Ecological characterization of Términos Lagoon, a tropical lagoon-estuarine system in the Southern Gulf of Mexico

Coastal lagoons
Estuary
System ecology

Lagunes côtières
Estuaire
Écologie

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ABSTRACT

Términos Lagoon was selected for study because of: 1) its biological diversity, in terms of both species and habitats; 2) its valuable fish, oyster, shellfish, and wildlife resources; 3) its relationships with Campeche Sound, the most important fishery area in the Gulf of México; and 4) its proximity to present and proposed oil industries. The ecological characterization is a description of the important components and processes that make up the ecosystem, stressing functional relationships and synthesizing existing information from the biological, chemical, physical, and environmental sciences. The ecological characterization collates what is known about the natural resources of the area, describes areas of probable environmental impacts, aids in development of mitigation procedures and alternatives for minimizing environmental damage, and helps identify research needs.

The lagoon has a moderate seasonal pulse of temperature and light, and the area has strong near-permanent physical gradients and a high diversity of estuarine habitats. Prevailing winds cause a net inflow into the eastern inlet and a net outflow from the western inlet, which creates high salinity and clear water conditions in the eastern end of the lagoon. The major river discharge is into the western part of the lagoon, creating turbid, nutrient-rich waters with low salinity. An inlet delta is being formed on the lagoon side of the eastern inlet. Most biological processes including assemblages of benthic and fish populations are strongly influenced by these gradients. Extensive grass beds occur in the northeastern end of the lagoon and a succession from grass beds to mangroves in taking place on the emerging delta. Extensive oyster reefs are located in the western part of the lagoon near the river mouths. Phytoplankton production, chlorophyll levels, and mangrove litter-fall are higher in the riverine area. Nekton larvae and juveniles generally enter the lagoon through the eastern inlet, reflecting prevailing currents. Peak river discharge is in October, when the highest primary productivity and entry of juveniles occur.

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RÉSUMÉ

Caractérisation écologique de la lagune de Términos, système lagunaire tropical du Golfe du Mexique.

La lagune de Términos a été choisie pour cette étude en raison de : 1) la diversité des espèces et des habitats ; 2) la qualité des ressources en poissons, huîtres, coquillages ; 3) ses relations avec le détroit de Campeche, la plus importante zone de pêche dans le Golfe du Mexique ; 4) la proximité de raffineries. La caractérisation écologique consiste en une description des composants et des mécanismes de fonctionnement de l'écosystème, en mettant l'accent sur les

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relations fonctionnelles et en synthétisant l'information disponible relative aux sciences biologique, chimique, physique et écologique. La caractérisation écologique fait le point sur les connaissances concernant les ressources naturelles de la zone étudiée, décrit les zones sensibles aux aménagements, aide le développement de techniques douces d'aménagement et propose des solutions de remplacement pour sauvegarder l'environnement ; enfin, sert à mettre en évidence des besoins de connaissance.
La température et la luminosité dans la lagune présentent une certaine stabilité saisonnière ; cette zone est caractérisée par un gradient permanent des facteurs physico-chimiques et par une grande diversité de biotopes estuariens. Les vents dominants sont à l'origine d'un flux entrant d'eau de mer dans la passe Est, et d'un flux sortant dans la passe Ouest, ce qui entraîne de fortes salinités dans la partie orientale de la lagune. Les apports fluviaux sont importants dans la partie occidentale de la lagune et provoquent de fortes turbidités et un enrichissement des eaux en nutriments. Dans la passe, un delta est en voie de formation du côté est. La plupart des phénomènes biologiques sont dépendants de ces gradients. Des herbiers très importants s'étendent dans la partie nord-est de la lagune ; les herbiers sont progressivement remplacés par la mangrove dans le delta en cours d'émergence. Des bancs d'huîtres très étendus sont situés dans la partie occidentale de la lagune près de l'embouchure de la rivière. La production phytoplanktonique, les concentrations en chlorophylle et les quantités de matière organique provenant de la mangrove sont plus élevées dans la zone fluviale.
Les larves et juvéniles de poissons pénètrent dans la lagune par la passe Est à cause des courants dominants. Le débit maximum du fleuve se situe en octobre en même temps que les plus fortes productions primaires et pendant l'immigration de juvéniles.

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INTRODUCTION

Estuarine ecosystems are dominated by a diversified physical environment. Estuarine physical factors include winds, tidal and riverine effects, heavy nutrient loads, high turbidity levels, and turbulence. Moreover, in higher latitudes there is a strong seasonal pulse of temperature and sunlight. Much of estuarine ecology is an investigation of the effect of this variable abiotic environment on the biota (Day, Yáñez-Arancibia, 1982).
Términos Lagoon is an excellent site at which to study physical-biological interactions for a number of reasons : 1) because of its tropical location, there is no strong seasonality in sunlight and temperature as in higher latitudes. Thus, in effect, the unique estuarine riverine-tidal interaction is isolated from temperate seasonal variability ; 2) there are two inlets connecting the lagoon with the Gulf of México. Regional winds and coastal currents cause a net inflow through one inlet and a net outflow through the other, a circulation pattern that leads to strong semi-permanent gradients in salinity, turbidity, sediment types, and nutrient levels ; 3) estuarine habitats in the lagoon are diverse, including mangroves, submerged sea grasses, marsh grasses, oyster reefs, areas of high sedimentation, and low salinity in the oligohaline zone. The effects of the physical environment can be studied in each case.

THE PHYSICAL ENVIRONMENT

Regional setting

Términos Lagoon is a large (± 2 500 km²), shallow (mean depth 3.5 m) coastal lagoon bordering the southern Gulf of México in Campeche, México (Fig. 1). Offshore is located the Bay of Campeche, an area with a broad continental shelf. This region supports one of the largest marine fisheries in México. The lagoon is at the base of Yucatán Peninsula and boarders two geologic provinces. To the east is the Yucatán Peninsula, characterized by low rainfall,

