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Community structure of macrobenthos and the results of macropredator exclusion on a tropical intertidal mud flat

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Abstract: A one year study (February, 1985 – March, 1986) was conducted to investigate changes in community structure within a 484 m^2 area of an intertidal mud flat (more than 30% silt +clay) in the Gulf of Nicoya, Costa Rica (10° N, 85° W). Core samples (core area: 17.7 cm^2) for macrofauna were collected monthly to a depth of 15 cm into the sediment, and preserved in 10% buffered formalin in sea water stained with Rose Bengal. Organisms retained on a 500 micron mesh sieve were considered as macrofauna. A total of 79 species was collected, with an approximate density of 14,798 individuals per m^2. This density is relatively high and very similar to that found the previous year. Diversity (H') ranged from 1.61 to 3.12 and evenness (J) varied from 0.46 to 0.85. Polychaete worms dominated the community in terms of the number of individuals and species, followed by microcrustaceans (the ostracod, *Cyprideis pacifica* and an undescribed cumacean), molluscs, and miscellaneous groups. The numerical dominance by the polychaetes was mainly due to the spionids, *Polydora citrona* and *Paraprionospio pinnata* and the capitellid, *Mediomastus californiensis*, which together represented 41% of the fauna. These results are in contrast with those found the previous year, when *C. pacifica* and the cumacean represented 43.4% of the fauna, and the polychaetes, *M. californiensis, P. pinnata* and, *Lumbrineris tetraura* accounted for 19.2% of the total. Most of the remaining species, however, were collected during both surveys and at very similar abundances. Thus, the observed abundance fluctuations of the dominant species are considered as natural oscillations of the community. Cluster analysis divided the biological data set into groups that corresponded in time with the observed dry and rainy seasons typical of the Gulf of Nicoya region. Four abundance patterns (a,b,c,d) were found among the top 25 important species: species with peaks of abundance coinciding with the dry (a) or rainy (b) seasons, and species increasing (c) or decreasing (d) in abundance during the sampling period. Multiple discriminant analysis on the environmental variables assigned relatively high scores to the organic matter, silt + clay, and very fine sand contents of the sediments. The abundances of some species showed significant association with one or several of the environmental variables. The importance of these factors in community structure needs further experimental work. Caging experiments (5 mm mesh size cages) resulted in non-significant changes in total abundance and species number inside cages after a period of three months. Cluster analysis, however, revealed differences between caged and uncaged sets of samples. *C. pacifica* and juveniles of an unidentified bivalve mollusc were more abundant inside cages, and the cumacean was more abundant outside. These results indicate that the role of macropredators (birds, crabs, fish) in community structure might be relatively unimportant. This benthic community is considered as representative of relatively unpolluted conditions since published information on trace metal concentrations and raw sewage discharges indicate that these appear characteristic of nonindustrialized estuaries. The main likely source of pollution (chemical compounds derived from agricultural practices) into the Gulf of Nicoya, however, needs to be quantified.

Studies of temporal fluctuations of tropical soft-bottom communities are scarce. Taxonomic problems, limited availability of support facilities, and the small number of scientists working on this specific field, have delayed such studies. Information on tropical intertidal communities in developing countries in needed to provide background information for coastal zone management programs. Sorensen and Brandani (1987) point out that "the coastal zone, in comparison to inland environments, is more

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richly endowed with renewable natural resources – most notably productive fisheries, soils and forests, as well as recreational–quality coastal waters, beaches, and shorelands. This appears to be particularly true for the world's tropical and semitropical zones within which the great majority of the developing nations are situated".

The increasing development of coastal areas and the resulting pollution often call for comparative studies based on data from relatively unpolluted systems. These comparisons must be based on studies covering at least a full year of sampling in order to separate seasonal fluctuations of populations from pollution induced changes.

Based on expeditions sponsored before 1970 by the New York Zoological Society and the Allan Hancock Foundation, there have been many publications on the taxonomy of Central American marine benthic invertebrates (see Brusca 1980). Although some of these expeditions included collections from Costa Rica, subsequent studies have been restricted to short sampling periods or have focused mainly on sandy beaches and rocky shores (see review in Brusca and Iverson 1985).

The Gulf of Nicoya is an estuarine embayment on the Pacific side of Costa Rica, and the main fishing ground of the country. The Gulf is a locale where coastal zone development has increased in recent years. Thus, surveys of the physical (Voorhis et al. 1983), chemical (Epifanio *et al.* 1983; Dean *et al.* 1986), and biological (Epifanio and Dittel 1982; Bartels *et al.* 1984; Dittel *et al.* 1985) characteristics of the system were initiated in 1979 as part of a multidisciplinary research program. The study of soft-bottom subtidal communities was emphasized during the first years of this program (see Maurer *et al.* 1984; Maurer and Vargas 1984; Vargas *et al.* 1985). More recently the emphasis has been shifted to the study of muddy intertidal environments (Fournier and De la Cruz 1987; De la Cruz and Vargas 1987).

I studied for a period of one year the benthic community on a relatively unpolluted mud flat in the Gulf (Vargas 1987). The macrofauna was numerically dominated by an ostracod (*Cyprideis pacifica* Hartmann), an undescribed cumacean (Bodotriinae), an unidentified flat-worm (Turbellaria), and the polychaetes, *Mediomastus californiensis* Hartman, *Paraprionospio pinnata* (Ehlers), and *Lumbrineris tetraura* (Schmarda), which together accounted for more than 70% of the total number of individuals. Several species showed seasonal peaks of abundance, while others increased or decreased in abundance during the sampling period. Predation by benthic feeding fish, portunid crabs and other crustaceans, shore-birds, and infauna, was considered as an important source of disturbance at the site. However, no experimental manipulation of the community was performed to bring support to this impression.

The role of predation in community structure may be indirectly estimated by excluding predators with the use of wire-mesh cages placed on the bottom (Naqvi 1968; Reise 1977; Quammen 1981). The results of caging in soft-bottoms, however, are difficult to interpret due to the numerous artifacts induced by the cages (Gray 1981). Moreover, total exclusion of predators from soft-bottoms is difficult since a high percentage of the caged species are themselves predators (Ambrose 1984). In spite of these problems caging experiments in different environments have produced, with a few exceptions, an increase in the abundance of organisms within the cages (Peterson 1979). Perhaps this effect is more pronounced in temperate mud flats. The distribution of experimental work on tidal flats around the world, however, is still too patchy to allow meaningful generalizations to be made. Basic research is needed on the subject in tropical intertidal environments. Thus, the objetives of the second year of observations reported herein are: to continue the study of the soft-bottom intertidal community described by Vargas (1987), and to describe the response of the community to the placement of cages on the sediment.

METHODS

Description of the study site: The intertidal mud flat, where the sampling reported herein was done, is located on the Punta Morales peninsula, on the eastern shore of the mid upper Gulf of Nicoya, Costa Rica. This is the same site sampled by Vargas (1987), who included detailed information of its environmental characteristics. The Gulf of Nicoya is a tectonic estuary located at 10° N, 85° W on the Pacific coast of Central America. The Gulf is nearly 90 km long and 50 km wide at the mouth. The upper Gulf is less than 20 m deep, more estuarine than the lower Gulf, and is surrounded by

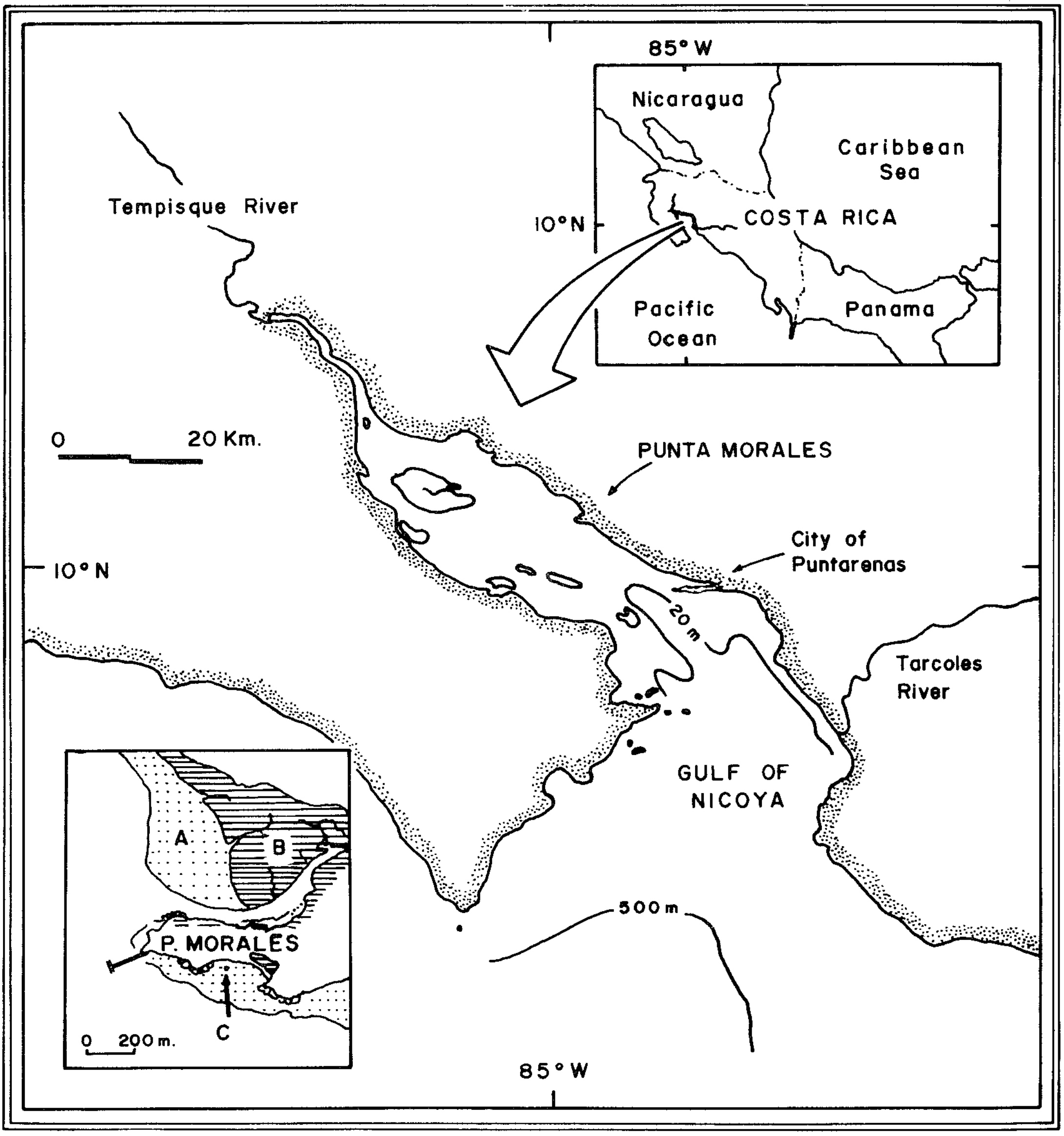

Fig. 1. Gulf of Nicoya, Pacific coast of Costa Rica. Location of the Punta Morales site on the upper Gulf. A: mud flot; B: mangrove; C: sampling site

