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FUNCTIONAL GROUPS AND ECOLOGICAL BIODIVERSITY, IN TERMINOS LAGOON, MEXICO*

Grupos Funcionales y Biodiversidad Ecológica en la Laguna de Términos, México

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ABSTRACT

An integrated approach, as required to comprehend the complexity of tropical coastal biodiversity (374 flora species, and 1468 macro fauna species at the study site) is discussed within a framework of lagoon-estuarine system gradients of habitats, of forcing functions (or *production mechanisms*), and seasonally stable assemblages of biota with similar biological behavior and ecological strategies (or *functional groups*). These assemblages play an important ecological role by coupling life-history strategies with the environmental variability and estuarine gradients. The complementarity of planktonic and macrofloral primary production and their coupling with secondary production are also discussed and we conclude that sequential pulsing is one of the functional processes that sustain high estuarine production and species diversity. The concept of *seasonal programming* describes how the functional groups of estuarine primary producers interact, and how functional groups of fish population assemblages use the lagoon habitats in time and space to reduce the effects of competition and predation, to enhance food availability and to secure their recruitment.

Key words: tropical estuary, functional groups, seasonal programming.

RESUMEN

Para comprender la complejidad de la biodiversidad costera tropical (374 especies de flora y 1468 de especies de macro fauna en el área de estudio) se requiere de una aproximación integral y esto debe ser discutido en el marco de un sistema lagunar-estuarino que presenta diversos gradientes de habitats, diferentes funciones de fuerza (o mecanismos de producción) y numerosos conjuntos bioticos -estacionalmente estables- que tienen comportamiento biológico y estrategias ecológicas similares (o grupos funcionales). Estos conjuntos juegan un importante papel ecológico vinculando las estrategias del ciclo de vida con la variabilidad ambiental y los gradientes estuarinos. Complementariamente se discute la producción planctónica y de la macroflora y su vínculo con la producción secundaria, concluyendo que los pulsos estacionales son el proceso funcional que sostiene la alta productividad estuarina y la diversidad de especies. El concepto de "programación estacional" describe como los grupos funcionales de conjuntos de poblaciones de peces usan los hábitats lagunares-estuarinos en tiempo y espacio para reducir los efectos de competencia y predación, favoreciendose ante la abundante disponibilidad de alimento y asegurando su reclutamiento.

Palabras clave: tropical, grupos funcionales, programación estacional.

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Introduction

Biodiversity is usually defined at three levels, i.e., genetic, species/population, and ecosystem (Ray and McCormick, 1992). The biodiversity of coastal environments is generally high in all respects; however information on tropical lagoon-estuarine ecosystems is usually not as detailed as required, given the variety of responses to environmental changes, the diverse space and time scales with which organisms interact with their habitats, and the general lack of information on these areas as compared to temperate systems (Longhurst and Pauly, 1987). The diverse biological, ecological and physical interactions which occur within tropical estuaries and the adjacent ocean produce a highly dynamic and variable mosaic of ecosystems (Yáñez-Arancibia *et al.*, 1991).

From an ecological standpoint, the term biodiversity can have several meanings when applied to tropical lagoon-estuarine ecosystems (Day and Yáñez-Arancibia, 1982). It can mean that there is a high diversity of species, or that there is a high diversity of environmental factors, habitats, connections in the food webs, and a high diversity of couplings, both internally and with neighboring systems. Also the diversity of forcing functions effectively modulating ecosystem functioning is high, and include wind, tide, rivers flows, littoral currents, sediment input, and others. Moreover there is a high diversity among primary producers and consumers, many with different types of life history. Grassle *et al.* (1991) and Lasserre (1992) pointed out that large-scale experiments are needed on whole system responses and on carefully selected tropical sites in order to identify a new paradigm for understanding coastal-marine diversity.

More information is needed on tropical estuaries for their complexity and biodiversity to be understood. Thus, in this paper, we focus on the functional biodiversity of these ecosystems, and describe the diversity of forcing functions; using the habitats and the seasonality of functional groups, i.e., primary producers and consumers, in Terminos lagoon, as example (see Fig. 1).

