Temporal Variations in a Tropical Soft-Bottom Community, Venezuela

David Bone† and Eduardo Klein‡

†Departamento de Biología de Organismos
Universidad Simón Bolívar, A. P. 89.000
Valle de Sartenejas
Caracas, Venezuela
e-mail: dbone@usb.ve

‡Departamento de Estudios Ambientales
Universidad Simón Bolívar, A. P. 89.000
Valle Sartenejas
Caracas, Venezuela
e-mail: eklein@usb.ve

ABSTRACT

The relationship between macrofaunal density fluctuations and temporal variations of environmental parameters were studied. Physico-chemical, sediment, and biological parameters from a tropical soft-bottom community were followed monthly during a 2½ years survey, and their possible relationships were elucidated using multivariate analyses. The community at the study site was composed of 37% polychaetes, 21% crustaceans (mainly amphipods), 15% nematodes, 5% oligochaetes and 22% shared among gastropods, bivalves, and other minor groups. Results showed little temporal variation for environmental and sediment variables, except for the grain-size fractions, and clear fluctuations in macrofaunal densities. Polychaete total abundances showed two annual peaks, one during the summer months (mainly June to July, but May and July in 1991) and a second one towards the end of the year (November to December). Crustaceans, the second major group, showed only one annual peak, either early (April–May 1990 and 1991) or late summer (July–August 1989). Similar temporal density variations were also noted for the nematodes, with one annual peak during June and July (but exceptionally high values in February 1990 and 1991) and lowest values in April 1990 and January 1991. The molluscs (gastropods and bivalves) occurred with very low densities and showed no clear temporal trend. Polychaetes, the dominant group, were represented by 22 species belonging to 15 families, with spionids, paraonids, and capitellids as the families with the highest richness. Maximum species richness was obtained in October 1990 and April 1991 and minimum richness in July 1990 and January 1991, with 10 polychaete species (< 2 species) as a monthly average. In terms of abundance, 21% of the polychaetes were represented by Lumbrineris tetraura, 10% by Prionospio pygmaea, 5% by the cirratulid Tharyx sp., 5% by Magelona pettiboneae, and less than 2% for the rest of the species of this group. Lumbrineris tetraura, the dominant species, had two annual density peaks per year except in 1990, where no peak for the summer months was evident. Prionospio pygmaea had the highest densities during September–October 1989 and the lowest during April, June, and August 1991. Maximal values were also observed for Tharyx sp. in November–December 1989, and during April, June, and July of the same year for Magelona pettiboneae. Results of the ordination analyses by CCA revealed little association between faunal densities and sediment parameters suggesting that other factors may be responsible for the macrofaunal density patterns at the study site, such as factors related to biological interactions between species or factors extrinsic to the community, related to the input of external pulses of organic material. We propose that macrofaunal density peaks may be a consequence of a combination of the above factors at our study site.

ADDITIONAL INDEX WORDS: Macroinfauna, soft-bottom, Caribbean, Polychaeta, multivariate analyses.

INTRODUCTION

Soft bottom benthic communities exhibit considerable temporal variation, whether it is seasonal, annual, interannual or longer. The patterns of abundance of benthic species from temperate and subtropical latitudes show seasonal peaks of their populations, due to the incorporation and subsequent mortality of new recruits (Giangrande et al., 1994; Olafsson et al., 1994). These seasonal pulses have been described for coastal and continental shelf environments (Frankenberg and Leiper, 1977; Buchanan et al., 1978; Gray and Christie, 1983; Gray et al., 1984; Gaston et al., 1995) as well as for estuarine systems (Grassle and Grassle, 1974; Vierne, 1977; Díaz, 1984; Coull, 1985). These pulses may be regular and predictable, defining cycles (although their intensity may vary interannually) (Boesch et al., 1976; Coull, 1985; Boero, 1994) or non-periodical (Boesch et al., 1976; Boero, 1994). The existence of such cycles (in the case of periodical events) or non-periodical pulses has been frequently related to seasonal or interannual variation of environmental parameters, mainly, water temperature (Buchanan et al., 1978; Coull, 1985), salinity (Boesch et al., 1976; Coull, 1985), sediment characteristics and organic matter content (Volckaert, 1987; Miron and Desdouiers, 1990), dissolved oxygen content (Santos and Simon, 1980;
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Gaston and Edds, 1994), and nutrient inputs (Pearson, 1975; Tsutsumi et al., 1990).