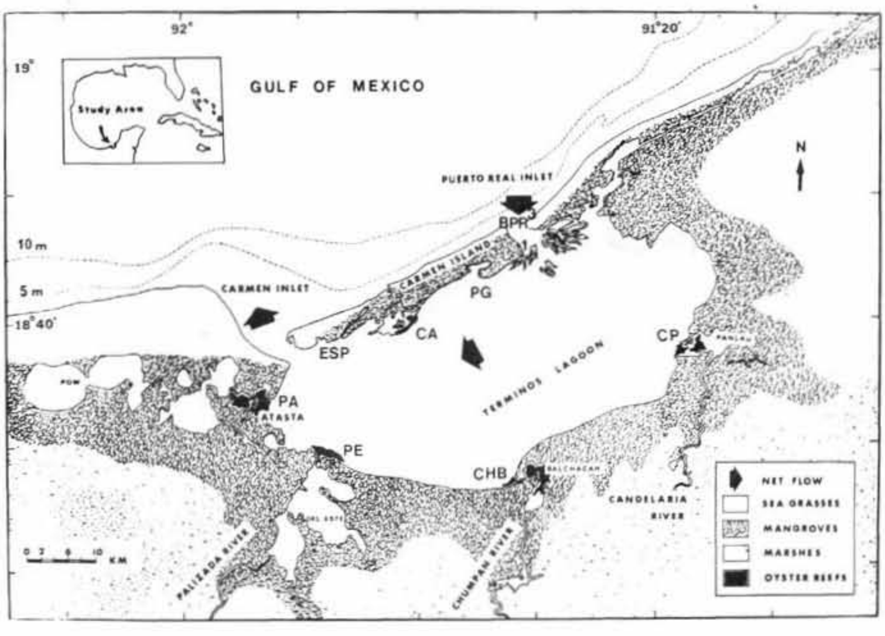


Figure 1
Términos Lagoon on Campeche coast, southern Gulf of México, showing the main ecological subsystems. Localities with marine influence are BRP : Puerto Real Inlet, PG : Punta Gorda, CA : Bajos del Cayo, ESP : Estero Pargo. Fluvial lagoon systems are CP : Candelaria-Panlau, CHB : Chumpan-Balchacah, PE : Palizada-del Este, PA : Pom-Atasta.

calcareous soils, and no significant surface drainage. To the west and south are the lowlands of Tabasco and the highlands of Chiapas and Guatemala, an area of high rainfall and fluvial soils. The Usumacinta-Grijalva river system (the largest in México and second largest in the Gulf of México) discharges into the Gulf about 70 km to the west. Three main rivers enter the lagoon : the Candelaria, the Chumpan, and the Palizada (a distributary of the Grijalva-Usumacinta).

Climatic and circulation patterns

There are three « seasons » in this region (Fig. 2). From June until the end of September, there are almost daily afternoon and evening showers. From October into March is the season of « nortes » or winter storms. These storms are generally strongest and associated with rains during

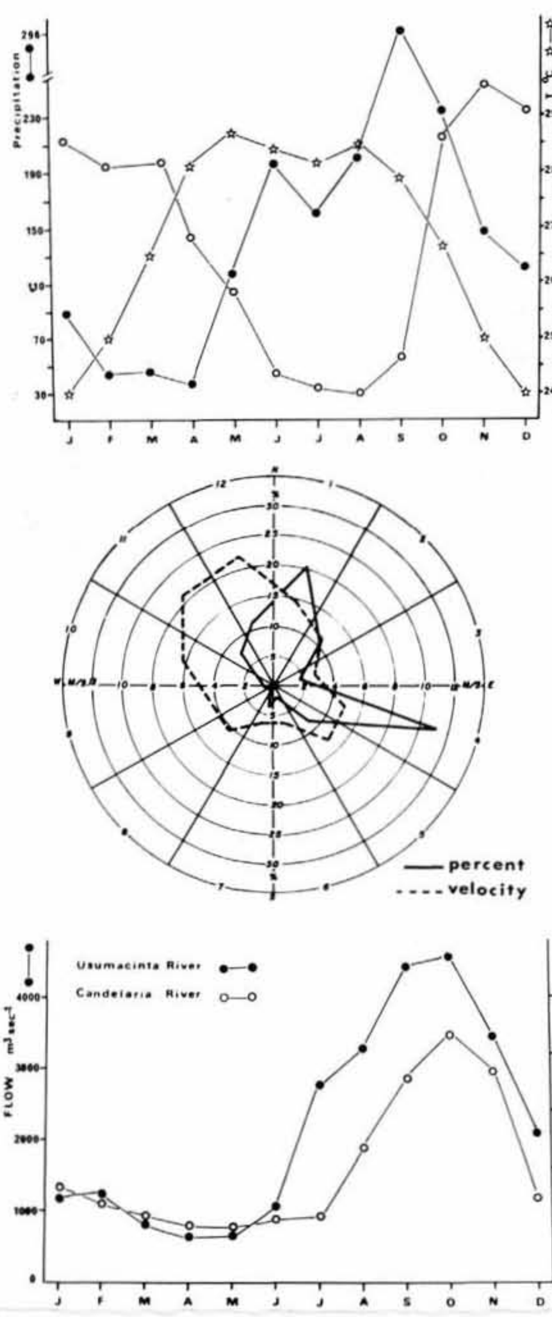


Figure 2

Climatic relationships in Términos Lagoon. Data for temperature, precipitation (in mm), and days with « nortes » are monthly mean values (adapted from Bravo Núñez, Yáñez-Arancibia, 1979). Wind direction and velocity are mean values for each of the 12 directions indicated (adapted from Mancilla, Vargas, 1980). River discharge data are from S. R. H. (1976).

November, December and January. February through May is the dry season. Annual precipitation averages 168 cm. Seasonal precipitation patterns over the drainage basin are similar to the local pattern. Temperatures in open lagoon waters range between 27 and 33 °C. River discharge into the lagoon reflects rainfall, as indicated by annual discharge patterns for the Candelaria and Usumacinta rivers (Fig. 2). Total average river discharge into the lagoon is estimated at 6×10^9 m^3 yr^{-1} (Phleger, Ayala-Castañares, 1971). The southwestern part of the lagoon receives more than 50 % of the freshwater input. The replacement time for lagoon waters lost through river discharge is about 1.5 years.

There are two quite distinct wind systems (Fig. 2). During « nortes », winds are from the northwest (segments 11 and 12, Fig. 2). Mean wind speeds are slightly higher than 8 m $sec.^{-1}$. For almost all the rest of the year, there is a sea breeze system, with winds predominantly from the north-northeast (segment 1, Fig. 2) and east-southeast (segment 4, Fig. 2). Average sea breeze velocity is between 4 and 6 m $sec.^{-1}$. The easterly orientation of the sea breezes reflects the regional influence of the trade winds. There are essentially no winds from the southwest.