The lagoon-estuarine system

Terminos Lagoon is located in the southern Gulf of Mexico at 18° N, were tropical climatic conditions occur: a rainy season from June to September, winter storms ("nortes") from October to February, and a dry season, from February to May. Terminos Lagoon is the most conspicuous part of the Usumacinta Delta, formed by a river with the second highest discharge in the Gulf of Mexico after the Mississippi. The area is one of the world's best known tropical estuaries (Yáñez-Arancibia and Day, 1988; Yáñez-Arancibia *et al.* 1988, 1993a; Rojas Galaviz *et al.*, 1992). In terms of functional characterization, this area of 2500 km^2 can be divided into three regions (Fig. 1), following Kjerfve (1989, 1993) and Yáñez-Arancibia (1987), as follows:

1) ***A tidal river zone***. Fluvial-deltaic zone characterized by lack of ocean salinity, but subject to tidal rise and fall of water level;

2) ***A mixing zone***. Characterized by water mass mixing and existence of strong gradients of physical, chemical and biotic features, and reaching from the tidal river zone to the seaward location of river mouth bar or ebb-tidal delta;

3) ***A near shore turbid zone***. In the near-shore ocean, between the mixing zone and the seaward edge of the tidal plume at full ebb tide.

This subdivision of Terminos Lagoon differs from those previously proposed in that it recognizes and includes nearshore marine components that are estuarine in character, and implicitly considers the five main habitats in the system as a whole, described, by Yáñez-Arancibia and Day (1982).

Habitat diversity

The semi-permanent gradients from the tidal wetlands to the estuarine plume on the inner shelf and adjacent sea leads to the identification of seven main habitats in the study area, as discussed by Yáñez-Arancibia and Day (1988) and summarized in Figure 1:

The fluvial-deltaic systems in the southern littoral zone of Terminos Lagoon have very low salinity, high turbidity, high nutrient concentrations, silty-clay sediments, *Crassostrea virginica* reefs, riverine mangrove forests, and in some areas of clear water, submerged fresh water vegetation. ***The central basin***, which is the transition zone between marine conditions and the zone influenced by the rivers, is characterized by mesohaline salinity, medium water transparency, silty-clay to sandy sediments and a typical estuarine phytoplankton production system including some benthic macroalgae. ***The inner littoral zone of El Carmen Island***, is dominated by *Thalassia testudinum* and fringe mangrove habitat with near