mangrove forests and mud flats. Tides are semi-diurnal, with a mean tide range of 2.3 m. Circulation time in this region of the estuary is on the order of one week. A dry season, usually lasting from December through April, and a rainy season from May through November, exert a significant impact on water characteristics of the system (Epifanio *et al.* 1983; Voorhis *et al.* 1983).

Punta Morales is a small peninsula located on the east side of the mid upper Gulf of Nicoya. It is surrounded by mangrove swamps, rocky shores, mud flats, and a white sand beach. This study was done on a mud flat lying off and sharply demarcated from the western end of the conspicuous white sand beach. The sampling site was 15 m from the offshore edge of that beach (Figure 1).

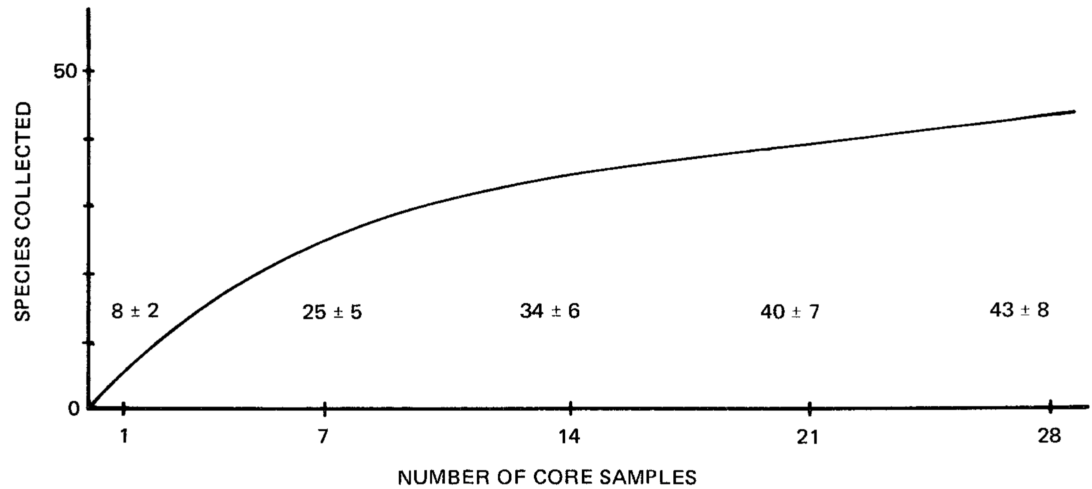

Fig. 2. Number of macroinvertebrate species collected as a function of the number of core samples (Species per area curve). The curve is based on 700 core samples collected from February, 1984 thru February, 1985. (Data from Vargas 1987). Mean number of species ± S.D. is indicated. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica.

Sample collection and processing: Gonor and Kemp (1978) point out that "differences between areas or changes in one location through time cannot be interpreted unless they can be distinguished from the spatial and temporal variations which are normally present at the locations". Thus, in order to minimize spatial variations in the distribution of organisms, sampling was restricted to a small area of the mud flat which was assumed to enclose a single community. The area was divided into four sections of 25 squares each, with 2 m wide access paths separating the sections, and each square was 4 m^2 (total area: 484 m^2). The selection of a particular square was made following Vargas (1987) methodology. That is, a random number was assigned to each one of the squares and selections were made by drawing from a container, without replacement, numbers previuosly written on paper tags.

Vargas (1987) sampled two squares per date and collected 14 core samples from each one. However, suspecting 28 cores per date might have included redundant information, a species per area curve (Gray 1981) was plotted using the information contained on all 700 cores analyzed in that first study. The results indicated that the first core included on the average 8 ± 2 species. Seven cores yielded 25 ± 5 species; 14 cores 34 ± 6, and 28 cores yielded a mean of 43 ± 8 species (Figure 2). Thus, the final samples yielded only 5 to 11 new, but rare species. Since this effort was costly in terms of the amount of new information gained, the present study is based on the collection of fourteen cores for each sample date: seven cores from each of two squares.

All core samples were collected at low tide with a plastic corer (core area: 17.7 cm^2) to a depth of 15 cm into the sediment. Samples were preserved in 10% buffered formalin in sea water stained with Rose Bengal. A 500 micron mesh sieve was used to separate the organisms from the sediments. Identification of species was accomplished as indicated in Vargas (1987).

Two cores were taken per square for sediment analysis, and analyzed following methods in Buchanan (1971). Sediment and water temperatures at the time of collection of samples were recorded. Salinity was measured with an optical refractometer. This study is based on a monthly sampling scheme initiated on February 7, 1985, and concluded on March 13, 1986.

Caging experiments were performed at the site and organized in two series. The "dry season" series was initiated on February 2 and concluded on June 6, 1985. The "rainy season" series was started on August 19 and concluded on December 16 of the same year. Cages remained on the sediment for periods of 1, 2, and 3 months. The experimental design is illustrated in Figure 3.

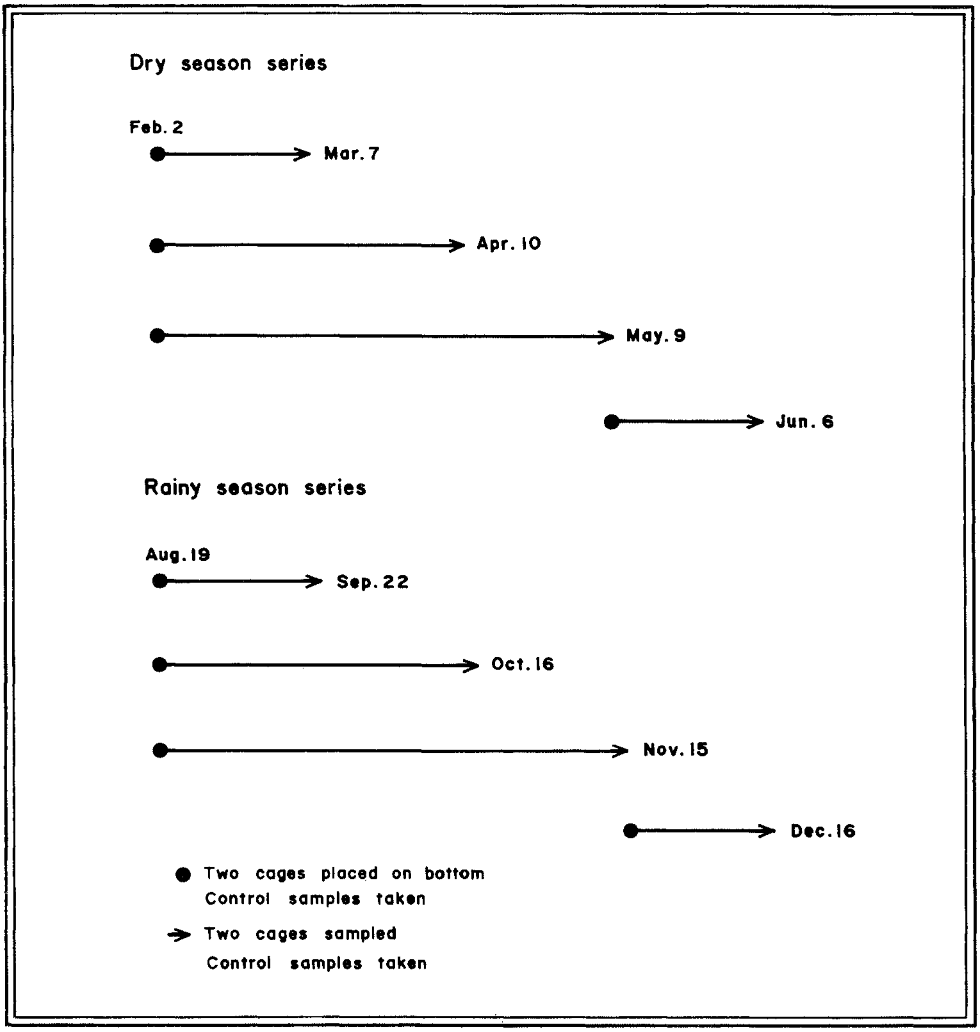

Fig. 3. Sampling scheme for the dry and rainy seasons series of caging experiments. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica. February 2 thru December 16, 1985.

Cages were made of galvanized steel wire mesh (mesh size is 5 mm) and had dimensions of 0.5 x 0.5 x 0.2 m. Each cage enclosed an area of 0.25 m^2 and was pushed 10 cm into the sediment. A total of 16 cages was used in this study and allocated randomly within the study area. Sampling dates were scheduled to coincide with tide levels low enough to uncover the cages completely. The cage to be sampled was carefully lifted and 7 core samples were taken randomly inside, and 10 cm away from the edges where the cage had been removed. The same number of reference samples were taken randomly outside each caged area and at least 1 m away from it (see Hulberg and Oliver 1980; Berge and Alvarez 1983). Sample preservation and processing, and species identifications, were conducted as indicated above. Two cores for sediment analysis were taken inside and outside each cage for sediment analysis as above. Water temperature and salinity were recorded at the time of collection of samples.

