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**ECOLOGICAL STRUCTURE OF ESTUARINE FISH COMMUNITIES:
HABITAT LINKAGES AMONG DOMINANT SPECIES GROUPS
IN TERMINOS LAGOON MEXICO**

A Dissertation

**Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy**

in

The Department of Oceanography and Coastal Sciences

by

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August, 2001

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DEDICATION

I want to dedicate this dissertation to my sons, Anton and Rodrigo because they are the most beautiful thing in my life, without them I don't have a reason to continue.

To my husband, Eduardo Sainz, for his constant support since our lives coincided.

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TABLE OF CONTENTS

DEDICATION	ii
ACKNOWLEDGEMENTS	iii
ABSTRACT	vii
CHAPTER 1. INTRODUCTION	1
1.1 Introduction	1
1.1.1 Background	3
1.1.2 Objectives	9
1.2 Study Area	10
1.3 Literature Cited	12
CHAPTER 2. ECOLOGICAL STRUCTURE OF ESTUARINE FISH COMMUNITIES: ABUNDANCE AND DIVERSITY PATTERNS IN TERMINOS LAGOON A TROPICAL COASTAL LAGOON	22
2.1 Introduction	22
2.1.1 The Problem	24
2.1.2 Objectives	26
2.2. Study Area	27
2.3 Material and Methods	30
2.3.1 Field and Laboratory Measurements	30
2.3.2 Analysis of Community Structure	31
2.3.3 Community Structure Parameters	31
2.3.3.1 Diversity	31
2.3.4 Statistical Analysis	41
2.4 Results	42
2.4.1 Environmental Trends	42
2.4.2 Community	51
2.4.2.1Community Structure	52
2.4.3 The Relation of Diversity Indices to Physical Parameters	71
2.5 Discussion	73
2.6 Literature Cited	78
CHAPTER 3. ECOLOGY OF DOMINANT FISH POPULATIONS, ENVIRONMENTAL FACTORS REGULATING BIOLOGICAL STRATEGIES IN A TROPICAL LAGOON	
.....	90
3.1 Introduction	90
3.1.1 Background	91
3.1.2 Objectives	95
3.2 Study Area	96
3.3 Material and Methods	98
3.3.1 Field and Laboratory Measurements	98
3.3.2 Analysis of Dominant Species Population Structure	98
3.4 Results	100
3.4.1 <i>Cathorops spixii</i> (mandamango sea catfish)	102

3.4.2 <i>Sphoeroides testudineus</i> (checkered puffer)	106
3.4.3 <i>Bairdiella chrysoura</i> (silver perch)	110
3.4.4 <i>Ariopsis felis</i> (hardhead sea catfish)	112
3.4.5 <i>Archosargus rhomboidalis</i> (sea bream)	116
3.4.6 <i>Eucinostomus gula</i> (silver jenny)	121
3.4.7 <i>Anchoa mitchilli</i> (bay anchovy)	123
3.4.8 <i>Chaetodipterus faber</i> (Atlantic spadefish)	128
3.4.9 <i>Cynoscion arenarius</i> (sand seatrout)	130
3.4.10 <i>Orthopristis chrysoptera</i> (pigfish)	132
3.4.11 <i>Diapterus rhombeus</i> (caitipa mojarra)	138
3.4.12 <i>Stellifer lanceolatus</i> (star drum)	141
3.4.13 <i>Citharichthys spilopterus</i> (bay whiff)	144
3.4.14 <i>Cetengraulis edentulus</i> (Atlantic anchoveta)	145
3.4.15 <i>Cyclichthys schoepfi</i> (striped burrfish)	145
3.4.16 Factor Analysis	147
3.5 Discussion	149
3.5.1 Residents or Typical Estuarine Species	150
3.5.1.1 <i>Cathorops spixii</i> (mandamango sea catfish)	150
3.5.1.2 <i>Sphoeroides testudineus</i> (checkered puffer)	154
3.5.1.3 <i>Bairdiella chrysoura</i> (silver perch)	155
3.5.1.4 <i>Ariopsis felis</i> (hardhead sea catfish)	156
3.5.1.5 <i>Eucinostomus gula</i> (silver jenny)	157
3.5.2 Seasonal or Cyclical Visitors	158
3.5.2.1 <i>Archosargus rhomboidalis</i> (sea bream)	158
3.5.2.2 <i>Chaetodipterus faber</i> (Atlantic spadefish)	159
3.5.2.3 <i>Cyclichthys schoepfi</i> (striped burrfish)	161
3.5.2.4 <i>Citharichthys spilopterus</i> (bay whiff)	162
3.5.3 Occasional Visitors	163
3.5.3.1 <i>Anchoa mitchilli</i> (bay anchovy)	163
3.5.3.2 <i>Cynoscion arenarius</i> (sand seatrout)	166
3.5.3.3 <i>Orthopristis chrysoptera</i> (pigfish)	167
3.5.3.4 <i>Diapterus rhombeus</i> (caitipa mojarra)	167
3.5.3.5 <i>Stellifer lanceolatus</i> (star drum)	168
3.5.3.6 <i>Cetengraulis edentulus</i> (Atlantic anchoveta)	170
3.5.4 Population Structure	171
3.6 Literature Cited	172

CHAPTER 4. ESTUARINE NEKTON ASSEMBLAGES COUPLED WITH HABITAT HETEROGENEITY: INTERACTIONS BETWEEN PRIMARY AND SECONDARY PRODUCTION

4.1 Introduction	181
4.1.1 The Problem	185
4.1.2 Habitat Diversity	186
4.1.2.1 Functional Groups	188
4.1.3 General Objective	194
4.2 Study Area	194
4.3 Material and Methods	197
4.4 Results	198
4.5 Discussion	200

4.6 Literature Cited	207
CHAPTER 5. SUMMARY	217
APPENDIX A: DATA TABLES FOR CHAPTER 2	225
APPENDIX B: DATA TABLES FOR CHAPTER 3	249
APPENDIX C: DATA TABLES FOR CHAPTER 4	267
VITA	271

ABSTRACT

Terminos Lagoon in the southern Gulf of Mexico has 5 ecological subsystems:

1) *fluvial lagoon systems* (FLS) with permanent river discharge, low salinity, high turbidity and nutrients. 2) *Central basin* (CB) between marine and river conditions, intermediate salinity and variable transparency. 3) *Inner littoral of Carmen Island* (ILCI) with strong marine influence, high transparency and extensive seagrass meadows. 4) *Carmen inlet* (Estero Pargo, ESP) with a net outflow of water and high turbidity. 5) *Puerto Real inlet* (PR) with a net inflow of waters, high transparency and seagrasses.

During a 15-month sampling, 13,691 individuals of 79 different species were collected in 264 trawls. Mandamango catfish, checkered puffer, silver perch, hardhead catfish and sea bream accounted for 63% of the total capture. Seventeen species accounted for 90% of all individuals, and 25 species had less than 5 individuals. Biomass and density peaked during the rainy and norte seasons at ESP, ILCI and FLS; and during the dry season at CB. Small individuals were captured in ESP and the FLS, and larger sizes in CB and ILCI, suggesting the role of the lagoon as nursery and feeding grounds. Salinity in ESP, and Secchi depth in the ILCI were the environmental controlling factors. In the FLS, the community ecology is controlled by numerous factors that limit the patterns of diversity and abundance.

The dominant species were classified as: 1) *resident* species: a) typically estuarine with reproduction in the lagoon and, b) typically estuarine with spawning areas located in the inner shelf; 2) *Seasonal* species with a marked periodicity; and 3) *Occasional* visitors with limited spatial distribution.

Fish usage for PR and at ESP showed 53% of common species for both areas, 30% exclusive to ESP and 15% to PR. Adults enter through PR in the fall, and spawn near-shore in the vicinity of the inlet. During the dry season, the density and biomass

(juveniles and pre-adults) was highest in the ILCI and ESP areas coincidental to the highest primary production and the most rapid growth period of their life history.

