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Ecosystem dynamics and nichthemeral and seasonal programming of fish community structure in a tropical estuarine inlet, Mexico

Estuarine ecosystem
Fish
Seagrass

Ecosystème estuarien
Poissons
Herbiers

A. Yáñez-Arancibia, A. L. Lara-Domínguez, P. Sánchez-Gil, I. Vargas Maldonado, P. Chavance, F. Amezcua Linares, A. Aguirre León, S. Diaz Ruiz
Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Apartado postal 70-305, 04510 México, D.F.

ABSTRACT

A one-year study revealed that the Puerto Real Inlet (*Thalassia testudinum* environment) is utilized by a variety of immature and adult fish as an immigration pathway to the Términos Lagoon and/or as a nursery. In this unpolluted ecosystem, 7 670 fish representing 59 species and 27 families were captured in 168 trawl collections between August, 1980, and July, 1981. Ninety-five percent of the salinity, temperature and transparency measurements ranged from 28 to 39 ppt, 23.8 to 32.8 °C and 32 to 100 %, respectively.

Diurnal (24-h) and seasonal variations of several diversity indices — density, biomass, frequency and numerical abundance — were statistically related to changes in salinity, temperature, tide, and light periods. Nichthemeral variations in density and biomass are probably related to specific trophic behavior (night or day feeding) which influences catchability, as was corroborated by cluster analysis. There were seasonal variations in all parameters of the community. Great variations in the population structure were correlated with climatic periods and river discharge, but temperature was the best correlate, as shown by a multifactorial analysis. These ecological parameters of the fish community remained high, reflecting a daily and seasonal succession of dominant fish species. The similarity in nichthemeral and seasonal changes exhibited by certain assemblages of species indicates that some dominant groups are influenced more by light period than by tidal stage.

The largest number of fish species (45) was collected in October, the season of immigration of immature fishes. The smallest number of species (22) occurred in February, by which there many fish have left the inlet system.

Community inhabitants and consumers of different trophic categories were seasonally quantified. Cyclical visitors (49 %) and second-order consumers (49 %) were dominant throughout the entire year. 20 species were quantitatively important in terms of frequency, biomass and numerical abundance ; the families represented were Sparidae, Pomadasyidae, Balistidae, Diodontidae, Tetraodontidae, Lutjanidae, Sciaenidae, Scaridae, Gerridae, Ariidae and Urolophidae.

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RÉSUMÉ

Écologie, évolution nycthémérale et saisonnière des peuplements de poissons à l'entrée d'une lagune tropicale, Mexique.

Une étude, portant sur une année, a montré que la Passe de Puerto Real (faciès à *Thalassia testudinum*) est empruntée par un grand nombre de poissons juvéniles et adultes comme voie de migration vers la lagune de Terminos et/ou sert de nursery. Dans cet écosystème non pollué, 7 670 poissons représentant 59 espèces et 27 familles ont été capturés au cours de 168 prélèvements entre août 1980 et juillet 1981. Les mesures de salinité, de température et de transparence ont varié entre 28 et 39 %, 23,8 et 32,8 °C, 32 et 100 % respectivement.

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Les variations nycthémérales et saisonnières de plusieurs paramètres — densité, biomasse, fréquence, indice de diversité — sont statistiquement corrélées avec les variations de salinité, de température, de marée et de photopériode. Les variations nycthémérales de densité et de biomasse sont probablement reliées au comportement trophique des espèces qui influence l'efficacité de capture comme le montre l'analyse des groupements spécifiques. Les variations saisonnières de tous les paramètres sont importantes. Ces grandes variations de la structure des peuplements sont mises en relation avec la climatologie et le débit fluvial, mais la meilleure corrélation est obtenue avec la température comme le montre l'analyse multifactorielle. D'une manière générale on observe une succession d'espèces au cours de la journée et au cours de l'année. La similitude des variations nycthémérales et saisonnières manifestée par certains groupements d'espèces montre que ceux-ci sont influencés davantage par la photopériode que par les mouvements de marée.

La plus grande richesse spécifique en poissons (45) est notée en octobre, période d'immigration des juvéniles. La plus faible richesse spécifique est observée en février (22), beaucoup de poissons ayant quitté la lagune.

Les espèces sont classées saisonnièrement d'après leurs comportements migrateur et trophique. Les immigrants temporaires (49 %) et les consommateurs de deuxième ordre (49 %) sont dominants toute l'année. 20 espèces sont particulièrement importantes en termes de fréquence, de biomasse et d'abondance ; elles appartiennent aux familles suivantes : Sparidae, Pomadasyidae, Balistidae, Diodontidae, Tetraodontidae, Lutjanidae, Sciaenidae, Scaridae, Gerridae, Ariidae et Urolophidae.

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INTRODUCTION

A number of studies have been concerned with seasonal variation of estuarine fish (Fox, Mock, 1968 ; McErlean *et al.*, 1973 ; Wagner, 1973 ; Sabins, Truesdale, 1974 ; Livingston, 1976 ; Ogren, Brusher, 1977 ; Yáñez-Arancibia, 1978 ; 1981 *a*). In other studies, there has been an emphasis on the use of various community parameters such as species richness, diversity and biomass to estimate functional characteristics of such assemblages (Dahlberg, Odum, 1970 ; Bechtel, Copeland, 1970 ; Headrich, Headrich, 1974 ; Livingston, 1976 ; D'Croz, Averza, 1979). At the same time, a number of papers have considered the use of subsystems and fish populations (Horn, Allen, 1976 ; Livingston *et al.*, 1978 ; Warburton, 1978 ; Daniels, 1979 ; Chávez, 1979 ; Yáñez-Arancibia *et al.*, 1980).

There is a paucity of information on the occurrence of immature marine fish in seagrass meadows, which are distinct and important components of marine and estuarine environments. Among their most important attributes are their ability to support high densities and diversities of fish and invertebrates, and their use as nursery and feeding grounds for macrofauna, as sediment stabilizers, and, in general, as complex habitats (Hoese, Jones, 1963 ; Fergusson-Wood *et al.*, 1969 ; Carr, Adams, 1973 ; Adams, 1976 *a* ; 1976 *b* ; 1977 ; McRoy, Helfferich, 1977 ; Thorhaug, Roessler, 1977 ; Weinstein, Heck, 1979 ; Yáñez-Arancibia *et al.*, 1980 ; Heck, Orth, 1980 ; Yáñez-Arancibia, 1981 *b* ; Vargas Maldonado *et al.*, 1981). Moreover, there are few published studies specifically directed to research on fish ecology in tidal passes or on the status of immature coastal-marine fishes in these habitats (Simmons, Hoese, 1959 ; King, 1971 ; Sabins, Truesdale, 1974 ; Bravo-Núñez, Yáñez-Arancibia, 1979).

Barrier islands are interspersed with relatively narrow openings, the tidal passes, which allow for the exchange of organisms and nutrients between the sea and estuarine bays and marshes. About 75 % of the commercial fish of the southern Gulf of Mexico spawn in the sea and along the shoreline. Their postlarval and juvenile stages enter the estuaries through the tidal passes (Yáñez-Arancibia *et al.*, 1981). The early life history stages are a critical part of the life cycle, and many estuarine-dependent marine species spend a portion of this critical period in tidal passes (Gunter, 1967 ; Sabins, Truesdale, 1974). Some fishes spawn in the immediate vicinity of tidal passes and a few complete their entire life cycles there (Bravo-Núñez, Yáñez-Arancibia, 1979).

Puerto Real, a natural tidal inlet, is a particular subsystem of the Términos Lagoon areas. Because of the presence of *Thalassia testudinum* beds and the nature and characteristics of its fish communities, it must be considered as very important in the productivity and composition of the communities in all internal environments of the lagoon, for it is the entryway for a number of nektonic species. The existence of a flood tide delta is the consequence of net transportation toward the interior of the lagoon. Marine influence is highest in this area and diminishes proportionally with movement into the lagoon. There is no strong light, thermal or salinity stratification, in the inlet. Therefore, these factors, together with turbulence, do not provide for any strong vertical distribution of the communities. The estuary and adjacent continental shelf, together with the intervening pass, form a recognizable ecological system influenced by physical factors. Exchange of living organisms is related to the physical processes, but it also reflects reproductive and behavioral activities. Juvenile and adult fish actively traverse the pass and display regular seasonal patterns of migration. As a physically-dominated nutritionally rich ecological system, the pass is a distinct habitat. In this paper we discuss strategies of fish succession, diversity, biomass, community inhabitants, and trophic balance in terms of nichthemeral and seasonal programming.

STUDY AREA

Puerto Real Inlet (91°30'E-18°50'N, Fig. 1) in Términos Lagoon is located in the southern Gulf of Mexico, off Campeche Sound on the Mexican coast. The area has a warm humid climate with three climatic seasons. From June until the end of September, there are almost daily afternoon and evening showers. From October to March is the season of " nortes " or winter storms. These storms are generally strongest and associated with rains during October, November, December and January. February through May is the dry season. Water temperatures range from 36 °C in summer to 25 °C in winter, and precipitation ranges between 1 200 and 2 000 mn per year with an average of 1 681 mm. The lagoon is large (+ 2 500 km^2) and shallow (mean depth 3.5 m) with a limited channel system at the two wide inlets, Puerto Real on the east and El Carmen on the west.