Cages with holes (cage controls) were used at the beginning of the study; however, since this type of cage attracted hermit crabs in high numbers, their use was discontinued. As a consequence the results presented herein do not separate the effect of macropredator exclusion from that of artifacts, if any, induced by the complete cages. The overall response of the community to the placement of a cage is evaluated in this study.

Data analysis: As a first step in the analysis the species, from the uncaged areas, were ranked according to their relative numerical contribution over the sampling period. Species diversity (H') and evenness (J) were measured per date (14 cores), and computed according to Gray (1981).

Groups of similar samples (normal classification), and similar species (inverse classification) were produced by cluster analysis using the BMD computer package (Vargas 1987). When data are frequency counts, clusters are formed based on the Chi-square statistic as a distance measure. All species found during the study were included in normal classification. Before inverse classification was attempted, however, the data matrix was reduced by removing all species ranked below the 25th place by the Biological Index (Maurer and Vargas 1984).

Analysis of variance (ANOVA) was used to test for significant differences between the total number of individuals of all species collected per date, as well as for each one of the 25 species included in inverse classification.

Samples from caged and reference areas were organized into two sets of 112 core samples each, 56 cores taken inside cages and an equal number outside (= 7 cores x 2 cages + 2 reference plots x 4 dates). Species from each set were ranked according to their relative numerical contribution over the four sampling dates (see Figure 4). Student's "t" tests were conducted to compare the mean number of individuals and species collected in caged and uncaged areas.

Groups of similar sets of samples were produced by cluster analysis as indicated above. Based on these results a close inspection of the raw data was performed in order to select those species which by their change in abundance may have influenced the clustering procedure. The mean number of individuals per core of the selected species was compared between caged and reference plots by means of "t" tests. Anova and "t" tests were computed according to Sokal and Rohlf (1969).

Vargas (1987) applied multiple discriminant analysis (MDA) to relate the biological data to some measured environmental variables.

The same approach has been followed in this study as an attempt to relate the biological data, from the uncaged samples only, to seven sedimentary variables (organic matter content, amounts of shell fragments, coarse sand, medium sand, fine sand, very fine sand, and silt-clay). Four replicate samples were included per sampling date. Rainfall (mm) was also included in the analysis and the four days with the highest precipitation per month were included as replicates. Salinity and water temperature were not included due to the small number of replicate measurements taken per sampling date. A total of 12 dates were included and comprised the period from March 7, 1985 through March 13, 1986. Biological data were log (x + 1) transformed, and sedimentary variables were subjected to an angular transformation (Shin 1982). Student's "t" were also used to compare mean values, for each sedimentary variable, between caged and uncaged sites. Spearman's rho rank correlation (Sokal and Rohlf, 1969) was used to test for the degree of association between the abundances of the top 25 numerically dominant species and the environmental variables included in Table 6.

RESULTS

Uncaged community

A. Species diversity and abundance

A total of 168 core samples (total area: 0.3 m^2) was analyzed yielding 4,412 individuals belonging to 78 species of macroinvertebrates and the gobiid fish, *Gobionellus sagitulla* (Gunther). Polychaete worms dominated the community in terms of the number of individuals and species, followed by crustaceans, molluscs, and miscellaneous groups (Table 1).

Numerical dominance by the polychaetes was mainly due to the relatively high contributions of two species: the spionid, *Polydora citrona* Hartman, and the capitellid, *Mediomastus californiensis* Hartman, which represented 38.4% of the fauna (Table 2). These two species, together with the polychaetes, *Paraprionospio pinnata* (Ehlers) and *Prionospio delta* Hartman, the crustaceans, *Cyprideis pacifica* Hartmann, *Pinnixa valerii* Rathbun, an undescribed cumacean, and juveniles of an unidentified bivalve species accounted for 93% of the individuals

TABLE 1

Total number of individuals (N) and species (S), and percentage (%) of polychaete worms, crustaceans, molluscs, and miscellaneous groups. Punta Morales intertidal mud falt, Gulf of Nicoya, Costa Rica, 1985-1986

	N	%	S	%
Polychaeta	2 413	54.70	30	37.97
Crustacea	1 286	29.15	21	26.58
Mollusca	525	11.90	15	19.00
Miscellaneous*	188	4.26	13	16.45
Total	4 412	100.01	79	100.00

* Brachiopoda, Cephalochordata, Echinoidea, Hemichordata, Nemertina, Ophiuroidea, Sipuncula, Tuberllaria, Pisces.

collected (Table 2). The remaining 54 species contributed with 310 individuals, and included the snails, *Nassarius luteostoma* (Broderip and Sowerby), and *Natica unifasciata* Lamarck represented by 14 and 7 individuals respectively, the portunid crab, *Callinectes arcuatus* Ordway (6 individuals), and the cephalochordate, *Branchiostoma californiense* Andrews (6). Other groups collected included 16 individuals of the ophiuroid, *Amphipholis geminata* (Le Conte), the echinoid, *Encope (Mellitella) stokesii* Agassiz (8), and the burrowing brachiopod, *Glottidia audebarti* Broderip (5).

The relative percentage represented by the 25 numerically dominant species collected during this study, and by Vargas (1987) the previous year, are included in Table 2 for comparative purposes.

The total number of individuals per date ranged from 158 (June 6) to 663 (March 7), with a mean of 367 ± 153 (Table 3). When abundances per date are converted to approximate densities, a minimum of 6,345 m^{-2} and a maximum of 25,421 m^{-2} were found, with a mean of 14,798 ± 6,170. The number of species collected per date ranged from 29 (August 19) to 41 (October 16), with a mean of 34 ± 4. Diversity (H') ranged from 1.61 (March 7) to 3.12 (September 22), and Equitability (J) ranged from 0.46 to 0.85 (same dates, respectively), Table 3.

The number of individuals per core (17.7 cm^2) ranged from 3 to 106, with a mean of 26 ± 17. The number of species ranged from 3 to 15, with a mean of 8 ± 3. No core was found devoid of macroinvertebrates.

Results of the analysis of variance (Anova) indicate that significant differences exist between dates in terms of the total number of individuals collected per date. Those species showing non-significant changes in the number of individuals collected per date are indicated by an asterisk in Table 2.

In addition to the 79 species collected by coring, at least 13 species of birds were observed foraging at low tide on the mud flat. Among these species, the herons, *Casmerodius albus* (Linnaeus) and *Egretta caerulea* (Linnaeus), the plover, *Pluvialis squatarola* (Linnaeus), and the sandpipers, *Numenius phaeopus* (Linnaeus), *Catoptrophorus semipalmatus* (Gmelin) and, *Limnodromus griseus* (Gmelin), were observed frequently. Portunid crabs, stomatopods, shrimps, and benthic fish were also observed.

B. Classification analysis

1. Dates (14 cores pooled, all species included) Two clusters are joined last as a result of the clustering procedure (Figure 4). Cluster A is made of samples taken from March 7 through June 6, 1985. Cluster B-1 includes samples from December 1985 and January 1986, and cluster B-2 those of February and March 1986. Cluster B-3 is made of samples corresponding to the period September 22 through November 15, 1985.

2. Species (top 25 species ranked by the Biological Index). Clusters are made of species having their peak abundances at about the same

TABLE 2

Relative percentages represented by the 25 numerically dominant species collected by coring at the Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica, during this study (A), and by Vargas (1987) de previous year (B).

	Species	A	B
P	*Polydora citrona* Hartman	21.74	0.14
C	Cumacea, Bodotriinae, sp. 1	17.88	20.77
P	*Mediomastus californiensis* Hartman	16.70	11.09
M	Bivalvia, juveniles sp. 1	6.19	0.81
C	*Pinnixa valerii* Rathbun	4.28	0.71
C	*Cyprideis pacifica* Hartmann	3.63	22.64
P	*Paraprionospio pinnata* (Ehlers)	2.58	4.59
P	*Prionospio delta* Hartman	2.27	1.31
M	*Tagelus bourgeoisae* Hertlein	2.06	0.42
P	*Glycinde armigera* Moore*	1.90	1.06
M	*Tellina rubescens* Hanley	1.63	2.01
C	*Panopeus* sp. 1	1.61	0.51
	Platyhelminthes, Turbellaria sp. 1	1.59	8.33
P	*Armandia salvadoriana* Hartmann-Schroeder	1.29	0.17
P	*Ceratocephale crosslandi* (Monro)*	1.04	1.94
P	*Lumbrineris tetraura* Schmarda*	1.02	3.58
P	*Sigambra tentaculata* (Treadwell)*	0.97	0.44
P	*Spiophanes soederstroemi* Hartman	0.82	2.55
	Oligochaeta sp. 1*	0.73	3.32
C	Pinnotheridae sp. 2*	0.68	0.02
P	*Acesta lopezi* Reish*	0.57	0.68
P	*Pectinaria californiensis* Hartman*	0.48	1.02
P	Syllidae sp 1. (*Sphaerosyllis*?)	0.48	0.05
M	Calyptreidae sp. 1*	0.43	0.12
	Hemichordata sp. 1*	0.41	0.81
	Total:	92.98	89.09

P = Polychaeta, C = Crustacea, M = Mollusca

* Non significant change in the number of individuals collected per date.