CHAPTER 1. INTRODUCTION

1.1 Introduction

Coastal areas are transition zones with strong interaction among the sea, lowland terrestrial habitats, rivers and the atmosphere. These interactions strongly affect the dynamics of the environment and result in a high diversity of habitats. Each habitat has specific physical characteristics and biological assemblages (Nixon, 1982; Yáñez-Arancibia and Day, 1982, 1988; Day and Yáñez-Arancibia, 1985; Yáñez-Arancibia, 1987; Day et al., 1989; Blaber et al., 1994). Coastal lagoons and estuaries are two ecologically important and widespread types of coastal systems. These are open systems that are subsidized by physical processes (Odum, 1980). There are important exchanges of biological and non-biological materials with adjacent ecosystems, including water, salts, nutrients, sediments, and organisms (Childers et al., 2000).

There is a high degree of variability in coastal lagoons and estuaries. Salinity changes with tide and river flow, water levels fluctuate, the intertidal area is subject to wetting and drying and extremes of temperature, deltas grow and erode, and barrier island grow, shift and disappear (Day et al., 1989, 2000). But estuarine organisms have developed physiological and behavioral patterns to deal with these dynamic environmental conditions (Day and Yáñez-Arancibia, 1985; Day et al., 1989). These ecosystems have a high diversity of habitats, which are used as feeding, reproduction or spawning grounds by many different species, especially fishes. There is also a high connectivity in food webs and high diversity of coupling both internally and with neighboring systems (Yáñez-Arancibia and Day, 1985).

Coastal lagoon estuarine systems have high ecological and economic value in terms of such factors as fish production, wetland health, wildlife natural protected areas, potential for water quality improvement, freshwater storage, agriculture and tourism (Reyes et al., 1993; Day et al., 1999; Chesney et al., 2000; Yáñez-Arancibia, 2000). Despite these high values, there are serious environmental problems in many lagoon-estuarine ecosystems. The most important are: subsidence due to drainage, urban expansion, lowered freshwater input, which can lead to reduced accretion and salinity intrusion, water quality deterioration, and decreased biological production (Boesch et al., 1994; Day et al., 1995, 1997; Coleman et al., 1998). In tropical coastal wetlands, these problems are often the result of habitat destruction (Diegues, 1999), a reduction in the influence of pulsing events such as storms and river floods that lead to accretion (Botero and Salzwedel, 1999), lower biological production (Windevoixhel, et al., 1999), and reduced delta building (Mendelssohn and McKee, 1988; Day et al., 1997).

In coastal lagoons, fish: 1) transform energy from primary sources, 2) actively transfer energy through the food web, 3) exchange energy with neighboring ecosystems through migration patterns, 4) act as a form of energy storage within the ecosystem, and 5) are agents of energetic regulation (McHugh, 1967, 1985; Yáñez-Arancibia and Nugent, 1977). The ecological role of coastal lagoons and wetlands for fish is to provide food, spawning and nursery areas, protection, and serve as pathways for migration (Yáñez-Arancibia et al., 1980; Deegan and Thompson, 1985). This suggests that the ecology of the fish communities in estuarine systems is very complex. Fish, as an ecological group, are characterized as having multiple

interactions through their life history related to environmental heterogeneity, particularly in coastal lagoon and estuaries.

1.1.1 Background

Several authors have emphasized the importance of estuaries to marine fisheries and fishery resources (McHugh, 1967, 1985; Deegan and Thompson, 1985; Chesney, et al., 2000; Velasco and Wolff, 2000 among many others) by demonstrating that a large part of the total landings worldwide is made up of species that spend an important part of their lives in estuarine waters. At the same time, a number of human impacts are affecting marine and coastal diversity including chemical pollution and eutrophication, physical alterations of coastal habitats, invasion of exotic species, global climate change and fishing itself. These are factors that directly influence the coastal zone, especially estuaries and coastal lagoons (CDB, 1995; Duffy and Baltz, 1998; Blaber et al., 2000).

The goal to understanding biodiversity in ecosystem function is particularly important for the conservation and management of coastal marine systems. May (1994) concluded that there was a lack of databases for most marine species, and this was particularly evident for coastal zones rich in species. There are, however, studies of fish communities where assessment of biological diversity has been carried out. A number of authors, including Yáñez-Arancibia et al. (1980, 1985a, 1985b, 1988, 1993), Sanchez-Gil et al. (1981), Deegan and Thompson (1985), Ross and Epperly (1985), Subrahmanyam (1985), Arrivillaga and Baltz (1999), have studied fish community structure in coastal ecosystems and described patterns of spatial and temporal variation associated with physical parameters. Others used diversity indices as indicators of pollution (Bechtel and Copeland, 1970). Generally, there is a trend to

studying fish communities as a natural resource that can be exploited (Pauly 1998). Ecological studies often refer to the importance of essential habitat in considering the fishery as part of the ecosystem, indicating that fishery management must be done from a holistic perspective (Magnuson, 1991; Fluharty, 2000).

Diversity indices have been used to evaluate the structure of biological communities. Shannon's diversity index (Shannon, 1949) is the most popular with marine biologists (Washington, 1984). This index is biased towards the species abundance aspect of diversity. Since dominance is often more relevant in the analysis of environmental impact, Simpson's index is more appropriate because it analyzes species by abundance (Platt et al., 1984). Nevertheless, because this index is difficult to interpret alone, it is often necessary to use it in conjunction with other indices or models so that comparisons between communities from different locations can be more easily made (Hushland, 1976; Crema and Pagliai, 1980; Iglesias, 1981; Death and Winterbourn, 1995; Blanchard, 2001).

Diversity consists of two components; variety and relative abundance (Magurran, 1988; Southwood, 1978, 1996). Species diversity measures can be divided into three categories: 1) species richness indices are a measure of the number of species in an area; 2) species abundance models provide a descriptor of the abundance distribution, which represent situations where there is high evenness to those which characterize cases where the abundance of species is very unequal (May, 1975; Southwood, 1978; Magurran, 1988); and 3) indices based on the proportional abundance of species. These diversity indices have been used to describe fish communities by Yáñez-Arancibia et al. (1980, 1985a, 1985b, 1988, 1993), Brun et al. (1990), Death and Winterbourn (1995), Griffiths (1997), Madrid et al. (1997), Duffy and

Baltz (1998), Rhodes (1998), Lekve et al. (1999), Bianchi et al. (2000), Guidetti and Bussotti (2000), Blanchard (2001).

Another important aspect in the analysis of estuarine fish communities is habitat-fish species relationships. In this sense, the fish community is an assemblage of different fish species located in a particular area, many of which are commercially important. When particular species are captured, as target species or bycatch, the fishery mortality can affect the whole assemblage structure. Therefore, fishery scientists and managers have become increasingly aware and concerned about the direct, indirect and cumulative impacts of habitat change on commercial and recreational fisheries, and conversely the effects of these fisheries in an ecosystem context (Fluharty, 2000; Blaber et al., 2000).

Thus, an understanding of the diversity, behavior and microhabitat requirements of estuarine-dependent fishes is important for the conservation of the nursery function of coastal wetlands (Baltz, et al., 1993). Enhanced survival and growth of early life history stages in nursery habitats is known to increase recruitment success. It is not clearly known how environmental factors influence survival and growth in estuaries, nor the extent to which habitat preferences affects recruitment success for many estuarine-dependent fishes.

Baltz (1990) defined the microhabitat of an individual fish as the site that it occupies at a given point in time. This site may be characterized by physicochemical variables that describe resources or environmental constraints. And microhabitat use describes the intensity of use of values on a site-resource axis by a life stage or population. The frequency of use distribution indicates the relative intensity of use by intervals of environmental variables (Baltz, 1990). Thus, a site is presumably selected

by the fish in response to proximate factors to optimize net energy gain while avoiding predators and minimizing interactions with competitors (Baltz et al., 1993). Baltz et al. (1993) approached the question of habitat preferences by fine scale studies of distribution and abundance at the microhabitat level. At the same time, to begin to understand the linkages between fish habitat preferences and recruitment, studies are needed which interrelate microhabitat use, prey selection and, and daily growth.