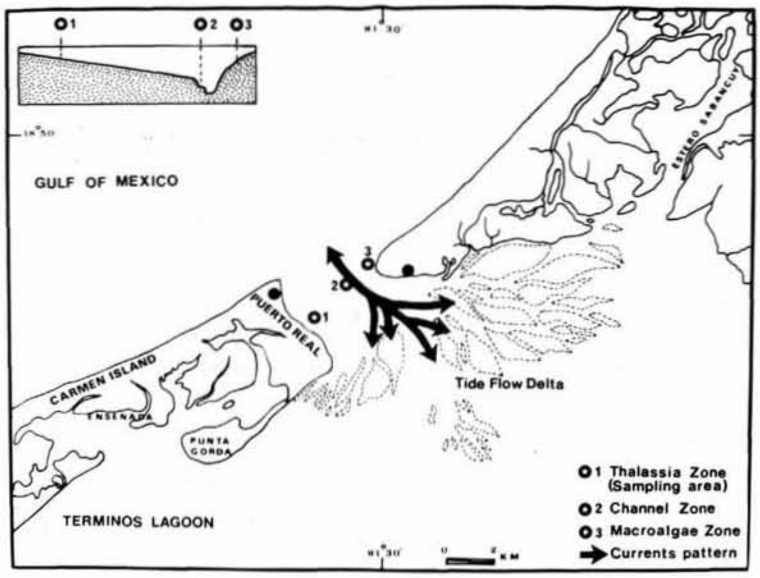


Figure 1

The study area. Physical, hydrodynamic and biological features of Puerto Real Inlet, Términos Lagoon in the southern Gulf of Mexico.

Prevailing easterly wind, longshore currents, and river discharge cause a strong net flow into the eastern inlet and out of the western inlet. Three main rivers enter the lagoon : the Palizada, the Chumpan, the Candelaria, and, in part, the Atasta system, forming important fluvial-lagoon systems. The season of high river flow is from August to November (especially in October) with an average total discharge into the lagoon of $6 \times 10^9 m^3 yr^{-1}$. Tidal range is 0.3 to 0.7 m. More detailed ecological descriptions of the lagoon are found elsewhere (Phleger, Ayala-Castañares, 1971 ; Gierloff-Emden, 1977 ; Bravo-Núñez, Yáñez-Arancibia, 1979 ; Amezcua Linares, Yáñez-Arancibia, 1980 ; Mancilla, Vargas, 1980 ; Vargas Maldonado *et al.*, 1981 ; Graham *et al.*, 1981 ; Yáñez-Arancibia, Day, 1981).

On the lagoon side of Puerto Real Inlet, a broad delta of calcareous sediment is forming as a result of the net import of water and sediment through that inlet. The *Thalassia testudinum* areas of Puerto Real have salinities of 28 to 39 ppt, temperatures from 21 to 33.5 °C, oxygen from 2.6 to 6.4 ml 0/1, a muddy substrata of fine slime clay with 50 to 60 percent $CaCO_3$ and significant quantities of organic matter, depth up to 4 m, varied and abundant macroepifauna, clear waters, high availability of food and complex trophic structure of communities (Yáñez-Arancibia, 1981 *b*).

MATERIALS AND METHODS

Fish were sampled over 24-h periods during Ausgust, October and December, 1980, and February, April, June and July, 1981. On each date two hauls were made in opposite directions every two hours, for a total of 168 trawl collections. These were made with a 5 m trawl (mouth opening during sampling was 2.5 m, mesh size 3/4"). Collections were classified in two ways, as flow or counter-flow and as seaward haul or lagoonward haul. The two classifications concur in flood stage and are opposite in ebb stage, both situations occurring in a 24-hour cycle. During each collection, salinity, temperature, transparency and tidal stage were measured, and substrate, vegetation, and macroepifauna were observed. In the laboratory fishes were identified, counted, weighed and measured. In order to characterize the size of fish of each species populations, an index (g ind^{-1}) was calculated by dividing total weight of capture per species by the total number of individuals.

On the basis of gut content, morphology of gut, mouth and gill rakers, and size, trophic position was determined using the criteria of Yáñez-Arancibia (1978) and following earlier studies in the area by Bravo Núñez and Yáñez-Arancibia (1979), Amezcua Linares and Yáñez-Arancibia (1980), Yáñez-Arancibia *et al.* (1980) and Vargas Maldonado *et al.* (1981). The trophic categories are : 1) first-order consumers : plankton feeders (phyto-and/or zooplankton) feeders on detritus and other vegetable remains, and omnivores (feeders on detritus, vegetable material and small animals) ; 2) second-order consumers : predominantly carnivorous fish, even when they consume small amounts of plant material and detritus. These fish consume primarily macro- and microbenthos and small fish ; 3) third-order consumers : fish that are exclusively carnivorous and feed primarily on macrobenthos and second-order consumer fish. Based on frequency of occurrence, gonad maturity, food habits, migration patterns and size, the fish species were classified as : 1) occasional or accidental visitors (Occ), 2) cyclical or seasonal visitors (Cv) and 3) resident or typical estuarine species (Sed). These groupings are based on earlier classifications by Yáñez-Arancibia *et al.* (1980). Dominant species were determined by ecological indices as well as by frequency, biomass and numerical abundance. The information function H' of Shannon and Weaver (1963), which increases as both the number of species (richness) and the equitability of species abundance (evenness) increase, was calculated. All diversity calculations were based on use of natural logs. The abundance of fish was calculated by number, density (individuals by area), and biomass (standing crop). The Wilhm (1968) function (H'w) was used to evaluate weight heterogeneity by species. To compare the degree of similarity of fish fauna by hour, cluster analysis was performed. Cluster analysis is a descriptive tool which objectively groups data into similar units based on their characteristics. The similarity measure was the simple matching coefficient, and the clustering method used was that of single linkage (Sneath, Sokal, 1973 ; Davies, 1971). Each sampling hour was compared to each of the remaining 11 in terms of species composition and was given a value ranging from 1.0 for complete similarity (all species in common) to 0.0 for complete dissimilarity (no species in common). The hours were then compared and grouped again according to similarity. This procedure was repeated at lower levels until distinct major groupings occurred. Results were displayed in a dendrogram in two ways : hours by species, and species by hours (Horn, Allen, 1976 ; Warburton, 1978 ; Yáñez-Arancibia *et al.*, 1980).

In order to compare the between-hauls variations the Wilcoxon non-parametric test for paired data (*in* Snedecor, Cochran, 1957) was used considering the direction of the trawl and the density, biomass, and diversity of fish populations.

To summarize the information obtained on seasonal evolution of population, the factorial method of principal components first described by Hotteling (1933) was utilized. The data considered the monthly (7) average densities (in a 24-hour cycle) of the 59 fish species encountered formed a

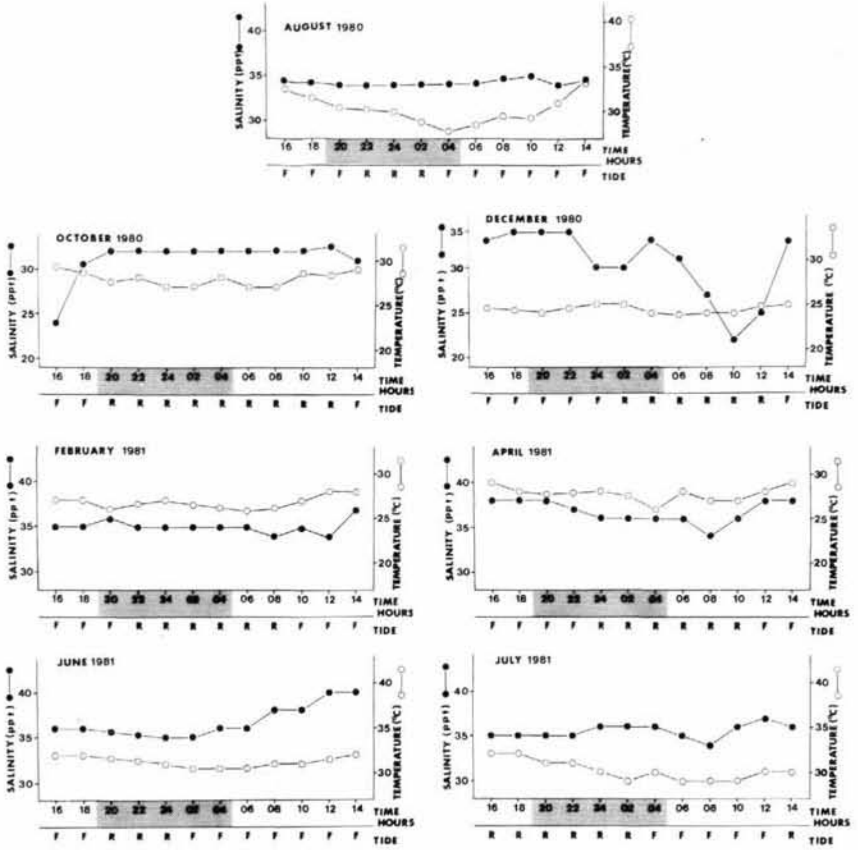


Figure 2

Temporal and nichthemeral distribution of salinity and temperature in Puerto Real Inlet. Selected months, hours, tide stage (R = ebb, F = flood) and dark period, are indicated. Lowest values of temperature and salinity occur in December and highest in June to August.