The most comprehensive long-term studies on the ecology of tropical intertidal habitats are the Scottish-Indian IBP Project (Ansell et al., 1972; Ansell et al., 1978) for the wet tropics area, and the studies done in Australia by Alongi (1988, 1990) for the dry tropics. Despite their importance, the existence of short and long-term studies addressing the temporal variability in the composition and abundance of soft-bottom benthos in other tropical areas such as the Caribbean, are scarce in the current literature.

In Venezuela, several reports on benthic studies have been produced (Penchaszadeh, 1979, 1983; Perez Nieto, 1980; De Mahieu, 1984; Penchasadeh and Losada, 1987; Perez, 1991), although these studies focused on the characterization of coastal benthic assemblages for environmental impact studies, and the majority have been conducted in the west coast of the country where most industrial and touristic activities take place. These studies have been mostly descriptive and non-periodical in their sampling frequency.

In view of the necessity to gather knowledge on the importance of such aspects, the main goal of this research was to conduct a long-term study where seasonal trends could be evaluated. The specific objectives were to measure environmental parameters (physico-chemical variables and sediment characteristics) and determine their temporal variation; to describe the community structure and temporal trends of the macroinfauna with special emphasis on polychaete species, and finally, to determine possible relationships between macroinfaunal and environmental variables.

METHODS

Study Site

This research was conducted at Isla Raton (10°29'15"N, 68°58'5"W), Golfo Triste, Edo. Carabobo, Venezuela, a reef-type key located at the sandy beach of Quizandal, and close by to the Universidad Simon Bolivar’s Marine Research Station (Figure 1). The sampling site was established at the bottom of a 7-m deep and 25-m wide natural channel located between the south side of Isla Raton and the beach. The channel is sheltered from the wind and waves due to the presence of the key, which consequently reduces current velocity within the channel (Bone, 1994).

Field Sampling

Samples were taken monthly, during 2½ years, from January 1989 to September 1991. Subsurface water temperature and dissolved oxygen content were measured using a standard YSI equipment, whereas salinity was measured with a hand-operated refractometer. These measurements were also made for bottom water samples from October 1990 until the end of the study. Two sediment samples were taken for sediment analyses every two months during the first year, in February and April of the second year, and in February, April and June of the third year. This sampling scheme was adopted since a previous study indicated small variation among sediment parameters (Ordaz, 1991). Twelve monthly samples for macroinfaunal characterization were taken using a 20.45 cm² corer which was driven into the sediment (25 cm deep), pulled and sealed underwater with two rubber caps. The samples were preserved in 10% buffered formaldehyde at surface, and then taken to the Marine Laboratory for further processing.

Laboratory Procedure

Sediment samples were separated into sand and silt-clay fractions, and grain-size analysis was performed for the sand fraction, after which median grain size (phi 50), sorting (ds), skewness (sk), and kurtosis (kg) were calculated. Organic matter content was determined with the ash-free dry weight technique (AFDW) (550°C for 1 hour) (RoA and Berthois, 1975). Samples for macroinfaunal analyses were passed through a 0.5 mm sieve, hand-picked from the sieved material, separated into taxonomical groups and quantified. Counts were reported as total densities (number ind/m²) based on pooled values for the 12 monthly cores. Polychaetes were identified to the lowest taxonomic level possible, as it was the dominant faunal group, and counts were similarly reported as species densities (number ind/m²).

Data Analyses

Canonical Correlation Analysis (CCA) (Ter Braak, 1986), were performed to determine possible associations between environmental and species variables. Only monthly data with complete sediment and species information sets were used for the analyses (n = 11, see Table I for sediment parameters used), and the results presented as a biplot of linear combination scores. Faunal attributes used for the sample-species matrix data included only total densities for the four major taxa (see Figure 3) and the four main polychaete species (see Figure 4). No transformations were used in these data sets.
Table 1. Results for the sediment analyses of the samples from Isla Raton.