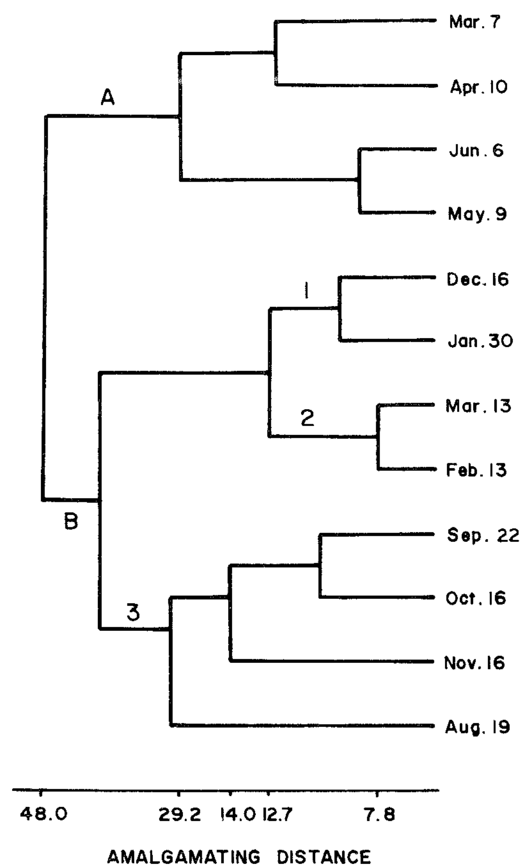

Fig. 4. Cluster analysis of dates (14 cores per date) Punta Morales mud flat, Gulf of Nicoya, Costa Rica, March 7, 1985 to March 13, 1986. Clusters B–1 and B–2 include all samples collected during 1986.

time of the year. Three clusters were formed as a result of inverse classification (Figure 5). Cluster A includes species with peak abundances towards the middle of the sampling period. Cluster B includes the species with abundances increasing towards the end of the sampling period. Cluster C-1 is made of species more abundant at the beginning of the year and declining afterwards. Cluster C-2 includes species with peaks in abundance being more frequent during the dry season months. The four main abundance patterns, outlined at the bottom of Figure 5 are illustrated in Figures 6, 7, 8 and 9 by the species, *Mediomastus californiensis* (pattern C-2), *Paraprionospio pinnata* (pattern A), *Pinnixa valerii* and, *Polydora citrona* (pattern B) and, *Cyprideis pacifica* (pattern C-1).

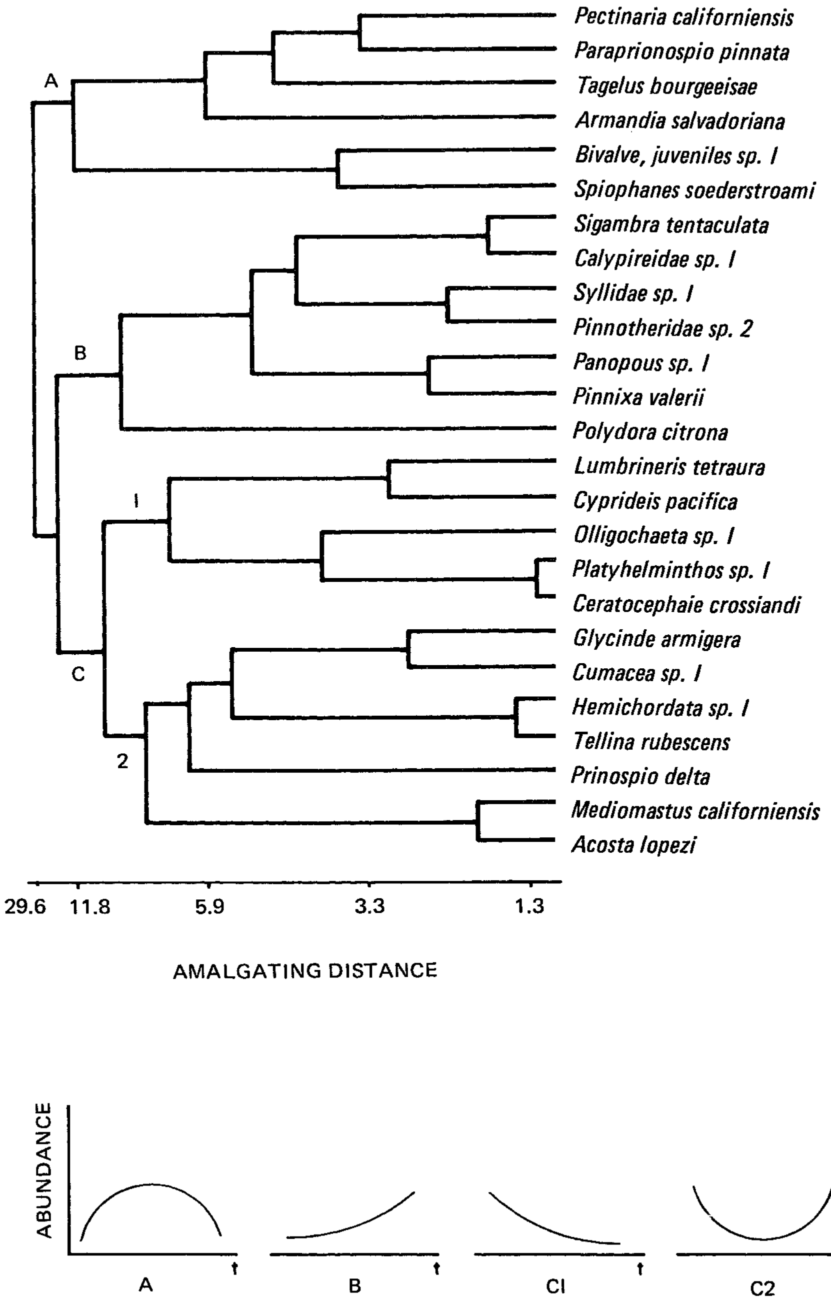

Fig. 5. Classification analysis of species groups. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica, 1985-1986. Small figures at the bottom indicate generalized abundance patterns characterizing the four main clusters.

Caged community

A list of the 10 more important species collected in the uncaged and caged plots, together with the total number of individuals and species, are included in Table 4 for the periods March 7 to June 6 ("dry season series"), and September 22 to December 16 ("rainy season series"). No

TABLE 3

*Total number of individuals (N), species (S), Shannon-Weiner diversity function H', and evenness (J). Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica. 1985-1986**

	N	S	H'	J
February 7	496	34	1.90	0.54
March 7	633	33	1.61	0.46
April 10	526	33	1.76	0.50
May 9	286	34	2.42	0.69
June 6	158	35	2.42	0.68
August 19	244	29	2.50	0.74
September 22	162	40	3.12	0.85
October 16	340	41	2.71	0.75
November 15	422	39	2.53	0.69
December 16	277	38	2.63	0.72
January 30	342	28	2.12	0.63
February 13	517	33	1.82	0.52
March 13	505	31	1.84	0.53

* Values listed are based on 14 core samples per date (core area: 17.7 cm^2). No samples were collected during July.

significant differences were detected for the total number of individuals and species collected. The results of cluster analysis, however, revealed a clear division of the data set into a dry season and a rainy season series (Figure 10). This indicates that the species composition and relative abundance is different on each series.

Caged and uncaged sets of samples from June 6, September 22, and October 16 were grouped in matched pairs by cluster analysis. This was not the case for pairs corresponding to March 7, April 10, May 9, November 15, and December 16. Caged samples from November 15, are the most dissimilar. An inspection of the raw data revealed that certain species were more abundant inside or outside cages for those particular dates. The results of Student's "t" test comparing the mean number of individuals found per core for these particular species are included in Table 5.

Environmental data

Rainfall at the port of Puntarenas (Figure 1) ranged from no precipitation during the months of February and March (1985 and 1986) to a maximum of 400 mm during the month of October. Water temperatures ranged from 31^{o} C (December) to 38^{o} (February and November, 1985). Salinity ranged from a low of 28 ^{o}/oo, to a maximum of 36 ^{o}/oo (October and March 1985, respectively). Based on tide tables, the number of tide levels below 0.1 m (the tide level at which the mud flat usually becomes exposed) ranged from a maximum of 32 (February, 1985) to a mimimum of 13 during July (Table 6).

The percentage of sand (all size fractions) in the sediment ranged from 50% (May) to 74% (February, 1986), with a mean percentage of 64.8%. The percentage of silt + clay ranged from 21% to 48% (February 1986 and May 1985, respectively), with a mean percentage of 31.6% . Organic matter content of the sediments ranged from less than 1% (March, 1985) to a maximum of 4.1% (October), with a mean percentage of 2.2% (Table 6).

Results of the multiple discriminant analysis (MDA) performed on the environmental variables indicate that the first three discriminant functions (DF's) account for 88% of the variance. Moreover, these functions were highly significant. Organic matter content of the sediment had the highest coefficient (1.1) on DF 1, followed by the amount of very fine sand (0.58). The second DF had the amount of shell fragments with the highest score (1.1) followed by the amount of very fine sand (0.85). The third DF had silt and clay, and rainfall with the highest coefficients (0.98 and 0.27, respectively)

Results of the Spearman's rho rank correlation analysis, between the environmental variable and the abundance of the top 25 numerically dominant species, are included in Table 7.

The cages did not affect sedimentary characteristics significantly inside. Moreover, no change in sediment level, color, or topographic relief was observed inside cages when compared to conditions outside.