general data matrix of 59 rows and 7 columns. For the analysis itself, the SPSS (Statistical Package for the Social Sciences) Version 6 (Nie *et al.,* 1975) was utilized on a Burroughs 6 700 computer. The specific nature of the analysis procedure is as follows : principal components are determined from a Bravais-Pearson correlation matrix between months (Q-type) ; original data is transformed into log 10 (1 + x) eigenvectors which have a length unity and are normalized to the length of their standard deviation (λ 1/2) ; a Varimax rotation is made on the first 6 factors. Considering these particularities, the interpretation must bear essentially on the angles formed between the axis joining each point with the origin as well as those formed with the factors which correspond to correlation measures (Legendre, Legendre, 1979). Since samples were homogeneous in regard to species content, double-absence frequency was low and was considered to be of little prejudice to the analysis. A similar analysis from a Kendall correlation matrix gave very comparable results, thus confirming the above assumption.

RESULTS AND DISCUSSION

Habitat characterization

Water temperatures ranged from 33.5 °C (14 : 00 hrs, August) to 23.8 °C (06 : 00 hrs, December), with an average water temperature of 28.4°C. Salinities recorded during the study ranged from 40 ppt (12 : 00 hrs, June) to 22 ppt (10 : 00 hrs, December), with an average salinity of 34.3 ppt (Fig. 2). Salinities in the pass area are influenced mainly by the introduction of saline waters from the Gulf of Mexico and local freshwater runoff. However, during periods of high river discharge (October), salinities in the pass area were appreciably reduced by diluted estuarine waters. On three occasions (October, 1980, December, 1980 and July, 1981) flood tides from the Gulf were associated with decreasing pass salinities, probably reflecting the movement of low salinity water from shelf into the pass area.

Tides along the southern Gulf of Mexico are normally diurnal ; semi-diurnal tides occur infrequently. Tropic and equatorial tides occur semi-monthly at intervals of about 8 days. Tides ranged from 0.30 to 0.70 m with an average annual tidal range of 0.50 m. The basic tidal patterns were modified by various meteorological phenomena, especially wind. Strong northerly winds dampened tidal fluctuations by length increasing the duration of flood tides and by reducing the range of ebb tides. Periods of strong southerly winds had the opposite effect. All collections for the study were made during periods of diurnal tides ; no semidiurnal tides were sampled. Tidal levels in the pass area were lowest during times of prevailing southerly winds (August, 1980, and October, 1980) and highest during times of prevailing northerly winds (February, 1981 ; April, 1981).

The seasonal pattern of salinity was highly correlated with the temperature pattern (Fig. 3). Lowest average values were recorded in December (" nortes " season), with salinities of 30.5 ppt and temperatures of 24.4 °C. Highest

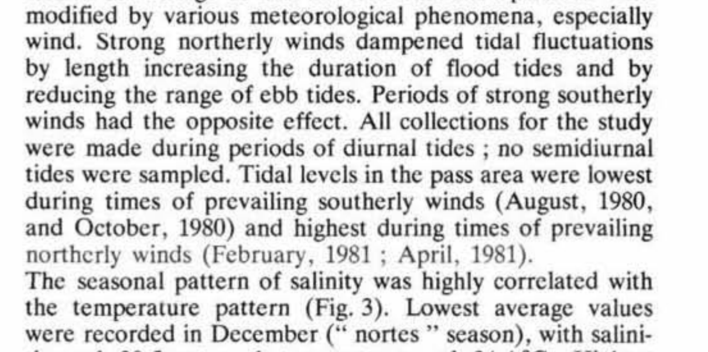


Figure 3

Bimensual averages and standard deviations of salinity, temperature and transparency in Puerto Real Inlet. Lowest values of parameters occur in December and highest in June (see Fig. 2 for nichthemeral variations).

Table 1

Wilcoxon non parametric test for paired data. Values of the smallest ranks' sums of differences. The sign indicates the positive or negative differences' sum (0.05 significant level, ** 0.01 significant level). A significative positive sum means that the parameter values are higher in countercurrent hauls or seaward ones depending the classification considered.*

	Counter flow		Versus		Flow directions		
Months	August	October	December	February	April	June	July
Number of pairs	10	12	10	10	10	10	12
Density	− 12	− 35	+ 12	− 25	+ 23	+ 20	+ 38
Biomass	− 11	− 22	− 18	+ 20	− 16	+ 25	− 30
Diversity	− 13	+ 32	+ 19	+ 14	+ 17	+ 17	− 33

	Seaward		Versus		Lagoon ward		
Months	August	October	December	February	April	June	July
Number of pairs	10	12	10	10	10	10	12
Density	− 17	+ 9*	+ 16	− 5*	+ 20	− 23	+ 37
Biomass	− 21	+ 4**	+ 24	− 20	+ 14	− 20	− 21
Diversity	− 16	− 33	+ 6*	− 11	− 25	− 10	− 17