The most striking feature with regard to circulation in the lagoon is the strong net flow from east to west caused by the prevailing easterly winds (Gierloff-Emden, 1977). Mancilla and Vargas (1980) measured a net westerly flux of 1 350 m^3 $sec.^{-1}$. Results from a preliminary hydrodynamic model of the lagoon (Graham *et al.*, 1981) indicate a maximum flux in the passes of about 6 000 m^3 $sec.^{-1}$. Thus, roughly one-fourth to one-third of the water that enters Real Inlet on a typical tidal cycle ultimately leaves through Carmen Inlet. The net flux is also indicated from model output of net currents (after tidal currents have been filtered out, Fig. 3). The strong westerly flow is a reflection of wind-driven currents. There is a mixed diurnal tide with a range of about 0.5 m which is in phase at the two inlets.

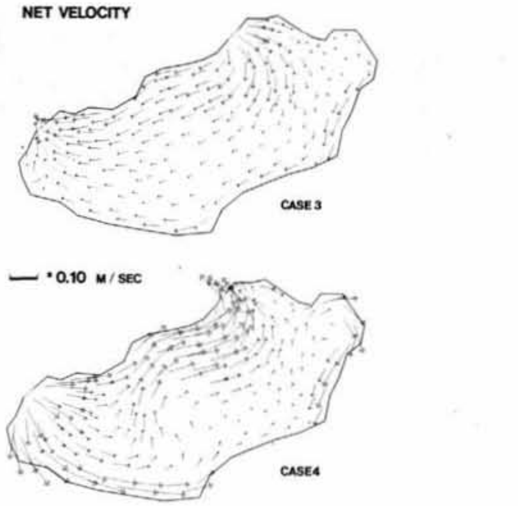


Figure 3

Net current velocity in Términos Lagoon after tidal currents are filtered out. Case 3 presents the following conditions : 5 m $sec.^{-1}$ wind is imposed from the NE (45 deg. relative to the X-axis) ; river inflows are 133 m^3 $sec.^{-1}$ and 38 m^3 $sec.^{-1}$ (average annual discharge) for the Palizada and Candelaria rivers, respectively ; this is the case which steady trade winds are hypothesized to induce the westward net flux. Case 4 was intended to observe the likely effects of the « norte » wind : a 10 m $sec.^{-1}$ wind from NW (135 deg. relative to the X-axis) is imposed ; river flows were set at 19 m^3 $sec.^{-1}$ (from a hydrodynamic model of the lagoon by Graham et al., *1981).*

Three historic Landsat images which portray gross circulation patterns are presented. Figures 4, 5 and 6 are band 5 images take by Landsat 2 on 8 October, 1979 (the end of the rainy season), 16 January, 1978 (« nortes » season), and 16 February, 1979 (dry season), respectively. It is surmised that Figures 5 and 6 were taken during flooding tide under

Figure 4

Landsat 2 image of Términos Lagoon, 8 October, 1979, at the end of the rainy season. Band 5, for sediments and circulation. Photograph courtesy of Donald S. Graham (Tudor Engineering Company, San Francisco, California) and John M. Hill (Dept. Civil Engineering, Louisiana State University, Baton Rouge, Louisiana).

Figure 5

Landsat 2 image of Términos Lagoon, 16 January, 1978, during « nortes » season. Band 5, red for sediments and circulation. Photograph courtesy of Donald S. Graham (Tudor Engineering Company, San Francisco, California) and John M. Hill (Dept. Civil Engineering, Louisiana State University, Baton Rouge, Louisiana).

Figure 6

Landsat 2 image of Términos Lagoon, 16 February, 1979, it the end of the « nortes » season and during dry season. Band 5, red for sediments and circulation. Photograph courtesy of Donald S. Graham (Tudor Engineering Company, San Francisco, California) and John M. Hill (Dept. Civil Engineering, Louisiana State University, Baton Rouge, Louisiana).

« norte » conditions, which commonly prevail during the winter (Fig. 2). The turbidity (which is high-lighted in band 5) follows the patterns indicated. Circulation close to the island is evident, as are the intrusions along the SW and NE shores, and the two large whirls in the center of the lagoon. An ebb tide sequence on a somewhat cloudy October day is depicted in Figure 4. From this image the scale of the outlet plume at Puerto Real Inlet can be seen, as well as its deflection to the east (Graham *et al.*, 1981). Regarding the net flows of cases 3 and 4 (Fig. 3), it can be seen that either can produce the westward flow, although the transverse distribution of velocity is different. The net flux for case 4 (« nortes » season) is fascinating. The general flow patterns shows that the wind set-up in the southeastern part of the lagoon forces the net flux along the barrier island, while producing a local outflow along the southern shore (Fig. 3 case 3 ; Fig. 4).

The results of the cited studies and our observations indicate several factors : 1) a significant portion of the water entering Puerto Real Inlet leaves through Carmen Inlet, but the water entering through Carmen affects, at most, the western third of the lagoon ; 2) water flows in for a longer period (± 15 hrs.) than out during a typical tidal cycle at Puerto Real Inlet, while the reverse is true at Carmen Inlet ; 3) a freshwater buffer from the rivers generally prevents the saline water that enters Carmen Inlet from flowing directly along the southwestern shore.

Geological processes

There are two principal sediments sources in the lagoon : riverine fluvial sediments and calcareous sediment from the beach zone east of the lagoon (Phleger, Ayala-Castañares, 1971). These two sediment sources and the circulation pattern result in a strong sediment-type gradient.

Calcareous sands predominate in the Puerto Real Inlet area and along the back of the island, while silty sediments are found in the southern and western zones. The water is much clearer in the eastern part of the lagoon. Most of the sediments in the central lagoon contain about 50 % calcium carbonated ; at the river mouth the content is 30-35 %, and

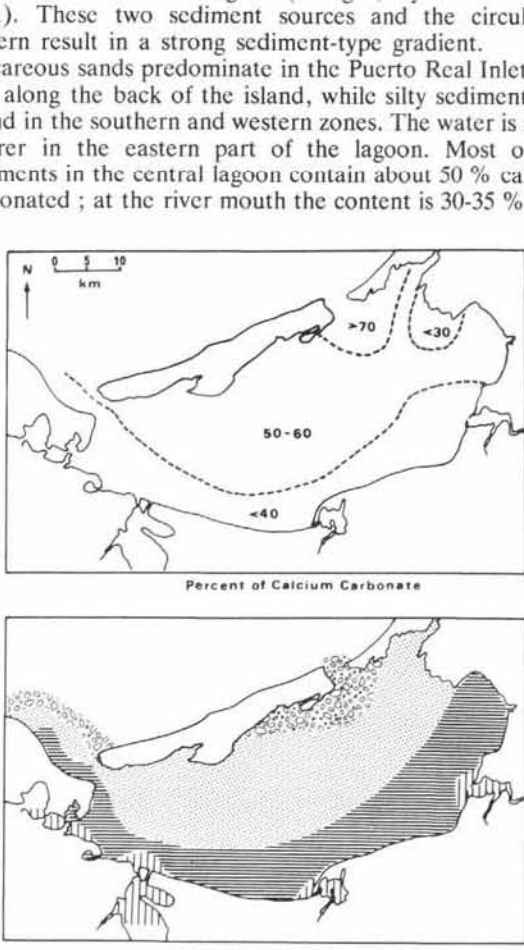


Figure 7

Distribution of calcium carbonate in sediments, and assemblages of foraminifera (adapted from Phleger, Ayala-Castañares, 1971).