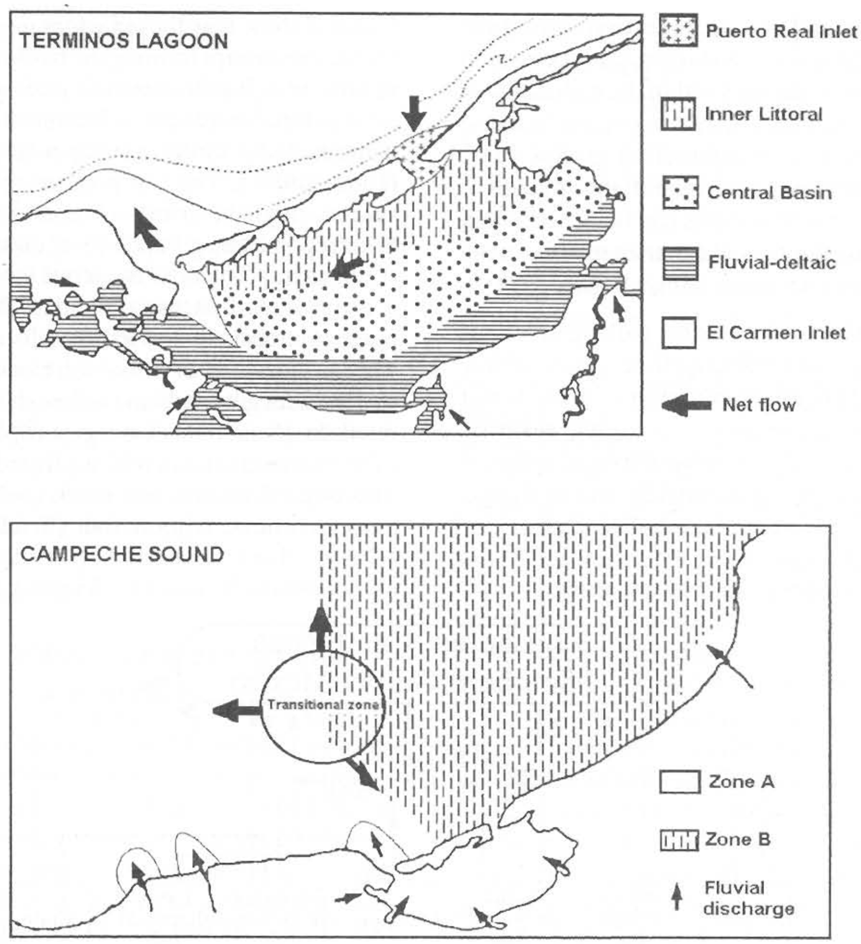

Figure 1. Habitat diversity in the estuarine ecosystem of Terminos Lagoon (above) and the adjacent Campeche Sound (below), showing the different habitats (or ecological subsystems). The inner shelf shows Zones A and B, associated with El Carmen and Puerto Real inlets respectively. The lagoon-estuarine system consists of five main habitats related to water circulation, river discharge, salinity and water depth. (After Yáñez-Arancibia and Day, 1988).

marine salinity, high water transparency, sandy sediments and a high diversity of both benthic and nektonic consumers. ***The Puerto Real Inlet***, where there is a net flow of Gulf water into the lagoon, is characterized by calcium carbonate sediments, clear waters and extensive seagrass beds. ***El Carmen Inlet***, the estuarine connection with the shelf, has a net transport from the lagoon to the ocean, producing an extensive estuarine plume of medium salinity on the shelf. There are silty-clay sediments and highly turbid waters without submerged vegetation in this area.

In Campeche Sound adjacent to Terminos Lagoon, there is a ***terrigenous subsystem (Zone A)*** strongly influenced by estuarine waters with medium water transparency, no benthic vegetation and with a high content of organic matter in the silty-clay-sandy sediments; and a ***calcareous subsystem (Zone B)*** with clear water of full salinity, calcium carbonate sand sediments, and with seagrass beds and macroalgae.

Diversity of forcing functions

Within the physical framework provided by the wetlands, the lagoon-estuarine environment and the continental shelf; the living resources maintain a complex biological organization in the study area. Figure 2 illustrates the complexity of the system (which couples the fish resources with the coastal ecological processes) and the biological production mechanisms (i.e., the forcing functions modulating the structure and functioning of the ecosystem).

Functionally, fish resources are related to ecological interactions in the coastal zone, and changes in fish resources in space and time are reflection of the natural variability of physical and biological processes in that zone. However, changes within the high diversity ecosystem are generally difficult to predict, because of the large number of interacting groups (e.g., competition, predation). Still, quantitative models of aspects of the resource systems can be constructed, e.g., for managing the coastal fisheries relying on the fish resource base (Arreguín-Sánchez *et al.*, 1992).

The most conspicuous factors (or forcing functions in terms of this paper) affecting fishery production, are: 1) physical/chemical conditions in the water column i.e., transparency, nutrients, salinity, temperature, 2) latitude, 3) bathymetry and sediment types, 4) meteorology and climate, 5) river discharge, 6) tidal range, 7) the area of coastal vegetation i.e., marshes, swamps, lagoons and estuaries, and 8) the interactions between the estuaries and the sea.

Figure 2 show how these factors interact to support the various groups forming the basis of fisheries in the region, in a highly dynamic interactive system in various time/space scales. The block of small pelagic fishes includes sardines (Clupeidae) and anchovies (Engraulidae). The top predator block comprises sharks, dogfish, grunts (Pomadasyidae), snooks (Centropomidae), groupers (Serranidae) and snappers (Lutjanidae). The small demersal fish block (<15 cm) is comprised of flatfish (Soleidae, Bothidae), silver perch (Gerreidae), and scorpion fish (Scorpenidae). The medium-sized demersal fish block (between 15-25 cm) includes gilt heads and yellow jacks (Carangidae), croakers (Sciaenidae), porgies (Sparidae), puffers (Tetraodontidae), sea robins (Triglidae) and others. The large demersal fish block (>25 cm) includes among others, ribbon fish (Trichiuridae), rays (Dasyatidae), seacatfish (Ariidae), lizard fish (Synodontidae), croakers (Sciaenidae) and others.

