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The benthic community of an intertidal mud flat in the Gulf of Nicoya, Costa Rica. Description of the community*

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Abstract: Structural changes of the soft-bottom community of a tropical intertidal mud flat (more than 30% silt + clay) in the Gulf of Nicoya, Costa Rica, were evaluated from February, 1984 through February, 1985. Core samples (core area: 17.7 cm^2) were collected, at semi-monthly intervals, within a 484 m^2 area and to a depth of 15 cm into the sediment. Samples were 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 92 species of macro-invertebrates and the gobiid fish, *Gobionellus sagitulla* (Gunther) were collected. The community was numerically dominated by deposit feeders. The ostracod, *Cyprideis pacifica* Hartmann and an undescribed cumacean (Bodotriinae) were the most common organisms found, representing 43.4% of the total. The polychaetes, *Mediomastus californiensis* Hartman, *Paraprionospio pinnata* (Ehlers), and *Lumbrineris tetraura* (Schmarda) accounted for 19.2% of the total. An unidentified flatworm (Turbellaria) represented 8.3% of the total number of individuals. Mean density of macrofauna (± 1 SD) was 13,827 ± 10,185 individuals per m^2. Diversity (H') ranged from 1.75 to 3.36 per date (28 cores) and equitability (Evenness) ranged from 0.48 to 0.87.

Cluster, principal components, and multiple discriminant analyses revealed a seasonal pattern of the community (dry and rainy seasons). Most species appear to reproduce throughout the year. Peaks of reproductive activity, however, were detected for a group of species.

In addition to biological and physical disturbance, spatial and temporal variability of water currents and water characteristics, coupled with an inferred preponderance of planktotrophic larvae, are considered as the main factors promoting changes in community structure.

The importance of deposit feeding invertebrates, the types of feeding modes and habitat utilization, 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, the community is named after a surface deposit-feeding spionid polychaete, a burrowing pinnotherid crab, and a scavenger snail, as the *Paraprionospio pinnata - Pinnixa valerii - Nassarius luteostoma* community.

Beginning with the pioneer work of Petersen (1914) the quantitative description of benthic communities has occupied the attention of scientists for over seventy years; yet, the definition of what constitutes a community remains one of the critical operational problems in ecology. Communities have been considered either as discrete units or as abstractions from a continuum. Field evidence from softbottom intertidal environments suggests that for such habitats species are distributed spatially in more or less defined curves of abundance along an environmental gradient (Gray 1981). Thus, a community is considered as a segment from a continuous distribution of species. The definition of community by Mills (1969) as a "group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups", is appropiate in this context.

After a community has been identified, it can be described in terms of its structure. According to Gray (1974), community structure means "the quantitative variation of individuals and species in space and time". Data

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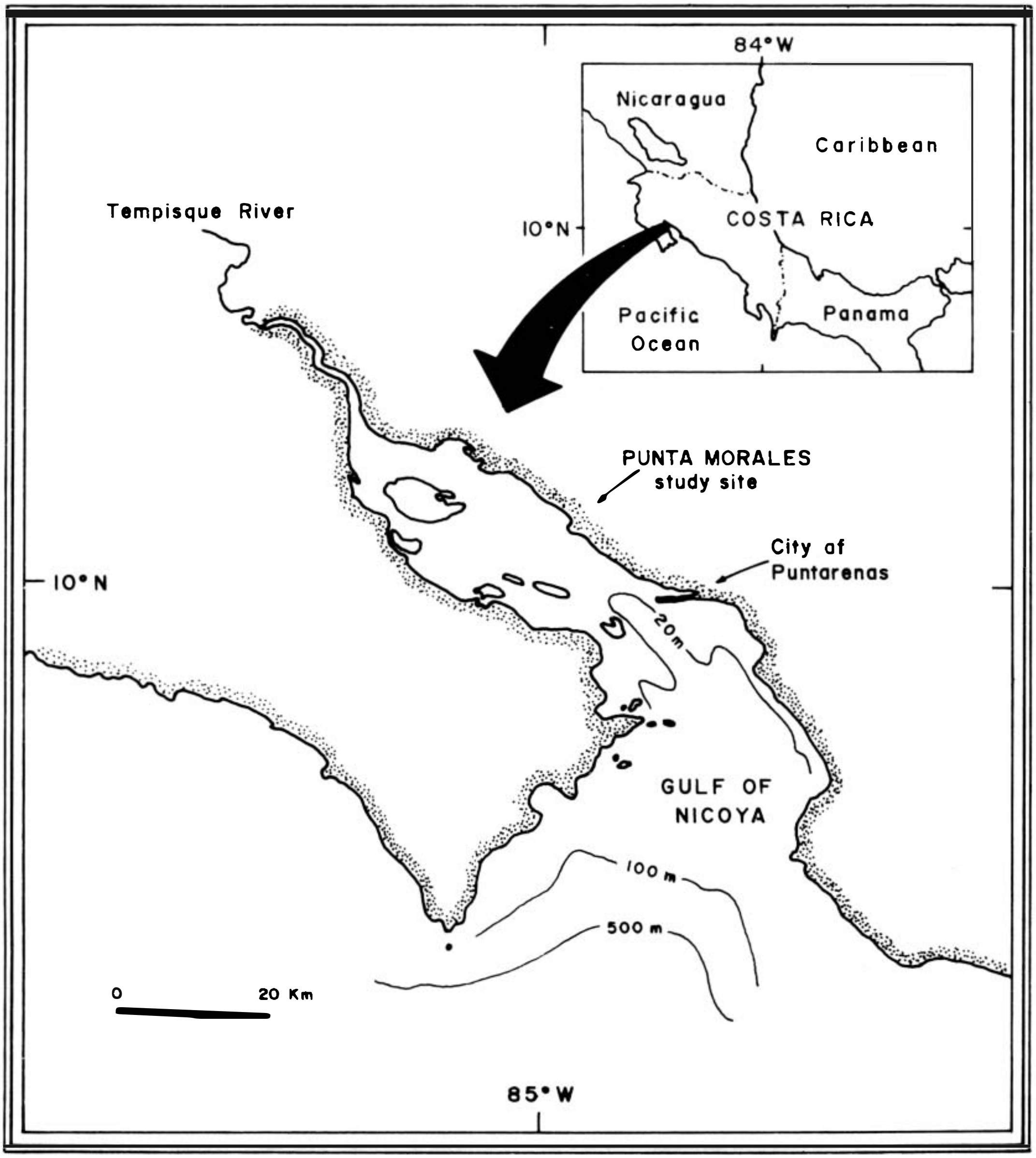

Fig. 1. Gulf of Nicoya, Pacific coast of Costa Rica. Location of the Punta Morales site on the Upper Gulf.

collected over the period of one year is the minimum to account for the most obvious seasonal effects. Surprisingly, intertidal soft-bottom studies covering a full year are scarce, even in temperate regions. Clearly, more research on tropical benthic systems will improve our conceptual framework to better understand marine communities and their structure.

From another point of view the worldwide increase in the development of coastal areas, and the resulting disturbance of the biota, often call for comparative studies based on data from undisturbed areas. Without this information changes due to pollution, and other disturbances, cannot be evaluated.