<table>
<thead>
<tr>
<th>Year</th>
<th>Months</th>
<th>Sand (%)</th>
<th>Silt-clay (%)</th>
<th>Org. Matt. (%)</th>
<th>Phi Values (S)</th>
<th>Sorting (S)</th>
<th>Skew.</th>
<th>Kurtosis</th>
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<td>2.9</td>
<td>0.98</td>
<td>0.19</td>
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<tr>
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<td>78.7</td>
<td>18.1</td>
<td>3.2</td>
<td>3.2</td>
<td>0.94</td>
<td>0.02</td>
<td>0.93</td>
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<td></td>
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<td>80.9</td>
<td>15.4</td>
<td>3.7</td>
<td>2.9</td>
<td>0.91</td>
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<td>0.98</td>
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<td>18.3</td>
<td>4.1</td>
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<td>5.8</td>
<td>-</td>
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<td>0.18</td>
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<tr>
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<td>0.6</td>
<td>0.1</td>
<td>0.21</td>
<td>0.72</td>
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<td>0.81</td>
<td>0.05</td>
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<tr>
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<td>4.72</td>
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<td>0.46</td>
<td>0.23</td>
<td>0.35</td>
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RESULTS

Environmental Parameters

Water temperature, salinity and dissolved oxygen content showed little variation during the study (Figure 2). Water temperature varied from 24 °C to 29 °C at the surface, and from 22 °C to 26 °C at the bottom, but with small differences between bottom and surface values. The highest value was recorded during the third trimester of each year (30 °C), and the lowest during March-April of 1990 and January-February of 1991. Salinity showed mean annual values of 36.9% for the surface and 36.4% for the bottom, with a small range of annual variation, except for 1991, where greater variation was recorded, both at the surface and the bottom. Dissolved oxygen values remained practically constant during the study, both, at the surface and the bottom (6.4 and 5.6 mg/l O₂ as annual means, respectively).

Sediment analyses indicated the presence of fine to very fine sands (median grain size for the sampling period = 3.11 phi, ± 0.46), moderately to well-sorted (S = 0.81 ± 0.23), and with variable skewness (0.05 ± 0.35) (Table 1). The sand fraction varied from 87.2% (in April 1990) to 68.5% (in June 1991), with a grand mean for the study period of 78% (±4.95%). The silt-clay fraction ranged from 28.5% (in June 1991) to 10.8% (in April 1990), with a grand mean of 18.35% (± 4.72%) for the sampling period. Organic matter content averaged 3.38% (±0.46%) for the study period, with a maximum value of 4.1% (in February 1991) and a lowest value of 3.0% (both months of 1990) (Table 1).

Macroinfauna Characterization

The community at Isla Ratón was composed of 37% polychaetes, 21% crustaceans (mainly amphipods), 15% nematodes, 5% oligochaetes, and 22% shared among gastropods, bivalves, and other minor groups. Polychaete abundances
showed two annual peaks, one during the summer months (mainly June-July, but May and July in 1991) and a second one towards the end of the year (November–December). The highest densities were observed in May and July 1991 (7,275 and 6,637 ind/m² respectively), and lowest in February and March 1989 (1,452 and 1,580 ind/m²), with a mean density of 3,303 (± 351.2) ind/m² for the sampling period (Figure 3, see Table II for details on annual means). Crustaceans, the second major group, showed only one annual peak, either early (April–May 1990 and 1991) or late summer (July–August 1989), with a maximum density of 8,000 ind/m², and a mean value of 2,046 (± 1,198.2) ind/m² for the sampling period (Figure 3, Table II). Similar temporal density variations were also noted for the nematodes, with one annual peak during June and July, and exceptionally high values in February 1990 and 1991 (4,225 and 4,066 ind/m², respectively). The lowest values were found in April 1990 and January 1991 (260 and 417 ind/m², respectively), with a mean of 1,491 (± 327) ind/m² (Figure 3, Table II). The molluscs (gastropods and bivalves) occurred in very low densities and showed no clear temporal trend. Polychaetes, the dominant group, were represented by 22 species belonging to 15 families (Table II), with spionids, paraonids, and capitellids as the families with the highest richness. Maximum species richness was obtained in October 1990 and April 1991 (14 and 13 species, respectively), and minimum richness in July 1990 and January 1991 (7 and 8 species respectively) with 10 polychaete species (±2 species) on the average. In terms of abundance, 21% of the polychaetes were represented by Lumbrineris tetraura Hartmann-Schröder (1971), 10% by Prionospio pygmaea (Hartman, 1961), 5% by the cirratulid Tharyx sp., 5% by Magelona pettiboneae Jones, (1963), and less than 2% for the rest of the species of this group. Lumbrineris tetraura, the dominant species, had a mean density of 666.5 ind/m² (±45.5) for the sampling period, with two annual density peaks per year except in 1990, where no peak for the summer months was evident (Figure 4, Table II). Prionospio pygmaea had the highest densities during September–October 1989 and the lowest during April, June, and August 1991, with a mean value of 314.6 ind/m² (±157.6) for the sampling period. Maximal values were also observed for Tharyx sp. in November–December 1989, and during April, June, and July of the same year for Magelona pettiboneae (Figure 4, Table II).

