

# The ecology and *Penaeus* fishery of a coastal lagoon system in West Mexico

Ecology  
Fishery  
Trophic relationships  
Mexico

Écologie  
Pêcherie  
Relations trophiques  
Mexique

R. K. G. Paul<sup>a</sup>, A. B. Bowers<sup>b</sup>

<sup>a</sup> Overseas Development Administration, Eland House, Stag Place, London SWLE 5 DH, UK.

<sup>b</sup> Department of Marine Biology, University of Liverpool, Port Erin, Isle of Man, UK.

## ABSTRACT

Quantitative sampling by cast-net, seine-net and beam trawl provided data concerning the distribution, relative abundance, migrations and composition of populations of penaeid shrimp, portunid crabs and dominant fish species in the Huizache-Caimanero lagoon system on the Pacific coast of Mexico. Data concerning lagoon hydrography were also obtained and qualitative studies were made of the lagoon vegetation, bird fauna and benthic infauna. *Penaeus (Litopenaeus) vannamei* Boone and *Penaeus (Litopenaeus) stylirostris* Stimpson were the dominant penaeids and, numerically, *Lile stolifera* (Jordan and Gilbert), *Anchoa panamensis* (Steindachner) and *Mugil curema* (Cuvier and Valenciennes) were the dominant fish species within the lagoon. Two species of portunid crab, *Callinectes arcuatus* Ordway and *Callinectes toxotes* Ordway, occurred in the lagoon with the former by far the more abundant. Population densities of shrimps, crabs and some fish species were generally higher in the "esteros" and canals than in the open lagoons. Crabs and fish were both seasonally abundant, maximum biomasses occurring in the dry season.

Postlarval penaeid immigration was maximum in the wet season. Subsequent growth was rapid and estimates of growth rate of up to 0.4 mm carapace length/day were obtained for *P. vannamei*. Growth rate estimates were also obtained for *C. arcuatus* and some fish species. The natural diets of penaeid shrimps and portunid crabs, and the feeding modes of some important fish and bird species are discussed. Models of the lagoon system are presented and discussed.

*Oceanol. Acta*, 1982. Proceedings International Symposium on coastal lagoons, SCOR/IABO/UNESCO, Bordeaux, France, 8-14 September, 1981, 383-388.

## RÉSUMÉ

Écologie et pêche de *Penaeus* d'une lagune côtière du Mexique Occidental

Des prélèvements quantitatifs réalisés par « cast-net », « seine-net », et « beam-trawl » nous ont permis d'obtenir des données sur la distribution, l'abondance relative, les migrations et la composition des populations de crevettes pénéides, des crabes portunides et des espèces dominantes de poissons dans le système lagunaire de Huizache-Caimanero sur la côte pacifique du Mexique. Nous avons également obtenu des données sur l'hydrographie, et, en outre, réalisé des études qualitatives sur la végétation, les oiseaux et la faune benthique des lagunes.

Parmi les crevettes pénéides, *Penaeus (litopenaeus) vannamei* Boone et *P. (Litopenaeus) stylirostris* Stimpson sont dominantes et, numériquement, *Lile stolifera* (Jordan et Gilbert), *Anchoa panamensis* (Steindachner), *Mugil curema* (Cuvier et Valenciennes) sont, parmi les poissons, les espèces dominantes à l'intérieur des lagunes. Deux espèces de crabes portunides : *Callinectes arcuatus* Ordway et *C. toxotes* Ordway existent dans la lagune, la première étant de loin la plus abondante. Les densités de populations de crevettes, de crabes et de certaines espèces de poissons sont généralement plus élevées dans les « esteros » et les canaux que dans les grandes lagunes. Les crabes et les poissons sont tous deux d'abondance saisonnière, leurs biomasses maximales se situant pendant la saison sèche. La migration des postlarves de penaeidae est maximale pendant la saison humide. En conséquence, la croissance est rapide et des taux de croissance de 0,4 mm/jour de la longueur de la carapace

ont été obtenus pour *P. vannamei*; on a également obtenu des estimations du taux de croissance de *C. arcuatus* et de certaines espèces de poissons.

Les nourritures naturelles des crevettes pénaïdes et des crabes portunides, ainsi que les modes d'alimentation de certains poissons et oiseaux importants sont discutés. Les modèles du système lagunaire sont présentés et discutés.

*Oceanol. Acta*, 1982. Actes Symposium International sur les lagunes côtières, SCOR/IABO/UNESCO, Bordeaux, 8-14 septembre 1981, 383-388.