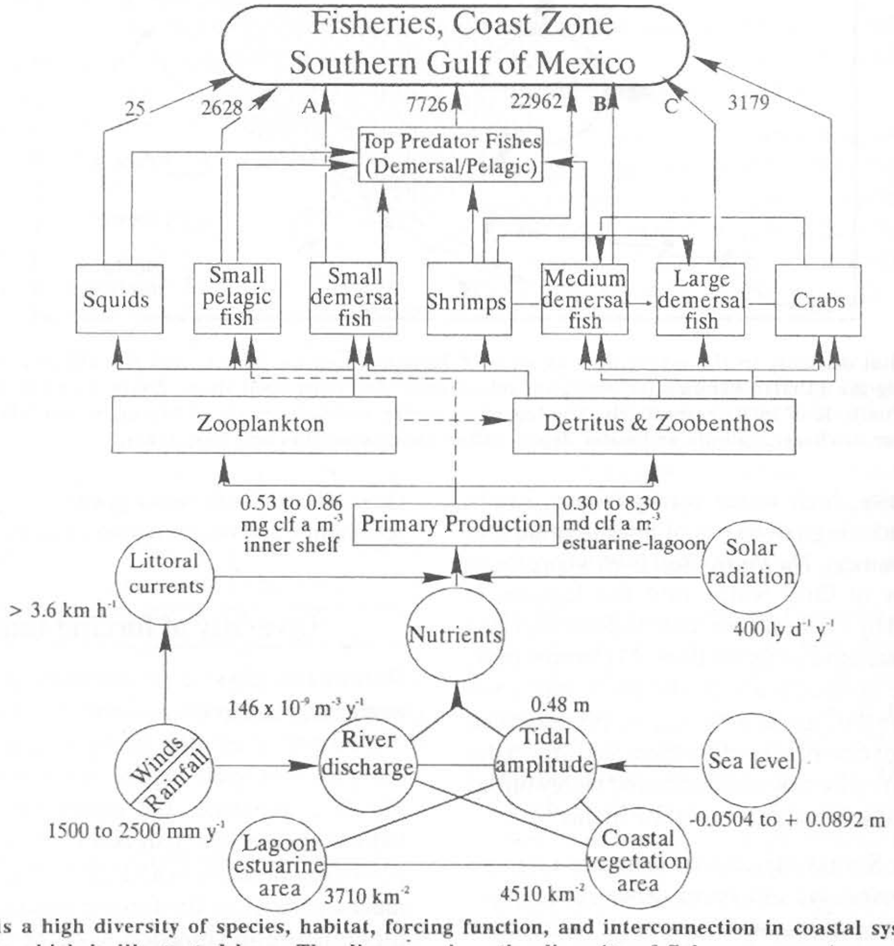

Figure 2. There is a high diversity of species, habitat, forcing function, and interconnection in coastal systems, such as Terminos Lagoon which is illustrated here. The diagram show the diversity of fishery groups (squares), and their interrelationship with coastal and biological processes, and production mechanisms, (forcing function, indicated by circles) in the lower part of the diagram. The catches are in metric tons per year. Values of fisheries catch are given in tons/year and the sum of the flows in A,B, and C is 34 x 10^5 tons/year. (After IOC-UNESCO, 1984).

Species diversity

Because of its high biological diversity, in terms of both habitats and species, Terminos Lagoon is at present being proposed to become an "ecologically protected coastal ecosystem" under the framework of the Mexican *"Federal Law for Ecological Equilibrium and Environmental Protection"*, (Yáñez-Arancibia *et al.*, 1993b). Results of the last 20 years of research on its valuable wildlife resources led to the information summarized as follow. The list of total species is included in the above cited report, consist of 374 plant species (of which 3 are endangered and 64 are endemics), and 1468 species of macrofauna (of which 510 are invertebrates and 958 are vertebrates). From the land vertebrates, 67 species are endangered, 30 are endemics, 22 are under protection and have economic value.

Diversity of functional groups and seasonality

Terminos Lagoon has a number of important functional groups, both of primary and secondary producers (or consumers). A *functional group* is a conspicuous assemblage of biota with similar biological behavior and ecological strategies. These assemblages, which contain a number of different species and are characteristic elements in the structure and functioning of the ecosystem play an important ecological role by the coupling life-history strategies of their constituent species with the environmental variability and estuarine gradients.