In relation to this topic, several authors have discussed habitat requirements for fish early life-history stages. Blaber and Blaber (1980) studied how physical factors affect the distribution of juvenile estuarine and inshore fish. Day et al. (1982) conducted an analysis of environmental factors regulating metabolism and fisheries production in a Louisiana estuary. Boehlert and Mundy (1988) discussed the role of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Pinto (1987) related environmental factors to the occurrence of juvenile fish in mangroves in Pagbilao, Philippines. Weinstein (1985) studied the role of the distributional ecology of fishes inhabiting warm-temperate and tropical estuaries on community relationships.

The abundance and importance of some fish species and families in coastal lagoons and estuaries have been studied particularly well because of their commercial importance. A number of studies have been carried out in Terminos Lagoon. The family Ariidae, for example, is common in many temperate, tropical and subtropical coastal ecosystems. In Terminos Lagoon, Lara-Domínguez et al (1981) and Yáñez-Arancibia and Lara-Domínguez (1988) studied the biological strategies and abundance patterns of three species of sea catfish. Also, Yáñez-Arancibia et al (1985c) reported on the environmental factors that regulate biological strategies and production of dominant fish populations. Several authors (Díaz et al., 1982; Aguirre Leon et al., 1982;

Mallarad Colmenero et al., 1982; Aguirre Leon and Yáñez-Arancibia, 1986) reported on the families Pomadasidae, Gerreidae and Tetraodontidae, which are important. Chavance et al. (1984, 1986) studied the population dynamics of *Bairdiella chrysoura* and *Archosargus rhomboidalis*.

Habitat and primary production are important determinants controlling fish community structure and distribution. For example, Yáñez-Arancibia et al. (1988) related fish abundance patterns to aquatic primary productivity in Terminos Lagoon. A number of authors have shown that mangroves are important nursery sites. Pinto (1988) studied the population dynamics and community structure of fish in mangroves in Pagbilao, Philippines and Lewis et al. (1985) related mangrove habitat to fishery resources in Florida. Other studies documenting the importance of mangroves include comparisons of the abundance and species composition of fish and crustaceans in mangroves and other near shore habitats in tropical Australia (Robertson and Duke, 1987), the utilization of red mangrove prop root habitat by fishes in South Florida (Thayer et al., 1987), the relationship of fish trophic dynamics to mangrove ecosystems in the north littoral of the Yucatan (Vega Cendejas, 1998), and the coupling of primary and secondary production in mangrove and seagrass habitats in Terminos Lagoon (Yáñez-Arancibia et al., 1993)

Seagrasses and salt marshes have also been shown to be important habitat for fishes. For example, Arrivillaga and Baltz (1999) documented the nursery value of seagrasses to fishes and macroinvertebrates on the Atlantic coast of Guatemala. Bell and Pollar (1989) also related the ecology of fish assemblages and fisheries with seagrass. Other studies have documented the importance of seagrass habitats including: the role of habitat complexity, competition and predation in structuring fish

and motile macroinvertebrates assemblages (Heck and Orth, 1980), the trophic organization of fish in coastal seagrass systems (Livingston, 1982), and the response of the organization of fishes in coastal seagrass system to stress (Livingston 1985). Food, density, and microhabitat relationships have also been studied for salt marshes including factors affecting the growth and recruitment potential of juvenile saltmarsh fishes (Baltz et al., 1998), microhabitat use by marsh-edge fishes in a Louisiana estuary (Baltz et al., 1993), the role of food and refuge on the dependence of fishery species in salt marshes (Boesch and Turner, 1984), shallow marsh habitats as primary nurseries for fish and shellfish in the Cape Fear River, North Carolina (Weinstein, 1979), and the ecology of fish communities in the Mississippi River deltaic plain (Deegan and Thompson, 1985),

In Terminos Lagoon (the largest tropical coastal lagoon in Mexico), numerous studies have addressed ecological role of the fish community in the system. It has been determined that fish communities are seasonally related, through structural parameters of biomass and diversity, to the different estuarine habitats. Reflecting this, the dominant species, as indicators of these relationships, are coupled to the different habitats and climatic periods during different periods of their life cycles in the lagoon (Yáñez-Arancibia and Day, 1982; Yáñez-Arancibia et al., 1980, 1985a, 1985b, 1985c, 1988, 1993, 1994; Yáñez-Arancibia and Lara-Domínguez, 1988).

The structural parameters of fish populations for each habitat often undergo regular changes (Yáñez-Arancibia et al., 1980, 1985c, and 1988). The seasonality of these changes is related to the biological adaptations of the different fish species to changes in environmental parameters during the year (Yáñez-Arancibia et al., 1993). Adaptations and tolerances to certain physical and biological parameters determine fish

species diversity and distribution. Different fish life history stages occur along spatial and temporal gradients that should reflect optimum conditions (physical, chemical and biological) for each stage (Baltz et al., 1993).

1.1.2 Objectives

In this work, I assess temporal and spatial changes in patterns of the structure of fish communities in Terminos Lagoon based on patterns of abundance and diversity. Based on this analysis, I address the ecological function of the different ecological subsystems of the lagoon for dominant species using measures of biomass, density, and frequency of capture as they are related to biological strategies. I address in more detail these relationships for fish populations in seagrasses and establish couplings between primary and secondary production.

- **General Objectives**

To identify what physical factors influence fish community structure in Terminos Lagoon in terms of species diversity, biomass and density. To determine spatial distribution patterns in terms of abundance, biomass and density.

To document seasonal changes in diversity and determine if these patterns are related to the life cycles or migration patterns of different fish species.

To determine for each major habitat in Terminos Lagoon, the dominant species unique to that habitat and dominant species shared with other habitats.

To establish the linkages among habitats with respect to different biological strategies of habitat utilization.

To define fish habitat use patterns and the environmental parameters that are associated with each these patterns.

To describe the ecological linkages among the dominant fish communities in different habitats related to their seasonal patterns of migration.

To analyze the seasonal biomass variation for each dominant fish species in each habitat and define its relationships with patterns of primary production.

1.2 Study Area

Terminos Lagoon is a large (about 1700 km² for the lagoon surface area surrounded by about 2500 km² of mangroves and freshwater wetlands), shallow (mean depth 3.5 m) coastal lagoon located at the base of the Yucatan Peninsula in the state of Campeche, Mexico (Fig. 1). The lagoon is separated from the Gulf of Mexico by Isla del Carmen and water exchange with the Gulf occurs through two deep inlets. There is a mixed diurnal tide with a range of about 0.5 m. Trade winds induce a net inflow into the lagoon through the eastern inlet at Puerto Real, and a net outflow through the western inlet at Carmen (Mancilla and Vargas, 1980; Graham et al., 1981). This net flow has resulted in the formation of a flood-tide delta in the lagoon at Puerto Real inlet and an ebb-tide delta in the Gulf at Carmen Inlet (Phleger and Ayala Castañares, 1971; Coll de Hurtado, 1975; Gutierrez Estrada and Castro del Rio, 1988; Kjerfve et al., 1988).

Climatically, this tropical area is characterized by three seasons with distinct patterns in precipitation, river discharge, winds and temperature (Yáñez-Arancibia and Day, 1982): the dry season from February to May, the rainy season from June to September, and the "Norte" season from October to January. Rainfall is very low during the dry season (66 mm/month), occurs during afternoon and evening thunder showers in the rainy season (289 mm/month) and is associated with frontal systems during the norte season (175 mm/month).