DISCUSSION

Uncaged community. The macrofaunal community inhabiting the Punta Morales intertidal

TABLE 4

*Total number of individuals collected for the 10 most abundant species, total number of individuals and species, in the uncaged and caged plots for the periods February 7 through June 6 (A), and August 19 through December 16 (B). Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica. 1985**

Uncaged (reference)		Caged (treatment)	
A. Dry season series			
Cumacea, Bodotriinae sp. 1	672	*C. pacifica*	411
Mediomastus californiensis	357	*M. californiensis*	410
Cyprideis pacifica	149	Cumacea sp. 1	365
Turbellaria sp. 1	68	*T. rubescens*	53
Lumbrineris tetraura	45	*L. tetraura*	52
Glycinde armigera	39	*G. armigera*	47
Tellina rubescens	36	*T. bourgeoisae*	44
Tagelus bourgeoisae	23	Turbellaria sp. 1	34
Paraprionospio pinnata	17	*P. pinnata*	28
Ceratocephale crosslandi	15	*Acesta lopezi*	21
	1,421		1,465
Total number of individuals	1,603		1,685
Total number of species	62		60
B. Rainy season series			
Polydora citrona	246	Bivalvia, juveniles	573
Bivalvia, juveniles sp. 1	186	*M. californiensis*	177
Mediomastus californiensis	179	*P. citrona*	147
Pinnixa valerii	88	*P. valerii*	66
Paraprionospio pinnata	44	*T. bourgeoisae*	46
Cumacea, Bodotriinae sp. 1	31	*P. pinnata*	34
Tagelus bourgeoisae	31	*P. delta*	32
Ceratocephale crosslandi	28	*Glycinde armigera*	29
Panopeus sp. 1	27	*Panopeus* sp. 1	23
Prionospio delta	27	*Spiophanes soederstroemi*	22
	887		1,149
Total number of individuals	1,201		1,414
Total number of species	66		58

* Cage mesh size is 5 mm. Sieve mesh size is 500 microns. Each cage enclosed an area of 0.25 m^2, and 16 cages were sampled during the study. No change in sedimentary characteristics was detected inside cages. Mesh fouling was minimum after a period of three months.

mud flat had been characterized as numerically dominated by deposit-feeding polychaete worms and microcrustaceans (Vargas 1987). This dominance pattern was repeated in this second year survey (Table 1). Moreover, all species collected in this study (79), with the exception of 5 rare species, were represented in the total of 93 found by Vargas (1987) the previous year. The mean number of species collected per core (8) is the same in both studies, and mean densities per m^2 (13,827 and 14,798) did not differ significantly either. Densities of 9,269 and 13,991 m^2 have been reported for sandy environments in the Pacific coast of Panama by Kaufman (1976) and Lee (1978), respectively.

The relative abundance (%) of several species, however, changed during this study when compared with their relative abundance the first year (Table 2). The most obvious changes are those of the spionid polychaete, *Polydora citrona* (+ 21.6% difference), the ostracod, *Cy-*

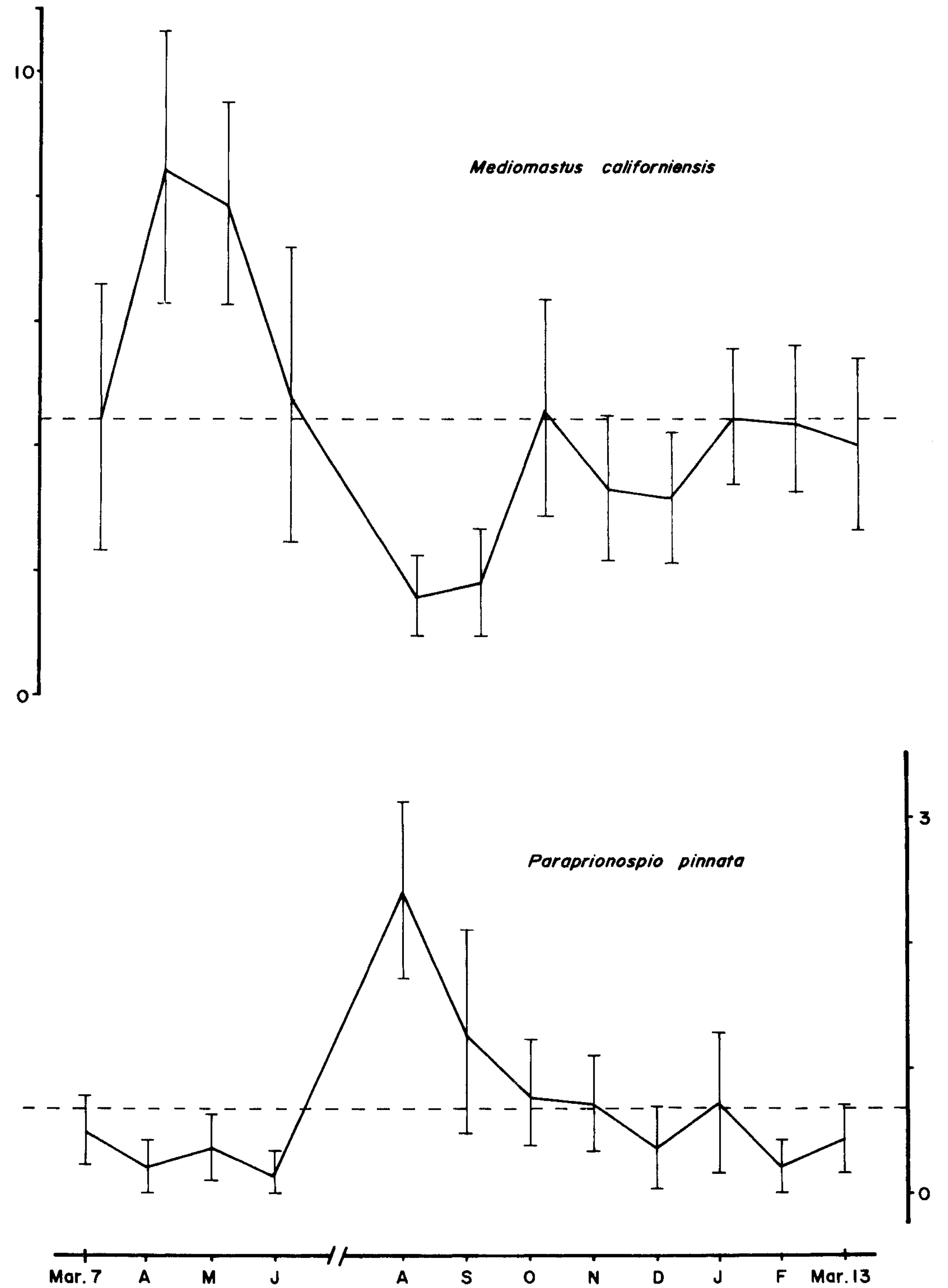

Fig. 6. Mean number of individuals per core (± 95%C.I.) for the polychaetes *Mediomastus californiensis* and *Paraprionospio pinnata.* Dashed line indicates mean number of individuals over the sampling period. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica, 1985-1986.

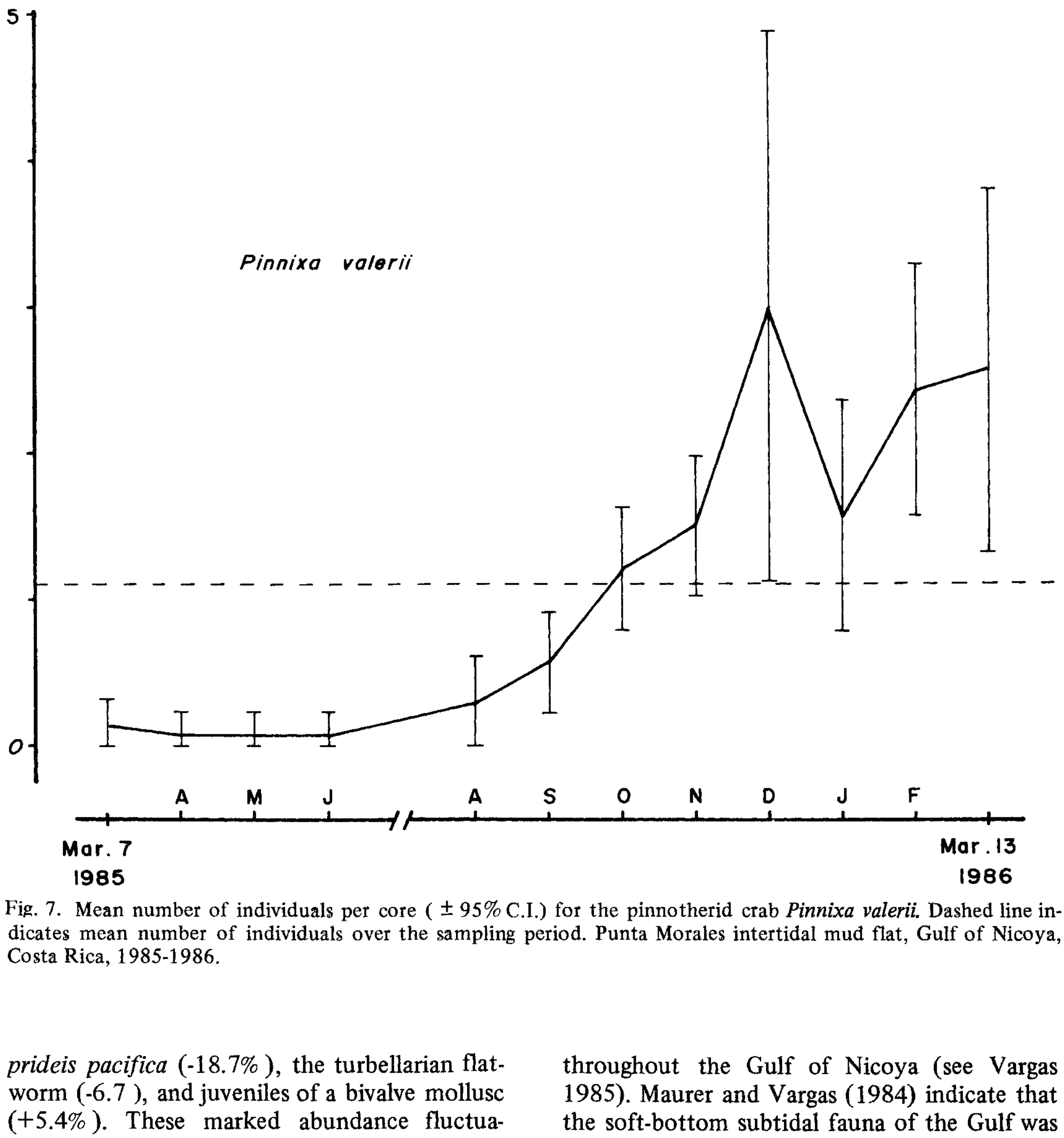

Fig. 7. Mean number of individuals per core (± 95% C.I.) for the pinnotherid crab *Pinnixa valerii.* Dashed line indicates mean number of individuals over the sampling period. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica, 1985-1986.

prideis pacifica (-18.7%), the turbellarian flatworm (-6.7), and juveniles of a bivalve mollusc (+5.4%). These marked abundance fluctuations support the comment by Lee (1978, p. 122) that population oscillations of at least certain tropical species are as great as those in temperate species (see Witlatch 1977). In contrast, the remaining 21 species (of those included in Table 2) fluctuated less than 4% each over the two year period. These observations lead the view that the community has some degree of temporal stability (*sensu* Gray 1981), and that the observed differences in structure over the two year period are natural fluctuations of the community.