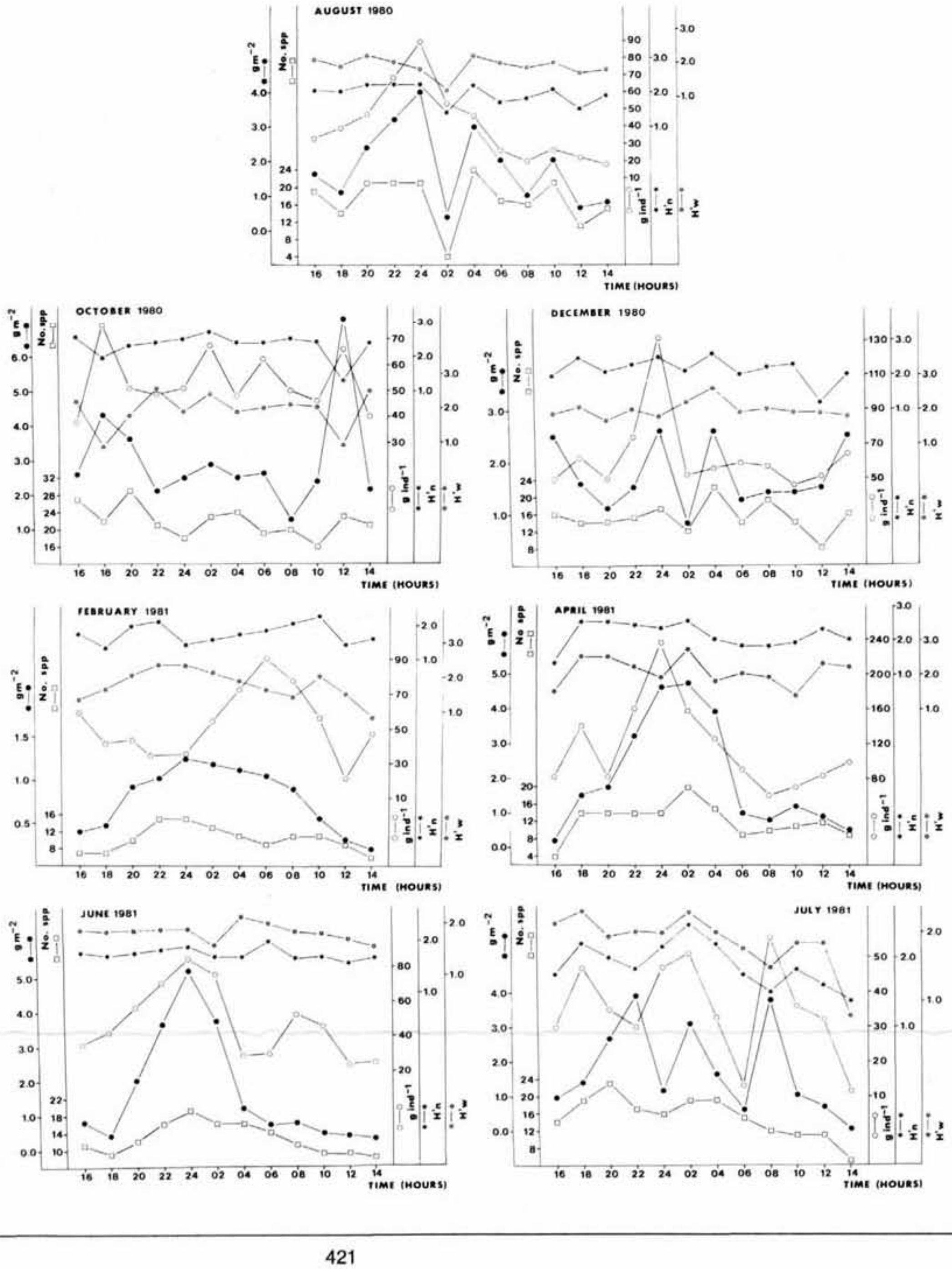


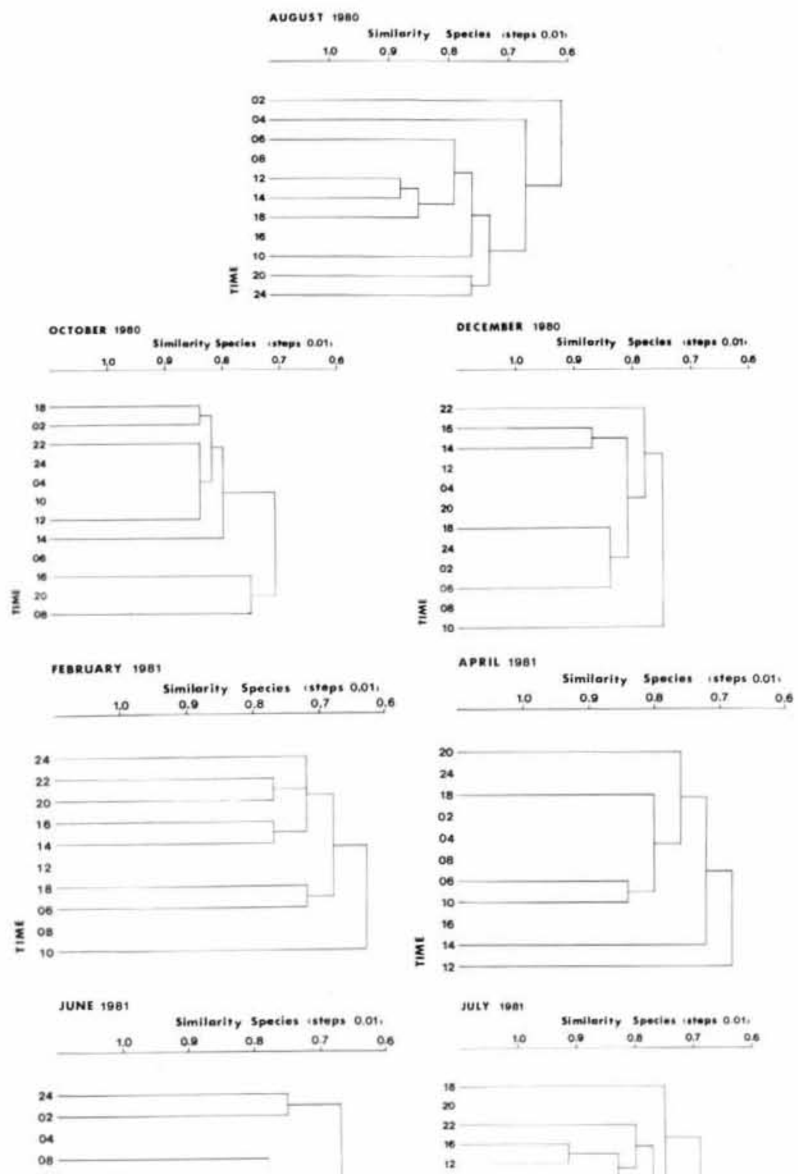
Figure 4

Temporal and nichthemeral comparison of the distribution of ecological parameters of the fish community : biomass (g m^{-2}), species number, numerical diversity (H'n) weight diversity (H'w) and average size of populations (g ind^{-1}) ; in Puerto Real Inlet.

average values occurred in June (the end of dry season), with salinities of 37.0 ppt and temperatures of 31.2 °C. Transparency, associated with winds and river discharge, showed the same pattern. The lowest monthly average value was 39 % in December after the period of greatest riverine influence, and the highest was 100 % during June and July.

Influence of haul direction on parameters of collections

Each two-hour collection was composed of two hauls in opposite directions. The results of the Wilcoxon test indicated that direction of the haul with respect to tide current was not statistically related to the ecological parameters of the community (Table 1). Therefore the two hauls were considered equivalent and combined in the subsequent analysis. By contrast, the geographic direction (sea or lagoonward) of the haul was highly correlated (Table 1). The significant cases correspond to the following months : October, 1980, when densities and biomass were higher in seaward hauls ; December, 1980, when diversities were higher in seaward hauls ; February, 1981, when densities were higher in lagoonward hauls.
These results demonstrate that the geographic orientation of the trawl has a definite influence on sample characteristics. Although the sampling method used in this study does not take into account the directional selectivity of other sample methods (traps for example), it is possible to interpret the observed differences between seaward and lagoonward hauls as a reflection of the relative importance of immigration and emigration at the end of winter.
Several authors have discussed the inherent variability of sampling methods, with different conclusions. Clark (1974, *in* Livingston, 1976) did not find any effect of sampling procedure and tidal stage on his trawl catches. On the other hand, Subrahmanyam and Drake (1975) found a significant difference between high tide and low tide collections using a seine in tidal creeks.
It seems difficult, therefore, to draw any general conclusions about the sampling best method. This could be due to the fact that estuarine changes are so evident that the inherent variability of sampling methods does not significantly the overall variation. However, general statistical considerations indicate that there is a marked advantage to collecting numerous small samples rather than a few large ones.



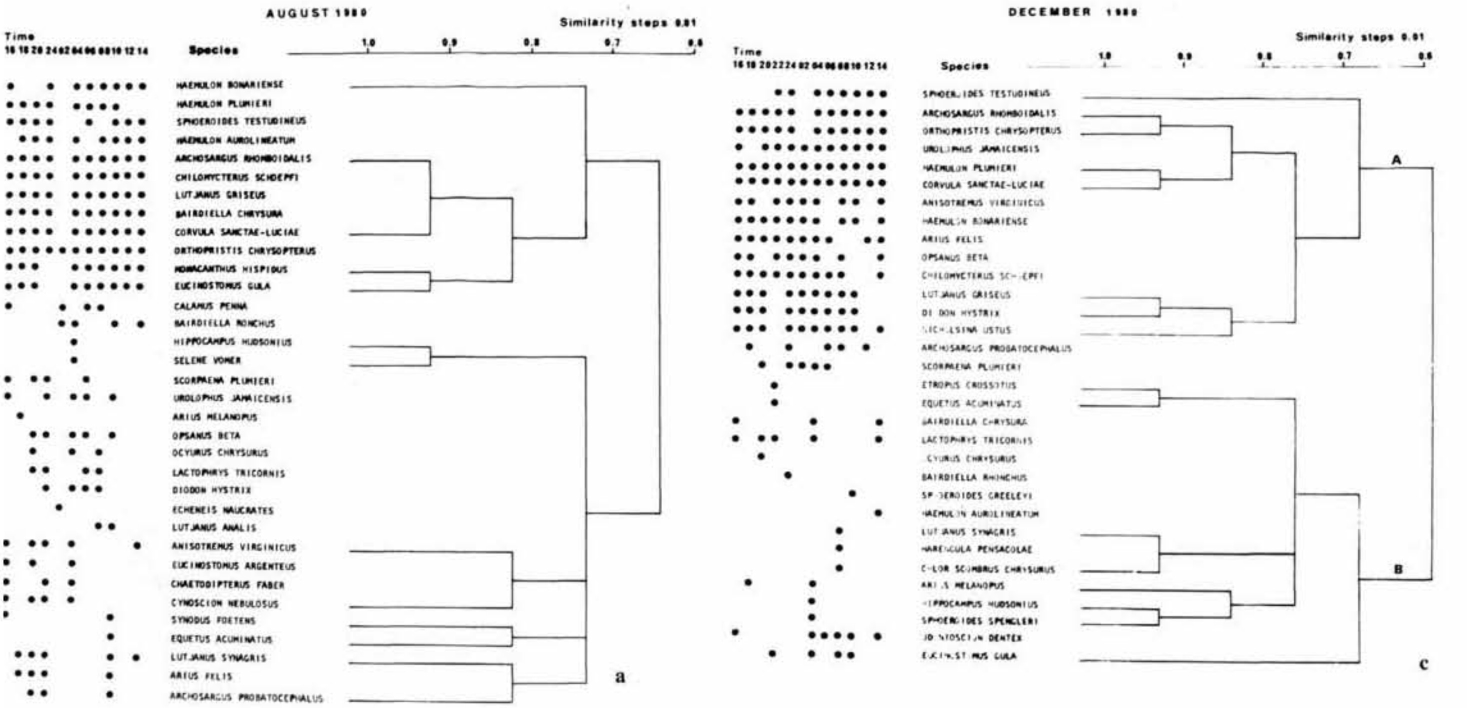
Nichthemeral variations of the fish community