## INTRODUCTION

The Huizache-Caimanero lagoon system, like most others on the Pacific coast of Mexico, supports an important seasonal fishery for penaeid shrimp. Young shrimp enter the lagoon and, after a rapid growth phase, are caught near artificial exit barriers ("tapos") as they migrate back to the ocean (Edwards, Bowers, 1974; Edwards, 1978 a). Registered shrimp catches in this lagoon system varied between 1014-1348 tonnes/year during the period 1976-1979 (Blake *et al.*, 1981). *Penaeus* (*Litopenaeus*) *vannamei* Boone and *P.* (*Litopenaeus*) *stylirostris* Stimpson form the basis of commercial lagoon shrimp fisheries in this area of Mexico and in some months are also important in the coastal trawler shrimp fishery (Chapa, Soto, 1969; Soto, Bush, 1973). *P.* (*Farfantepenaeus*) *californiensis* Burkenroad and *P.* (*Farfantepenaeus*) *brevirostris* Rathbun also occur in the lagoons but are more typical of the coastal fishery. Other fisheries in the lagoon system are much less developed and principally exploit finfish such as the mullet (*Mugil curema* Cuvier and Valenciennes), portunid crabs (*Callinectes arcuatus* Ordway and *C. toxotes* Ordway) and oysters (*Striostrea iridescens*).

Between 1973 and 1979 a joint project existed between the Department of Marine Biology of the University of Liverpool and the Centro de Ciencias del Mar y Limnología of the National Autonomous University of Mexico (UNAM), with funding for British participation from the Overseas Development Administration. The purpose of the project was to study lagoon ecology, with particular reference to the populations of penaeid shrimp, portunid crabs and dominant fish species, with an eventual aim of formulating plans to improve fishery management.

The present paper gives a review of some of the aspects of research undertaken by the University of Liverpool team.

## STUDY AREA

The Huizache-Caimanero lagoon system (22° 48'-23° 06'N, and 106° 00'-106° 16'W, see Fig. 1) has been described by several authors (Edwards, 1977; 1978 b; Warburton, 1978 a; 1979; Menz, Bowers, 1980; Paul, in press a). A double lagoon occupies the area between two rivers, and is connected to them by narrow winding mangrove-lined channels (called "esteros"). During the wet season (from late June to October) fresh water enters the lagoons via land run off, by direct precipitation and through the esteros via the rivers. At the height of the wet season the lagoons cover an area of about 175 km<sup>2</sup>. From October onwards, the esteros conduct seawater from the ocean compensating for the effects of evaporation and reduced precipitation. Then, the mean tide level of the lagoon system falls by 47 cm, and the net flow is reversed. The minimum water level is reached around May each year when the lagoons cover an area of about 81 km<sup>2</sup>. The maximum depth reaches 2 m in Caimanero and 1.5 m in Huizache in the wet season, although the average depth is around 1 m. In the dry season large areas of both lagoon basins dry up and the average depth of the open lagoons is below 0.5 m. The sea mouth of Estero Ostial, which connects Huizache lagoon to the

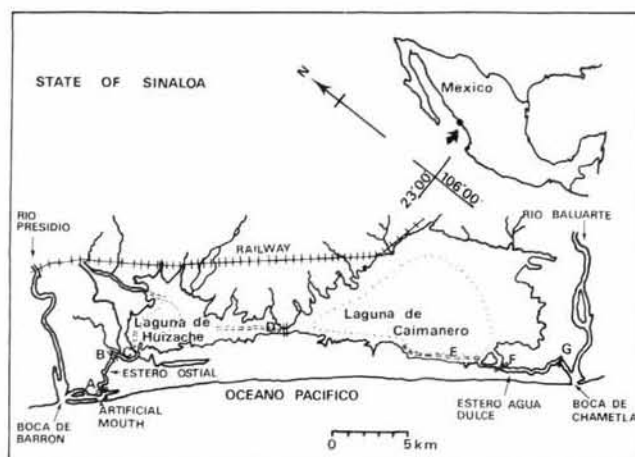


Figure 1

A map of the Huizache-Caimanero lagoon system. The mean minimum limits of the lagoons (late dry season) are dotted. Canals are shown by a broken line. Important sampling stations are indicated as: A, Tapo Botadero; B, Tapo Ostial; C, Las Garzas; D, Tapo Pozo de la Hacienda; E, El Tanque Canal; F, Tapo Caimanero; G, Tapo Agua Dulce.

ocean, is blocked by a sand bar for about 4 months each year during the dry season and it is usually opened by bulldozers around July each year. The mouth of Estero Agua Dulce remains open throughout the year and permanently connects Caimanero lagoon to the ocean. Within the lagoons there are artificially dredged canals which aid navigation and are important fishing areas. Ayala-Castanares *et al.* (1969) and Phleger and Ayala-Castanares (1972) have described the topography of the area and the bottom deposits; they showed that the lagoon bottom is predominantly silty clay mud with some large patches of clayey sand in the Caimanero basin.