Many of the species collected at the Punta Morales mud flat have been found previously throughout the Gulf of Nicoya (see Vargas 1985). Maurer and Vargas (1984) indicate that the soft-bottom subtidal fauna of the Gulf was characterized as broadly occurring species fluctuating in abundance with change in depth and bottom type. It may be speculated that the faunal homogeneity of the Gulf is partially attributable to the type of circulation patterns and relatively fast circulation time of the Gulf of Nicoya waters (Voorhis *et al.* 1983), which may scatter planktonic larvae throughout most of the estuary (see Epifanio and Dittel, 1982; Stancyk and Feller, 1986).

On a local scale, however, the Punta Morales peninsula is a physical obstacle for coastal currents. Small, larvae-trapping eddies may be formed with the reversal of the semidiurnal

TABLE 5

Significance of the difference in the mean number of individuals per core ("t" tests, n = 14) between caged and uncaged plots for the species listed and dates indicated. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica, 1985

	Mar. 7	Apr. 10	May 9	Jun. 6
Cumacea, sp. 1	**UN	NS	NS	NS
Cyprideis pacifica	NS	** C	* C	NS
Mediomastus californiensis	§ NS	NS	NS	NS
	Sep. 22	Oct. 16	Nov. 15	Dec. 16
Polydora citrona	NS	NS	NS	NS
Bivalvia, juveniles sp. 1	NS	NS	** C	*** C
M. californiensis	NS	NS	NS	NS

* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

UN: UNCAGED SAMPLES, C: CAGED SAMPLES, NS: NON-SIGNIFICANT

§ Capitellid worms have been shown to be insensitive to caging experiments perhaps because their deep position in the sediment allows them to avoid predation pressure (Reise 1977).

tide. Levin (1986) concluded that tidal circulation can lead to water mass oscillations which retain larvae in back-bay habitats. These larvae essentially reseed the parent population. Whether or not this mechanism contributes both to the stability and the species changes of the Punta Morales community is an interesting topic for further research.

Brood protection may reduce wastage of planktonic larvae. The cumaceans are examples of this type of development as larvae develop to a manca stage within the female brood pouch. Female cumaceans, bearing young in their brood pouches, were collected frequently at Punta Morales during the dry season. Moreover, among the factors that may have allowed the tubiculous polychaete, *Polydora citrona,* to reach high densities at the site (this worm was first collected at the site in December, 1984) is the fact that this species deposits ova in the tube where the young develop (Hartman, 1941). Thus, young worms may be more likely to settle near the parent with the effect of a rapid density increment at the site (Figure 9).

Changes in the abundance of a given species thru time may be represented by a modified sinusoidal wave (Gray, 1981). It may be assumed that the small diagrams at the bottom of figure 6 represent segments of waves over a period of one year each. Certain species show population fluctuations characterized by annual peaks of abundance coinciding either with the dry season (e.g., *Mediomastus californiensis,* Figure 6), or with the rainy season (e.g., *Paraprionospio pinnata,* Figure 6). Other species, however, may show peaks of abundance at intervals of more than a year (e.g., *Pinnixa valerii,* Figure 7 and, *Cyprideis pacifica,* Figure 9).

When abundances of all species are evaluated by cluster analysis, a seasonal pattern of the community becomes more evident (Figures 4 and 10). A seasonal pattern was also found by Vargas (1987) the previous year.

Lee (1978) and Dexter (1979) found a marked seasonality in the reproductive patterns, abundance, and diversity of invertebrates living in sandy beaches on the Bay of Panama. These changes coincided with strong seasonal upwelling conditions in the region. Broom (1982) reports evidence of seasonality on Malaysian mud flats triggered by the onset of the north-east monsoon.

In the Gulf of Nicoya water properties and currents vary seasonally, and during the rainy season horizontal and vertical gradients are well

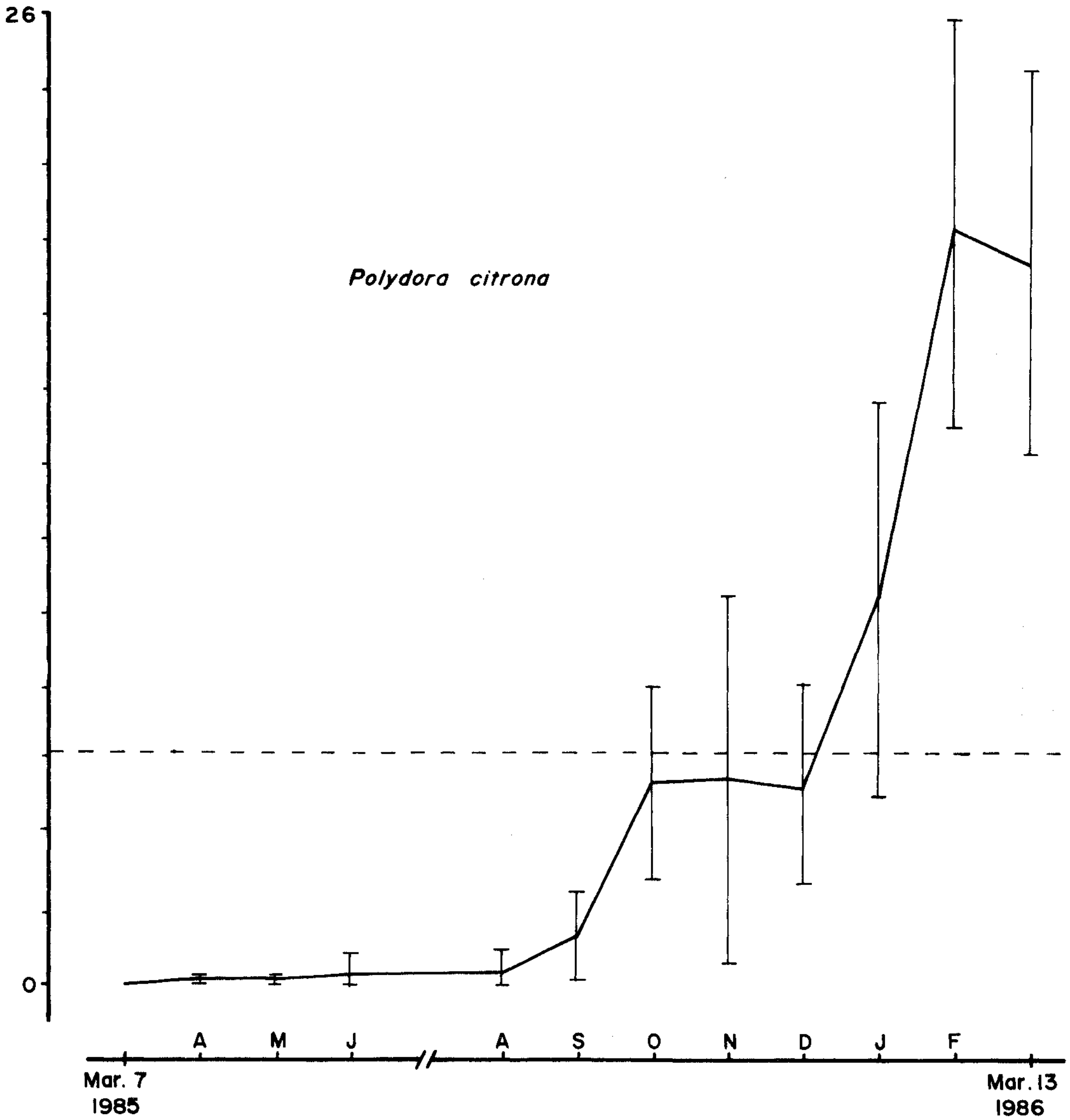

Fig. 8. Mean number of individuals per core (± 95% C.I.) for the spionid polychaete *Polydora citrona.* Dashed line indicates mean number of individuals over the sampling period. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica, 1985-1986.

developed. These gradients are diminished during the dry season due to wind and tidal mixing (Epifanio *et al.* 1983; Voorhis *et al.* 1983). Thus, the existence of seasonal patterns of the soft-bottom intertidal fauna is not surprising.