The tropical benthic area reported on herewith is a representative site in the Gulf of Nicoya, an estuarine embayment on the Pacific coast 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. Surveys of the physical (Voorhis *et. al.* 1983) and chemical (Epifanio *et al.* 1983; Dean *et al.* 1986) characteristics of the Gulf were initiated in 1979. Studies of the fish (Bartels *et al.* 1984) and crab (Dittel *et al.* 1985) populations, subtidal epibenthic (Maurer *et al.* 1984) and infaunal communities (Maurer and Vargas 1984; Vargas *et al.* 1985) were also conducted. In focussing on intertidal soft-bottom communities this study, coupled with the research referred to above, we begin to acquire an integrated picture of this productive estuarine embayment, providing valuable information for the management of its resources. The specific objective of this study is to describe the benthic community and its structural changes over a period of one year at a sampling locality of a relatively unpolluted intertidal mud flat in the Gulf of Nicoya.

METHODS

I. Environmental setting

The Gulf of Nicoya is an estuary located at 10^{o}N, 85^{o}W on the Pacific side of Costa Rica. The Gulf extends approximately 90 km from the mouth of the Tempisque River to the 200 m isobath (Figure 1). Tides are semidiurnal, with a mean tide range of 2.3 m. 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 (Voorhis et al., 1983). Rainfall over the estuary varies from less than 50 mm to over 600 mm per month during the rainy season (Epifanio et al., 1983). However, salinities in excess of 25 ppt and water temperatures above 25 ^{o}C are characteristic of most of the Gulf regardless of season.

Punta Morales, where the sampling reported herein was done, is a small peninsula located on the eastern shore of the mid upper Gulf. It is bordered by mangrove swamps, rocky shores, and a white sand beach. Inmediately offshore most of Punta Morales is bordered by a mud flat. On the Punta there is a research station and, at the very end, a loading pier for sugar (Figure 2).

This study was done on a mud flat lying off and sharply demarcated from the western end of a conspicuous white sand beach. The sampling site was 15 m from the offshore edge of that beach. Here the mud flat is exposed only at tide levels below + 0.1m (referred to the chart datum), and is characterized by almost no topographic relief, except for a low ridge and trough relief present occasionally.

II. Sample collection and processing

In this homogeneous mud flat an area 484 m^2 was selected for sampling with the assumption that it enclosed a single community. The area was divided into four sections of 25 squares each, with 2 m wide access paths separating the sections. Each square was 4 m^2. Wooden stakes were placed as markers at the corners and center of the area. A random number was assigned to each square and no one was sampled more than once during the study. Thus, the collecting scheme chosen consisted of sampling two randomly selected squares per date, each one located on different sections of the sampling area. A true random sampling would have involved some trampling and excesive disturbance of the study area.

The collection of samples, initiated February 22, 1984, was concluded on February 21, 1985, for a total of 25 sampling dates. Sampling intervals ranged from 12 to 18 days (mean = 15 days), with the exception of the period from June to July when sampling was conducted on June 18 and July 19. All samples were collected during the late morning hours at tide levels from -0.4 m to + 0.5 m.

Coring devices are routinely used for sampling the macrofauna of intertidal environments (Gonor and Kemp 1978). Thus, samples were collected with a cylindrical corer (core area: 17.7 cm^2) to a depth of 15 cm into the sediment. Fourteen cores were collected per square for a total area of 0.025 m^2. A total of 50 squares (700 cores) was sampled during the study.

Samples were put in heat sealable polyester bags where they were preserved in 10% buffered formalin in sea water stained with Rose Bengal (Maurer and Vargas 1984). Once the bags were sealed, sediment clumps were disintegrated by gently squeezing the bags. This method increased the recovery of whole organisms that otherwise might be fragmented by the usual sieving and preserving technique. Prior to analysis, samples were poured into a 500 micron mesh sieve and gently agitated on a container filled with fresh water. The residue on the sieve was transferred to a white enamel

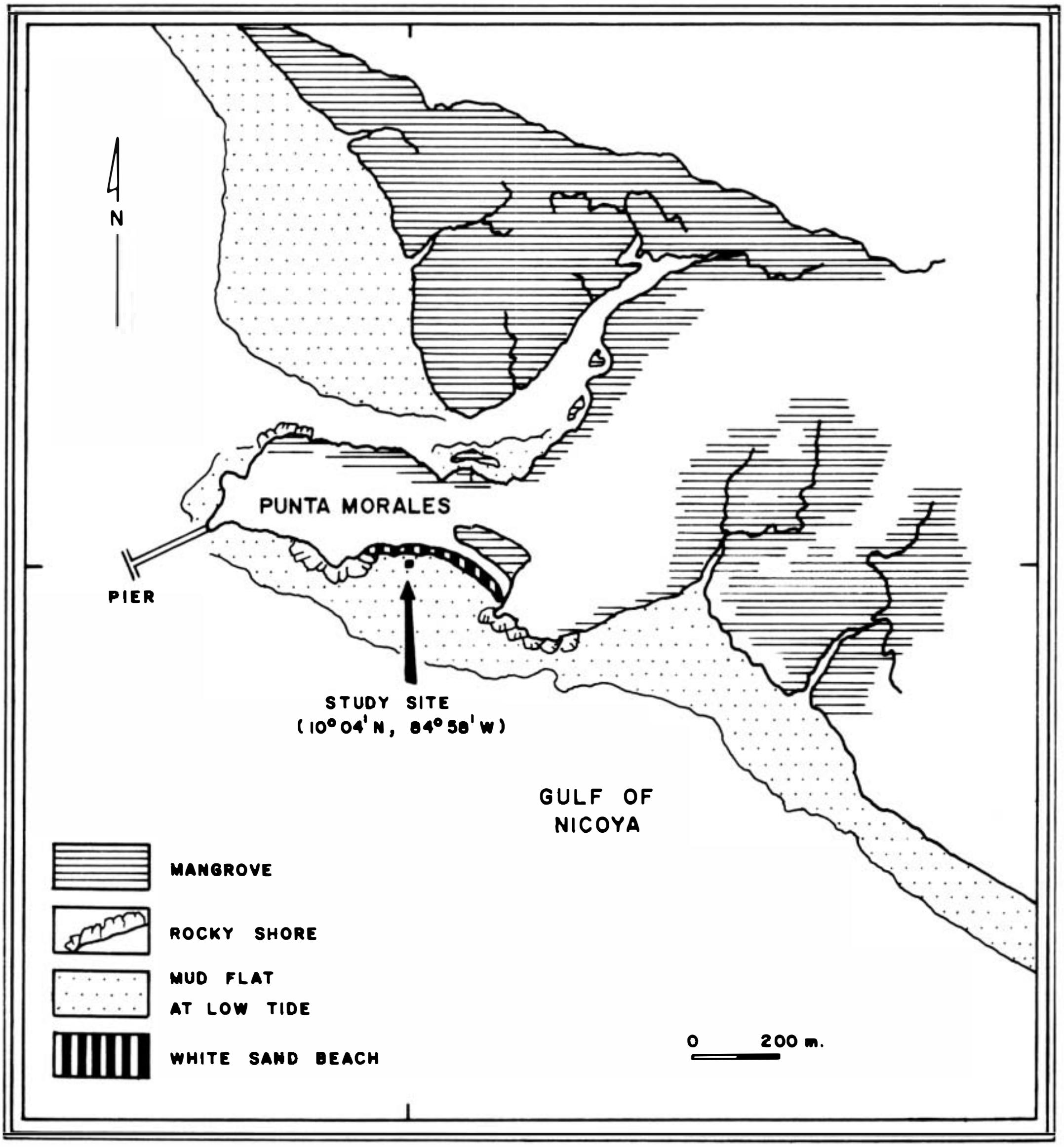

Fig. 2. Punta Morales Peninsula, Gulf of Nicoya, Costa Rica. Location of the study site on the intertidal mud flat.

sorting tray and scanned under a dissection microscope (10 X). All organisms were removed and stored in glass vials filled with 70% ethanol.