near Puerto Real Inlet there is more than 70 % (Phleger, Ayala-Castañares, 1971 ; Fig. 7).
Two major inlet deltas are being formed. 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 sediments through that inlet. The outline of a similar delta, a relic, can be seen in the middle of the island (Fig. 1), indicating that Puerto Real Inlet will eventually close (Thom, 1969). The delta at Carmen Inlet is being formed on the Gulf of México side and is composed mainly of riverine sediments.

Lagoon chemistry

Salinity is higher in the eastern part of the lagoon and during the dry season. During the period from 1964 to 1966, Phleger and Ayala-Castañares (1971) recorded values from 25 to 36.5 ppt in the northeastern part of the lagoon near Puerto Real Inlet, and from fresh water to 28 ppt in the southern and western parts. Bravo Núñez and Yáñez-Arancibia (1979) measured values from 26 to 39 ppt in Puerto Real Inlet during 1976-1977. Salinities as high as 40 ppt have been recorded in semi-isolated small bodies of water during the dry season (Ley-Lou, 1979 ; Vargas Maldonado *et al.,* 1981) of 1976-1978. In 1972 the average salinity in the lagoon was 33 ppt in the dry season and 26 ppt in the wet season (Carvajal, 1973). In 1974, the values were 33.5 and 21.9 ppt, respectively (Botello, Mandelli, 1975).
Nutrient chemistry in the lagoon is determined by circulation, river flow, and biology. This is reflected in the results of Botello and Mandelli (1975), who measured a number of chemical parameters at 27 stations in May and November, 1974. May is the final month of the dry season, and peak river flow occurs just before November. Mean salinity during May and November was 33.5 and 21.9 ppt, respectively. The concentrations of PO_4-P and $NO_2 + NO_3 - N$ were 2.6 × and 2.2 × higher, respectively, in November ; however, the concentration of NH_4^+ was 3.8 × higher in May. Dissolved oxygen reached 147 % saturation in November and 99 % saturation in May. The higher PO_4 and $NO_2 + NO_3$ concentrations were obviously due to riverine input. This leads to higher gross and net aquatic primary productivity (to be discussed later), and thus to higher oxygen levels. Higher NH_4^+ during May is perhaps due to benthic regeneration combined with lower flushing, more reduced conditions, and biological activity. Plots of nutrient concentration *versus* salinity indicate a negative relationship during the wet season for phosphorus and to a lesser extent for $NO_2 + NO_3$ (Fig. 8). The three wet season points that fall above the general cluster occur in a zone where waters with low and high salinity mix and probably represent transient conditions. For $NO_2 + NO_3$, all stations with values above 10 μg at l^{-1} were sampled close to oyster reefs or *Thalassia* beds. They may reflect high community metabolism and low flushing.
In summary, salinity and riverine input seem to be correlated to phosphorus and the oxidized forms of inorganic nitrogen during the wet season. During the dry season, inorganic chemical levels seem to be more a factor of local conditions such as turbulence, sediment type, and biological activity. There is a decrease in both nitrogen and phosphorus with increasing salinity, but it is especially pronounced for nitrogen. This may reflect the fact the nitrogen is normally limited in estuaries (Postma, 1969 ; Mee, 1978). Supersaturation of oxygen during the wet season indicates net primary production.

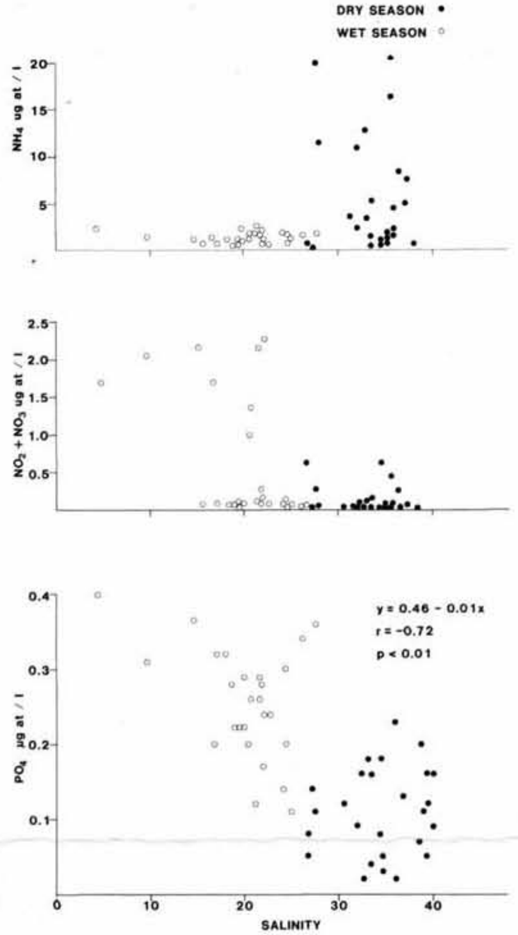


Figure 8
Distribution of and relationships between nutrient levels and salinity in Términos Lagoon (adapted from Botello, Mandelli, 1975).