The shrimp fishery is centred in both the lagoons and the esteros. Barrier fences called tapos, which impound shrimps within the lagoons, are situated at the junctions of the lagoons and esteros, across the main esteros and across the narrow neck of water between Caimanero lagoon and Huizache lagoon (Fig. 1). The tapos are closed between mid-August and mid-April each year by screens erected on a framework of permanent posts. Shrimps are caught by means of cast nets called "atarrayas" thrown by fishermen operating from canoes. Details of the fishery are given by Edwards (1978 a).

## MATERIALS AND METHODS

Edwards (1978 b) made a general survey of the fauna of the lagoon system in the initial phase of the project. Subsequent sampling was more intensive. During the period 1974-1976 regular samples (ranging in frequency from biweekly to monthly) of shrimps (Menz, Bowers, 1980), portunid crabs (Paul, in press a) and finfish (Warburton, 1978 a; 1979) were obtained from the lagoon system using cast nets, seine

nets and a small beam trawl. Less intensive qualitative surveys were also made of the lagoon vegetation, bird populations and benthic infauna.

Sampling was carried out at fixed stations representing the main lagoon ecotopes in open lagoon areas, artificial canals and esteros. In the wet season, up to a total of 16 stations were sampled in Caimanero and 9 in Huizache but, in the dry season, the numbers were reduced to a maximum of five and three respectively as many became inaccessible or dried up. The most important sampling stations were those that could be sampled throughout the year and these are indicated in Figure 1 as stations A-G.

During sampling, the water temperature was measured to the nearest 0.1 °C using Gallenkamp total immersion thermometers and salinity was measured to the nearest 1 ‰ using American Optical Corporation temperature-compensated Refractometers. Depth was measured using a pole and a 30 cm rule. Samples were stored on ice or were preserved in 10% formalin in the field and brought to the laboratory for analysis. All samples were identified to specific level and were sexed before being measured and weighed. The principal measurements taken included carapace length and total length (shrimp), carapace breadth including lateral spines (portunid crabs) and total length (fish).

## RESULTS AND DISCUSSION

### Hydrography

Figure 2 gives variation in mean monthly water temperature and salinity at selected locations for the period February 1975 to August 1976. Local rainfall is also shown. Lagoon water temperatures were similar at all stations and were highest between June and September each year (maximum

36 °C) and lowest between December and March (minimum 18 °C). Salinity is the main environmental variable, showing large fluctuations related to the wet and dry season. During both years lagoon salinity declined rapidly with the onset of the rains in June and the flooding of the rivers, from fully saline or hypersaline to below 10 ‰ in Caimanero and to almost zero in Huizache. Rainfall was much lower in 1976 than in 1975 and this is reflected in the salinity data for Caimanero lagoon. After the rains, salinity slowly increased and reached its maximum values between March and May. Tapo Pozo de la Hacienda in Huizache became isolated from the main lagoon body during the dry season of both years and salinities in excess of 125 ‰ were recorded. The sudden drop in salinity in Huizache during February 1976 was due to a temporary diversion of freshwater into the lagoon from the Rio Presidio. A salinity gradient exists across the lagoons, especially during August and September each year, with levels of about 2 ‰ in Huizache, 4 ‰ at Tapo Pozo de la Hacienda and 8-11 ‰ in Caimanero.

The general pattern was similar in all years during the period 1974-1979 and variations were due to differences in the amount of rain and the date of initiation of the wet season each year, both locally and in the nearby mountains which form the catchment area of local rivers. The lagoon hydrography is discussed more fully by Mendoza von Borstel (1972), Edwards (1978 b) and Moore (1979).

### Vegetation

Mangroves occur in dense stands along the esteros and also are common in the peripheral areas of the lagoon system, particularly along the western shore. Three species dominate: *Rhizophora mangle* (the red mangrove); *Avicennia nitida* (the black mangrove) and *Laguncularia racemosa*. The button mangrove, *Conocarpus erecta*, is much less common. Also common in the peripheral areas of the lagoon system are the saltwort (*Salicornia* spp.), cordgrass (*Spartina* spp.) and several species of rush. These tend to colonise mudflats during the dry season. In the lagoon diatoms and dinoflagellates are common (Gomez-Aguirre *et al.*, 1974) as are the macroalgae *Enteromorpha* sp. and *Cladophora* sp. The widgeon grass (*Ruppia maritima*) is also very abundant in the lagoon especially during the wet season.