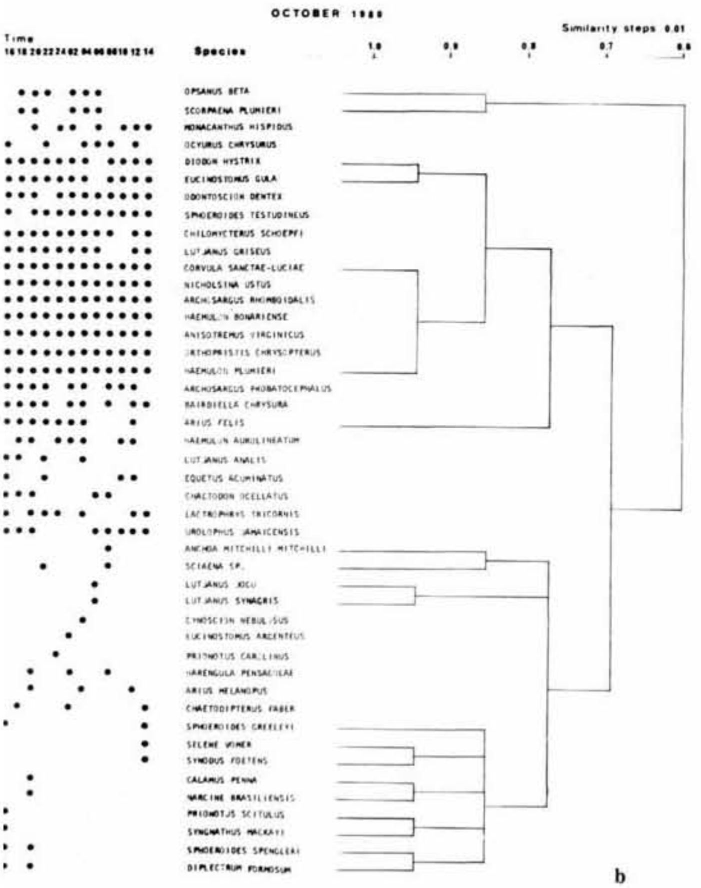
A total of 7 670 fish from 59 species were collected.
Figures 4*a* and 6*a* to 6*g* show all ecological parameters for the fish community in 24-h samples and during different months. A broad variation, mainly of biomass, species number and average size of fish (g ind^{-1}), is evident. During the months of August, December, February, April and June, the biomass shows a peak beginning at 18 : 00 hours and reaching a maximum at 24 : 00 hours. A similar pattern occurred for species number and average fish size. This pattern can be explained by major feeding activities of large carnivorous fish (second and third-order consumers) which feed largely on molluscs, polychaetes and crustaceans which are more available and abundant during early night hours. Some dominant species produce a second peak (i.e., October, *Arius melanopus, Nicholsina ustus, Lutjanus griseus, Urolophus jamaicensis, Diodon hystrix, Corvula sanctaeluciae ;* Fig. 6*b* and 8.
February shows the most simple pattern of variation. This can be explained by the simple community structure during this month as indicated by the low diversity and biomass values (Fig. 7). By contrast, August, October, December and July show a complex pattern related to the more complex structure of the community, as indicated by the highest values of diversity and biomass.
Figures 5 and 6*a* to 6*g* show the general nichthemeral community structure in terms of species diversity, frequency and presence/absence of fish species. Certain hours of the day are characterized by particular species. Figure 5 indicates that early night hours are ecologically related to each other as well as to the hours with maximum light. Dendrograms 6a to 6g indicate two main groups of fish : a group of species which have broad distribution all day, and a group of species distributed only at certain hours, mainly during the night. Other species do not present a regular pattern.

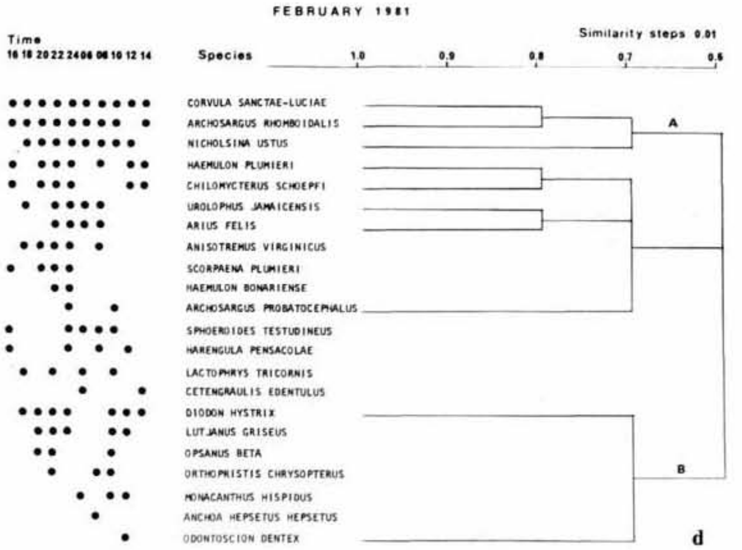
Annual cycle

The lowest values of community ecological parameters were recorded in February, but this marks the beginning of a pulse which shows the highest values of diversity (H'n), biomass (g m^{-2}) and species number in October. In April

Figure 5
Dendrograms of the clustering of sampling hours showing ecological affinities in different months, based on presence/absence of fish species. Groups are defined for hours which present a similar composition of fish populations. Dark hours are ecologically related (see Fig. 2).







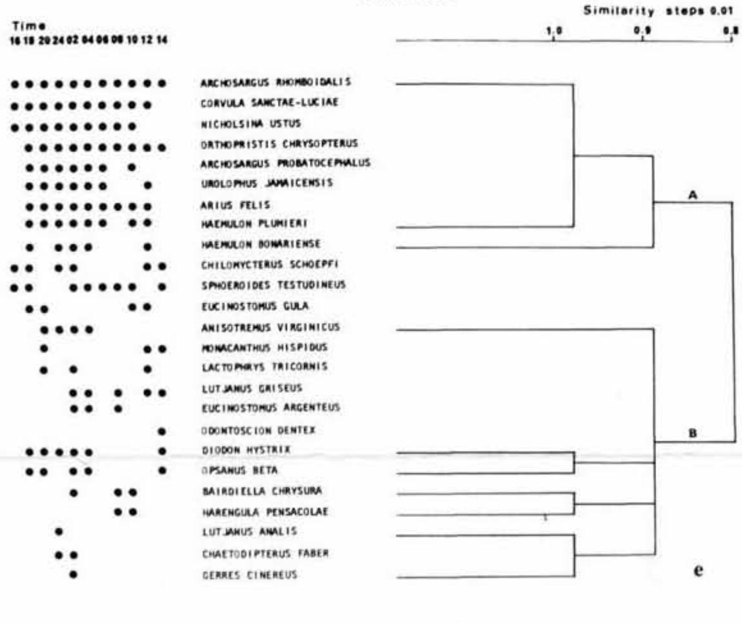


Figure 6

Dendrogram of the clustering of fish populations showing ecological affinities based on frequency and presence/absence during a nichthemeral cycle. Fish species were placed in distributional categories (indicated by the dark spot) based on a two-way table (24-h vs. species) generated with the cluster analysis. The dendrogram reflects groups A and B defined for fish populations which co-occur spatially and temporally in different hours.