BIOLOGICAL PROCESSES

Flora and primary production

The distribution of plant communities within the lagoon clearly reflects conditions of circulation, water clarity, and salinity (Fig. 1). Sea grasses occur in dense beds along the lagoon side of Carmen Island and especially on the delta of Puerto Real Inlet. Less vigorous stands grow along the eastern and southeastern shore. The most abundant species is *Thalassia testudinum.* Hornelas (1975) measured 382 g dry weight m^{-2} of total biomass of *Thalassia* along the inner side of Carmen Island. *Halodule wrightii* is the colonizing species, especially in the delta region. Red mangrove, *Rhizophora mangle,* is presently invading the shallower parts of the delta.
Diatoms dominate the net phytoplankton of the lagoon. Gómez-Aguirre (1974) identified 45 genera of phytoplankton. Thirty-four were diatoms, 4 dinoflagellates, 3 chlorophytes, 2 cyanophytes, and 2 rhodophytes. There were very few unidentified species of silicoflagellates and coccolithophores. Diatoms in the sediment samples are marine types and appear to be generally distributed throughout the lagoon (Silva-Barcenas, 1963).
Almost all of the lagoon is bordered by mangrove swamps which extend up the rivers and associated lakes to the limit of marine influence. Three species, *Rhizophora mangle* (red mangrove), *Avicenia germinans* (black mangrove), and *Laguncularia racemosa* (white mangrove) dominate the swamps, while *Conocarpus erectus* is encountered occasionally. Day *et al.* (1982) measured the composition of mangrove swamps on transects at the mouth of the Palizada River and at a site with high salinity on the lagoon side of Carmen Island. *R. mangle* was the most abundant at the river site. The abundance of *L. racemosa* was similar at both sites. Trees at the river site were on the average taller (15-25 m as compared to 5-10 m at the island site) and in general more robust.
The productivity of mangroves and chlorophyll levels are higher in riverine areas. Day *et al.* (1982) measured mangrove litter-fall at the mouth of the Palizada River (Boca Chica) and along a small high-salinity channel on the

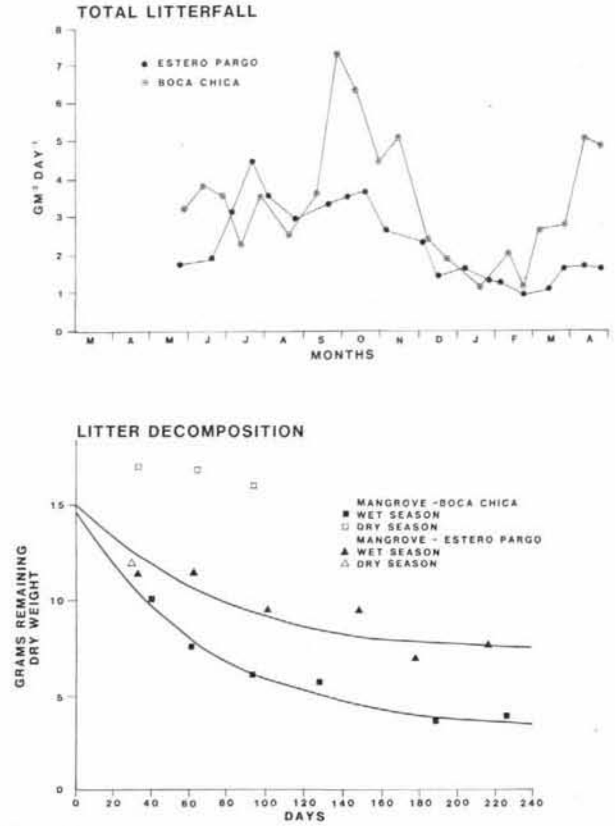


Figure 9

Total litter-fall and litter-bag decomposition at a low salinity riverine site (Boca Chica) and a high salinity site (Estero Pargo ; adapted from Day et al., *1982).*

lagoon side of Carmen Island (Estero Pargo). The highest total litterfall at both sites occurred during a season of rains and high river flow (Fig. 9). Total litter-fall was 1 365 g dry weight m^{-2} yr^{-1} at the riverine site and 986 g dry weight m^{-2} yr^{-1} at the high salinity site. Litter decomposition was 50 % more rapid at the riverine site (Fig. 9). Light-dark bottle oxygen productivity and chlorophyll concentration were measured at a number of sites throughout the lagoon by Day *et al.* (1982). Planktonic photosynthesis, respiration, and chlorophyll were higher in turbid, low-salinity, river-influenced areas. Riverine input affected mangrove productivity and chlorophyll levels. Litter bag decomposition measurements of mangrove leaves were also higher at the riverine site, with 24 % remaining after 6 months as compared to 50 % at the high-salinity site. Chlorophyll *a* concentrations ranged from 0.3-8.2 mg/m^3. There was a seasonal pattern in Chl *a* concentration, with the lowest mean values (± 1 mg/m^3) during the dry season (February-June) and the highest mean values (± 5 mg/m^3) during and following the rainy season. Phytoplankton productivity ranged from 0.87 to 5.5 g O_2 m^{-3} day^{-1}. The productivity of *Thalassia* was highest during the dry season and ranged in clear high-salinity waters from 0.68 to 4.6 g cm^2 day^{-1} : Benthic microalgal productivity was low (0.3 g cm^2 day^{-1}) and limited to a narrow zone near shore. Overall gross production in the lagoon was 2.6 g O_2 m^{-3} day^{-1}.

This is the same area for which Botello and Mandelli (1975) reported high nutrient levels (see Fig. 8). Gómez-Aguirre (1974) found the highest volumes of net phytoplankton in the passes and the lowest volumes in low-salinity areas. This may indicate that most of the metabolism and chlorophyll are associated with nanoplankton, a finding similar to those in other areas (Williams, 1973). Near the river mouths there is a strong seasonal pattern for chlorophyll which correlates with river flow ; this pattern is less evident in areas with high salinity.

Benthos

The distribution of foraminifera in the lagoon reflects circulation and sediment patterns. Four distinct assemblages were reported by Phleger and Ayala-Castañares (1971 ; Fig. 7). A mixed fluvial assemblage occurs in and near the river mouths. Open gulf foraminifera are found in Puerto Real Inlet and along the southeastern side of Carmen Island, and lagoon foraminifera occur in the Gulf at Carmen Inlet. The living population ranges from about 250 to 900 specimens/10 cm^2. These standing stocks suggest relatively high rates of organic production in much of Términos Lagoon, probably as a result of the high river runoff, which carries into the basin the trace materials that encourage the development of these organisms.

The micromollusca in the lagoon are typical of saline bays and nearshore areas and are somewhat more related to open-ocean assemblages than to those in a closed bay. Gastropods are more abundant than pelecypods, and the assemblage is fairly uniform over the entire area (García-Cubas, 1963). García-Cubas (1981) found at least 171 macromollusca species : 96 gastropods, 72 pelecypods, 2 cephalopods, and 1 polyplacophoran. There is a pattern of distribution, diversity and frequency ; it is possible to identify and characterize five faunal assemblages, highly correlated with salinity, substrate, and primary producers in the different habitats : a) limnetic areas ; b) fluvial-lagoon systems ; c) inner lagoon associated with Términos Lagoon ; d) Términos Lagoon central area ; and e) marine-influenced areas. Species with commercial importance in the area are : *Rangia flexuosa, Rangia rangianella cuneata,* and *Polymesoda carolineana* (in fluvial-lagoon systems) ; *Crassostrea virginica* (in inner lagoons associated with Terminos Lagoon) ; *Crassostrea rhizophora* (in marine-influenced areas) ; *Melongena melongena, Pleuroploca gigantea,* and *Strombus alatus* (in marine-influenced areas).