Functioning of primary producers

The main ecological role of primary producers is to provide food via photosynthesis. In tropical estuarine and lagoon systems, some primary producers also provide important critical habitats: mangrove swamps, submerged grass beds. The diversity of *functional groups* of primary producers can be high in estuarine ecosystems (Rojas Galaviz *et al.*, 1992). Salinity gradients, turbidity, sediments, nutrients, and tidal range, control the distribution of primary producers, in the three above mentionned regions as follows:

1) tidal freshwater delta areas with riverine mangrove swamps, submerged freshwater aquatic vegetation, and fresh water marshes. In this areas, organic carbon in river input provides an important additional food source;
2) the central basin with salinity ranges from 10 to 25 ‰, and where phytoplankton are the dominant primary producers;
3) shallow intertidal and subtidal zones with high marine influence (> 25 ‰) dominated by fringing mangroves and submerged seagrass beds.

These regions includes the habitats in Figure 1. Each of these is dominated by specific primary producers forming functional groups. The importance of these groups is that they represent a food source for estuarine and coastal consumers, besides acting, as the case might be, as a critical habitats for a great number of organisms during various life stages, and regulating important components of the estuarine chemical cycles (Odum, 1988; Day *et al.*, 1989; Rojas Galaviz *et al.*, 1992).

Figure 3 shows the clear seasonality of the pulses of abundance and productivity of different primary producers functional groups. Primary production is generally high during all year, but each functional group has a different seasonal pattern, in relation to the environmental parameters specific to each gradient. The main productivity peak of mangroves occurs during the rainy season and may be related to freshwater input (nutrients and lowered salinity). For submerged grasses, the highest biomass and productivity generally occur during the dry season, while the lowest biomass values occur during the rainy and "nortes" seasons. Both marine and freshwater grasses start their productivity pulse at the end of the "nortes". Maximal productivity of freshwater macrophytes occur in February and slowly declines during the dry and rainy seasons, while peak seagrass biomass and productivity occur during the dry season (March-May). Phytoplankton productivity and biomass in the mid-lagoon has a seasonal pattern opposite that of the aquatic macrophytes. Planktonic primary productivity and chlorophyll *a* levels increase through the rainy season, reaching a peak during the beginning of the "nortes" season from September until December. Aquatic primary productivity in mangrove bordered tidal channels is highest during the dry season. Day *et al.* (1982, 1988 a, b) showed that dissolved organic matter exported from mangrove stimulated aquatic primary productivity.

These results suggest that high year-round production in Terminos Lagoon is maintained by sequential pulses of different primary producers, this seasonal programming being one of the functional processes sustaining high estuarine production.