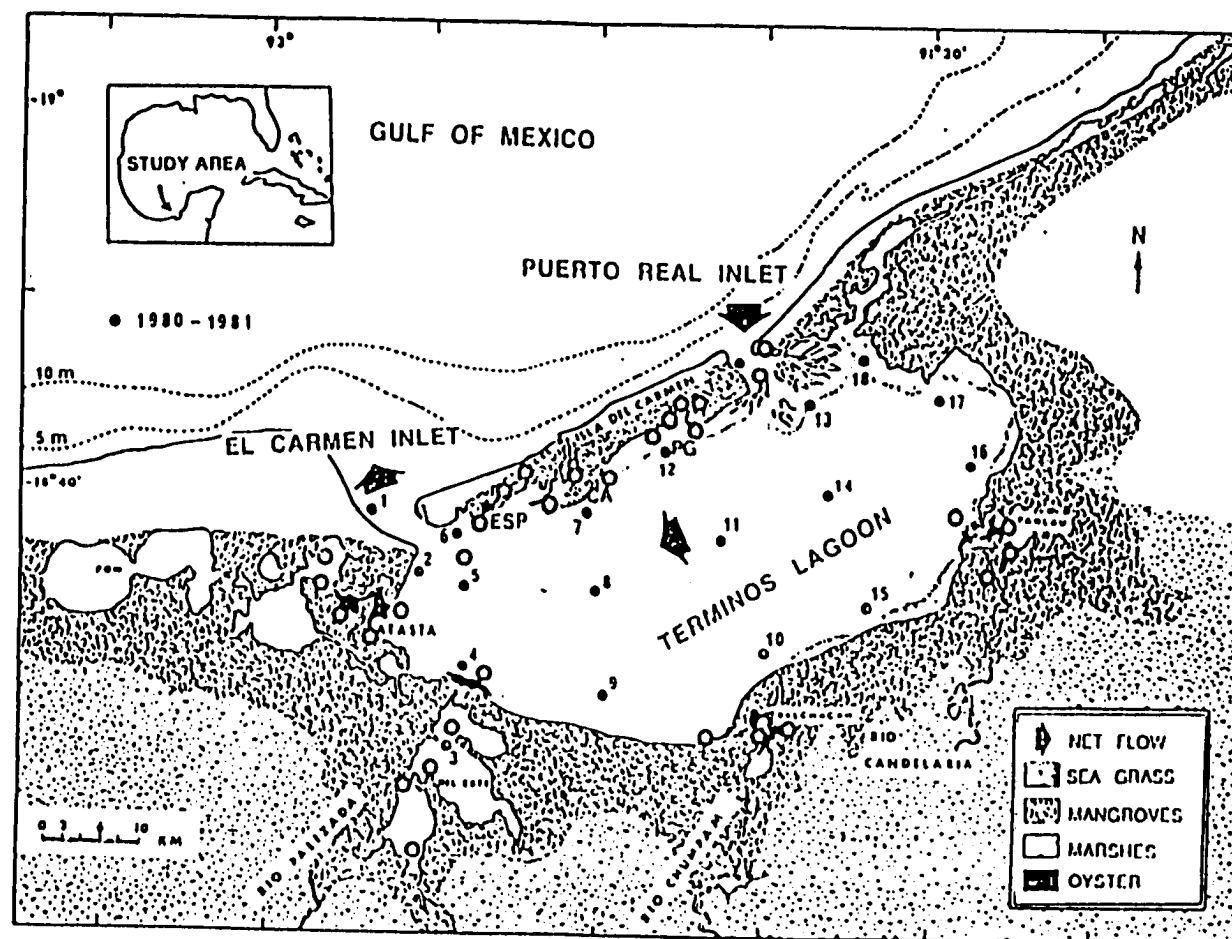


Fig. 1.1. Location of study area, Terminos Lagoon in the Southern Gulf of Mexico. Location of sampling stations are indicated.

The same rainfall pattern occurs over the drainage basin of the lagoon resulting in a similar pattern of river discharge with peak discharge in the months of September, October and November. Three main rivers discharge to the lagoon: the Candelaria, the Chumpan and the Palizada (a distributary of the Usumacinta River) (Phleger and Ayala-Castañares, 1971; Amezcua Linares and Yáñez-Arancibia, 1980; Vera Herrera et al., 1988). The Palizada has the highest discharge resulting in a pronounced lowering of salinity in the western part of the lagoon.

Seagrass beds occur in shallow areas along shores in the eastern end of the lagoon (Moore and Wetzel, 1988). *Thalassia testudinum* is the most abundant species, but *Diplantera wrightii* and *Syringodium filiforme* also occur. Extensive mangrove swamps dominated by *Rhizophora mangle*, *Avicennia germinans* and *Laguncularia racemosa* surround the lagoon (Day et al., 1982, 1988, and 1997).

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CHAPTER 2. ECOLOGICAL STRUCTURE OF ESTUARINE FISH COMMUNITIES: ABUNDANCE AND DIVERSITY PATTERNS IN LAGUNA DE TERMINOS, A TROPICAL COASTAL LAGOON

2.1 Introduction

Coastal areas are transition zones with strong interactions among the sea, lowland terrestrial habitats, rivers and the atmosphere. These interactions strongly affect the dynamics of the environment and result in a high diversity of habitats. Each habitat has present specific physical characteristics and biological assemblages (Nixon, 1982; Yáñez-Arancibia and Day, 1982, 1988; Day and Yáñez-Arancibia, 1985; Yáñez-Arancibia, 1987; Day et al., 1989; Blaber et al., 1994). Coastal lagoons and estuaries are two ecologically important and widespread types of coastal systems. These open systems are subsidized by physical processes (Odum 1980). There are important exchanges of biological and non-biological materials with adjacent ecosystems, including water, salts, nutrients, sediments, and organisms (Childers et al., 2000).

There is a high degree of variability in coastal lagoons and estuaries. Salinity changes with tide and river flow, water levels fluctuate, the intertidal area is subject to alternating wetting and drying and extremes of temperature, deltas grow and erode, and barrier island grow, shift and disappear (Day et al., 1989, 2000). Estuarine organisms, however, have developed physiological and behavioral patterns to deal with these dynamic environmental conditions (Day and Yáñez-Arancibia, 1985). These ecosystems have a high diversity of habitats, which are used as feeding, reproduction or spawning grounds by many different species, especially fishes. There is also a high connectivity in food webs and high diversity of coupling both internally and with neighboring systems (Day and Yáñez-Arancibia, 1985).

Many tropical coastal nekton use tropical coastal lagoons during part or all of their life history. Fish are the main component of nekton and they have different migration patterns related to their ecological strategies. Coastal wetlands serve as both seasonal residence and nursery habitats for many estuarine dependent fishes and invertebrates such as penaeid, drums, snappers, and many others (Weinstein, 1979, 1985; Blaber and Blaber, 1980; Herck and Orth, 1980; Yáñez-Arancibia et al, 1980; Day et al., 1982a; Livingston, 1982, 1985; Boesch and Turner, 1984; Zimmerman and Minello, 1984; Deegan and Thompson, 1985; Lewis et al., 1985; Claridge et al., 1986; Pinto, 1987, 1988; Robertson and Duke, 1987; Thayer et al., 1987; Boehlert and Mundy, 1988; Yáñez-Arancibia and Lara-Domínguez, 1988; Yáñez-Arancibia et al., 1988a, 1993, 1994; Bell and Pollar 1989; Baltz et al., 1993, 1998; Chesney et al., 2000).

Coastal lagoon estuarine systems have high ecological and economic value in terms of such factors as fish production, wetland health, wildlife natural protected areas, potential for water quality improvement and freshwater storage, agriculture and tourism (Reyes et al., 1993; Day et al., 1999; Chesney et al., 2000; Yáñez-Arancibia, 2000). Despite these high values, there are serious environmental problems in many lagoon-estuarine ecosystems. The most important are: subsidence due to drainage, urban expansion, lowered freshwater input, which can lead to reduced accretion and high salinity intrusion, water quality deterioration, and decreased biological production (Boesch et al., 1994; Day et al., 1995, 1997; Coleman et al., 1998). These problems are the result of habitat destruction in tropical coastal wetlands (Diegues, 1999), blocking the influence of pulsing events such as storms and river floods that lead to accretion and fresh water input (Botero and Salzwedel, 1999), higher net biological

production (Windevoixhel et al., 1999), and enhanced delta building (Mendelssohn and McKee, 1988; Day et al., 1997).