### Fauna

The lagoon system supports a very extensive and diverse fish, bird and invertebrate fauna. No attempt is made to list all species present but merely to draw attention to the most abundant and characteristic types.

#### Benthic infauna

Edwards (1978 b) reported that in most areas polychaetes of the family Spionidae (e.g. *Prionospio* spp.) predominated in the infauna followed, in Caimanero, by amphipods of the family Corophidae, the bivalve mollusc *Tagelus affinis* and cumaceans (family Leuconidae) predominated in the infauna with polychaetes and amphipods in smaller numbers.

#### Benthic epifauna

The predominant invertebrate on Caimanero mud-flats, in terms of biomass, is the gastropod *Cerithidea mazatlanica* (Edwards, 1978 b). Garcia-Cubas (1969) reported this gastropod to be present in large numbers in Caimanero but absent from Huizache. Its distribution seems related to that of the macrophyte *Ruppia maritima*, its major food source. The oyster *Striostrea iridescens* is common in Estero Agua Dulce. Burrowing shrimps (*Callinassa* spp.) and palaemonid shrimps (*Macrobrachium* spp.) are also common in the lagoon system. Associated with the mangrove communities and lagoon shores are considerable populations of crabs of the families Ocypodidae (e.g. *Uca* spp.), Gecarcinidae (e.g.

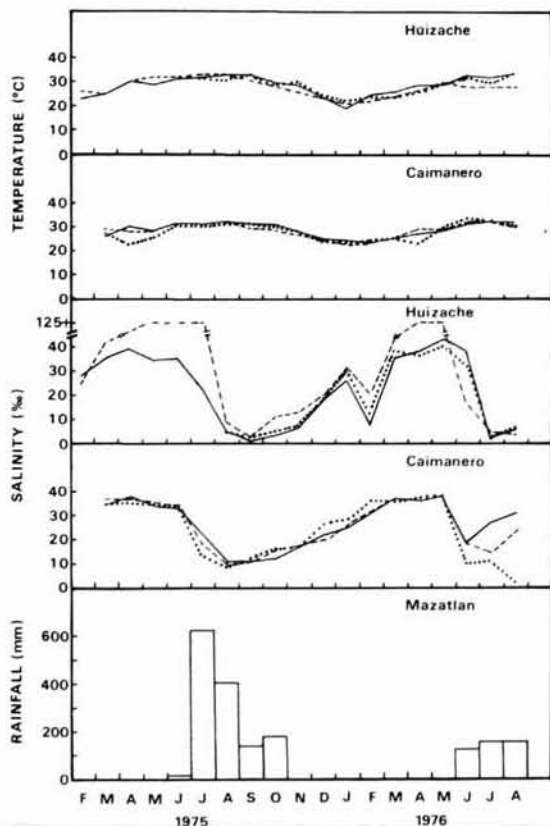


Figure 2  
Mean monthly water temperature and salinities at El Tanque (—), Tapo Caimanero (---) and Tapo Agua Dulce (...) in Caimanero lagoon and Las Garzas (—), Tapo Pozo de la Hacienda (---), and Tapo Ostial (...) in Huizache lagoon for the period February 1975 to August 1976. Rainfall data for the adjacent city of Mazatlan are shown.

*Cardiosoma crassum*, *Gecarcinus* spp.) and Grapsidae (e.g. *Sesarma* spp.)

#### Penaeid shrimp

Mexican Pacific penaeid shrimps spawn in the ocean (Edwards, 1978 a) with peaks of spawning between March and October. Subsequent postlarval immigration to the lagoons is maximal between June and October (Watkins, 1980). Shrimp densities were higher generally in the canals and esteros than in the open lagoons (Menz, 1976; Edwards, 1978 b). Densities of small juvenile *P. vannamei* of up to 5.4/m<sup>2</sup> were recorded in the open lagoons with 7.5/m<sup>2</sup> at Tapo Ostial and up to 34/m<sup>2</sup> at Tapo Pozo de la Hacienda (Blake *et al.*, 1981). Densities of larger shrimp were normally around 3/m<sup>2</sup> in the open lagoons during the summer. Within the lagoon the white shrimp (*P. vannamei*) and the blue shrimp (*P. stylirostris*) were by far the most abundant although *P. californiensis* and *P. brevivirostris* sometimes occurred. Shrimp numbers and biomass were highest in the late spring and summer after which they declined due to the closing of the tapos and the initiation of fishing in August and September respectively. The growth of juvenile shrimp in the lagoon is rapid. Estimates were obtained from cage experiments (Edwards, 1977), length-frequency analyses (Menz, Bowers, 1980) and from tagging and enclosure experiments (Menz, Blake, 1980). Summarizing the results, it was shown that there was a high negative correlation between size and growth rate. Growth rates of *P. vannamei* of 4-20 mm carapace length (CL) were in the range of 0.3-0.4 mm CL (1.35-1.80 mm total length) per day, and those of shrimp above 20 mm CL were around 0.2 mm CL (0.9 mm total length) per day. Above 28 mm CL growth rates further decreased. Shrimp growth was faster in the summer than in the winter.