Macroinfauna–sediment Relationships

The results of ordination with CCA using sediment characteristics as sample-environment matrix and the densities of the benthic organisms in each sampling date as sample-species matrix are shown in Figure 5. The results explained 54.2% of the variance in the first axis and 27.5% in the second, accounting for 99.4% of the total variance in the first four ordination axes. The first ordination axis was defined mainly by high densities of Lumbrineris tetraura, Prionospio pygmaea and Tharyx sp., in addition to mollusces, and low densities of crustaceans and nematodes. The second axis was represented by high densities of this same group and low densities of Tharyx sp. and crustaceans. The environmental data showed low correlation among the variables except for kurtosis and the sorting coefficient (r = 0.202). A low correlation was obtained between the silt-clay fraction and the organic matter content, (r = 0.147) probably due to the fact that the latter was measured in whole samples. The components of the benthic community showed little correlation with the environmental data except for the nematodes and crustacean. Nematodes seemed to be more related to the high variability of the silt-clay fraction in the sediments, while the crustaceans appeared to be influenced by variations in organic matter content. The molluscs and dominant polychaete species showed no apparent relationship with any environmental variable. With respect to the sampling dates, no consistent temporal pattern was observed. Moreover, the same month of different years appeared to be distinct from one other. Four sampling dates (Apr 91, Jun 91, Feb 91 and Feb 90) were separated from the others. These dates were more related to the variation of the environmental variables rather than that of the biological component. For example, Apr 91 was highly

Figure 3. Temporal variation of total densities for the four dominant macrofaunal groups of Isla Ratón during the study, January 1989 to August 1991 (each bar represents the total count of individuals of the 12 cores/month, expressed as ind/m²).
related to organic matter content, while Apr 89 was related to *Prionospio pygmaea*, *Lumbrineris tetraura* and molluscs. These results suggest that some months with relatively high values of environmental variables may override the influence that may be exerted by the biological component, although this pattern was not consistent throughout 2½ years.

**DISCUSSION**

Measurements of seasonal variation of environmental parameters related to soft-bottom benthic studies have been previously reported for other Venezuelan coastal systems (Penchaszadeh, 1979; Bone and Bock, 1983; Feragotto and Rodriguez, 1987). Most of these studies were conducted at Punta Morón, Golfo Triste, a sandy beach system located 20 km west of Isla Ratón, and may be considered a “typical” sandy beach system along Golfo Triste’s coast (Penchaszadeh, 1979, 1983; De Mahieu, 1984; Penchaszaideh y Losada, 1987; Pauls et al., 1991). The results of these studies coincide with the general trend found for Isla Ratón: low water temperatures at the beginning of the year and high values around September and October; salinity between 35–37 ppt at the water surface and 36–37 ppt for the bottom, (annual mean = 36.5 ppt) and dissolved oxygen content showing little annual variation. Seemingly, the sediment characteristics were not very different from the ones reported for other coastal areas of Golfo Triste, including Punta Morón (RoA, 1983, 1987), except for the fact that the sediments of Isla Ratón had a greater percentage of fine material (5–6% for Punta Morón vs. 18% for Isla Ratón).

