacean samples taken in Montepio, Veracruz, Mexico.

tats in subtropical and temperate areas where community composition is stable and predictable. Gore *et al*. (1978) described as stable and predictable the decapod species composition associated with a sabellariid worm reef in Florida. Based on stomach contents, they argued that the constant supply of food provided by the sabellariid worms was the main factor that maintained the community without noticeable changes. Other studies have identified predictable temperature regimes (Thomson & Lehner, 1976), predictable recruitment rates and population growth of keystone species (Flores & Negreiros-Fransozo, 1999), and the strength of certain predator-prey interactions (Farrell, 1988), as the factors that prevent communities from undergoing constant changes.

Regarding the species richness estimates for this ecosystem, it is clear that with such high species replacement rate and a large percentage of rare species, only continuous samplings for more than a year would start to produce reliable results. The cumulative species curve presented here indicates that more species are still to be added. Supporting this interpretation, diversity (H') levels do not clearly increase with time in this community, suggesting that a typical succession process is not taking place here. Rather, diversity seems to completely depend on the random recruitment of species, which is taking place continuously throughout the year. The constant presence of disturbances in tropical intertidal ecosystems, rather than predictable seasonal changes, has been found to be responsible for the maintenance of high diversity in other tropical systems (Ben-Eliahu *et al.*, 1988).

Crustaceans are usually conceived as a numerically dominant group in coastal habitats; however, our results show that annelids and mollusks have higher densities than crustaceans. A salient point is that the maximum density obtained for crustaceans does not coincide with the maximum for the whole community. When analyzing community structure in tropical rocky intertidal sites, the difficulties imposed by the taxonomy of each group and the countless possible interactions among all the species often promote that the analysis be restricted to a small set of taxa. However, as shown with the results presented herein, interpretations about community composition can be seriously biased, overestimating the importance of the studied groups.

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