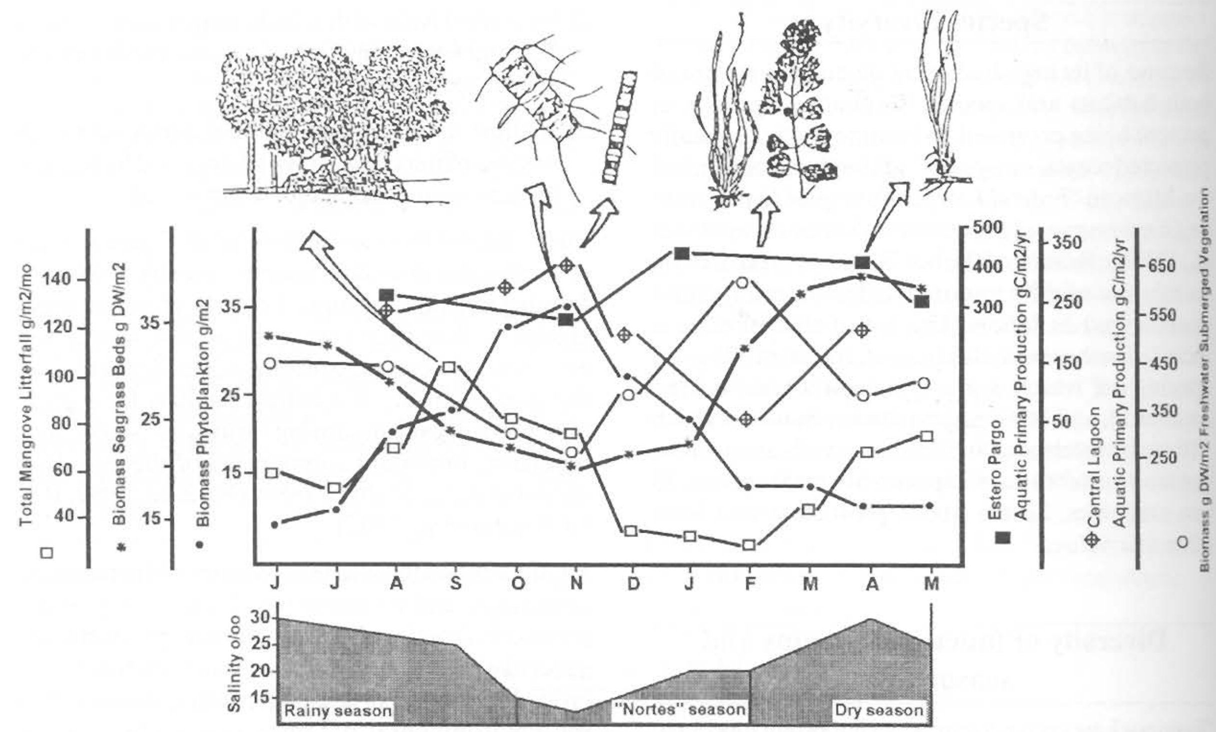

Figure 3. Seasonal patterns of primary production and plant biomass of the different functional groups of primary producers in Terminos Lagoon. The illustration above the graph are common representatives of different primary producer groups (left to right) black (*Avicennia germinans*), and red (*Rhizophora mangle*) mangroves; two genera of diatoms (*Chaetoceros, Skeletonema*), an important gropus of estuarine phytoplankton; two species of freshwater submerged aquatic vegetation, *Vallisneria americana* and *Cabomba palaeformis;* and the dominant marine seagrass of the lagoon, *Thalassia testudinum*. The decrease of salinity (below) during the rainy and "nortes" seasons corresponds to the period of high river flow. And high input of river borne organic matter (From Rojas Galaviz *et al.*, 1992).

Functioning of macro-consumers

The primary producers discussed above and the dynamics of the ecological system summarized in earlier sections, sustain a high diversity of nektonic species. There are clear fish-habitat relationships and a sequential use of the gradients in various time/space scales (Yáñez-Arancibia and Lara-Domínguez, 1988; Yáñez-Arancibia *et al.*, 1988, 1993a).

More than 150 fish species in different functional groups occur in Terminos Lagoon (Yáñez-Arancibia *et al.*, 1980) and there are more than 250 species in different functional groups from Campeche Sound, i.e., the adjacent continental shelf (Yáñez-Arancibia *et al.*, 1985; Sánchez-Gil and Yáñez-Arancibia, 1986).

The widespread use of estuaries by larvae and juveniles of so many species has let to the concept of "estuarine dependence", implying that the estuary is required for some part of the life cycle of these organisms. There is consistent evidence of the ecological value of Terminos Lagoon and Campeche Sound habitats for refuge, reproduction, feeding, recruitment, nursery, and growth for a number of coastal fishes. In this paper we consider *recruitment* as the key factor that separates the "estuarine-dependent" from "estuarine-related" (or estuarine opportunistic) fish species. For example, for estuarine-dependent species, juvenile habitats are spatially separate and structurally different from the habitat of the adults and the early the stages (eggs and larvae).

Fish assemblages or *functional groups* are very important in maintaining the structure and functioning of consumers. At least three groups of fishes occur in the lagoon-estuarine system (Fig. 4) as discussed by Pauly and Yáñez-Arancibia (1993):

1) ***Resident species:*** Those which spend their entire life cycle within the system;

2) ***Seasonal migrants:*** Those which enter the lagoon during a more or less well-defined season (from either the marine or the freshwater side) and leave it during another season;

3) *Occasional visitors:* Those which enter and leave the system without clear pattern within and among years;

To these, two other groups may be added:

4) *Marine, estuarine-related species.* Those which spend their entire life cycle on the inner sea shelf under the estuarine plume influence; and

5) *Fresh water, estuarine-related species.* Those which spend their entire life cycle in the fluvial-deltaic riverine zone, associated with the upper zone of the estuarine system.

One mechanism which allows high standing stock to be maintained in the lagoon-estuarine ecosystem is small-scale between-habitat migration. The functional group which mainly exists in the fluvial-deltaic riverine zone of the estuary (Fig. 4) utilizes the estuarine system mainly as a feeding and nursery ground. This pattern is similar for the functional group in the inner shelf. The recruitment of these functional groups depend on the habitats inside the system. Here, the relative level of recruitment into the lagoon-estuarine system is determined locally by the ease with which fish can sequentially use the habitats, and between years, by the overall number of potential recruits along the coast.