In coastal lagoons, fish serve 5 ecological roles: 1) transform energy from primary producers, 2) actively transfer energy through the food web, 3) exchange energy with neighboring ecosystems through migration patterns, 4) act as a form of energy storage within the ecosystem, and 5) are agents of energetic regulation (Yáñez-Arancibia and Nugent, 1977). The ecological role of coastal wetlands for fish is to provide food, spawning and nursery areas, protection, and serve as pathways for migration (Yáñez-Arancibia et al., 1980; Deegan and Thompson, 1985). This suggests that the ecology of fish communities in estuarine systems is very complex. Fish, as an ecological group, are characterized as having multiple interactions through their life history related with environmental heterogeneity, particularly in coastal lagoon and estuaries.

2.1.1 The Problem

Several authors have emphasized the importance of estuaries to marine fisheries and fishery resources (McHugh, 1967, 1985; Deegan and Thompson, 1985; Chesney, et al., 2000; Velasco and Wolff, 2000) by demonstrating that a large part of the total landings worldwide is made up of species that spend an important part of their lives in estuarine waters. At the same time, a number of human impacts are affecting marine and coastal diversity including chemical pollution and eutrophication, physical alterations of coastal habitats, invasion of exotic species, global climate change and fishing itself (Blaber et al., 1994; Duffy and Baltz, 1998). These are factors that directly influence the coastal zone, especially estuaries and coastal lagoons (CBD, 1992).

Understanding the role of biodiversity in ecosystem function is particularly important for the conservation and management of coastal marine systems. May

(1994) concluded that there was a lack of databases for most marine species, and this was particularly evident for the coastal zone which is rich in species. There are, however, studies of fish communities where assessment of biological diversity has been carried out. A number of authors, including Yáñez-Arancibia et al. (1980, 1985a, 1985b, 1988a, 1993), Sanchez-Gil et al. (1981), Deegan and Thompson (1985) Ross and Epperly (1985), Subrahmanyam (1985), and Death and Winterbourn (1995) and Arrivillaga and Baltz (1999) have studied fish community structure in coastal ecosystems and described patterns of spatial and temporal variation associated with physical parameters. Others used diversity indices as indicators of pollution (Bechtel and Copeland, 1970). Generally, there is a trend to studying fish communities as a natural resource that can be exploited. Ecological studies often refer to the importance of essential habitat in considering the fishery as part of the ecosystem, indicating that fishery management must be done from a holistic perspective (e.g., Magnuson, 1991; Fluharty, 2000).

Diversity indices have been used to evaluate the structure of biological communities. Shannon's diversity index (Shannon, 1949; Meffe and Carroll, 1997) is the most popular with marine biologists (Washington, 1984). This index is biased towards the species richness aspect of diversity. Since dominance is often more relevant in the analysis of environmental impact, Simpson's index is more appropriate because it analyzes species by abundance (Platt et al., 1984). Nevertheless, because this index is difficult to interpret alone, it is often necessary to use other indices or models so that comparisons between communities from different locations can be more easily made (Kushland, 1976; Crema and Pagliai, 1980; Iglesias, 1981; Death and Winterbourn, 1995; Blanchard, 2001).

Diversity consists of two components; species richness and abundance (Magurran, 1988; Southwood, 1978, 1996). Species diversity measures can be divided into three categories: 1) species richness indices are a measure of the number of species in an area; 2) species abundance models provide a descriptor of the abundance distribution. There are four models to describe abundance, ranging from those which represent situations where there is high evenness to those which characterize cases where the abundance of species is very unequal (May, 1975; Southwood, 1978; Magurran, 1988). In this paper, I use these models for the first time to describe tropical fish communities; and 3) indices based on the proportional abundance of species. These diversity indices have been used to describe fish communities in Yáñez-Arancibia et al. (1980, 1985a, 1985b, 1988a, 1993), Brun et al. (1990), Sedberry and Carter (1993), Griffiths (1997), Madrid et al. (1997), Duffy and Baltz (1998), Rhodes (1998), Lekve et al. (1999), Bianchi et al. (2000), Guidetti and Bussotti (2000), Blanchard (2001).

2.1.2 Objectives

This study was carried out to address concerns described in the Convention on Biological Diversity (1992) on the environmental interactions and species composition on functional groups of marine organisms and to try to establish what specific characteristics of a habitat directly or indirectly influence species diversity. There is a paucity of published data on diversity analysis in fish communities to formally test the fit of the main species abundance models. Thus, the general objective is:

- **General Objective**

To identify what physical factors influence fish community structure in Terminos Lagoon in terms of species diversity, biomass and density. To determine spatial distribution patterns in terms of abundance, biomass and density. To document

seasonal changes in diversity and determine if these patterns are related to the life cycles or migration patterns of different fish species.

- **Specific Objectives**

To evaluate fish community richness in terms of number of species and Margalef's index of species richness.

To evaluate fish community structure in terms of numbers of individuals, biomass, density, and average mass.

To analyze the structure of fish communities using four conventional abundance models (geometric series, log series, log normal and broken stick) as suggested by Magurran (1988). In addition, the graphical k-dominance curves and the Q-statistic were used. These models make data sets easier to compare and it is possible evaluate the use of available resources in each habitat.

To evaluate fish community diversity using indices such as Shannon, Whilm, Pielou, and Simpson.

To establish what physical characteristics directly or indirectly influence species diversity.

2.2. Study Area

Terminos Lagoon is a large (about 1700 km² for the lagoon surface area surrounded by about 2500 km² of mangroves and freshwater wetlands), shallow (mean depth 3.5 m) coastal lagoon located at the base of the Yucatan Peninsula in the state of Campeche, Mexico (Fig. 2.1). The lagoon is separated from the Gulf of Mexico by Isla del Carmen and water exchange with the Gulf occurs through two deep inlets. The tide is a mixed diurnal tide with a range of about 0.5 m. Trade winds induce a net inflow into the lagoon through the eastern inlet at Puerto Real, and a net outflow