Little work was carried out on shrimp feeding but Edwards (1978 b) indicated that penaeids in the lagoon are detritus and deposit feeders, consuming sediment and infaunal organisms such as small crustaceans and polychaetes.

#### Portunid crabs

*Callinectes arcuatus* and *C. toxotes* are the only two species of portunid crab which occur in the lagoon system and the former is by far the more abundant (Paul, in press a). Their distribution and general ecology has been described by Paul (in press b). Their commercial exploitation is at a very low level as yet although their fisheries potential is high (Paul, 1981 a). The crabs are seasonally abundant, maximum numbers occurring in the dry season (particularly between February and May). Crab density and biomass/m<sup>2</sup> in all areas were 3-17 and 3-32 times higher, respectively, in the dry season than in the wet season (Paul, in press a). Density and biomass were also up to 14 times higher in the esteros and canals than in the open lagoons. Densities of up to 5 crabs/m<sup>2</sup> (a corresponding biomass of 500 g/m<sup>2</sup>) were recorded. Female crabs tended to dominate at the seawards end of the lagoon and they migrated to the sea to spawn between March and August, followed by the males (Paul, in press a). Growth estimates for *C. arcuatus* of different sizes were derived from breadth-frequency analyses (Paul, in press a). Estimates ranged from 5-11 mm carapace breadth/month. Growth was faster in the summer than in the winter and ceased when the crabs completed the terminal moult. The spawning season of *C. arcuatus* was from March to August and that of *C. toxotes* from November to January. The subsequent immigration of small juvenile *C. arcuatus* to the lagoon was maximum between January and May each year. Stomach analyses showed that *C. arcuatus* and *C. toxotes* are omnivores and that they feed as predators, scavengers and, when juveniles, as detritivores (Paul, 1981 b). They feed on molluscs (particularly bivalves), crabs (including *Callinectes*), fish and to a lesser extent on shrimps, polychaetes, amphipods and plant material.

#### Fish

57 species representing 26 families have been recorded in the whole lagoon system (Warburton, 1978 a). Numerically, the anchovy (*Anchoa panamensis*), sardine (*Lile stolidifera*) and mullet (*Mugil curema*) were the most abundant and constituted over 90 % of the fish caught. In terms of biomass the most abundant were the mullet, anchovy, catfish (*Galeichthys caerulescens*) and weakfish (*Cynoscion xanthulus*) (Warburton, 1979). Fish, generally, were most abundant between November and March each year (up to 18.3/m<sup>2</sup>) and were least abundant between May and August. Fish densities were higher in the canals and esteros than in the open lagoons and higher fish densities were obtained in Huizache lagoon than in Caimanero lagoon (Warburton, 1978 a). Most of the species recorded use the lagoons as nursery grounds and growth areas and occur mainly as juveniles. Others, such as the catfish and mullet, are more or less permanent residents and occur as adults. Fish growth is rapid in the lagoons and estimates obtained from length-frequency analyses and otolith check techniques varied from 0.5 cm/month (sardine), 0.7 cm/month (anchovy), around 1 cm/month (goby, *Gobionellus microdon* and sole, *Achirus mazatlanus*) up to 1-1.5 cm/month (catfish), 1.89-2.60 cm/month (weakfish) and 2.24-3.93 cm/month (mullet) (Warburton, 1978 b; 1979). The main recruitment periods for most species were during the period September to April each year. Published work (Carranza, 1969; Yanez, 1975; Warburton 1978 a) on fish feeding habits in lagoons allows six main feeding types to be identified. These are: herbivorous feeders (e.g. mullet); planktivorous feeders (e.g. sardine, anchovy); detritivorous feeders (e.g. sole, goby, mullet); omnivorous feeders (e.g. *Gerres cinereus*, *Eucinostomus californiensis*); omnivorous feeders and/or primary carnivores (e.g. *Diapterus peruvianus*, *Centropomus robalito*) and secondary carnivores (e.g. weakfish, catfish). In the lagoon system fish are not commercially exploited to anything like their full potential.