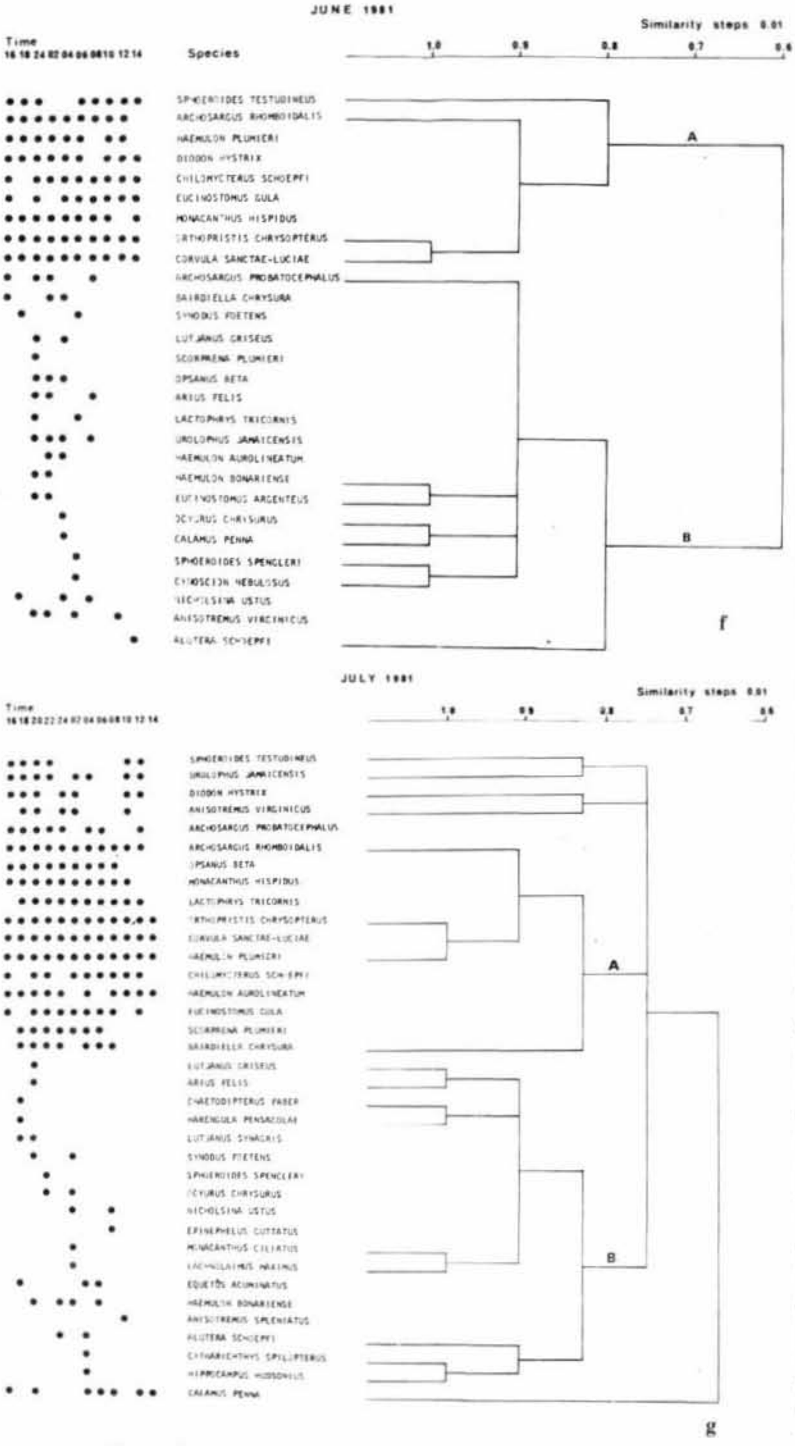


Figure 6

Dendrogram of the clustering of fish populations showing ecological affinities based on frequency and presence/absence during a nichthemeral cycle. Fish species were placed in distributional categories (indicated by the dark spot) based on a two-way table (24-h vs. species) generated with the cluster analysis. The dendrogram reflects groups A and B defined for fish populations which co-occur spatially and temporally in different hours.

adults of few species were caught, as is suggested by the g ind^{-1} index, and corroborated by the inverse relationship of the biomass (H'w) index with standing crop (g m^{-2}).

From October to February, the values of community ecological parameters decrease, as there is an evident immigration throughout the area, to the sea as well as to the lagoon. The results described in Figure 7 are correlated with climatic conditions (Fig. 3) and the environmental parameters of the habitat (Fig. 2 and 3).

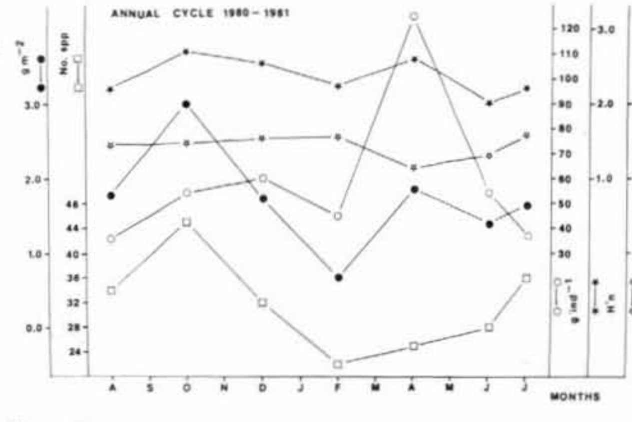


Figure 7

Temporal distribution of ecological parameters of the fish community: biomass (g m^{-2}), species number, numerical diversity (H'n), weight diversity (H'w) and average size of populations (g ind^{-1}), in Puerto Real Inlet. The figure reflects the bimodal distribution of biomass during the period of high juvenile immigration (October) and the presence of a more uniform population of larger fish during April. See text for explanation.

Dominant species, community inhabitants and ichthyotrophic catagories

Of the 59 species collected, 20 (Fig. 8) made up 28 % of the number and 75 % of the weight of the catch. They were *Archosargus rhomboidalis, Orthopristis chrysopterus, Haemulon plumieri, Monacanthus hispidus, Chilomycterus schoepfi, Sphoeroides testudineus, Lutjanus griseus, Bairdiella chrysura, Corvula sanctae-luciae, Haemulon aurolineatum, Anisotremus virginicus, Haemulon bonariense, Nicholsina ustus, Eucinostomus gula, Diodon hystrix, Odontoscion dentex, Arius melanopus, Urophus jamaicensis, Arius felis* and *Archosargus probatocephalus.*

These species were broadly distributed throughout the year. It must be remembered that this information is based on trawl-caught fish. Trawls can be selective for some fish but catch others very inefficiently. Fast swimmers are often underrepresented in trawls, while fish which live in very shallow habitats are common in these catches. Figures 7 and 8 show abundance, diversity and biomass in the different sampling months. The presence of a few large specimens explains the inverse relationship between density and biomass in this area (Fig. 7 and 8). Seasonal changes in density and biomass resulted primarily from the influx of juveniles from April to October.

Resident species (14 %) were found in Puerto Real Inlet at all times (Fig. 9). They reproduce and grow to maturity in or near the inlet and appear to leave rarely, if ever. Seasonal visitors (49 %) use the inlet in a regular repeating pattern and seem to be dependent on it at some stage of their life cycle. Common examples in this group are estuarine-dependent species spawn offshore, move into the inlet as juveniles, and return to the sea as adults. Occasional visitors (37 %) had no regular pattern of use of the lagoon. In placing each species into one of the three catagories, we took into account trawl selectivity and the ecological criteria mentioned under " methods ".

The penetration of fish species into Puerto Real Inlet is either of a trophic nature or is linked to reproductive cycles (i.e., pathway of immigration through Términos Lagoon or *vice versa*).

More than 49 % of the fish species were second-order consumers (Fig. 9). These species showed greater affinity for a particular habitat. This is not surprising since most of these species are demersal and many have fairly specific feeding habitats ; thus, they would associate themselves more closely with particular habitats than would higher consumers that range widely over the inlet. Second-order consumers are more important in determining characteris-

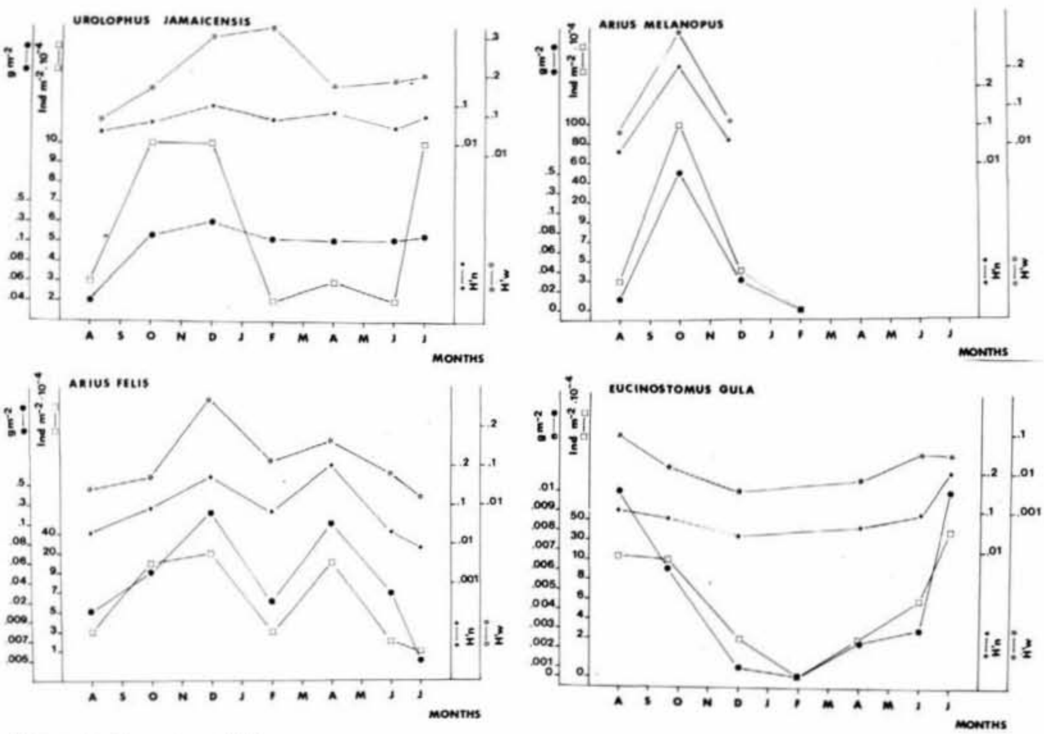


Figure 8*a* (legend p. 427)