For identification of species a reference collection of the morphologically recognizable types was developed and a code number assigned to each one. Preliminary identification of most species was accomplished using references in Vargas *et al.* (1985). These identifications were verified, whenever possible, by the specialists listed in the acknowledgements section. In this paper the code number, applicable to the reference collection mantained by the author, are used for all species mentioned. Voucher specimens for all species collected have been deposited at the Museo de Zoología, Universidad de Costa Rica.

Core samples were also taken for sediment analysis and stored in heat sealable polyester bags. Samples were kept frozen until analyses which were performed following methods in Buchanan (1971). Organic matter content of the sediments was determined by weight loss of the sediment after combustion at 550 °C for

TABLE 1

Total number of individuals (n), species (s), and percentaje (%) of polychaetes, crustaceans, molluscs, and miscellaneous groups. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica.

	n	%	s	%
Polychaeta	5563	33.04	38	40.86
Crustacea	7843	46.58	25	26.88
Mollusca	825	4.90	18	19.35
Miscellaneous*	2606	15.47	12	12.90
Total	16837	99.99	93	99.99

* Bachiopoda (1), Cephalochordata (1), Echinoidea (1), Hemichordata (1), Nemertina (2), Ophiuroidea (2), Pisces (1), Sipuncula (2), Turbellaria (1).

four hours. All values were expressed as percentages of the original weight of oven dryed (60 °C) sediment.

Sediment and water temperatures at the time of collection of samples were measured with a mercury in glass thermometer. Salinity of the water was measured with an optical refractometer. Data on rainfall was obtained from the Instituto Metereológico Nacional.

III. Statistical analyses

Data were organized into a species x core samples x date matrix. As a first step in the analysis the species were ranked according to their relative contribution over the 25 sampling dates. In order to obtain an indication of the frequency with wich a species was present during the year, the Biological Index (Maurer and Vargas, 1984) was computed for all species. Species diversity and equitability (Evenness) were measured with the Shannon-Weiner function H' and E, respectively (Gray 1981).

Cluster an alysis has been applied to benthic survey data as an exploratory technique to find similarities among samples or variables. The analysis starts with a raw table of "n" samples and "s" species containing abundance data. From this a similatity matrix is derived, and finally a dendrogram is constructed showing the relationship between groups of samples or species (Gray 1981). Groups of similar samples (normal analysis), and similar species (inverse analysis) were produced by cluster analysis using the BMD computer package and the Chi-square statistic as a distance measure (Dixon 1974). All species found during the study were included in normal analysis. Before inverse analysis was attempted, however, the data matrix was reduced by removing all species ranked below the 30th place by the Biological Index. These species were selected from Table 2 with the exception of a gastropod (Vitrinellidae sp. 1) and the polychaete, *Polydora citrona* Hartman. These two species (ranked 24th and 28th, respectively, by the Biological Index) were represented by less than 40 individuals each and, therefore, not included in Table 2.

Clusters are made of species having their peak abundances at about the same time of the year. Thus, the significance of seasonal differences in the mean number of individuals of the 30 species was assessed by Student's "t" tests (Sokal and Rohlf 1969). The periods included in the analysis were February through May, 1984, and January and February, 1985 ("dry season") *versus* June through December, 1984 ("rainy season"). The period of peak abundance of each species, and the period when juveniles appeared on the samples were also recorded for these species. Juveniles were classified as such is their size was one third or less than the size of the biggest specimen kept on the reference collection.

The use of ordination techniques, like principal components analysis (PCA), on which similar samples are placed near each other on a cartesian coordinate space, has been discussed by Field *et al.* (1982) as a complementary approach to cluster analysis. Therefore, PCA is used in this study to produce a complementary two-dimensional display of the biological data

TABLE 2

*Species code (C), Species name, taxonomic group and probable feeding mode (G–FM), number of individuals in order of decreasing abundance (n), percentage of number of individuals (%), frequency of occurrence over the 25 sampling date (Oc), and rank by Biological Index (BI) for the 35 more common species at the Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica, 1984–1985**

C	Species name	G–FM	n	%	Oc	BI
34	*Cyprideis pacifica* Hartmann	**C–DF	3812	22.64	25	5
38	Cumacea, Bodotriinae, sp. 1	C–DF	3497	20.77	25	2
13	*Mediomastus californiensis* Hartman	P–DF	1868	11.09	25	1
62	Platyhelminthes, Turbellaria sp. 1	CA	1402	8.33	16	15
04	*Paraprionospio pinnata* (Ehlers)	P–DF	772	4.59	25	4
19	*Lumbrineris tetraura* (Schmarda)	P–DF	602	3.58	25	3
30	Oligochaete, sp. 1	DF	559	3.32	24	6
05	*Spiophanes soederstroemi* Hartman	P–DF	430	2.55	21	10
50	*Tellina rubescens* Hanley	M–DF	339	2.01	25	7
25	*Ceratocephale crosslandi* (Monro)	P–CA	326	1.94	25	11
26	*Prionospio delta* Hartman	P–DF	221	1.31	25	9
06	*Neanthes succinea* (Frey & Leuckart)	P–CA	190	1.13	21	14
15	*Glycinde armigera* Moore	P–CA	179	1.06	19	12
01	*Pectinaria californiensis* Hartman	P–DF	171	1.02	22	21
71	Bivalvia, juveniles, sp. 1	M–SF	137	0.81	17	13
58	Hemichordata, sp. 1	DF	136	0.81	18	8
22	*Linopherus* sp. 1	P–CA	131	0.78	23	19
33	*Pinnixa valerii* Rathbun	C–OM	120	0.71	23	16
11	*Acesta lopezi* (Reish)	P–DF	115	0.68	23	22
57	Brachiopoda, *Glottidia audebarti* Broderip	SF	102	0.61	13	20
14	*Tharyx parvus* Berkeley	P–DF	97	0.58	24	29
86	*Panopeus* sp. 1	C–OM	86	0.51	19	18
20	*Sigambra tentaculata* (Treadwell)	P–OM	74	0.44	23	26
03	*Nephtys monroi* Hartman	P–CA	73	0.43	15	32
12	*Notomastus hemipodus* Hartman	P–DF	73	0.43	22	37
55	*Tagelus bourgeoisae* Hertlein	M–SF	71	0.42	17	30
60	Echinodermata, Ophiuroidea sp. 1	DF	70	0.42	18	17
02	*Chone mollis* (Bush)	P–SF	62	0.37	16	27
35	Ostracoda, sp. 2	C–DF	60	0.36	18	34
69	*Magelona pacifica* Monro	P–DF	59	0.35	14	25
63	Nemertina, sp. 1	CA	59	0.35	21	23
49	*Dosinia dunkeri* (Philippi)	M–SF	52	0.31	10	39
61	Echinodermata, Ophiuroidea sp. 2	DF	52	0.31	21	33
45	*Natica unifasciata* Lamarck	M–CA	45	0.27	21	40
59	Echinodermata, *Encope* sp. 1	DF	43	0.26	14	42

* The species listed include 95.5% of the 16,837 individuals collected.
** C = Crustacea, P = Polychaeta, M = Mollusca, DF = Deposit Feeder, SF = Suspension Feeder, CA = Carnivore, OM = Omnivore.

matrix only, without attempting to interpret the axes as environmental factors. This approach allows some flexibility in meeting the assumptions of multivariate normality and linearity of the data (Green and Vascotto, 1978; Tabachnick and Fidell, 1983). PCA was computed with SPSS (Statistical Package for the Social Sciences, Nie et al., 1975).