#### Birds

Large populations of many species of birds inhabit the lagoon area throughout the year. Some are permanent residents and others are seasonal visitors. Their impact on the lagoon ecosystem has not been studied quantitatively but it must be considerable since they are voracious feeders. A recent study (Watkins, pers. comm.) and personal observations indicate that four main feeding types exist amongst the lagoon avifauna. The ducks (*Anas* spp., *Spatula clypeata*) are mainly herbivorous feeders but they also include small benthic organisms (e.g. molluscs) and insects in their diet. Wading birds such as the avocets (*Recurvirostra americana*), dowitchers (*Limnodromus scotlapaceus*), godwits (*Limosa fedoa*) use their beaks to obtain small crustaceans (e.g. amphipods), polychaetes, molluscs and insects from the substrate. They also consume plant material. The larger birds such as the herons, egrets and ibis have a varied diet which, in addition to small benthic organisms, also includes penaeid shrimps, crabs and fish. These birds, particularly the herons (*Ardea* sp.) and egrets (*Egretta* sp.) commonly stalk their prey in shallow water before striking with their beaks. The final type includes the large piscivorous feeders such as the white pelican (*Pelecanus erythrorhynchus*), the brown pelican (*Pelecanus occidentalis*) and cormorants (*Phalacrocorax* spp.). Fish form the major part of the diet of all three species although all, particularly the cormorants, also feed on crustaceans (shrimps and crabs). The brown pelican catches fish by diving from the air, the cormorant by diving from the water surface and the white pelican feeds from the surface.

#### CONCLUSIONS

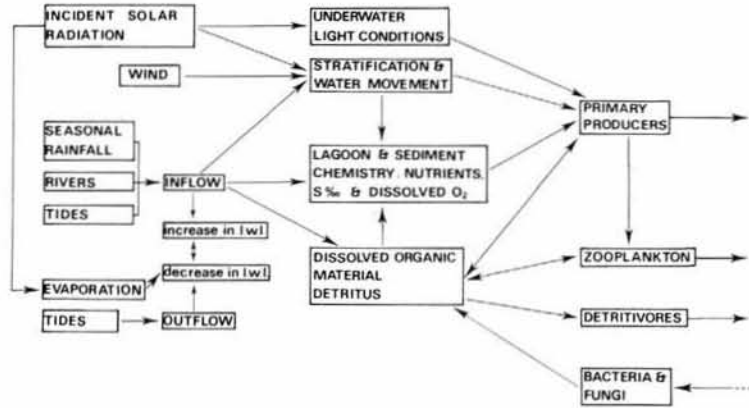
The Huizache-Caimanero lagoon system is a highly productive area. It is utilized by penaeid shrimps, portunid crabs

and many species of fish as a nursery and growth area. As well as supporting a well established shrimp fishery there is considerable potential for the further development of finfish and crab fisheries in this area. Recommendations concerning dredging operations, tapo maintenance, timing of the fishing season, mesh size regulation and the control of predators by the diversification of lagoon fishing effort, with an aim to improve the management of the shrimp fishery, are fully discussed by Blake *et al.* (1981). The fisheries potential of portunid crabs of the genus *Callinectes* in this area is discussed by Paul (1981 *b*).

The research undertaken in this project has elucidated many aspects of the ecology of this lagoon system. Edwards (1978 *b*) constructed a hypothetical model of trophic relationships in the lagoon system, which, whilst an oversimplification, represented the chief components of the ecosystem as revealed by the sampling methods employed. This work indicated that net production in the water column was

ecosystem. Most of these factors have been discussed previously and these are summarized outside the main body of Figure 4 which gives a modified version of the model of trophic relationships (Edwards, 1978 *b*) in the lagoon system. Direct grazing of primary producers or their decomposition by bacteria and fungi supports a variety of deposit and filter feeders (e.g. *Prionospio*, *Corophium*, *Tagelus*, *Cerathidea*) and omnivores (e.g. *Callinectes*, *Penaeus*, *Geres*, *Eucinostomus*) which, in turn, are fed upon by primary carnivores (e.g. *Diapterus*, *Centropomus*) in the mixed trophic level. Secondary and tertiary carnivores (e.g. *Cynoscion*, *Galeichthys*, *Ardea* and *Pelecanus*, *Phalacrocorax*, *Man*) are supported by the mixed trophic level and there is a considerable immigration of larval invertebrates (e.g. *Penaeus*, *Callinectes*) into the lagoons, together with larvae of many fish species. Other more direct pathways support populations of herbivorous and planktivorous fish and birds (e.g. *Mugil*, *Anas*, *Anchoa*, *Lile*) and detritivo-

Figure 3  
Model of the interrelationships of the main physical components of the Huizache-Caimanero lagoon ecosystem (l.w. l. = lagoon water level).



sufficient to support the metabolic requirements of the relatively sparse infauna in the wet season but that the input necessary to support the epifauna was to some extent dependent on the contribution made by macrophytes. A simplistic overall picture of energy pathways in relation to shrimp ecology was formulated (Blake *et al.*, 1981). The flooding of the rivers into the lagoons during the rainy season provides an input of nutrients, detritus and suspended sediment. This in turn stimulates primary production, particularly of diatoms, *Ruppia*, macroalgae and mangroves. The subsequent bacterial and fungal decomposition of primary producers enhances the organic content of the substrate together with direct deposition of sediment from the rivers, and this benefits shrimp production, either directly, or indirectly through the benthic fauna.