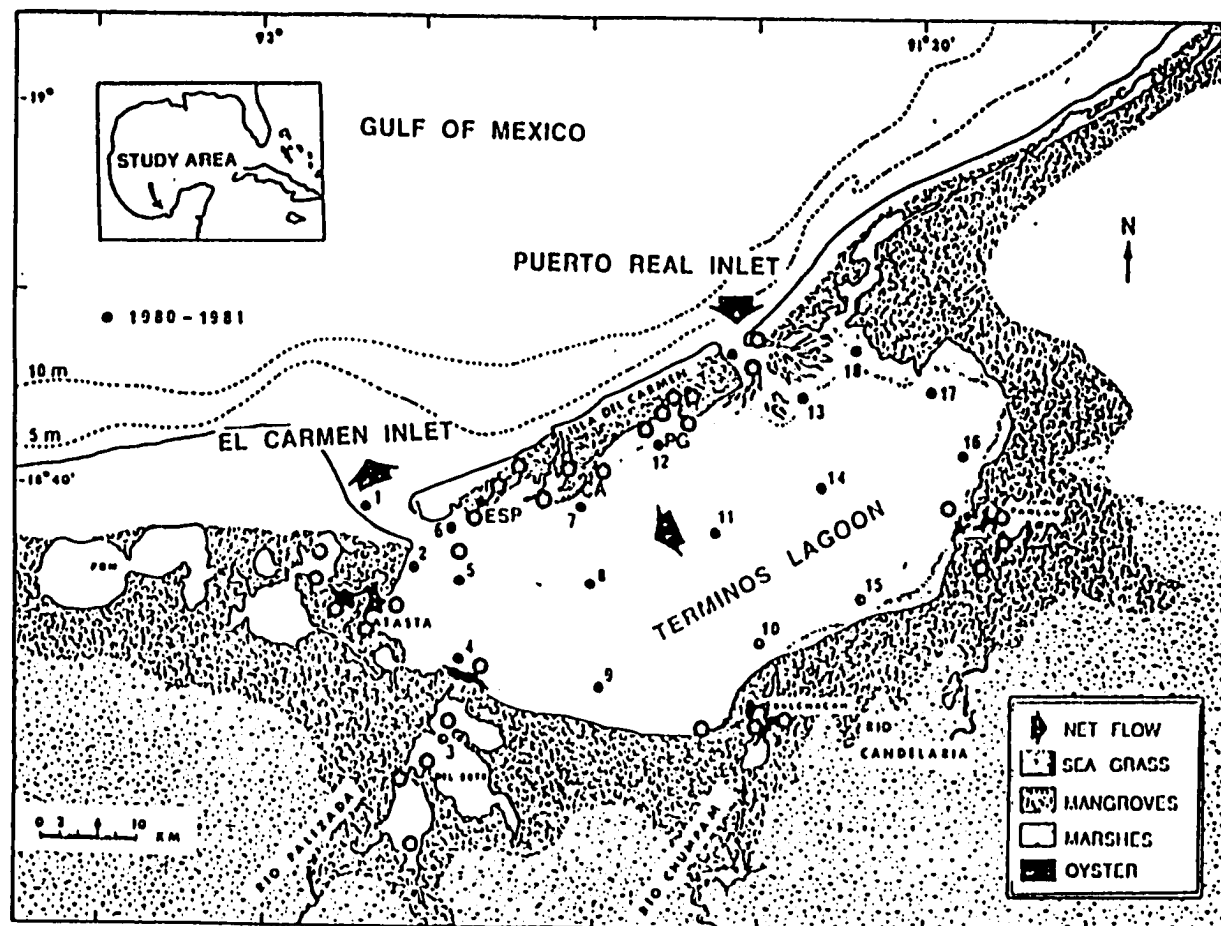


Fig. 2.1. Location of study area. Terminos Lagoon in the Southern Gulf of Mexico. Sampling stations are indicated.

through the western inlet at Carmen (Mancilla and Vargas, 1980; Graham et al., 1981). This net flow has resulted in the formation of a flood-tide delta in the lagoon at Puerto Real Inlet and an ebb-tide delta in the Gulf at Carmen Inlet (Phleger and Ayala Castaños, 1971; Coll de Hurtado 1975; Gutierrez Estrada and Castro del Rio, 1988; Kjerfve et al., 1988).

Climatically, this tropical area is characterized by three seasons with distinct patterns in precipitation, river discharge, winds and temperature (Yáñez-Arancibia and Day, 1982): the dry season from February to May, the rainy season from June to September, and the "Nortes" season from October to January. Rainfall is very low during the dry season (66.1 mm/month), occurs during afternoon and evening thunder showers in the rainy season (289.0 mm/month) and is associated with frontal systems during the norte season (175.2 mm/month).

The same rainfall pattern occurs over the drainage basin of the lagoon resulting in a similar pattern of river discharge with peak discharge in the months of September, October and November. Three main rivers discharge to the lagoon: the Candelaria, the Chumpan and the Palizada (is a tributary of the Usumacinta River; Phleger and Ayala-Castaños, 1971; Amezcua and Yáñez-Arancibia, 1980; Vera Herrera et al., 1988). The Palizada has the highest discharge resulting in a pronounced lowering of salinity in the western part of the lagoon.

Carmen Inlet is a highly variable environment due to the interaction with the Gulf of Mexico, lagoon, and riverine water masses. Sediments are clay-silts with less than 30% CaCO_3 . The area is mostly fringed with mangroves and macroalgae also occurs. The Central basin of the lagoon is a transition area where mixing of fresh and marine waters occurs. Sediments are fine sands and clays of 30-40% CaCO_3 . Submerged macroalgae, mainly rhodophytes, is abundant in this area. The fluvial

lagoon systems are directly influenced by river discharge and fringed by mangroves. Two areas in this region can be distinguished. The eastern portion is located in the southern-most extent of the Yucatan Peninsula with sediments of clay with fine sand and 20 to 40% CaCO_3 . There is abundant submerged sea grasses and macroalgae. The western portion of the region is in the northeastern part of the alluvial plain of the Grijalva-Usumacinta delta. Sediments are clay-silt with 10 to 30% CaCO_3 . There is no submerged vegetation and oyster reefs are common. The Inner Littoral of Carmen Island is an area of semi-permanent marine influence due to waters that entering through Puerto Real Inlet. There are carbonate sands with 30 to 70% CaCO_3 . Submerged vegetation, dominated by *Thalassia testudinum*, is very abundant and mangrove swamps border the area. It is important to note that this area has no freshwater inflow and the only direct freshwater input is precipitation during the rainy and norte seasons (Yáñez-Arancibia et al., 1982; Yáñez-Arancibia and Lara-Dominguez, 1983).

Seagrass beds occur in shallow areas along shallow shorelines in the eastern end of the lagoon (Moore and Wetzel, 1988). *Thalassia testudinum* (turtle grass) is the most abundant species, but *Diplantera wrightii* and *Syringodium filiforme* (manatee grass) also occur. Extensive mangrove swamps dominated by *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove) and *Laguncularia racemosa* (white mangrove) surround the lagoon (Day et al., 1982b, 1988b, and 1996).

2.3 Material and Methods

2.3.1 Field and Laboratory Measurements

Fish were collected by a 5 m shrimp otter trawl (2.5 m mouth with a 19 mm mesh). Tows lasted 10 to 12 min at 2 to 2.5 knots and covered an area of 1500 to 2000 m^2 . Sampling depth varied but never exceeded 3.5 m. Samples were collected

monthly at 18 stations from March 1980 to April 1981 (Fig. 2.1). Specimens were fixed in neutralized 10% formalin. Temperature (thermometer), salinity (temperature-compensated refractometer), Secchi depth and total depth, sediment type, presence of submerged vegetation, air temperature and wind direction were also measured in association with samples at each station. In the laboratory, individuals were identified to species, counted and measured to the nearest millimeter Total Length (TL).

2.3.2 Analysis of Community Structure

Cluster analysis (SAS Institute Inc., 1994) of the environmental parameters was used to characterize Terminos Lagoon. In addition to salinity, temperature and Secchi values, the analysis included monthly river discharge (Secretaria de Agricultura y Recursos Hidraulicos, Direccion de Hidrologia, 1981), sediment type (Ayala Castaños, 1963), and type of vegetation (Rojas Galaviz et al., 1993). The purpose of the cluster analysis was to characterize the sampling stations in different subsystems in the lagoon (Yáñez-Arancibia and Day, 1982, 1988; Yáñez-Arancibia et al., 1983).

2.3.3 Community Structure Parameters

For each ecological subsystem several structural parameters of the fish community were calculated based on the total number of individuals of each species occurring at each station. These are presented below. Biomass and density estimates per m² were calculated monthly for each subsystem and for the entire lagoon. Mean fish size (mass) in the community was calculated monthly for each subsystem and for the entire lagoon by dividing total biomass by density.

2.3.3.1 Diversity

Diversity can be measured by the number of species, relative abundance or a combination of the two components. Diversity measures can be divided into three main categories, 1) indices which measure the number of species in a sampling area, 2)

abundance models which describe the distribution of species abundance, and 3) indices based on the proportional abundance of species which measure richness and evenness in a single value. Species abundance models range from those that represent situations where there is high evenness to those which characterize cases where the abundance of species is very unequal. The diversity of a community may therefore be described by referring to the model that provides the best fit of the observed pattern of species abundance. In general, high diversity communities have a few species which are very abundant, an intermediate number of species of medium abundance, and many species represented by only a few individuals. The species abundance models utilize information of species abundance distribution in a community to describe an integrated mathematical description of the data (Magurran, 1988). Three types of diversity analyses were carried out.

2.3.3.1.1 Species Richness

For these analyses, the number of species in each ecological subsystem and for the entire lagoon was used. Margalef's index (1969) of diversity is a combination of S (the number of species recorded) and N (the total number of individuals summed over all S species). It is calculated as $D = \frac{(S-1)}{\ln N}$.

According to Peet (1975) the index of species richness of Margalef (1969) is the only diversity index that provides information on ecological diversity. According to this index, the maximum possible diversity occurs when each captured individual belongs to a different species.