Holland and Polgar (1976) used multiple discriminant analysis (MDA) to "demonstrate and evaluate quantitative temporal changes for a sandy intertidal community". With the same objective in mind, MDA was applied to the Punta Morales biological data. The main goal of MDA is to find linear combinations (Discriminant functions) of the variables that maximize differences among preexisting populations (dates in this particular case). MDA requires a significant difference among the population centroids. The test for the null hypothesis that that the centroids are equal is provided by a multiple analysis of Variance

(Pimentel 1979). The biological data were organized into a matrixof 25 dates x 93 species x 28 cores, and MDA was computed with SPSS.

MDA was also used in this study to relate the biological data to the following variables: organic matter content of the sediments, amount of shell debris on the sediments, coarse + very coarse sand content, medium sand, fine sand, very fine sand, silt + clay, and rainfall. The sedimentary variables were originally expressed as percentages; thus, an angular transformation was applied (Shin 1982). Salinity and water temperature were not included in MDA due to the small number of replicate measurements available per date. The analysis was based on samples collected at monthy intervals, and comprised the period from March 8, 1984, through February 7, 1985.

RESULTS

I. Species diversity and abundance

A total of 700 core samples was analyzed yielding 16,837 individuals belonging to 92 species of invertebrates and the gobiid fish, *Gobionellus sagitulla* (Gunther). Crustaceans dominated the community in terms of the number of individuals, followed by the polychaete worns, miscellaneous groups, and the molluscs. Polychaeta had the most species, followed by Crustacea, Mollusca, and others (Table 1).

A podocopid ostracod (*Cyprideis pacifica* Hartmann), an undescribed cumacean (Bodotriinae sp. 1), an unidentified flat-worm (Turbellaria), and the polychaetes, *Mediomastus californiensis* Hartman, *Paraprionospio pinnata* (Ehlers), and *Lumbrineris tetraura* (Schmarda), accounted for 71% of the total number of individuals. Moreover, thirty five species represented 95.5% of all organisms collected (Table 2). The remaining 58 species contributed with 752 individuals, and included several highly mobile taxa such as the cephalochordate *Branchiostoma californiense* Andrews (32 individuals, code 56), the alpheid shrimp, *Alpheus mazatlanicus* Wicksten (28 ind., code 39), juveniles of the portunid crab, *Callinectes arcuatus* Ordway (17 ind., code 31) and of the penaeid shrimp, *Trachypenaeus byrdi* Burkenroad (26 ind., code 43), hermit crabs, *Clibanarius panamensis* Stimpson (11 ind., code 67), and individuals of the burrowing stomatopod, *Gonodactylus* sp., (9 ind., code 36). Four species of gammaridean amphipods contributed with 126 individuals of which *Corophium* sp., contributed the most (40 ind., code 37). The gastropods, *Nassarius luteostoma* (Broderip and Sowerby), and *N. wilsoni* (C. B. Adams), codes 46 and 53, were represented by 32 and 6 snails respectively. Tubes of the onuphid polychaete, *Diopatra ornata* Moore (code 10), were common at the site but only 10 of these worms were collected. A list of all specie s collected during the study is included in Vargas (1986).

Rank positions by abundance or frequency of occurrence did not agree for most species (Table 2). When abundance and occurrence are combined in the Biological Index, a different sequence of dominants emerged. For example, *Mediomastus californiensis,* ranked 3rd by abundance, was assigned a first place by the Index. The flat-worm (Turbellaria), ranked 4th by abundance, was ranked 15th by the Index (Table 2). This indicates that the flat-worm occurred less frequently and in higher numbers than *M. californiensis.*

The total number of individuals per date (28 cores, 0.05 m^2) ranged from 184 (November 24) to 1996 (April 5), with a mean of 672 ± 495 (SD). When abundances are converted to approximate densities, a minimun of 3,787 m^{-2} and a maximun of 41,086 m^{-2}, with a mean of 13,827 ± 10,185 individuals per m^2 were found.

Abundance per sampling date was above 1,000 individuals during the period from February through April of 1984, declining to a low of 414 by May, then remaining below 500 until December, and increasing to a maximum of 1,062 by February of 1985 (Figure 3). The average number of species found per sampling date was 43, with 57 being the maximum found (December 26), and 28 the minimum (May 16). No clear trend in the number of species per date was evident (Figure 3).

The Shannon-Weiner diversity function H' ranged from 1.75 (April 17) to 3.36 (November 24). Diversity values above 2.5 were typical of the period from May through November, and those below it were more frequent during the dry season months. Equitability (Evenness) ranged from 0.48 (April 17) to 0.87 (Nov. 24), Figure 3.