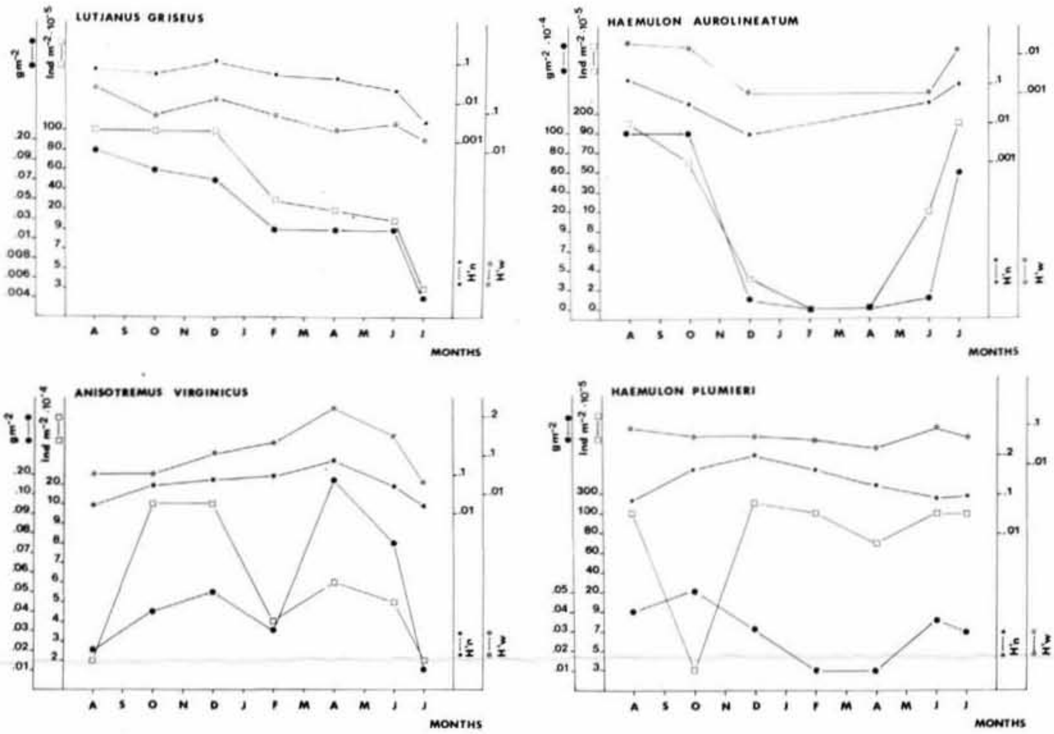
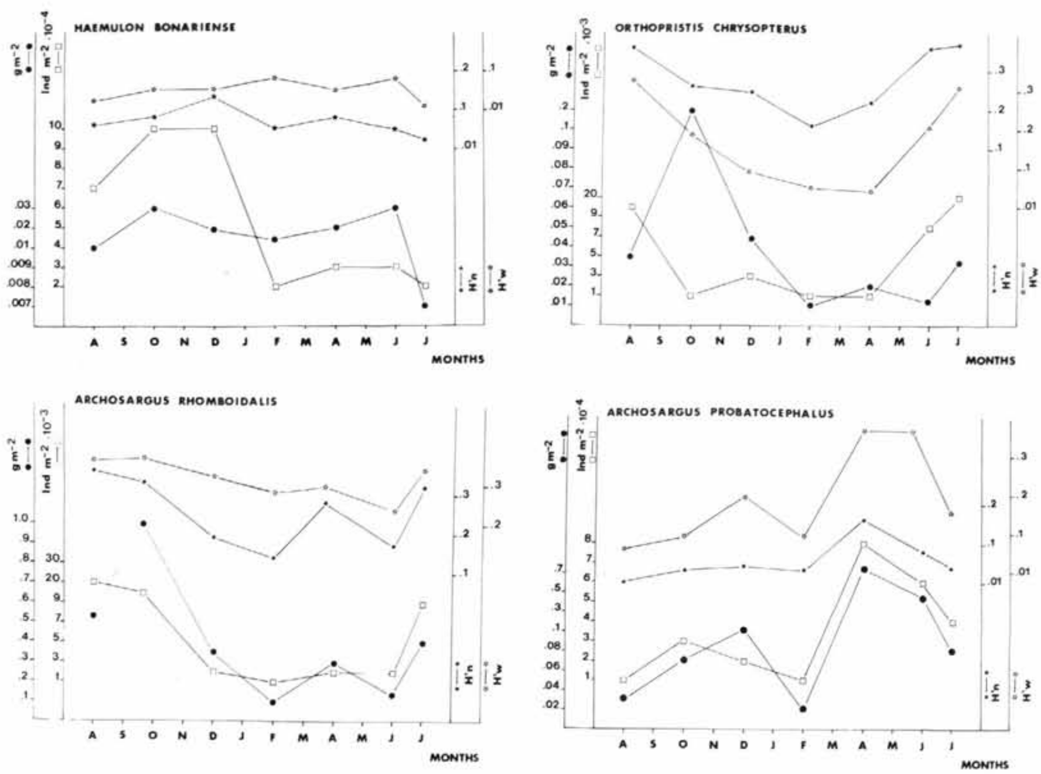
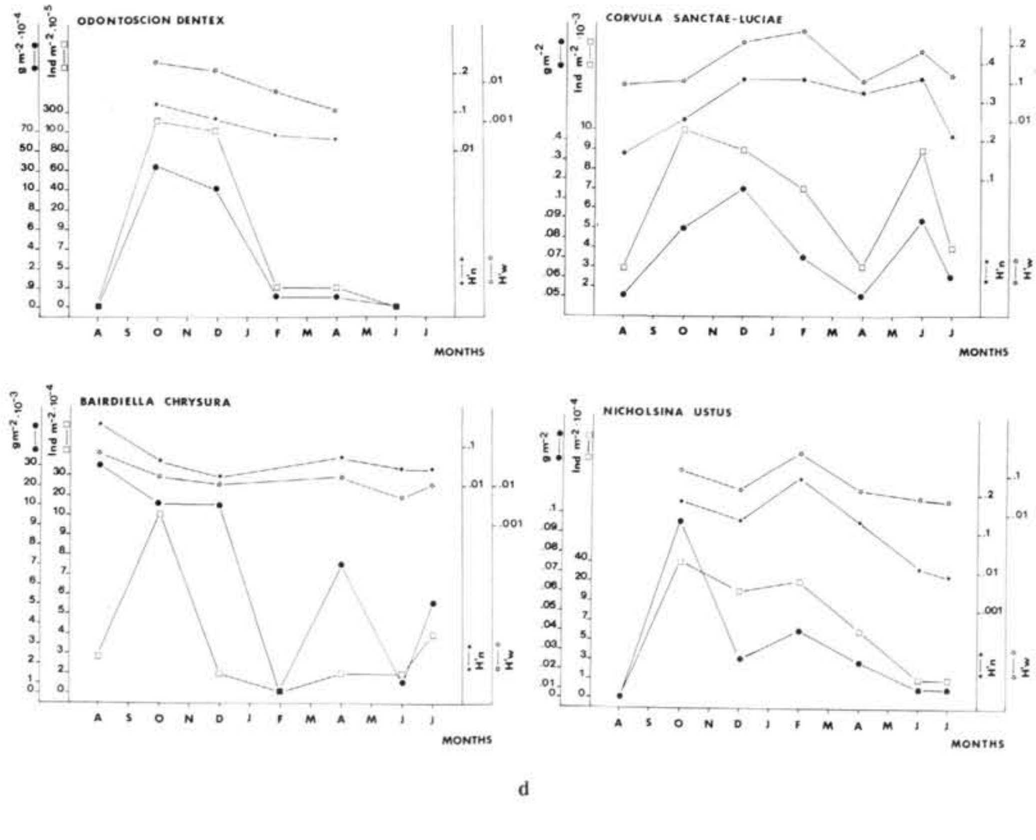


Figure 8*b* (legend p. 427)


HAEMULON BONARIENSE
ORTHOPRISTIS CHRYSOPTERUS
ARCHOSARGUS RHOMBOIDALIS
ARCHOSARGUS PROBATOCEPHALUS
A S O N D J F M A M J J
MONTHS
H'n
H'w