There is evidence that benthic species respond to natural cycles characterized by periods of several years in addition to the yearly seasonal cycle (Gray and Christie, 1983). Thus, a knowledge of long term fluctuations is needed in order not to attribute them to artificial causes, such as pollution. This is particularly important in the case of species such as *Polydora citrona.* From an abundance of about 200 individuals per m^2 in August 1985, this species reached densities in excess of 10,000 per m^2 by February of 1986. Sharp increases in abundance after a disturbance event have been reported for several

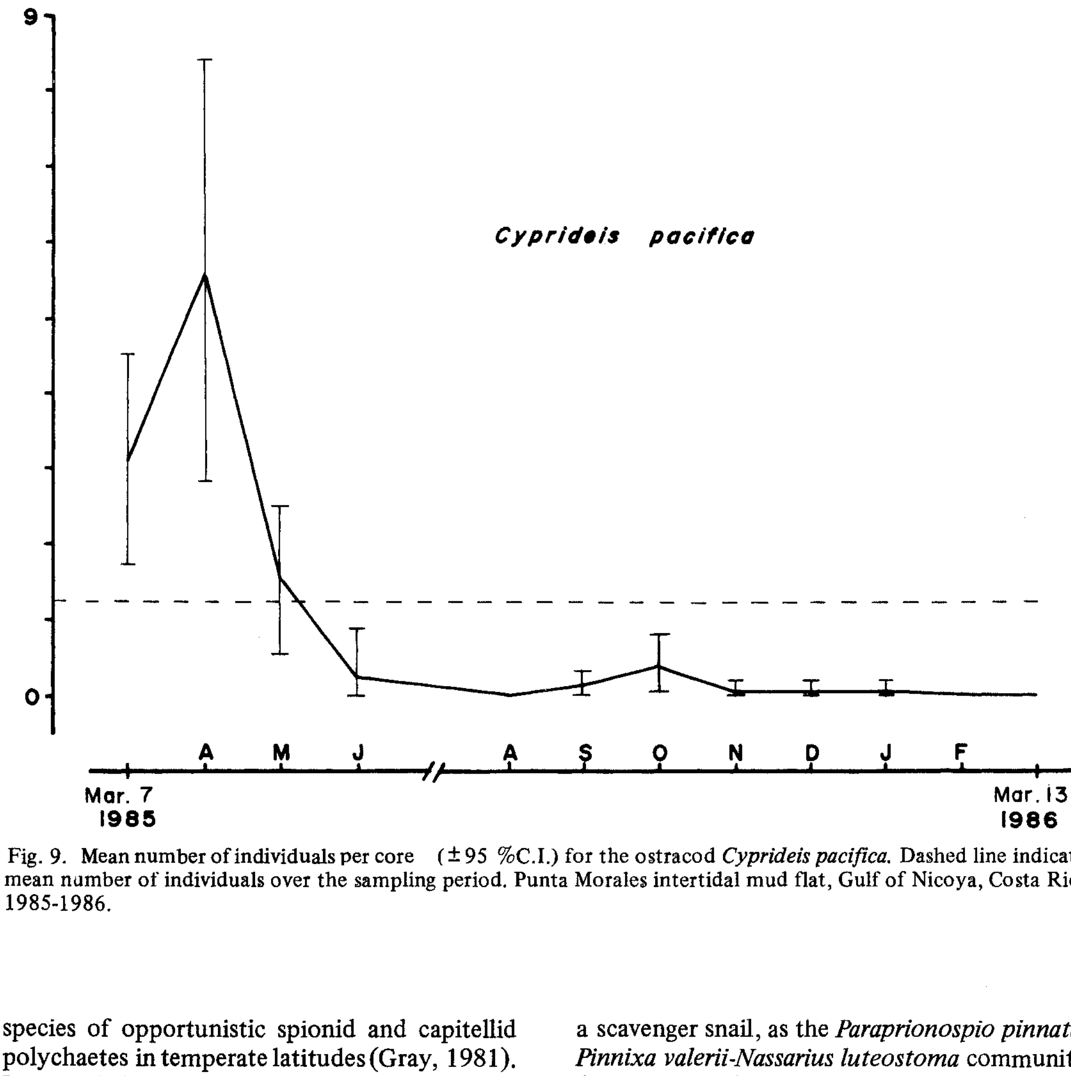

Fig. 9. Mean number of individuals per core (± 95 %C.I.) for the ostracod *Cyprideis pacifica.* Dashed line indicates mean number of individuals over the sampling period. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica, 1985-1986.

species of opportunistic spionid and capitellid polychaetes in temperate latitudes (Gray, 1981). It is probably premature, however, to categorically list, *P. citrona* as an opportunist since the numbers increase noted in this study did not relate to a marked environmental disturbance. The same argument may be valid in the case of the ostracod, *Cyprideis pacifica,* and the turbellarian flat-worm.

In conclusion, the importance of deposit feeding polychaetes, the magnitude of population fluctuations, the types of niches being exploited, and the existence of seasonal patterns, make this community similar to certain temperate zone counterparts. To emphasize these similarities, and for convenience in referring to this assemblage of species, I named the community after a surface deposit-feeding spionid polychaete, a burrowing pinnotherid crab, and a scavenger snail, as the *Paraprionospio pinnata-Pinnixa valerii-Nassarius luteostoma* community (Vargas, 1987), These species were collected during this second year survey. Thus, the name remains valid to refer to this particular assemblage of species and to provide a clue to the nature of the species present.

The high abundance of microcrustaceans (cumaceans and ostracods), and the relatively high number of species and macrofaunal densities separate this community from others living in muddy environments (see Broom, 1982). The scarcity of comparable published studies on tropical mud flats, however, makes premature to consider this community and its structural variations as typical for tropical mud flat environments. Moreover, this scarcity of information poses a problem when data from "unpolluted systems" is needed for comparison. Concen-

TABLE 6

A) Total rainfall (mm), B) Water temperature °C, C) Salinity °/oo, D) Number of tide levels below 0.1 m, E) Sand (%), F) Silt + Clay (%), G) Organic matter (%) Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica, 1985-1986.

	A*	B	C	D	E**	F**	G**
Feb.	0.0	38	31	32	67.9	28.7	2.9
Mar.	0.0	35	36	22	61.8	37.5	0.06
Apr.	16.0	36	35	18	50.1	47.4	2.10
May.	169.0	32	32	20	50.0	48.3	0.13
Jun.	145.5	35	32	14	64.4	33.1	2.37
Jul.	64.5	ND	ND	13	ND	ND	ND
Aug.	116.6	34	32	19	62.7	33.5	2.37
Sep.	240.0	32	35	20	67.6	28.6	2.25
Oct.	400.0	32	28	19	68.2	26.5	4.12
Nov.	151.0	38	30	16	70.2	25.6	2.63
Dec.	22.5	31	28	17	72.7	24.2	2.42
Jan.	0.0	34	30	18	68.0	25.3	2.73
Feb.	0.0	34	32	24	74.0	21.2	2.21
Mar.	0.0	35	33	29	64.6	31.8	2.70

* At the port of Puntarenas

** Mean of four replicates, percentages may not add to 100.

ND: No Data collected.

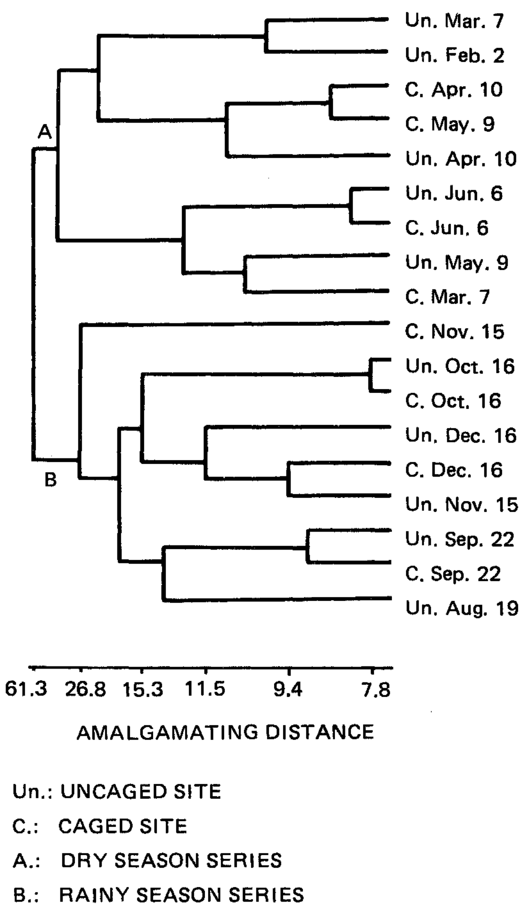

Fig. 10. Cluster analysis of dates included in the dry and rainy seasons series of caging experiments. Each date is represented by a set of 14 cores collected inside 2 cages ("C") and a set of 14 cores collected outside ("Un"). Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica. 1985.

trations of trace metals in the Gulf of Nicoya appear characteristic of non-industrialized estuaries (Dean *et al.* 1986), and raw sewage discharges from the city of Puntarenas (Figure 1) are, in theory, rapidly dispersed by tidal currents (Murillo 1983). The main source of pollution into the system, however, might be in the form of chemical compounds derived from agricultural practices and carried into the Gulf mainly by the Tempisque and Tárcoles rivers (Figure 1). This area of research deserves immediate attention. Provisionally, however, I consider the Punta Morales mud flat as representative of relatively unpolluted conditions.

Caged community. Though significant changes in the abundance of several species were detected inside and outside cages (Table 5), no significant change in total abundance was detected between caged and uncaged sites. In addition, sedimentary characteristics inside cages did not differ significantly from those of uncaged sites.

Caging experiments in different latitudes have produced, with a few exceptions, a significant increase in the number of individuals inside caged areas (Peterson, 1979). Reise (1977) placed cages of 0.5, 1, 2, 5, and 20 mm mesh sizes to exclude predators from an intertidal

TABLE 7

List of species (from those included in Table 2) showing significant (*) or highly significant (**) association between their abundances per date the environmental variables. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica. 1985-1986.

	Variables					
Species	1	2	3	4	5	6
P. pinnata	*	*(−)				
S. soederstroemi	*					
A. salvadoriana			*(−)			
M. californiensis					*	
G. armigera	*(−)	*				
L. tetraura	*(−)		*(−)	*		
S. tentaculata				*		
C. pacifica			*(−)			
Cumacea sp. 1	*(−)		**(−)			
T. rubescens		*	*(−)			
Hemichordata sp. 1			*(−)			
Turbellaria sp. 1			**(−)			*
			**(−)			
Pinnotheridae sp. 2			**(−)			
Calyptreidae sp. 1			**(−)			
P. citrona				*(−)		

Results based on Spearman's rho rank correlation. Sign of the correlation coefficient is indicated within brackets only for those tests showing a negative association.