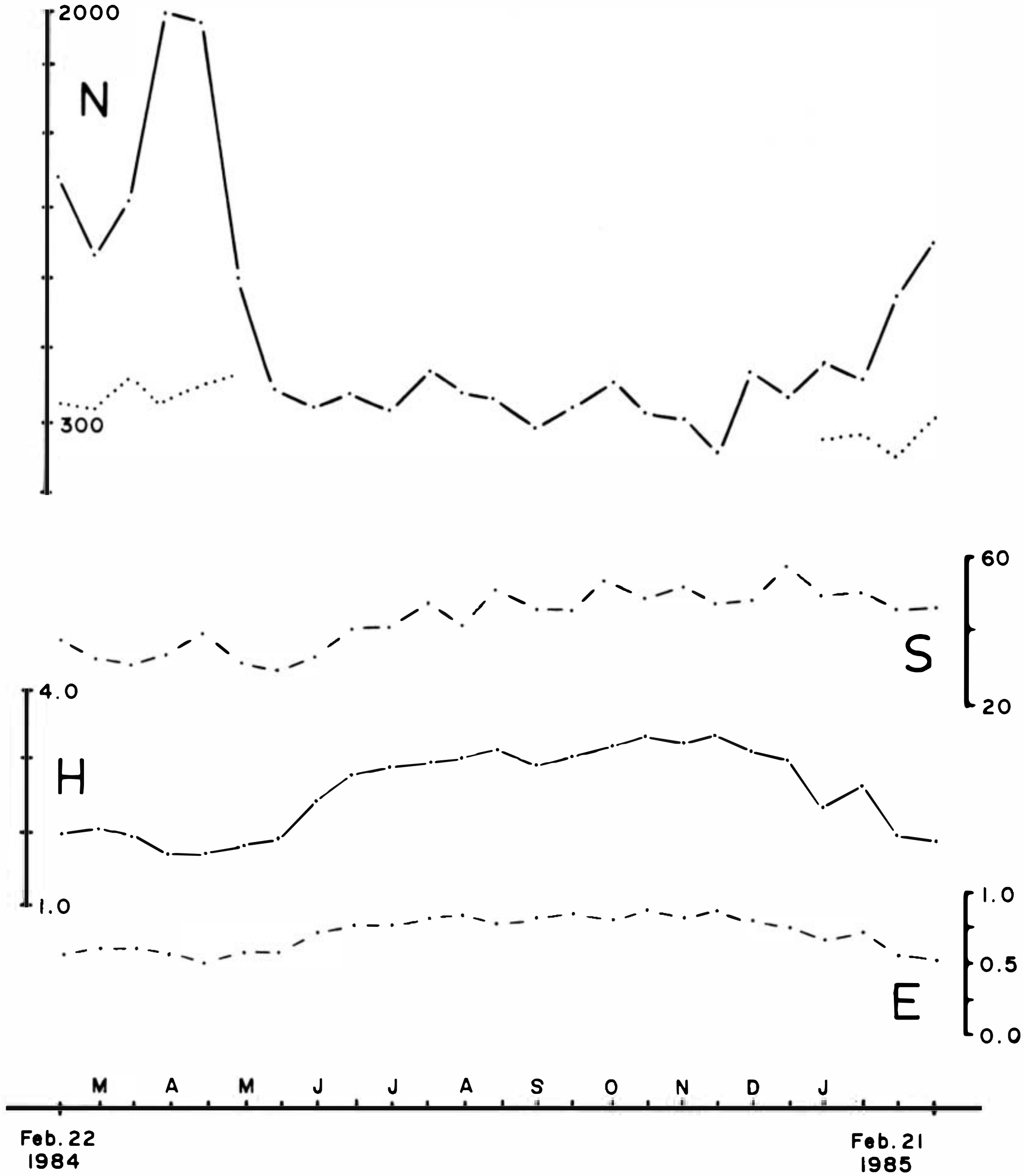

Fig. 3. Total number of individuals (N), Species (S), Shannon-Weiner diversity function (H'), and Equitability (E), per date (28 cores, 0.05 m^2). Dotted lines indicate the value of N when abundances of the cumacean sp. 1, flat-worm, and *Cyprideis pacifica* (Ostracoda) are removed from the periods indicated. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica.

II. Seasonal patterns

Two clusters are joined last as a result of the clustering procedure (Figure 4: A,B). Cluster A is made of samples taken June 1 through December 26, 1984. Cluster B includes samples corresponding to the period February 22 through May 16, 1984 (B-1), and those collected during January and February of 1985 (B-2). Species groups resulting from inverse cluster analysis are included in Table 3.

The 25 sampling dates were arranged into two main groups by principal components analysis (PCA), Figure 5. The upper group

TABLE 3

Groups of species as defined by cluster analysis. Period of peak abundance, period of high seasonal abundance, and period when juveniles were collected more frequently. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica. 1984–1985

Group	Species	Period of Peak abundance	Seasonal Peak*	Juveniles Collected
A–1	*Pectinaria californiensis*	Feb. – Apr.	** D	All year
	Tellina rubescens	Jan. – Apr.	*** D	All year
	Mediomastus californiensis	Jan. – May.	*** D	?
	Acesta lopezi	March.	* D	?
	Ceratocephale crosslandi	Mar. – Apr.	NS	Mar. – Jul.
A–2	*Lumbrineris tetraura*	Apr. – Jun.	NS	Feb. – Jul.
	Linopherus sp. 1	Apr. – Aug.	NS	Apr. – May
	Nemertina sp. 1	August	NS	?
	Prionospio delta	Apr. – May	NS	?
	Chone mollis	Jul. – Aug.	NS	Mar. – Oct.
A–3	*Spiophanes soederstroemi*	Mar. – Jul.	NS	Mar. – Oct.
B–1	*Neanthes succinea*	Aug. – Sep.	** R	Apr. – Nov.
	Magelona pacifica	August	* R	?
	Glottidia audebarti	Sep. – Oct.	** R	Aug. – Nov.
	Hemichordata sp. 1	Sep. – Oct.	** R	Jul. – Feb.
	Vitrinellidae sp. 1	August	* R	?
	Pinnixa valerii	Sep. – Oct.	** R	Sep. – Dec.
B–2	Bivalvia, juveniles sp. 1	December	NS	Dec.
B–3	Ophiuroidea sp. 1	All year	NS	All year
	Polydora citrona	Dec. – Feb.	NS	?
	Sigambra tentaculata	All year	NS	?
	Tagelus bourgeoisae	Aug. – Feb.	NS	Jul. – Feb.
	Glycinde armigera	Oct. – Feb.	NS	Jul. – Feb.
B–4	*Tharyx parvus*	All year	* R	All year
	Oligochaeta sp. 1	All year	* R	?
	Panope us sp. 1	All year	** R	Feb. – Nov.
	Paraprionospio pinnata	Jun. – Dec.	*** R	All year
C	Cumacea, Bodotriinae sp. 1	Jan. – Apr.	*** D	Feb. – May.
	Turbellaria sp. 1	Feb. – Apr.	** D	?
	Cyprideis pacifica	Feb. – May.	** D	?

* Student's "t" significance level: *P < 0.05, ** P < 0.01, *** P < 0.001 D = dry season, R = rainy season, NS = non significant. A question mark indicates that juveniles were difficult to identify as such by size difference only.

includes samples taken from February through May of 1984, and those of January and February of 1985. The lower group covers the period June through December. With the exception of date 12 (August 14), placed in a different group by cluster analysis, both techniques agree to a great extent, thus giving strong indication that the patterns are real.

Results of multiple discriminant analysis (on log x + 1 transformed data) are included in Figure 6. These results agree with those obtained by cluster and PCA in the sense that the biological data set is divided into two main phases that correspond in time with the dry and rainy seasons characteristic of the Gulf of Nicoya region. That is, dates 1 through 7, and 22 through 25, corresponding to the dry season months were discriminated from the compact "rainy season cloud" formed by dates 8 through 21 (July through December).

The period of peak abundance, and the statistical significance ("t" tests) of a seasonal peak in the mean number of individuals of the groups of species resulting from inverse cluster

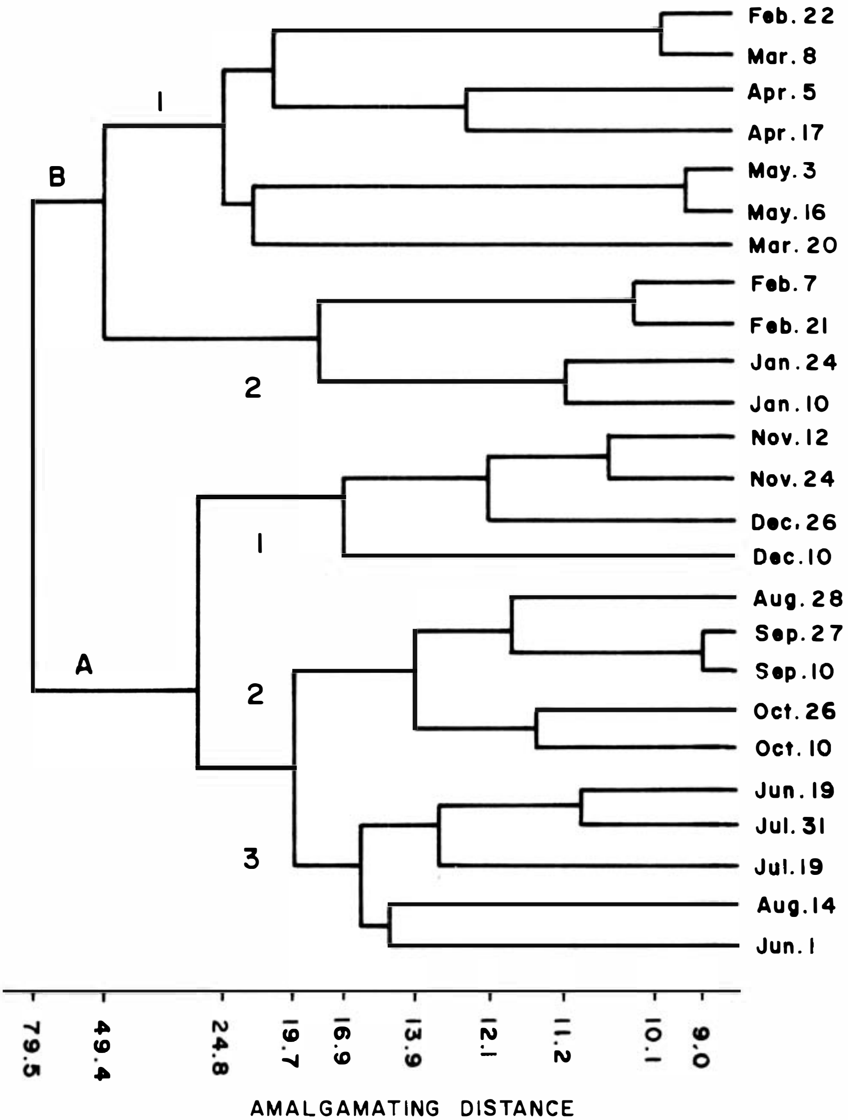

Fig. 4. Cluster analysis of dates (28 cores per date 0.05 m²). Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica. February 22, 1984 thru February 21, 1985. Cluster B–2 includes all samples taken during 1985.