Figure 3 is a diagrammatic representation of the interrelationships of the main physical components of the lagoon

rous fish (e.g. *Mugil*, *Gobionellus*, *Achirus*) as shown in Figure 4.

The general pattern of trophic relationships summarized in Figure 4 is likely to apply to many shallow coastal lagoons on the Pacific coast of Mexico and elsewhere in the tropics, though there will be differences in detail related to hydrographic conditions, sediment type and biotic components. There are strong similarities between the food web in the Huizache-Caimanero lagoon system and that in the Cochin Backwater, a tropical estuary in Kerala, India, investigated by Qasim (1970).

In contrast to aquatic ecosystems in relatively high latitudes and to open ocean systems, tropical lagoon food chains show a reduction in the role of phytoplankton as a primary producer and of zooplankton as the most important herbivores. Direct grazing of plant material, and utilisation of detritus from plant decomposition provide alternative pathways for energy transfer (Odum, 1970).

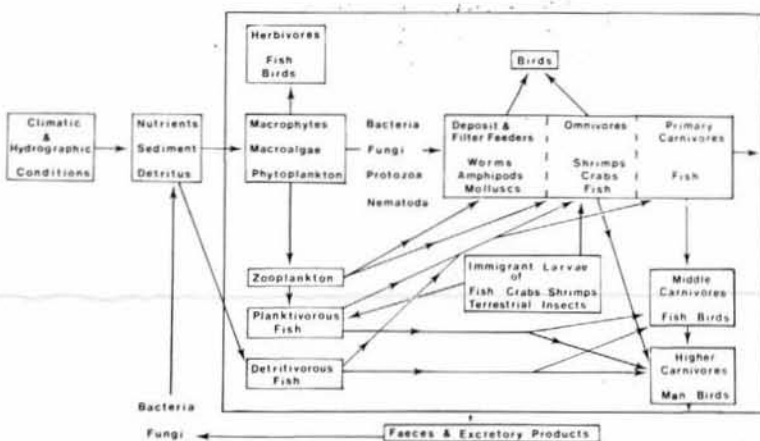


Figure 4  
Model of trophic relationships in the Huizache-Caimanero lagoon ecosystem (modified after Edwards, 1978 *b*).