2.3.3.1.2 Species Abundance Models

These models are based on the relative abundance of species in the community developed for the species: the abundance relationship will be a reflection of

the underlying distributions of the individual species in the community. For example, Fisher et al. (1943) stated "that if insect population were distributed at random and the mean varied for the various species, then the distribution of species abundance should be a negative binomial distribution. He further reasoned that such a distribution could be easily approximated by a simple log series, one of the parameters of which could be used as a measure of diversity" (Buzas, 1972) Six models have been described by May (1975), Southwood (1978, 1996), Magurran (1988) Kempton and Taylor (1976, 1978) and Platt et al. (1984).

2.3.3.1.2.1 Geometric Series

If species i occupies fraction k_i of a habitat, species $i+1$ occupies fraction k_{i+1} of the habitat, species $i+2$ occupies fraction k_{i+2} of the habitat, and so on, the resulting rank-abundance distribution will be a geometric series (Motomura, 1932; Magurran, 1988). This model is also called the 'niche-pre-emption hypothesis'. In a geometric series the abundance of species ranked from the most to least abundant will be:

$$n_i = NC_k k(1-k)^{i-1}$$

where n_i = the number of individuals of the i th species;

N = the total number of individuals;

$C_k = [1 - (1 - k)^S]^{-1}$ and is a constant which ensures that $\sum n_i = N$

k = the proportion of the available niche space or resource that each species occupies.

k is estimated interactively using the following equation

$$N_{min}/N = [k/(1-k)][(1-k)^S] / [1-(1-k)^S]$$

where N_{min} = is the number of individuals in the least abundant species. With k estimated from the equation, it is possible to obtain a value of C_k , and calculate the expected value of individuals for each species, S = number of species.

When this process has been repeated for each successive species, the observed and expected values can be compared using a χ^2 Goodness-of-Fit test, with degrees of freedom = number of species - 1. Because the ratio of the abundance of each species to the abundance of its predecessor is constant through the ranked list of species, the series will be a straight line if plotted on a log abundance/species rank graph.

2.3.3.1.2.2 Logarithmic (or log) Series

This analysis was originally suggested for description of species abundance data by Fisher (1958). The small number of abundant species and the large proportion of rare species predicted by the log series model suggests that it is most applicable in situations where one or two environmental factors (such as salinity or temperature) dominate the ecology of a community. To use these models, the observed abundance data is first put into abundance classes based on \log_2 (that is octaves or doublings of species abundance; Preston, 1948). The log series takes the form

$$\alpha x, \frac{\alpha x^2}{2}, \frac{\alpha x^3}{3} \dots \frac{\alpha x^n}{n}$$

with αx being the number of species with one individual, $\alpha x^2/2$ the number of species with two individuals, etc.

To fit the series, it is necessary to calculate how many species are expected to have one individual, two individuals and so on. The two parameters needed to fit the series are x and α . x is estimated by iterating the following term

$$S/N = [(1-x)/x] [-\ln(1-x)]$$

where S = total number of species and N = total number of individuals.

Once x has been obtained, α is calculated using the equation

$$a = [N(1-x)]/x$$

α is an index of diversity. When α and x have been obtained, the number of species expected to have 1, 2, 3, ... n can be calculated. These expected abundances are then put into the same abundance classes used for the observed distribution and a goodness of fit test is used to compare the two distributions. χ^2 is one commonly used test, with degrees of freedom = classes - 1.

The logarithmic series model is based mainly on the assumption that any biological parameter follows a positive binomial or normal Poisson distribution (Southwood, 1978). In the analysis of the fish community, the model establishes that the fish community is made up of a small number of dominant species and a large proportion of 'rare' species in which the class containing one individual per species is always the largest. This model describes patterns of species abundance of the where one or few factors dominate the ecology of the community.

2.3.3.1.2.3 Log Normal Distribution

Preston (1948) suggested that the normal distribution would give the best description of species-abundance patterns assuming that individuals were distributed among species in a normal or Gaussian distribution. May (1975) further discussed the biological reasons why the log normal might be considered to apply to both opportunistic and equilibrium species.

Species abundance was plotted using \log_2 classes and the resulting classes were termed octaves (Preston, 1948). The distribution is usually written in form:

$$S(R) = S_o \exp(-a^2 R^2)$$

where $S(R)$ = the number of species in the R th octave (i.e. class) to the right and the left of the symmetrical curve.

S_0 = the number of species in the modal octave

$a = (2s^2)^{\frac{1}{2}} =$ the inverse width of the distribution

In this study, I used the Pielou's truncated log normal distribution method (1975), which fits species abundance to a truncated log normal distribution because it reflects the fact that there are a number of rare species that escaped collection. Therefore, this method entails converting the observed number of individuals per species to logs and fitting a normal curve, disregarding the area to the left of the truncation point. This point is assumed to occur at a count of one individual, and it is called the 'veil line' (Preston, 1948). That is, the part of the normal curve lying to the left of one individual cannot be observed without further sampling. The area under the remaining part of the curve is then used to estimate S^* , the total number of species in the community. In this method, it is necessary to consult Cohen's table (1961) for truncated log normal distributions in order to obtain θ (the auxiliary estimation function) which permits the mean and variance of the distribution to be estimated.

The mean and variance of the sample are then calculated. Next, $\gamma = \sigma^2 / (x - x_0)^2$ is calculated where $x_0 = \log_{10} 0.5 = -0.30103$. Then, μ_x and V_x (the mean and variance of x) from the truncated log normal distribution is estimated using the equations $\mu_x = x - \theta (x - x_0)$ and $V_x = \sigma^2 + \theta (x - x_0)^2$. Then the standardized normal variable z_0 , which corresponds to the truncation point x_0 , is calculated as $z_0 = (x_0 - \mu_x) / \sqrt{V_x}$. With this value, p_0 is obtained using tables that give the area under the normal curve. This represents the species unsampled in the community; the ones to the left of the veil line.

The equation $[S^* = S / (1-p_0)]$ gives the total number of species in the community. With this, it is possible to estimate the number of species expected in each

class. It is helpful to construct a table with the following columns: a) The upper class boundary; b) the upper class boundary converted to \log_{10} ; c) the standardized form of these log classes with the equation $[(b - \mu_x) / \sqrt{V_x}]$; and d) the cumulative number of species expected. To obtain the values for column d, take each value in (c), and obtain from the tables that give the area under the normal curve, p_0 , and multiply the result by S^* . Differences between successive entries provide the expected number of species in each class. The log normal diversity statistic, λ , is then obtained from the equation $\lambda = S^* / \sigma_x$ (where $\sigma_x = \sqrt{V_x}$). Finally, the observed and expected number of species are compared using a χ^2 goodness of the fit test, with degrees of freedom = classes - 3.

2.3.3.1.2.4 The Broken Stick Model

MacArthur (1957) proposed this model which is generally called 'the random niche boundary hypothesis'. It reflects a much more equitable distribution than those suggested by the normal distribution, log series and geometric series. It is a biologically realistic expression of a uniform distribution. Like the geometric series, the broken stick distribution is conventionally written in terms of rank order abundance and the number of the individuals in the i th most abundant class of S species (N_i) is obtained from the equation:

$$N_i = N/S \sum_{n=i}^S 1/n$$

where N = total number of individuals; S = total number of species.

Nevertheless, May (1975) suggested an alternative approach to the model in terms of standard species abundance and the results is that it is possible to make comparisons with the other models. This approach is estimated by a χ^2 goodness of the fit test, with degrees of freedom = classes - 1.

$$S(n) = [S(S-1)/N](1-n/N)^{S-2}$$

where $S(n)$ is the number of species in the abundance class with n individuals. The observed species are allocated to abundance classes (using Log_2). The number of species expected to have one individual, two individuals, etc is then calculated. Next, these values are summed in relation to the class boundaries. When this procedure is complete, the expected number of species is compared with observed number by using a χ^2 goodness of the fit test, with degrees of freedom = classes - 1.