analysis, are included in Table 3. The period when juveniles were collected more frequently is also included in Table 3. Several species appear to reproduce throughout the year as evidenced by the continuous appearance of juveniles during the sampling period. The polychaetes, *Pectinaria californiensis* Hartman, *Tharyx parvus* Berkeley, and *Paraprionospio pinnata* (Ehlers), the bivalve, *Tellina rubescens* Hanley, an unidentified species of brittle star (Ophiuroidea), and perhaps the oligochaete sp. 1, are examples of this reproductive pattern. Juveniles of the predatory snail, *Natica unifasciata* Lamarck (ranked 40th by the index and, therefore, not included in cluster analysis) were collected throughout the year also.

Other species appear to have their reproductive peak activity restricted to one of the seasons. *Ceratocephale crosslandi* (Monro), *Lumbrineris tetraura* (Schmarda), and the cumacean (Bodotriinae, sp. 1) are species reproducing during the dry season, while the brachiopod, *Glottidia audebarti* Broderip and the crab, *Pinnixa valerii* Rathbun, may be reproducing during the rainy season only.

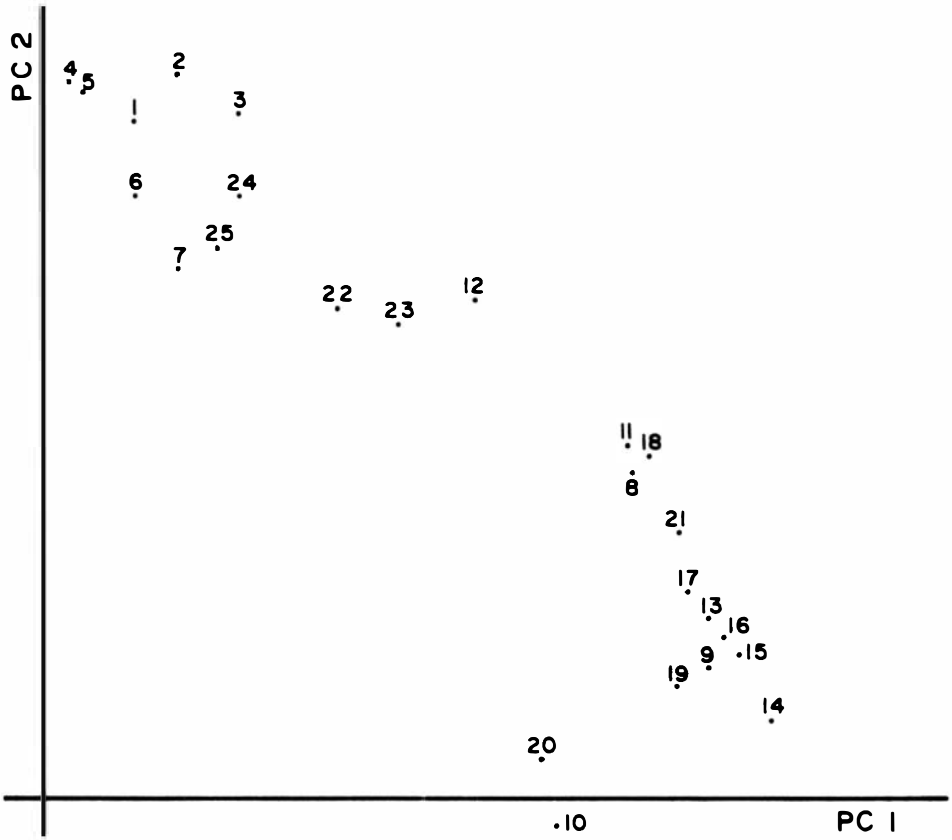

Fig. 5. First and second Principal Components (PC) calculated from the number of individuals per core in all 28 cores collected per date. Dates are numbered 1 thru 25. Date 1 is February 22, 1984; date 25 is February 21, 1985. Date 11 is July 31, and date 12 is August 14. All dates are included in Figure 4. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica.

III. Environmental data

A total of 48 sediment samples (4 per date) were analyzed and the results are included in Table 4. On the average the sediments at the site were made of 65% sand, 32% silt + clay, and about 2% organic matter content. Among the sand fractions, the very fine sand (62 to 125 microns) and the fine sand (125 to 250 microns) represented more that 40% of the total sand weight. Most of the shell fragments were made of empty shells of the bivalve *Corbula tumaca* (Olsson), but only five specimens of this bivalve were found alive during the study.

Sediments at the site were also characterized by a thin brown layer (less than 1 cm deep) of oxidized material. A few Eh measurements (Gray 1981) indicated reduction potentials of -200 mV at 1 cm below the sediment surface. No seasonal migration of the depth of the oxidiz ed layer was observed during the survey.

Salinity at the time of collection of samples ranged from 27 ppt (September) to 34 ppt (April), and water temperatures at low tide ranged from 27 ^{o}C (November) to a maximum of 40 ^{o}C (April), Table 4.

Rainfall at the port of Puntarenas (Figure 1) reached a maximum of 345 mm during the month of May. Occasional rains were reported duiing the dry season of 1984. Precipitation decreased significantly after October of 1984, and no rain was reported after November (Table 4).

The Punta Morales mud flat becomes exposed at tide levels near + 0.1 m. The number of times per month at which the flat was exposed is included in Table 4. Exposure was greater during the dry season (more than 20 times per month) than during the rainy season

TABLE 4

A: total rainfall (mm), B: water temperature (^{o} C), C: salinity (ppt), D: number of tide levels below + 0.1 m, E: sand (%), F: silt and clay (%), G: organic matter content of sediments (%). Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica, 1984-1985.

	A*	B	C	D	E**	F**	G**
February	23	34	32	20	58.0	39.4	1.3
March	7	36	32	22	59.0	40.4	1.3
April	63	40	34	24	62.3	34.4	2.1
May	345	36	32	21	62.3	34.2	2.4
June	160	34	30	13	53.8	44.0	1.9
July	200	30	29	15	71.0	26.0	2.0
August	182	31	30	19	73.9	23.1	2.5
September	254	31	27	20	71.0	26.8	1.9
October	83	33	30	18	65.4	32.1	2.1
November	43	27	30	16	71.7	25.1	2.5
December	0	36	32	15	70.3	26.1	2.3
January	0	36	32	15	70.3	26.1	2.3
February	0	38	31	22	67.9	28.7	2.9

* At the port city of Puntarenas.

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

(less than 17 times per month). The rising tide covers the mud flat slowly (in about 30 minutes) with no apparent disturbance of the sediments.

Waves with amplitudes greater than 0.5 m were seldom observed. The flat was then characterized by almost no wave induced relief. A low ridge and trough relief, however, was observed occasionally during the dry season months.