Thirty-nine species of ostracos were recorded in the lagoon by Morales (1966). Because of the wide range in water salinity, the ostracod fauna consists mostly of euryhaline species. Three moderately well defined ostracod groups characterize the oyster bank, lagoon, and washover delta. Approximately half the species of ostracods identified in Términos Lagoon were found at stations where there was rapid transition from clear water rich in submerged vegetation to turbid water. Morales (1966) reported that the ecological requirements differ widely from one species to another within a genus, so that using a single genus as an environment indicator may result in inaccuracies in paleoecologic work.

Polychaetes are typical of saline bays and are distributed in three assemblages controlled principally by salinity and sediments (Marron, 1975) : a) west zone ; b) central zone ; and c) east zone. Typical species in the west zone are *Cossura candida* and *Prionospio pinnata* ; in the central zone, *Onuphis quadricuspis* and *Diopatra cuprea* ; and in the east zone, the species found are *Sigambra bassi, Tharyx parvus,* and *Antionella sarsi.* The three zones are highly correlated with salinity, turbidity, and sediment type.

Porifera and echinoderms, which are essentially marine fauna occur in the lagoon in areas with great and persistent marine influence. There are numerous sponges that occur in association with sea grasses and macroalgae, i.e., *Dysidea etherea, Dysidea fragilis, Pellina coeliformis, Haliclona hogarthi, Ptilocaulis marguezii, Placospongia carinata, Anthosigmella varians,* and *Chondrilla nucula* (Núñez, 1979). The same ecological relationship is true for echinoderms ; and Caso (1979) reported the following species ; *Luidia clathrata, Echinaster serpentarius, Ophiotrix angulata, Ophiotrix suensoni, Ophictis savignyi, Ophiophragmus wurdemanis, Amphiodia guillermosoberoni, Ophioderma cinereum, Ophiolepis elegans, Arbacia punculata, Lytechinus variegatus,* and *Echinometra lacunter.* Both sponges and echinoderms are abundant in Puerto Real Inlet and on the

lagoon side of Carmen Island, while epibenthic animals are found frequently on mangroves roots (Espinoza, 1980).
Numerous marine and estuarine species of decapoda occur in Términos Lagoon. The dominant species are those that can be termed slow-swimming nekton, i.e., *Callinectes similis, Callinectes sapidus, Callinectes bocurti,* and four species of penaeid shrimp (Ibarra, 1979 ; Signoret, 1974). *Penaeus setiferus* is most abundant in the southwestern side of the lagoon, *Penaeus aztecus* in the west side of the lagoon near Carmen Inlet, *Penaeus duorarum* in the east side of the lagoon near Puerto Real Inlet, and *Xiphopeneus kroyeri* in the west side and in Carmen Inlet. The distribution and size of the population indicate that migration into the lagoon occurs through both inlets but mainly through Carmen Inlet (Signoret, 1974).

Nekton

Nekton are a very conspicuous and important component of the fauna of Términos Lagoon and Campeche Sound (Bravo Núñez, Yáñez-Arancibia, 1979 ; Amezcua Linares, Yáñez-Arancibia, 1980 ; Vargas Maldonado *et al.*, 1981 ; Lara Domínguez *et al.*, 1981 ; Sánchez-Gil *et al.*, 1981 ; Yáñez-Arancibia *et al.*, 1981 ; 1982 ; Aguirre León *et al.*, 1982 ; Diaz Ruiz *et al.*, 1982). This subject was treated in detail by Yáñez-Arancibia *et al.* (1980). They discussed the ecology for 121 fish species : 15 species (12 %) had a broad distribution and composed 78 % of the total number ; 12 species (10 %) were permanent residents ; 55 species (45 %) used the lagoon as a nursery ; and 55 (45 %) were occasional visitors ; the latter penetrations are probably either of a trophic nature or are linked to reproductive cycles. The presence of these species in estuarine waters is variable in time (Yáñez-Arancibia *et al.*, 1981), as it is often transient in nature and limited to particular areas and periods of the year (Yáñez-Arancibia *et al.*, 1982).
22 % of the fish species were herbivores, detritivores or omnivores ; 51 % were primary carnivores, and 26 % were higher carnivores. Organic detritus is a major dietary component of the first-order consumer fishes. Small crustaceans, molluscs, and polychaetes as well as some small first-order consumers serve as the main diet of the second-order consumers. The top carnivores feed largely on the first and second-order consumer fishes and macrobenthic forms. More than 50 % of the fish species are second-order consumers. These species showed the greatest affinity for a particular habitat (Yáñez-Arancibia *et al.*, 1981). This is not surprising since most of these species are demersal and many have fairly specific feeding habits ; thus, they would correlate more closely with particular habitats than would higher consumers that range widely over the lagoon. Also, because of their numerical abundance and habitat specificity, second-order consumers are more important in determining characteristics of particular fish communities (Yáñez-Arancibia *et al.*, 1981 ; 1982).
Cluster analysis was used to group fishes according to faunal similarity (Yáñez-Arancibia *et al.*, 1980 ; 1981). The groups corresponded to major differences in the physical makeup of the lagoon. Southern and northern shore groups of fishes were shown (Fig. 10 and 11). There was a consistent pattern of migration within the lagoon reflecting prevailing currents. The season of maximum juvenile influx from the sea (September to November) was during the time of maximum river flow and occurred primarily through Puerto Real Inlet (Yáñez-Arancibia *et al.*, 1982).
Fish productivity was 7.4 g wet weight m^{-2} $year^{-1}$ in beds of *Thalassia* near Puerto Real Inlet (Yáñez-Arancibia, 1980), and 8.5 g m^{-2} $year^{-1}$ in the fluvial-lagoon systems