For the coastal fish, randomly spawning on the shelf adjacent to the lagoon-estuarine system and letting the juveniles find their way into the lagoon would be inefficient (Yáñez-Arancibia *et al.*, 1993c). Rather, seasonal variations of abiotic parameters, seasonal changes of primary production and of competitors must be accommodated, and this is what leads to the phenomenon labeled here as "seasonal programming" (of consumers) which refers to the temporal and spatial sequence of lagoon-habitats used by juveniles and preadult fishes (Fig. 5). Fish migration also allows optimum utilization of primary production we have found that fish tend to visit different habitats during periods of peak primary production (as show in Fig. 3). This ensures high food availability and thus high fish growth rates.

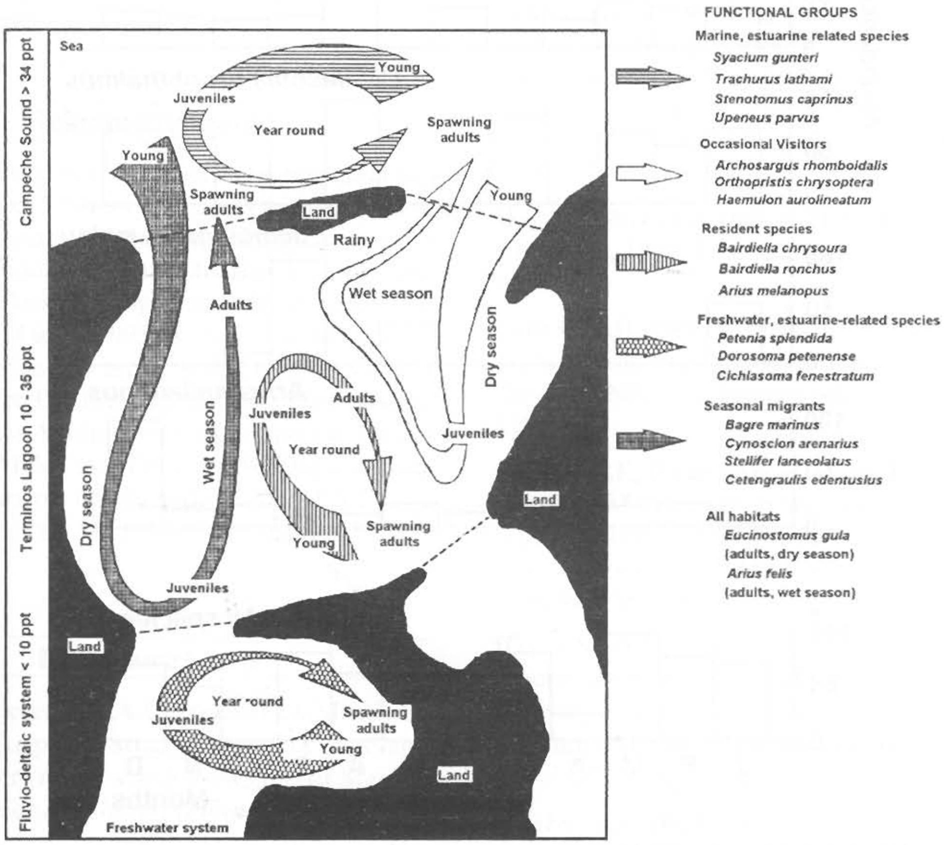

Figure 4. Diagramatic representation of functional groups of fishes with characteristic migration patterns and habitat utilization within, outside of, and into and out of Terminos Lagoon. The functional groups are defined in the text (From Pauly and Yáñez-Arancibia, 1993).