Macrofauna community structure of Isla Ratón was also similar to that reported for sand-bottom areas of Punta Morón, but different with respect to dominant taxa and relative abundances. Polychaetes, for example, were also the most abundant group in Punta Morón, representing between 46–59% of the total macroinfauna, but their densities were 2 to 3 times lower than those found in Isla Ratón for the same depths (Penchaszadeh et al., 1979; Bone et al., 1983; De Mahieu, 1984; Diaz et al., 1987; Pauls et al., 1991). Molluscs (bivalves and gastropods), the second most important group in Punta Morón, represented 25–40% of the total macrofauna; whereas this group represented a minor fraction in Isla Ratón (less than 10%). The crustaceans, the second most important taxa in Isla Ratón, showed a moderate richness in Punta Morón, but very low abundances. Finally, nematodes constituted only 5% of the total macrofauna at Punta Morón, representing a minor group for this area. With respect to polychaete species, there was more similarity in species composition between both sites (Punta Morón and Isla Ratón). *Prionospio pygmaea*, *Lumbrineris tetraura*, *Tharyx sp.* and *Magelona pettiboneae*, the most abundant species at Isla Ratón, were amongst the 10 most important species at Punta Morón (Bone et al., 1983; Diaz et al., 1987). Nonetheless, species abundances were consistently higher at our study site. These abundances are comparable to those reported for other latitudes. Flint and Rabalais (1980) reported polychaete densities between 500 to 13,000 ind/m² for a coastal shelf environment off the coast of Texas, U.S.A. Dauer (1980) reported mean annual densities of 316 ind/m² for *Magelona pettiboneae* and 239 ind/m² for *Prionospio pygmaea* at Tampa Bay, Florida, U.S.A. Alongi (1990) provided an extensive summary of mean density values for the macrofauna inhabiting several temperate and tropical regions. This data showed extreme variability, ranging from less than 100 ind/m² for the coast of Chile to over 60,000 ind/m² for areas such as SW Africa. Within the Caribbean, these values range from less than 2,000 ind/m² for the east coast of Venezuela and Colombia to over 16,000 ind/m² for a sandflat in Carrie Bow Cay (Belize), indicating less variability than in other tropical regions (Ansell et al., 1972; Alongi, 1990), but more similar with our results.

Our results showed that the benthic community established at Isla Ratón is distinct in terms of composition and relative abundances of the main invertebrate groups compared to those described for Punta Morón. These differences could be due to the sampling site at Isla Ratón, which is shel-
Table 2. Annual mean values per year (and standard error) for the main taxonomic groups and polychaete species present at Isla Ratón during the sampling period (n = number of months sampled per year; s.d. = standard deviation; n.p. = not present; n.d. = no data available).

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<th>1989 Mean</th>
<th>s.d.</th>
<th>1990 Mean</th>
<th>s.d.</th>
<th>1991 Mean</th>
<th>s.d.</th>
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<td>Tharyx sp.</td>
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<td>86.54</td>
<td>119.44</td>
<td>79.22</td>
<td>42.37</td>
<td>31.08</td>
<td>91.66</td>
<td>30.13</td>
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<td>63.78</td>
<td>64.23</td>
<td>54.69</td>
<td>70.13</td>
<td>44.12</td>
<td>83.26</td>
<td>9.84</td>
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<td>19.76</td>
<td>30.4</td>
<td>24.4</td>
<td>319.5</td>
<td>184.16</td>
<td>124.15</td>
<td>93.61</td>
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<td>44.6</td>
<td>n.p.</td>
<td></td>
<td>n.p.</td>
<td></td>
<td>n.p.</td>
<td></td>
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<td>818.7</td>
<td>66.89</td>
<td>83.6</td>
<td>527.25</td>
<td>517.89</td>
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<td>10.1</td>
<td>29.6</td>
<td>16.1</td>
<td>22.25</td>
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<td>4.24</td>
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<tr>
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<td>51.5</td>
<td>36.9</td>
<td>56.53</td>
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<td>30.2</td>
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<td>246.0</td>
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<td>n.p.</td>
<td>37.3</td>
<td>36.3</td>
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<tr>
<td>Prionospio dayi</td>
<td>n.p.</td>
<td>n.p.</td>
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<td>9.2</td>
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</table>

...tered from the direct impact of the natural wave energy and water currents that dominate the neighboring sandy beaches. Also the greater accumulation of fine sediment material at the bottom of the study site may have promoted a macrobenthic community of different composition and higher relative abundances than those established in the non-sheltered coast line.