Variables are: 1. Temperature (°C), 2. Number of tide levels below 0.1 m. 3. Rainfall (mm), 4. Salinity (ppt), 5. Organic matter content (%), 6. Percent Silt + clay.

mud flat in the North Sea (55°N). Reduced predation pressure on the benthos was only achieved with mesh sizes smaller than 5 mm due to the high number of crabs, shrimps, and gobiid fish able to pass thru the bigger meshes. In his 1 mm mesh cages macrofauna reached an abundance of 23 times the control density. Vargas (1979) used cages of 12 mm mesh gauze to exclude predators on a shallow (1m) coastal lagoon in Delaware (39°N), and abundances inside caged areas were 4.5 times greater than those at the control site. Naqvi (1968) placed cages of 12 mm mesh on an intertidal site in Florida (27°N), and densities inside cages were 2.5 times greater than at the controls. Lee (1978) utilized cages of 9.5 mm mesh to exclude predators from a subtidal (1.5 m) site on the Pacific coast of Panamá (8°N). He concluded that even though the cages were not completely effective in excluding predators, including portunid crabs, total density was greater inside cages than in controls.

Further from feeding rate experiments on *Callinectes arcuatus,* he suggested that the density of this crab was enough to cause significant changes in benthic mortality rates. Perhaps the common occurrence of *C. arcuatus* in Punta Morales, with some juveniles actually getting inside the cages, results in mortalities in this location.

The results mentioned above are difficult to compare due to the different sampling techniques used. For instance, sieves of mesh sizes ranging from 125 to 2000 microns were used to separate the organisms from the sediments.

The main results obtained in this study, however, are very similar to those obtained by Mahoney and Livingston (1982) in a Florida estuary, and by Berge and Alvarez (1983) on a subtidal (23 m) mud flat in Norway (59°N). Both studies used a 500 micron mesh to separate the organisms from the sediments, cages were made of comparable wire mesh sizes (6 and 4 mm, respectively), and kept on the sediment for periods ranging from 2 to 5 months. Both studies concluded that predation by epibenthic macropredators was not a key factor regulating macrofaunal densities at the study sites. Mahoney and Livingston (1982) argued that the short duration of the experiment (2 months) may be inadequate for the caged fauna to respond to predator exclusion. They also point out that variations in larval supply to the site may have prevented some species to recruit inside their cages. Berge and Alvarez (1983) found that cage-induced sediment disturbance was small; thus opportunistic species, which might have increased with disturbed sediments, did not colonize the caged habitat.

In spite of these interpretation problems, the results obtained by caging the Punta Morales intertidal community indicate that the role of macropredators (birds, benthic fish, portunid crabs and other crustaceans) in community structure may be relatively unimportant. Moreover, contrary to expectations the smallest changes between caged and uncaged areas were observed during the dry season (Table 4). This is the period of the year when migratory shorebirds are more common at the mud flat (Smith and Stiles, 1979), and when females of the crab, *Callinectes arcuatus* appear to migrate to the lower Gulf of Nicoya for spawning (Dittel *et al.* 1985).

Reise (1985) points out that it is often impossible to separate the effects of predation from those of disturbance. The importance of biological disturbance in benthic community structure has been emphasized by Thistle (1981). The role of disturbance might be more important than predation on a community where most of its species are potential sediment reworkers. The Punta Morales community has many species of microcrustaceans, small crabs, shrimps and other crustaceans, polychaetes, echinoderms, benthic fish, and a species of hemichordate, able to produce considerable sediment disturbance (Vargas, 1987). The relative role of their activities, however, remains to be investigated.

The conclussion reached above for the Punta Morales community must be regarded as preliminary. The following hypotheses are guidelines for further research at the site: 1. The 5 mm mesh is not effective in excluding certain predators. The use of smaller mesh gauzes might produce other results. 2. The response of the community to the placement of a cage takes more than three months. Cages kept in place for longer periods may induce a different response. 3. Predation by epibenthic predators is important but restricted to large and mobile prey not sampled efficiently by any corer. Prey population studies are suggested. 4. Recruitment of juveniles of, *Callinectes arcuatus* inside cages is important. 5. The role of predatory infauna is more important than that of macropredators. 6. The response of the community to caging may be evident at the meiofaunal size range (62 to 500 microns). Sampling the meiofauna inside and outside cages is recommended.

Environmental factors. The percentages or organic matter content, silt + clay, and shell fragments in the sediments are important variables in this study based on the results of multiple discriminant analysis (MDA). The main goal of MDA is to find the dimensions along which preexisting groups (dates in this particular case) are maximally different. Shin (1982) applied cluster analysis to his benthic survey data and four main groups were identified. He concluded that the delineation of such animal assemblages was related to the relative high organic carbon and silt + clay contents of the sediments. His conclusion was based on the relatively high scores obtained for these variables in MDA.

Following his approach the delineation of the groups (12 dates) in this study is related to the contents of organic matter, silt + clay, and shell fragments in the Punta Morales sediment. Organic matter content, and silt + clay have been considered as indicators of potential food sources for benthic invertebrates (Gray, 1981), while the amount of shell fragments may be enhancing microhabitat heterogeneity as suggested by Vargas (1987). At the individual species level significant associations were detected between the abundance of 15 species and the environmental variables (Table 7). Of particular relevance to the above discussion on seasonality is the fact that 10 of these species had their abundances apparently influenced by rainfall. Buchanan (1971), however, emphasized that such correlations "are far from an answer but rather and statement of an ecological problem, which only an intimate knowledge of the biology of the individual species will resolve". Unfortunately, this information is generally lacking for most tropical soft-bottom species. Thus, the importance of these variables on community structure needs to be evaluated further.

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M. L. Christoffersen (alpheid shrimps), H. K. Dean (polychaetes), Ana I. Dittel (decapod crustaceans), G. Fernández (molluscs), G. Hartmann (ostracods), G. Hendler (echinoderms), N.S. Jones and L. Watling (cumaceans), and Ana Pereira (birds), helped with the identification of the species. Les Watling and Odalisca Breedy are presently describing the cumacean species (Bodotriinae sp. 1) based on type material collected by the author.

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RESUMEN

Se hizo un estudio (febrero de 1985 a marzo de 1986) para investigar los cambios en la estructura de la comunidad presente en un área de 484 m^2, en una planicie fangosa (más del 30% de limo + arcilla), en el Golfo de Nicoya, Costa Rica (10°N, 85°W), y comparar los resultados con los obtenidos en el mismo sitio el año anterior. Las muestras de macrofauna fueron recolectadas, mensualmente, con un cilindro (área: 17.7 cm^2) hasta una profundidad de 15 cm en el sedimento, y preservadas en solución neutra de formalina en agua de mar teñida con Rosado de Bengala. Se consideró como macrofauna a los organismos retenidos en un tamiz de 500 micrómetros de abertura del poro. Se recolectó un total de 79 especies, con una densidad aproximada de 14,792 individuos por m^2. Esta densidad es relativamente alta y semejante a la encontrada el año anterior. La diversidad (H') osciló entre 1.61 y 3.12 y la uniformidad (J) varió entre 0.46 y 0.85. Los gusanos poliquetos dominaron la comunidad en términos del número de individuos y de especies, seguidos por los microcrustáceos (el ostrácodo *Cyprideis pacifica* y un cumáceo aún no descrito), los moluscos, y los grupos misceláneos. La dominancia numérica de los poliquetos se debió a los espiónidos *Polydora citrona* y *Paraprionospio pinnata* y al capitélido *Mediomastus californiensis*, que juntos representaron el 41% de la fauna. Estos resultados contrastan con los obtenidos el año anterior cuando *C. pacifica* y el cumáceo representaron el 43.4% de la fauna, y los poliquetos *M. californiensis*, *P. pinnata* y *Lumbrineris tetraura* el 19.2% del total. Sin embargo, la mayoría de las especies restantes fueron recolectadas durante ambos estudios y en densidades similares. Por lo tanto, se considera a los cambios en la abundancia de las especies dominantes como oscilaciones naturales de la comunidad. El análisis de conglomerados dividió los datos sobre abundancia en dos grupos que coincidieron con los períodos de las estaciones seca y lluviosa características de la región del Golfo de Nicoya. Se encontró cuatro patrones (a, b, c, d) de abundancia entre las 25 especies más importantes, a saber: especies con picos de abundancia en la estación seca (a) o lluviosa (b), y especies que aumentaron (c) o disminuyeron (d) en abundancia durante el año. El análisis discriminante múltiple de las variables ambientales seleccionó al contenido de materia orgánica en los sedimentos, limo + arcilla, y arena muy fina como las más importantes. Las abundancias de algunas especies mostraron una asociación significativa con una o varias de las variables ambientales. La evaluación de la importancia relativa de esas variables en la estructura de la comunidad requiere de un enfoque experimental. Experimentos con jaulas (malla de 5 mm de abertura del poro) para excluir depredadores dieron como resultado cambios no significativos en la abundancia total y número de especies dentro de las jaulas después de tres meses. Sin embargo, el análisis de conglomerados reveló diferencias entre grupos de muestras tomadas adentro y afuera de las jaulas. *C. pacifica* y juveniles de un molusco bivalvo no identificado fueron más abundantes dentro de las jaulas, mientras que el cumáceo fue más abundante afuera. Estos resultados indican que la influencia de los macrodepredadores (aves, cangrejos, peces) en la estructura de la comunidad podría ser de poca importancia. Esta comunidad béntica es considerada como representante de condiciones relativamente no contaminadas debido a que la información publicada, sobre la concentración de metales en trazas y descargas de desechos urbanos no tratados, indican que éstas son, aparentemente, características de estuarios no industrializados. Sin embargo, la fuente más probable de contaminación (compuestos químicos usados en agricultura) en el Golfo de Nicoya, no ha sido cuantificada.

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