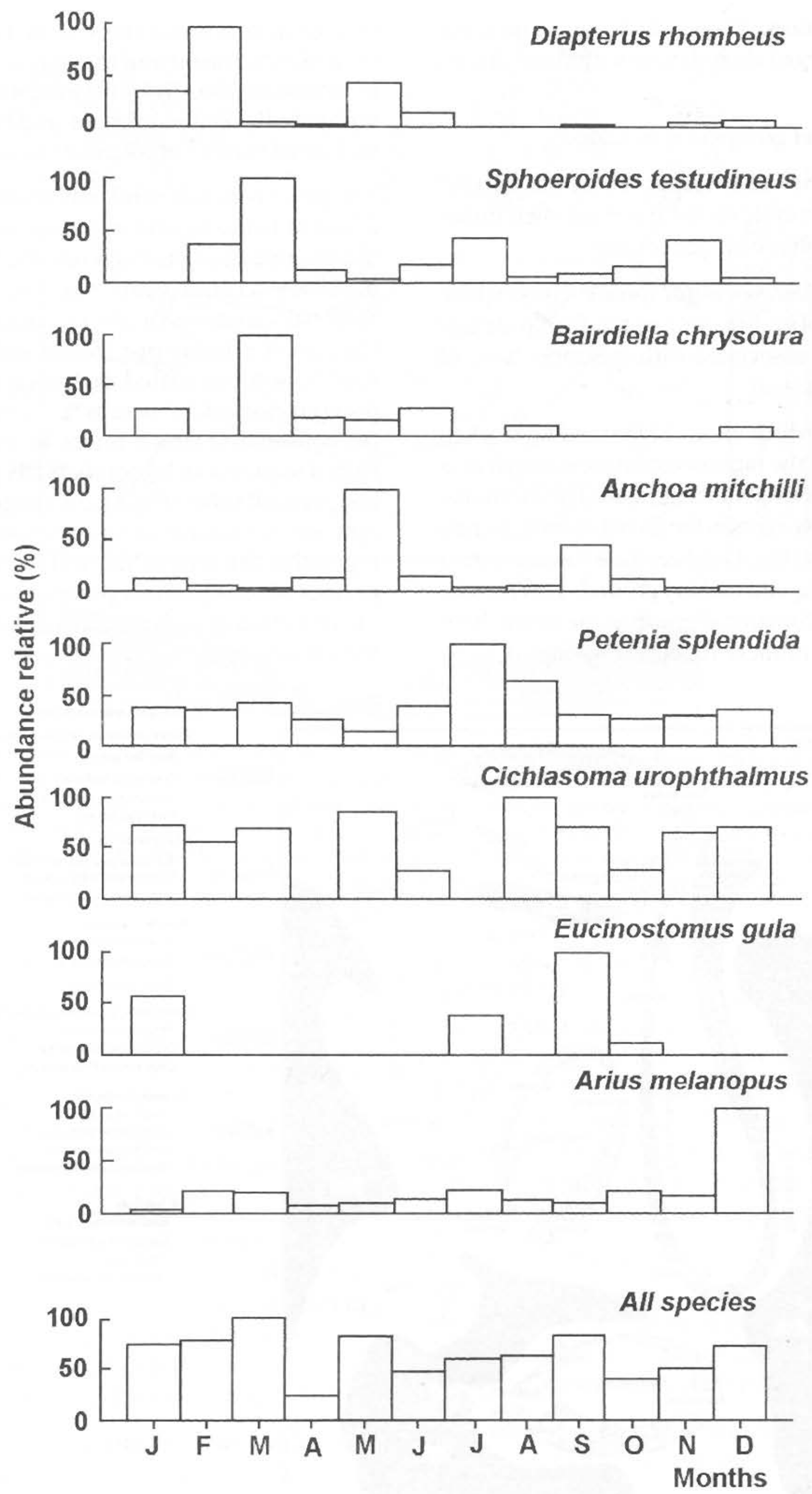

Figure 5. Seasonality of abundance of eight dominant fish species in Terminos Lagoon. These fishes show a clear seasonal sequence of abundance and habitat utilization, called here "seasonal programming". The sum of the relative abundance of these species (lower graph) suggest an even utilization of the lagoon-estuarine system throughout the year. After Yáñez-Arancibia *et al.* (1993c).

Synthesis

Tropical coastal ecosystems have maintained themselves over very long periods. The specific location of the coast has changed as sea level rose and fell, but the ecosystems have a long continuity. This has allowed the evaluation of mechanisms which stabilize and refine such seasonal programming, making the fish populations gradually more "dependent" on the lagoon system for the maintenance of high biomass and secondary production.

We believe that understanding biodiversity from an ecological point of view, e.g. the functional role of estuarine gradients and habitats, will lead to a better understanding of tropical coastal zones and is indeed the basis of their sustainable development. Along tropical coasts, only holistic habitat management approaches appear to be adequate (Fortes, 1991; Buttrick, 1992; Ray, 1991). The approach for interrelating resources flows, socioeconomic interactions and habitat gradients on transect of coastlines proposed by Pauly and Lightfoot (1992) may also contribute to this.

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