With respect to temporal density variations, most of the main polychaete species found at Isla Ratón showed a peak of abundance towards mid-year, and a minor peak during November and December. Although previous studies on macrobenthic communities along Golfo Triste’s coast had sampling frequencies less than our monthly routine (e.g., every three months), their results similarly indicate high polychaete densities from May to July and November to December, and low densities during February to April and August to September (Bone et al., 1983; De Mahieu, 1984; Diaz et al., 1987; Pauls et al., 1991). This is similar to that found for Isla Ratón, suggesting a general pattern for polychaetes inhabiting the sandy beaches of Golfo Triste. The abundance peaks are usually related to the reproductive events which is a well-known fact for polychaetes worldwide. The existence of reproductive peaks has been reported for Lumbrineris fragilis between September to November (Buchanan and Warwick, 1974), while Nishihira et al., (1980) have indicated a reproductive season for L. latreiili during April, when water temperature rose above 10 °C. These authors have reported the presence of mature gametes of L. tetraura in any season of the year. Dauer et al., (1984) reported abundance peaks for Prionospio pygmaea during late fall to early winter in the state of Virginia (U.S.A.); whereas Dauer and Simon (1976) found such peaks during the summer months at the area of Tampa Bay, Florida (U.S.A.). Dauer (1980), in his two years study of the same Tampa Bay area, found abundance peaks for P. pygmaea during January of the first year, and during June to July of the second year. Similar results have been found for other polychaete species represented in the macrobenthic community of Isla Ratón, such as Tharyx sp. (Dailes, 1951; Woodin, 1978; Maurer et al., 1979) and Magelona pettiboneae (Jones, 1963; Dauer, 1980). On the basis of these comparisons, we may conclude that in general, the two main reproductive seasons in Golfo Triste seems to be around mid-year and at the end of the year. No strong associations were evident from multivariate analyses, suggesting that these environmental parameters exerted little influence on macroinfaunal abundance fluctuations. A clear multidimensional pattern may be observed when both sets of variables were related, indicating that many variables would be necessary to explain a reasonable percentage of the total variation, thereby suggesting the limited influence of any single variable in...
macroinfaunal patterns. This observation was similarly found for the polychaete species. With respect to sampling dates (samples) a low tendency of aggregation could be seen for the different months, or between the same months of different years, suggesting, that at a certain extent, each sampling month is described by fluctuations of any environmental parameter. Hence, the variability in faunal abundances may likely be defined by conditions or by a set of variables other than those considered in this study (see SNELGROVE and BUTMAN, 1994 for review). We believe that such factors could be grouped into two categories:

- factors intrinsic to the community, mainly related to biological interactions between species, and
- factors extrinsic to the community, mainly related to the input of pulses of external organic material (“food” e.g., particulate and dissolved organic matter, nutrients)

The first category has been extensively discussed in the literature and has been regarded as important in determining the composition, structure and dynamics of soft bottom benthic communities (WOODIN, 1978; WATZIN, 1986; GIANGRANDE et al., 1994; OLAFSSON et al., 1994; THRUSH et al., 1994). WATZIN (1986) has reported that intense biological interactions between the meiofauna-macroinfauna components determined temporal variations of infaunal densities. Predation effects by macrocrustaceans, fish, and sea birds on the benthic biota associated with these organisms has also been documented (PETERSON, 1979; THRUSH et al., 1994).

The second category, represented by input of pulses of nutrients and/or organic matter, may cause a temporal or chronic enrichment of the sediments which, after assimilation within a short period of time by many benthic species, may produce changes in abundance patterns and generate recruitment peaks (TSUTSUMI et al., 1990). This external input of “food” is well represented in Golfo Triste by important river drainages, rather than by plankton blooms, providing shallow

Figure 5. Biplot of the Linear Combination Scores for the Canonical Correlation Analyses (CCA) for samples (sampling dates), environmental (sediment characteristics), and biological (density of main benthic groups and main polychaete species) data (Prion. pig = Prionospio pygmaea, Lum. tet = Lumbrineris tetraura, Mag. pet = Magelona pettiboneae).
coastal benthic communities with sediments rich in organic matter and other compounds, e.g., the northern coastal zones of Golfo Triste (Bone et al., 1983). Aller and Aller (1986) provided evidence of the effects of major river effluents in low latitudes, and found that areas closest to the river mouth were nearly devoid of benthic life, but at a distance from the mouth, high abundances of meiofauna and macrofauna were reached as a result of nutrients born by the river effluent. Indirect evidence of the occurrence of such events, at a smaller scale are available for Isla Ratón, e.g., high deposition rates of organic-rich sediment measured during December and January at the same sampling site (D. Bone, unpublished data). Sedimentation rates greater than 0.12 g/cm²/day were found, possibly related to terrestrial inputs provided by small river and creek drainages located a few kilometers to the east of the island.

Finally, we suggest that macroinfaunal density peaks may also be a consequence of the combination of the above factors, i.e., the appearance of abundance peaks may be synchronized with organic-rich sediment inputs that both, promote macroinfaunal secondary production, and subsequent rapid abundance declines due to intense biological interactions that could reduce densities to average annual values. Evidently, much more research will be needed to continue and expand on these aspects, which will be useful for the knowledge of the role of these factors in determining temporal variations in tropical soft-bottom communities.

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