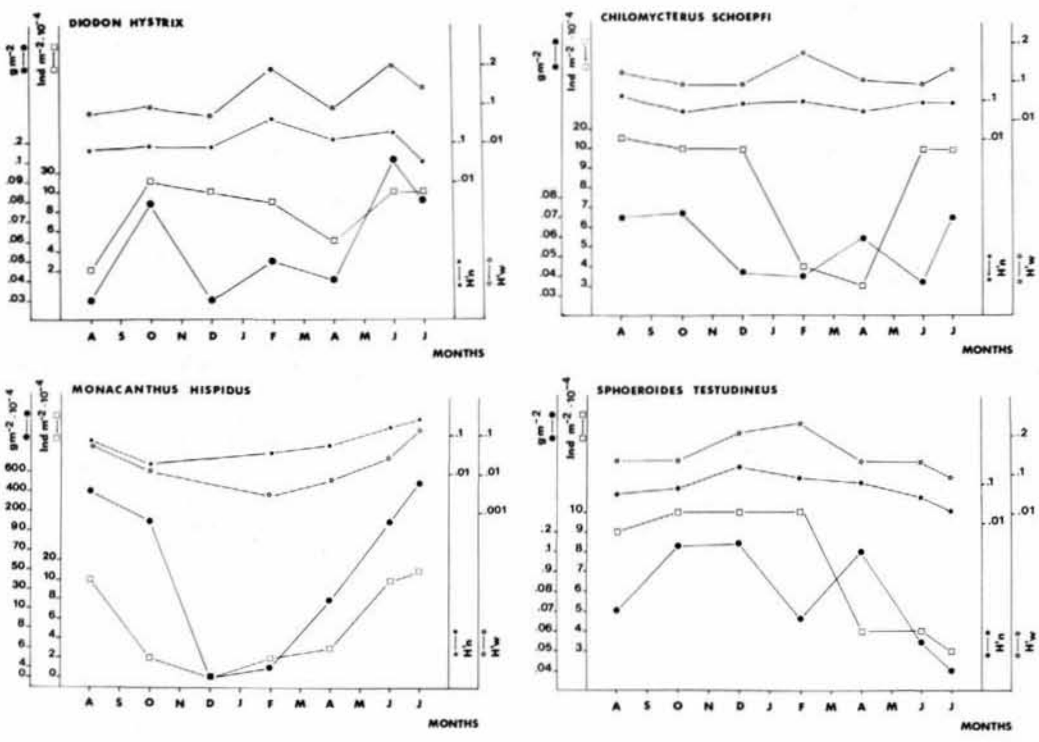
c


ODONTOSCION DENTEX
CORVULA SANCTAE-LUCIAE
BAIRDIELLA CHRYSURA
NICHOLSINA USTUS
A S O N D J F M A M J J
MONTHS
H'n
H'w

d

Figure 8

Monthly ecological parameters of dominant species: biomass (g m^{-2}), numerical diversity (H'n), weight diversity (H'w) and density of population (ind m^{-2}), in Puerto Real Inlet. Some of them show a bimodal distribution of biomass, highly correlated with Figure 7. Seasonal programming of different ecological patterns between species are conspicuous.



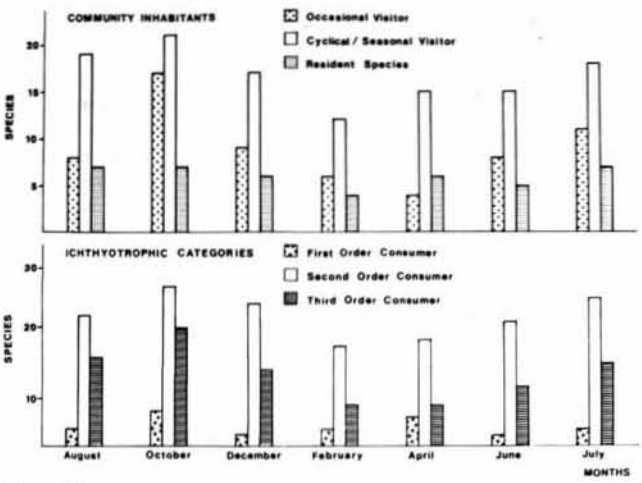


Figure 9

Temporal distribution of community inhabitants and ichthyotrophic categories of the fish community in Puerto Real Inlet. Cyclical or seasonal fish species and second order consumers are dominant in the community structure. October and February are the limits of the community pulse, correlated with Figure 7. See text for explanation.

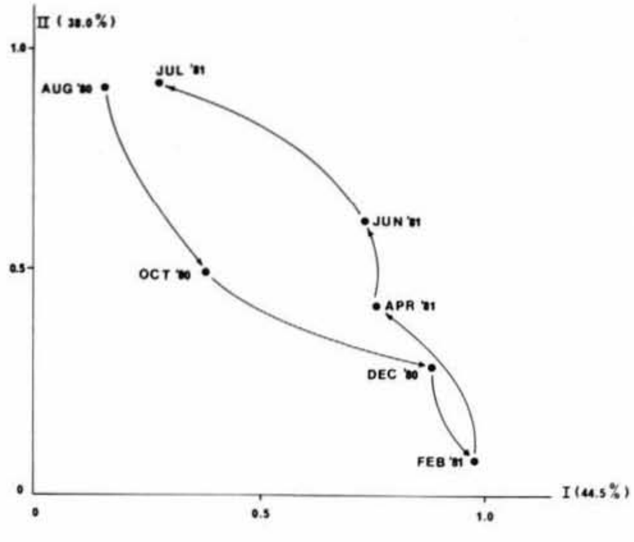


Figure 10

Principal components analysis. Relative position of the months in the first two factors and proportion of total variance. See text for explanation.

tics of particular fish communities because of their numerical abundance, habitat specificity and wide trophic range.

Multivariate analysis

In order to summarize the information obtained on the seasonal cycles of populations, the factorial method of principal components was utilized. After rotation, the first two factors (I and II) accounted for 44.5 % and 38.0 %, respectively, of the total variance. Thus, 82,5 % of the correlation matrix information is represented in the reduced space of these two factors and this representation may therefore be considered an excellent synthesis. The 7-month plot in this space follows the chronological order of sampling (Fig. 10). The sequence shows sudden changes between February and April, June and July, and August through December, which correspond precisely to the three major hydroclimatic changes. These are, respectively, the beginning of the dry season, the beginning of the rainy season, and the beginning of the winter storm (" nortes ") season. Between montly collections, Kendall correlation tests were made for each factor and the corresponding values of temperature, salinity, and transparency. Temperature appared as the only parameter significatively correlated (Table 2), showing an inverse relation with factor I and a direct one with factor II. Therefore, it seems that salinity, which is a highly variable parameter in the inner lagoon (4-35 %) but has attenuated variations in the pass, does not

Table 2

Kendall correlation coefficients between monthes' loadings and 3 abiotic parameters (0.005 significant level).*

	Temperature	Salinity	Transparency
Factor I	− 0.62*	− 0.05	− 0.15
Factor II	+ 0.62*	− 0.24	− 0.35
N of pairs	7	7	6

constitute an important factor for fish in this particular zone. However, temperature appears to be a good indicator of qualitative and quantitative changes in the fish community.
Daget (1976) in a similar study on a fish community in an African lagoon with marked salinity variations (Ébrié lagoon, Ivory Coast, Africa), found comparable results, but correlated both factors with salinity. On the other hand, Sabins and Truesdale (1974), studying a fish community in a natural tidal pass with attenuated salinity variation (like Puerto Real) in Louisiana, considered temperature to be a good criterion for defining species assemblages. There, a cold assemblage occurs from November to April and a warm one from May to October.
Therefore, the pass provides a unique and original habitat with relation to the entire lagoon. This analysis has shown that, while salinity variation constitutes an important parameter for fish populations in the inner part of the lagoon, the pass represents a typical marine feature with temperature as the dominant variable.

CONCLUSIONS

1) In 24-h cycles salinity and temperature were correlated with tidal stage and light period. Salinity and water temperature show a seasonal pulse with lowest values during the month of December and highest values in June.
2) The results demonstrate that the geographic orientation (sea or lagoonwards) of the trawl more than the tidal current direction, has a definite influence on sample characteristics, thus reflecting the relative seasonal importance of immigration and emigration of fish.
3) A broad variation, mainly of biomass, diversity and fish size, is evident during 24-h cycles. This finding is explained by major activities of large carnivorous fish (second and third-order consumers) : fish and their food are more available and abundant during early night hours.
4) The lowest values of the community ecological parameters were recorded in February, but this marks the beginning of a pulse which reaches its highest values of diversity and biomass in October and is evident in a migration throughout the pass, both to the sea and to the lagoon.
5) In the pass, 14 % of the fish species were permanent residents, 49 % seasonal visitors, and 37 % occasional visitors. The penetration of fish into Puerto Real Inlet is either of a trophic nature or is linked to reproductive cycles. More than 49 % of the fish species were second-order consumers, most of them are demersal. Because of their numerical abundance and habitat specificity, second-order consumers are more important in determining characteristics of particular fish communities.
6) The pass, a distinct habitat, is a particular subsystem of the Términos Lagoon complex. This analysis has shown that, while salinity constitutes an important parameter for fish populations in the inner part of the lagoon, the pass represents a typical marine feature with temperature as the dominant variable.
7) A succession of species is demonstrated in the community showing that the Puerto Real Inlet is a dynamic ecosystem of transitional ichthyofauna. The system represents the entrance to the estuarine lagoon ecosystem of the interior of the Términos Lagoon.

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