## RÉFÉRENCES

- Ayala-Castanares A., Gutiérrez M., Malpica V. M., 1969. *Informe final de los estudios de geología marina de los planes pilotos Escuinapa y Yavaros en la primera etapa*, Instituto de Biología, Univ. Nac. Autón. México, 5-34.
- Blake B. F., Bowers A. B., Naylor E., 1981. Ecology and *Penaeus* fishery of Mexican lagoons, *Spec. Rep. Overseas Development Administration, London*, 58 p.
- Carranza J., 1969. *Informe preliminar sobre la alimentación y hábitos alimenticios de las principales especies de peces de las zonas de los planes pilotos Yavaros y Escuinapa*, Instituto de Biología, Univ. Nac. Autón. México, 37 p.
- Chapa S. H., Soto R. L., 1969. Relación de algunos factores ecológicos con la producción camaronesa de las lagunas litorales del sur de Sinaloa, México, in: *Coastal lagoons. A symposium*, edited by A. Ayala-Castanares and F. B. Phleger, Univ. Nac. Autón. México, 653-662.
- Edwards R. R. C., 1977. Field experiments on growth and mortality of *Penaeus vannamei* in a Mexican coastal lagoon complex, *Estuarine Coastal Mar. Sci.*, **5**, 107-121.
- Edwards R. R. C., 1978 a. The fishery and fisheries biology of penaeid shrimp on the Pacific coast of Mexico, *Oceanogr. Mar. Biol. Ann. Rev.*, **16**, 145-180.
- Edwards R. R. C., 1978 b. Ecology of a coastal lagoon complex in Mexico, *Estuarine Coastal Mar. Sci.*, **6**, 75-92.
- Edwards R. R. C., Bowers A. B., 1974. Shrimp research in Mexican lagoons, *Fish. News Int.*, **13**, 11, 251-258.
- García-Cubas A., 1969. Resultados preliminares del estudio de los moluscos en las lagunas de Caimanero y Huizache, Sinaloa y Yavaros, Sonora, *Bol. Inst. Geol. Univ. Nac. Autón. México*, 115-134.
- Gomez-Aguire S., Licea-Duran S., Flores-Coto C., 1974. Ciclo anual del plancton en el sistema Huizache-Caimanero, México (1969-1970), *An. Centro Ci. Mar. Limnol., Univ. Nac. Autón. México*, **1**, 1, 83-98.
- Mendoza von Borstel X., 1972. Efectos de la marea sobre la producción camaronesa en lagunas litorales, *Mem. IV Congreso Nac. Oceanogr. México*, 407-418.
- Menz A., 1976. Bionomics of penaeid shrimps in a lagoon complex on the Mexican Pacific coast, *Ph. D. Thesis, Univ. Liverpool*, 145 p.
- Menz A., Blake B. F., 1980. Experiments on the growth of *Penaeus vannamei* Boone, *J. Exp. Biol. Ecol.*, **48**, 99-111.
- Menz A., Bowers A. B., 1980. Bionomics of *Penaeus vannamei* Boone and *Penaeus stylirostris* Stimpson in a lagoon on the Mexican Pacific coast, *Estuarine Coastal Mar. Sci.*, **10**, 685-697.
- Moore N. H., 1979. The annual physical hydrographical cycle of a tropical lagoon system of the Pacific coast of Mexico, *Ph. D. Thesis, Univ. Liverpool*, 323 p.
- Odum W. E., 1970. Utilization of the direct grazing and plant detritus food chains by the striped mullet *Mugil cephalus*, in: *Marine food chains*, edited by J. H. Steele, Oliver and Boyd, Edinburgh, 222-240.
- Paul R. K. G., 1981 a. The development of a fishery for portunid crabs of the genus *Callinectes* (Decapoda, Brachyura) in Sinaloa, Mexico, *Spec. Rep., Overseas Development Administration, London*, 78 p.
- Paul R. K. G., 1981 b. Natural diet, feeding and predatory activity of the crabs *Callinectes arcuatus* and *C. toxotes* (Decapoda, Brachyura, Portunidae), *Mar. Ecol. Prog. Ser.*, **6**, 91-99.
- Paul R. K. G., in press a. Abundance, breeding and growth of *Callinectes arcuatus* Ordway and *Callinectes toxotes* Ordway (Decapoda, Brachyura, Portunidae) in a lagoon system on the Mexican Pacific coast, *Estuarine Coastal Shelf. Sci.*
- Paul R. K. G., in press b. Observations on the ecology and distribution of swimming crabs of the genus *Callinectes* (Decapoda, Brachyura, Portunidae) in the Gulf of California, Mexico, *Crustaceana*.
- Phleger F. B., Ayala-Castanares A., 1972. Ecology and development of two coastal lagoons in northwest Mexico, *An. Inst. Biol. Univ. Nac. Autón. México, Ser. Ci. Mar. Limnol.*, **43**, 1, 1-20.
- Qasim S. Z., 1970. Some problems related to the food chain in a tropical estuary, in: *Marine food chains*, edited by J. H. Steele, Oliver and Boyd, Edinburgh, 45-51.
- Soto L. R., Bush R., 1973. Analisis de los muestreos de camarón en los esteros del sur de Sinaloa. Temporada 1973, *Programa Camaron del Pacifico INP/ISI*, **15**, Inst. Nac. Pesca, México, 15-36.
- Warburton K., 1978 a. Community structure, abundance and diversity of fish in a Mexican coastal lagoon system, *Estuarine Coastal Mar. Sci.*, **7**, 497-519.
- Warburton K., 1978 b. Age and growth determination in a marine catfish using an otolith check technique, *J. Fish. Biol.*, **13**, 429-434.
- Warburton K., 1979. Growth and production of some important species of fish in a Mexican coastal lagoon system, *J. Fish. Biol.*, **14**, 449-464.
- Watkins J. L., 1980. The immigration of postlarval penaeid shrimp into a lagoon system on the Pacific coast of Mexico, *Ph. D. Thesis, Univ. Liverpool*, 144 p.
- Yanez L. A., 1975. Relaciones tróficas de la fauna ictológica del sistema lagunar costero de Guerrero y aspectos parciales de dinámica de poblaciones de los peces de importancia comercial, *An. Centro Ci. Mar. Limnol., Univ. Nac. Autón. México, Publicación especial*, 284 p.