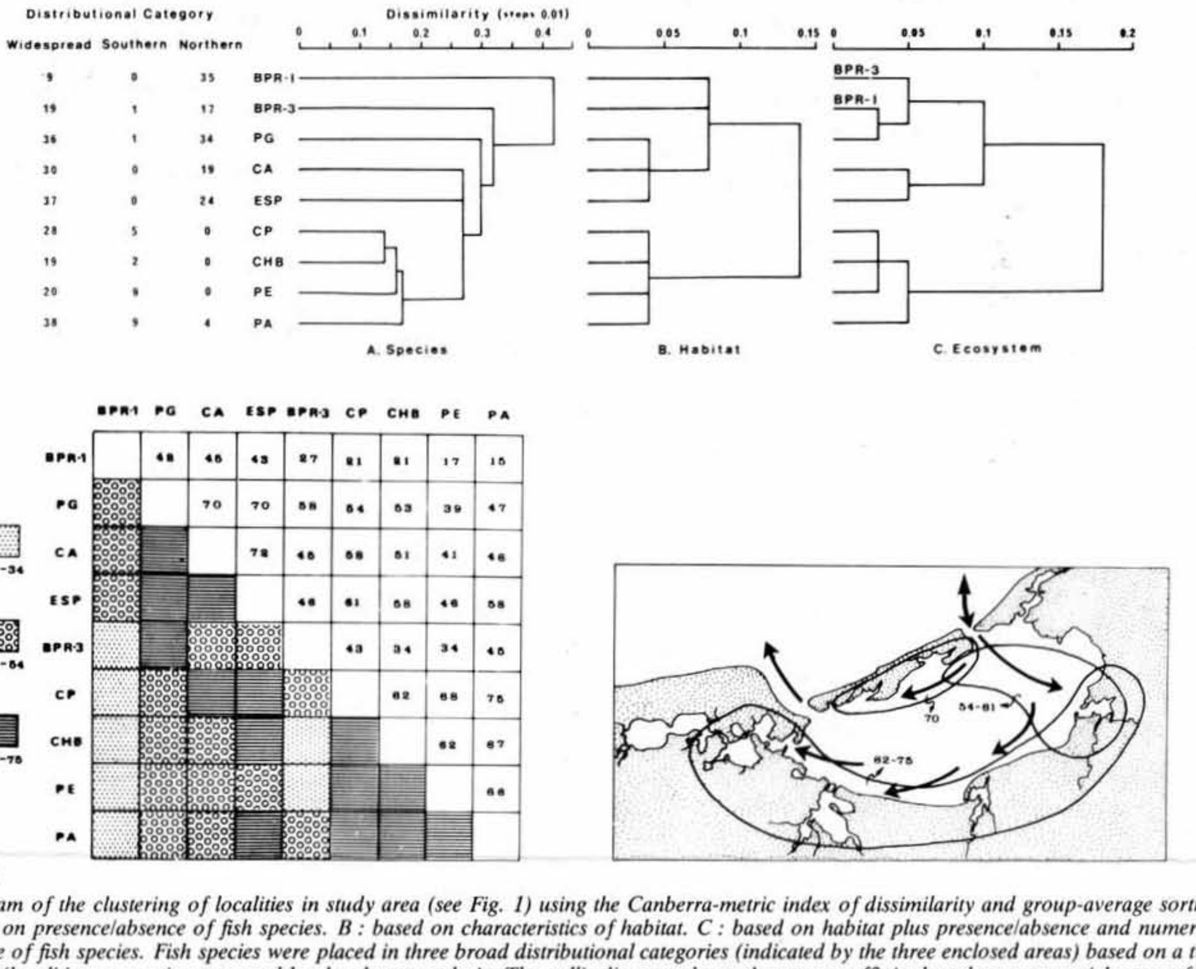


Figure 10

Dendrogram of the clustering of localities in study area (see Fig. 1) using the Canberra-metric index of dissimilarity and group-average sorting. A : based on presence/absence of fish species. B : based on characteristics of habitat. C : based on habitat plus presence/absence and numerical abundance of fish species. Fish species were placed in three broad distributional categories (indicated by the three enclosed areas) based on a two-way table (localities vs. species generated by the cluster analysis. The trellis diagram shows the present affinity based on presence/absence of fish species. The dendrogram and trellis diagram indicate a probable pattern of migration whithin the lagoon (indicated by arrows) reflecting prevailing currents and the diversity of estuarine habitats (adapted from Yáñez-Arancibia et al., *1980).*

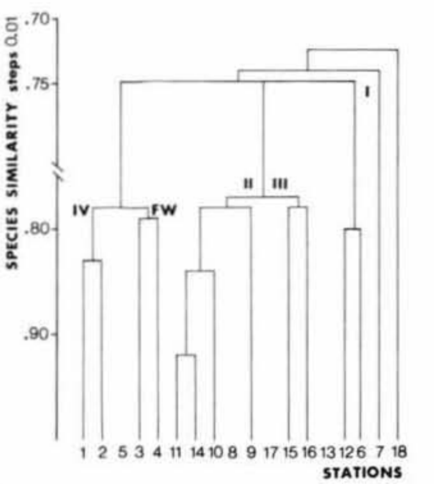


Figure 11

Dendrogram of the clustering of localities in study area (see Fig. 12 for sampling station) using the simple matching coefficients index of similarity and the single linkage clustering method. The dendrogram reflects high statistical correlation of fish population structure with the ecological habitat of the ecosystem, illustrated in Figures 1 and 12. 35 425 fish individuals were processed from July 1976 to April 1981, including 134 fish species, 27 species (20 %) have a broad distribution and comprise 88 % in number and 89 % in weight of total catches (after Yáñez-Arancibia et al., *1981 and unpublished data).*

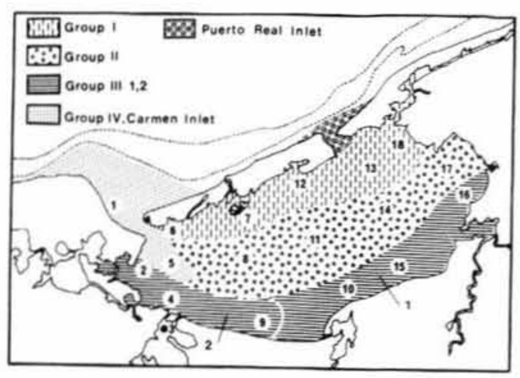
(Amezcua Linares, Yáñez-Arancibia, 1980). Diversity and biomass indices reflected changes in number of species and individuals during the year, and some were highly correlated with temperature and salinity. Mean biomass at different sampling stations ranged from 0.95 to 4.2 g wet weight m^{-2} and H′ from 0.4 to 3.2. Fishery research in the lagoon is complicated by 1) the large number of species present in a community (134 fish species, Yáñez-Arancibia *et al.*, 1981), and 2) the difficulties of determining fish ages and growth rates. In the absence of true production data, yield expressed as weight/area is often used as an index of production. In general, fishes in this area grow faster and have shorter life cycles than many fish in temperate climates. The growing season extends over the whole year and recruitment occurs throughout most of the year. Ecologically complementary species help increase yields ; many species can withstand poorly oxygenated waters ; and food is generally available. Typical fish species of Términos Lagoon with broad distribution in all subsystems are : *Chloroscombrus chrysurus, Cynoscion nebulosus, Chaetodipterus faber, Arius felis, Arius melanopus, Bairdiella chrysura, Citharichthys spilopterus, Eucinostomus gula, Sphoeroides testudineus, Anchoa mitchilli* and *Diapterus rhombeus.* At the same time, particular fish species are also distributed in particular habitats inside the lagoon (Fig. 10, 11 and 12).