Results of multiple discriminant analysis of the sedimentary variables and rainfall indicate that the first three discriminant functions accounted for 81% of the variance. However, only the first function was significant and accounted for 45% of the variance. The amount of shell debris had the highest coefficient (1.00) along this function, followed by the amount of silt + clay (0.67) and organic matter (0.45). Rainfall was the least important (0.01).

DISCUSSION

I. The nature of the community

The Punta Morales mud flat community was numerically dominated by cumaceans, ostracods, and polychaetes (Table 2). The most interesting fact, however, is the seasonal shift from a preponderance of crustaceans over polychaetes during the dry season months to the reverse relationship during the rainy season (Table 5).

Crustaceans (mainly amphipods and isopods) have been reported as the dominant groups in certain temperate mud flats (e.g. Howard and Dorjes 1972) and in tropical sandy beaches (e.g. Dexter 1972). Iam not aware, however, of any tropical mud flat characterized by a seasonal alternation of dominance by cumaceans and ostracods, and polychaete worms. Thus, this

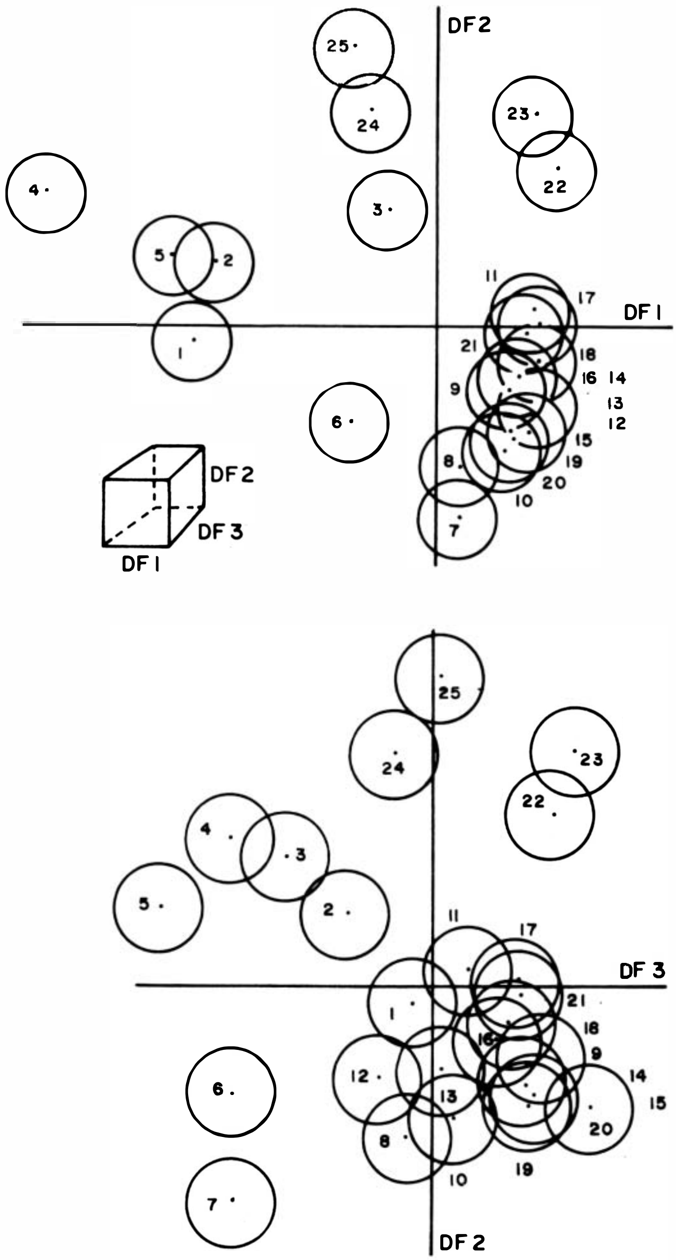

Fig. 6. Multiple Discriminant Analysis of biological samples. Data were log (x + 1) transformed. Points indicate groups centroids enclosed by 95% confidence circles (Pimentel 1979). Discriminant Functions DF 1, DF 2, and DF 3 account for 54% of the variance. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica, 1984 - 1985.

tropical community may be unique in the sense that its structural changes over a period of one year were mainly due to fluctuations of two species of microcrustaceans (an undescribed cumacean and the ostracod, *Cyprideis pacifica*), the polychates, *Mediomastus californiensis, Paraprionospio pinnata,* and *Lumbrineris tetraura,* and a turbellarian flat-worm.

Most of the numerically dominant species in Punta Morales probably are deposit feeders (Table 2). Thus, the area adheres to the well known dominance of deposit feeders over suspension feeders in sediments containing a relatively high proportion of silt and clay (Gray 1974). Food webs at the site seem to be based on a detritus pool receiving imput from autochthonous and allochthonous sources, benthic microalgae and mangrove leaf decomposition, respectively being likely sources (see Gocke *et al.* 1981). This topic deserves further research.

Tropical communities are expected to have more species than their temperate counterparts; thus, the number of species found in this study (93) is not surprising when compared, for instance, with the 30 species collected by Whitlatch (1977) on a temperate (41 °N) mud flat. However, species diversity and abundance at a given site are heavily influenced by sampling methods and by local conditions such as habitat heterogeneity, disturbance, and recruitment success. These factors make comparisons difficult.

At Punta Morales densities per m^2 ranged from 3,787 to 41,086 (mean: 13,827). Maurer and Vargas (1984) found a maximum density of 8,744 per m^2 in subtidal soft-sediment environments in the Gulf of Nicoya. Lee (1978) reports a minimum density of 5,007 and a maximum of 13,991 individuals per m^2 for a soft-sediment site in the Pacific coast of Panama. Thus, densities at Punta Morales are relatively high but near the range reported for unpolluted soft-sediments in the region.

In the work of Petersen (1914) and Thorson (1957) a community was named after the two or three conspicuous genera, either in terms of numbers or biomass. The intent was to facilitate the recognition of the same or closely related taxa in parallel benthic communities elsewhere.

One of the problems in naming a community based on numerical dominance, however, is that it implies similar intensity and nature of biological interactions, as well as similar larval settlement and survival rate, at the places expected to be inhabited by the same community. Moreover, the Petersen-Thorson concept of parallel communities identified by taxa is difficult to reconcile with the dynamic nature of benthic marine communities, where the same system may recur in variable combinations of individuals and species (see Johnson 1972). In spite of such variability Wade (1972) argues that naming a community is justified it the name is used for convenience. I feel this is valid; thus, the Punta Morales intertidal mud flat community may be named the *Paraprionospio pinnata-Pinnixa valerii-Nassarius luteostoma* community, after a deposit-feeding spionid polychaete, a tube dweller pinnotherid crab, and a surface scavenger snail. These species were chosen mainly because they were collected throughout the year and are easy to identify. *P. pinnata* has a wide geographical distribution (Dauer 1985), *P. valerii* was described from the Gulf of Nicoya (Rathbun 1931), and *N. luteostoma* is easily observed at the site at low tide.

Finally, my main goal in naming the community is to call the attention to fauna that might be playing a similar ecological role elsewhere. A comparison of Table 2 with similar examples from the literature (see Wiltlatch 1977; Reise 1985) supports the observation that intertidal mud flats are inhabited worldwide by roughly the same life forms. Tube dwellers and tube builders like deposit feeding crustaceans and polychaetes, scavenger and predaceous snails like nassarids and naticids, fast digging clams like tellinids and solenids, and microcrustaceans, are commonly found on mud flats throughout the world indicating that similar ecological roles are being played by morphologically similar species at different latitudes. Though this search for analogous ecological roles is more related to functional aspects of the community than to structural ones, feeding and other activities of these organisms cause disturbances (burrows, tubes, fecal mounds, fecal pellet accumulation, sediment reworking and stabilization, traces, etc) that are important in structuring a community (Gray 1981; Thistle 1981; Grant 1983; Nichols and Thompson 1985). In this sense the Punta Morales community and other mud flats elsewhere may be partially structured by comparable processes (the rate of specific processes, however, might be different). This topic is discussed in more detail by Vargas (1986).