CONCLUSIONS

1) Two inlets connect the lagoon with the sea, and there is a strong net westerly flow through the lagoon caused by prevailing easterly winds. This circulation pattern leads to strong semi-permanent gradients in salinity, turbidity, nutrient levels and sediment types, which result in assemblages of foraminifera, assemblages of benthic macrofauna, and migration of fish and shrimp.

2) There are three climatic seasons : the rainy season from June to September ; the season of « nortes », or winter storms, from November into March ; and the dry season from February to May. The southwestern part of the lagoon receives more than 50 % of the freshwater inflow.

3) There is a high diversity of estuarine subsystems in the lagoon, including low salinity and brackish-marine mangrove, swamps, sea grasses, marsh grasses, areas of high sedimentation, oyster reefs, and oligohaline areas.



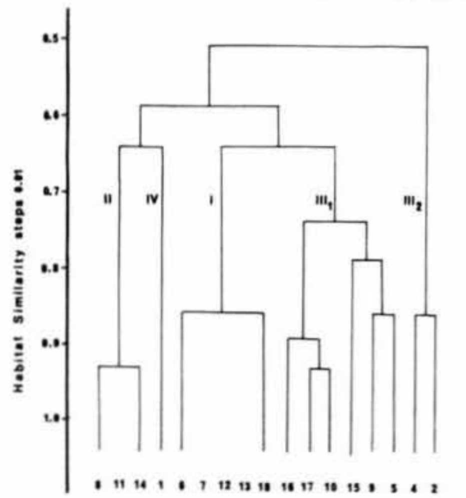


Figure 12

Dendrogram of the clustering of localities in study area using the simple matching coefficients index of similarity and the single linkage clustering method, based on annual environmental characteristics of the ecosystem (Table). The dendrogram reflects five (I to IV and Puerto Real Inlet) groups of stations which were defined as different habitats (after Yáñez-Arancibia et al., *1981 and unpublished data).*

4) There are two principal sediments sources in the lagoon : riverine fluvial sediments and calcareous sediments from the beach zone east of the lagoon.

5) Salinity is higher in the eastern part of the lagoon and during the dry season. Nutrient chemistry in the lagoon is determined by circulation, river flow, and biology. Salinity and riverine input are the main controlling factors for phosphorous and oxized forms of inorganic nitrogen during the wet season. During the dry season, the levels of inorganic chemicals seems to be caused by local conditions such as turbulence, sediment type, reducing state, and biological activity.

6) The productivity of both phytoplankton and mangroves is higher in riverine areas. The supersaturation of oxygen in some areas during the wet season also indicates high rates of net production.

7) Benthic populations are related to different subsystems in the lagoon and are controlled by salinity, river flow, turbidity, and sediment types.

8) The analysis of nekton affinity shows a high degree of statistical significance with habitats within the lagoon. In colonizing the lagoon, fish migrate mainly through Puerto Real Inlet, while shrimp on the other hand, seems to migrate mainly through Carmen Inlet.

9) There is relatively little commercial fishing in the lagoon, but the largest commercial fishery in México is in Campeche Bay. The lagoon is important to the fishery as a nursery and feeding area for various fish and shrimp populations.

10) This paper has described the ecology of Términos Lagoon in terms of biological processes adapted to the physical and chemical environment. Because of the complexity of the lagoon ecosystem, we believe that major efforts should be directed to modelling water resources.

Table
Main ecological characteristics of subsystems in Términos Lagoon.

	Subsystems (Fig. 12)	Annual salinity ($\overline{X}$ ppt)	(Cv %)	Transparency ($\overline{X}$ %)	(Cv %)	Water influence (sea)	(freshwater)	Observations
I	Puerto Real Inlet and Carmen Island Inner area	29	22	50	42	4+	1+	Strong sea water influence. Related with Habitat II during dry season. Sand and silty-clay with 30 to 70 % $CaCO_3$. Macroalgae, sea grasses and mangrove swamps.
II	Central basin	25	22	43	49	3+	2+	Transition zone. Related with Habitat I during dry season and with Habitat III in « nortes » and rainy season. Muddy with fine sand and clay-silt with 30-40 % $CaCO_3$. Macroalgaes.
III	Fluvial-lagoon systems							Strong riverine influence :
	Eastern (III. 1)	23	23	45	43	2+	4+	Related with Habitat II during dry season. Silty-clay with fine sand with 20-30 % $CaCO_3$. Seagrasses, mangrove swamps and oyster reefs.
	Western (III. 2)	20	36	29	47	1+	4+	Related with Habitat IV during dry season. Silty-clay with 10 to 30 % $CaCO_3$. Mangrove swamps and oyster reefs. During « nortes » and rainy season III. 1 and III. 2 are related with Habitat II.
IV	Carmen Inlet	25	29	24	36	3+	3+	Variable zone due to marine and freshwater interactions. Related with III. 2 during dry season and with Habitats I and II during « nortes » and rainy seasons. Clay-silt with lesser than 30 % $CaCO_3$. Mangrove swamps and macroalgae debris.

$\overline{X}$ = average, Cv = Coefficient of variations.

These models should simulate climatic conditions as derived statistically from empirical data for the lagoon. The index conditions of the lagoon that predict adverse effects should be made available to planners so that specific action programs can be designed. Important results have shown quantitatively four (I to IV and Puerto Real) main ecological subsystems (Table, Fig. 10, 11 and 12) ; these results open the way for studies which in the near future will provide : 1) an identification and quantification of ecological connections between Términos Lagoon and the fisheries ; 2) implementation of a hydrodynamic-ecological model of the lagoon ; 3) prediction of changes which may occur due to human activities ; and 4) development of a series of conceptual models for the analysis of ecological and economic connections in the Términos region.

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