II. Seasonality

When abundances of all species collected in Punta Morales are analyzed simultaneously by the multivariate techniques, the biological data set is divided in two main phases (Figures 4,5, and 6). Phase I extends from February through May ("dry season phase"), and phase II extends

TABLE 5

Percentage of the total number of individuals represented by each species for the periods indicated. Punta Morales intertidal mud flat, Gulf of Nicoya, Costa Rica, 1984–1985

Dates 1 – 7, 22 – 25*	%	Dates 8 – 12	%
Cyprideis pacifica	20.87	*M. californiensis*	4.25
Cumacea, Bodotriinae sp. 1	18.60	*P. pinnata*	3.88
Turbellaria sp. 1	8.23	Oligochaeta sp. 1	2.32
Mediomastus californiensis	6.85	Cumacea, sp. 1	2.17
Lumbreneris tetraura	1.90	*C. pacifica*	1.76
Tellina rubescens	1.55	*L. tetraura*	1.68
Ceratocephale crosslandi	1.30	*S. soederstroemi*	1.53
Spiophanes soederstroemi	1.01	*Neanthes succinea*	0.88
Oligochaeta sp. 1	1.00	Bivalvia, juveniles	0.71
Pectinaria californiense	0.76	Hemichordata sp. 1	0.67
Paraprionospio pinnata	0.70	*Glycine armigera*	0.66
Prionospio delta	0.68	*P. delta*	0.63

* Dates 1–7 (February through May, 1984). Dates 22–25 (January through February, 1985) Dates 8–21 (June through December, 1984).

The species included represent 84.6% of the total number of individuals collected during the study.

from June through December ("rainy season phase"). The results included in Table 5 indicate that such phases are more related to fluctuations in the abundance of certain species, than to changes in the composition of the species collected.

Abundance fluctuations of the adult populations can be better understood when data on the reproductive patterns of the species are available. Data in Table 3 indicates that at Punta Morales most species may be reproducing throughout the year but with peaks of reproductive activity restricted to short periods.

In the Gulf of Nicoya females of the blue crab, *Callinectes arcuatus* migrate to the lower Gulf to spawn during the dry season (DeVries *et al.* 1984), and the intertidal barnacle, *Tetraclita stalactifera* releases larvae towards late November and early December (Villalobos 1980). The bivalve, *Anadara tuberculosa* reproduces throughout the year in Punta Morales but greatest spawning activity was observed from May through September (Cruz 1984). Lee (1978) working on a Panamanian soft-bottom community found evidence of seasonality in several species. Broom (1984), working on a Malaysian mud flat, found evidence of seasonality on the reproductive pattern of several species of invertebrates, including the bivalve, *A. granosa.*

In the Gulf of Nicoya water properties and currents vary seasonally, and during the rainy season horizontal and vertical gradients are well developed. These gradients are diminished during the dry season months due to wind and tidal mixing (Voorhis *et al.* 1983) Epifanio *et al,* (1983) concluded that the upper Gulf, where Punta Morales is located, is a region heavily influenced by changes in rainfall as concentrations of nutrients varied by an order of magnitude between seasons. Since water characteristics in the Gulf vary seasonally, the possibility of seasonal fluctuations in larval recruitment to the mud flat is high. This possibility is particularly true if it is inferred that most of the invertebrates in Punta Morales may have planktotrophic larvae, a larval type easily transported by currents.

III. Role of environmental factors

Though dry season-rainy season seasonality occurs, it is difficult to relate this to observed conditions of the mud flat environment. While seasonal fluctuations in certain environmental parameters are noteworthy, the community responses are not in phase with the variables described.

Results of the multiple discriminant analysis (MDA) of the sedimentary variables and rainfall reflect this problem as rainfall proved to be the least important of the variables included in the analysis. The relatively high scores obtained by the amount of shell debris in the sediment, and the percentage of silt + clay may be regarded only as suggestive possibilities for further research. Shell fragments within the sediment may be enhancing habitat heterogeneity by providing crevices for small infauna, and perhaps allowing oxygen to penetrate deeper into the sediment. The amount of silt + clay might indicate sources of potential food for benthic organisms, as well as microhabitat conditions to which species may be responding; however, relating such possibilities to seasonality is perplexing.

In view of the existence of a marine research station in Punta Morales, it is highly desirable to pursue continuous monitoring of certain environmental variables such as salinity, water temperature, and rainfall, and studies of the reproductive biology of selected species, with the goal to unfold the mechanisms and rates by which the benthos responds to environmental change.

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RESUMEN

Se evaluó, desde Febrero de 1984 a Febrero de 1985, los cambios estructurales de la comunidad béntica en una zona fangosa ($>$ 30% limo + arcilla) de la zona de entre-mareas en el Golfo de Nicoya, Costa Rica. Se recolectó muestras con un cilindro de 17.7 cm^2 de area y hasta una profundidad de 15 cm en el sedimento. Las muestras fueron preservadas en una solución de formalina (10%) en agua de mar teñida con Rosado de Bengala. Se consideró como macrofauna a los organismos retenidos en un tamiz de 500 micras de tamaño del poro.

Se recolectó un total de 92 especies de invertebrados y al pez góbido *Gobionellus sagitulla* (Günther). La comunidad fue dominada numéricamente por organismos que se alimentan directamente del sedimento. El ostrácodo *Cyprideis pacifica* Hartmann y un cumáceo (Bodotriinae) no descrito aún, fueron los organismos más comunes, representando un 43.4% del total. Los poliquetos *Mediomastus californiensis* Hartman, *Paraprionospio pinnata* (Ehlers) y *Lumbrineris tetraura* (Schmarda) representaron un 19.2% del total. Un gusano plano (Turbellaria) no identificado, representó el 8.3% del total de individuos. La densidad promedio (± 1 SD) de la macrofauna fue de 13,827 ±10,185 m^{-2}, y la diversidad (H') osciló entre 1.75 y 3.36 por fecha (28 muestras). La equitabilidad osciló entre 0.48 y 0.87.

Los análisis de conglomerados, componentes principales y discriminante revelaron estacionalidad (estaciones seca y lluviosa). La mayoría de las especie s aparentemente se reproducen durante todo el año. Sin embargo, en varias especies se encontró períodos durante los cuales existe una actividad reproductiva alta.

Perturbaciones físicas y biológicas, variabilidad espacio-temporal de las corrientes y propiedades de las masas de agua, unido a una posible preponderancia de larvas de tipo planctotrófico, son considerados como los factores principales promotores de cambios en la estructura de la comunidad.

La importancia relativa de los organismos detritófagos, los tipos de alimentación y utilización de hábitat, y la existencia de estacionalidad hacen a la comunidad de Punta Morales

semejante a alg unas comunidades de ambientes fangosos en latitudes altas. Para enfatizar esas semejanzas, y por conveniencia al referirse a este grupo de especies, se ha denominado a la comunidad como la *Paraprionospio pinnata - Pinnixa valerii - Nassarius luteostoma* de acuerdo a los nombres de un poliqueto espiónido, un cangrejo excavador y un caracol que se alimenta de carroña.

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