2.3.3.1.2.5 The Q Statistic

This method is an interesting approach to the measurement of diversity, which takes the distribution of species abundance into account but does not entail fitting (Kempton and Taylor, 1976, 1978). This index is a measure of the inter-quartile slope of the cumulative species abundance curve and provides an indication of the diversity of the community with no weighting either towards very abundant or very rare species. The first step is to construct a table showing the cumulative number versus abundance and work out the position of the lower and upper quartiles. Once these are selected, the estimations are made with the following equation:

$$Q = \frac{\frac{1}{2}n_{R1} + \sum_{R1+1}^{R2-1} n_r + \frac{1}{2}n_{R2}}{\log(R2/R1)}$$

where $\frac{1}{2} n_{R1}$ = half of the number of species in the class where lower quartile falls.

$\sum n_r$ = the total number of species between the quartiles

$\frac{1}{2} n_{R2}$ = half of the number of species in the class where the upper quartile falls.

n_{R1} = the number of individuals in the lower quartile class

n_{R2} = the number of individuals in the upper quartile class

2.3.3.1.2.6 k-Dominance Curve

In addition to the number of species in a particular area, it is also useful to know the species frequency distribution. Dominance patterns can be visualized by plotting the percentage abundance of each species ranked in decreasing order of dominance. This is called a k-dominance curve, which is used when there is interest in the relative abundances of the most common species. The k-dominance curve ranks the species from the most to the least common. These curves are essentially a means of graphically representing the two aspects of diversity; the total number of species (species richness) and how evenly the individuals are apportioned among the species (evenness) (Platt et al., 1984).

2.3.3.1.3 Indices Based on the Proportional Abundance of Species

These indices provide an alternative approach to the measurement of diversity. The fact that no assumptions are made about the shape of the underlying species abundance distribution led Southwood (1978) to refer to them as non-parametric indices. This type of diversity measure has enjoyed a great deal of popularity in recent years. In this study, the diversity by number was taken as the number of species and the proportion of individuals per species in each sampling.

Shannon's diversity of index has been used often in studies of coastal fish communities. It is calculated as (Shannon, 1949):

$$H' = -\sum p_i \ln p_i$$

Where: p_i = the proportion of individuals in the i th species. The variance of H' is calculated as:

$$\text{Var}H' = \frac{\sum p_i (\ln p_i)^2 - \left(\sum p_i \ln p_i\right)^2}{N} + \frac{S-1}{2N^2}$$

and a t-test is calculated to test for significant differences between communities (Hutcheson, 1970) where N is the total number of individuals.

$$t = \frac{H'_1 - H'_2}{(\text{Var}H'_1 + \text{Var}H'_2)^{1/2}}$$

where H'_1 is the diversity of community 1 and $\text{Var. } H'_1$ is its variance. Degrees of freedom (= df) are calculated using the equation:

$$df = \frac{(\text{Var}H'_1 + \text{Var}H'_2)^2}{(\text{Var}H'_1)^2 / N_1 + (\text{Var}H'_2)^2 / N_2}$$

where N_1 and N_2 = the total number of individuals in community 1 and 2, respectively.

The index of Shannon is widely used in ecological studies of diversity, especially in marine systems (Washington, 1984). The Whilm (1968) adjustment for biomass, however, is used much less often in studies of the structure of communities. However, both indices were used in this study to evaluate seasonality in fish communities.

The evenness measure is the ratio of observed diversity to maximum diversity, which occurs where all species are equally abundant, e.g., if $H' = H_{\max} = \ln S$ (Pielou, 1969), therefore:

$$E = H' / \ln S$$

This parameter is constrained between 0 and 1.0 with 1.0 representing a situation in which all species are equally abundant.

Simpson's Index is a dominance measure, since it is weighted towards the abundance of the commonest species rather than providing a measure of species richness (Simpson, 1949). This index gives the probability of any two individuals drawn at random from an infinitely large community belonging to different species as:

$$D = \sum p_i^2$$

Where p_i = the proportion of individuals in the i th species. In order to calculate the index, the form appropriate to a infinite community is used:

$$D = \sum \left(\frac{n_i(n_i - 1)}{N(N - 1)} \right)$$

Where n_i = the number of individuals in the i th species and N = the total number of individuals. As D increases, diversity decreases. This index is presented in this study as an expression $1 - D$.

2.3.4 Statistical Analysis

Analysis of variance was used to characterize significant differences in diversity indices among combinations of season and station with a separate three by four factorial model with nested error structure (month within season). Since there was no replication within station and month, I considered habitat and season as fixed effects and stations and months were treated as random effects. Therefore, it was possible to compare the means of the diversity indices among the different seasons of the year and also across the different habitat types. I used the Tukey-Kramer adjusted p-values to make all possible pairwise comparisons. I used proc mixed that uses a maximum likelihood approach based on a variance covariance matrix. Logarithmic transformations of the indices were used to conform to the assumption of normality of the residuals. The following indices were transformed density (individual per square meter), biomass (grams per square meter) Shannon's diversity with natural logs and Pielou was transformed with natural log $(x+1)$. The Whilm, Margalef indices did not require transformation and normality of the Simpson's and mean size grams per individual could not be made to conform to the assumption of normality of the residuals. Contrasts on significant terms in the model, with appropriate adjustments for Type I error, were used to understand the relationship among factor levels.

Multiple regression analyses were carried out to establish relationships between diversity indices and physical parameters as independent variables. Stepwise multiple regression was used to choose subsets of possible independent predictor variables (i.e., physical parameters) to explain the variation in the dependent variables (i.e, indices of diversity and community structure). For each index the relationship was by using the environmental parameters to predict dependent variables.

Density: $\text{Ln}(\text{density}) = \text{Bottom salinity} + \text{Ln}(\text{secchi disk depth}) + \text{Ln}(\text{depth})$

Biomass: $\text{Ln}(\text{biomass}) = \text{square surface salinity} + \text{square bottom salinity} + \text{Secchi disk depth} \text{Ln}(\text{depth})$

Shannon index: $\text{Ln}(\text{Shannon}) = (\text{surface salinity})^2 + (\text{bottom salinity})^2 + \text{bottom temperature}$

Whilm index: $\text{Whilm} = \text{Ln}(\text{surface salinity}) + \text{bottom salinity} + \text{Secchi disk depth} + \text{depth}.$

Margalef index: was $\text{Margalef} = (\text{surface salinity})^2 + (\text{bottom salinity})^2 + \text{Secchi} + \text{depth}.$

Pielou index: $\text{Ln}(\text{Pielou}+1) = (\text{surface salinity})^2 + (\text{bottom salinity})^2 + \text{Secchi} + \text{Ln}(\text{depth} + 1)$

Simpson index: $\text{Simpson} = (\text{surface salinity})^2 + (\text{bottom salinity})^2 + \text{Secchi} + \text{depth}.$

Mean size in biomass (grams per individual): $\text{mean size} = \text{surface salinity} + \text{bottom salinity} + \text{Secchi} + \text{inverse of depth}.$

2.4 Results

2.4.1 Environmental Trends

The cluster analysis based on all sampling records allowed the identification of 4 groups of stations based on salinity, temperature, Secchi depth, sediment type and monthly river discharge. The resulting clusters corresponded to the following ecological subsystems: Carmen Inlet (stations 1,2 and 5). Fluvial-lagoon systems (3, 4, 9, 10, 15, 16, and 17), the inner littoral of Carmen Island with persistent marine influence and

seagrass meadows (6, 7, 12, 13 and 18), and the central basin of the lagoon (8, 11, and 14; Fig. 2.2).

The lowest salinity values occurred in areas directly affected by river discharge in the SW portion of the lagoon (stations 3, 4, 9, 10, 15, 16 and 17, Fig. 2.3). Mean monthly surface salinity in the fluvial lagoon systems ranged from a maximum of 25.8 in May to a low of 6.1 in November (Fig. 2.3). Mean bottom salinity ranged from 26.5 in May to 9.9 in November (9.9). The lowest salinities occurred in the Palizada-del Este System where freshwater was sometimes encountered (Fig. 2.3).

The central basin (stations 8, 11 and 14) is a transition zone between marine and brackish water parts of the lagoon. Surface salinity mean ranged from 25.8 during May to 6.1 in November and bottom salinity ranged from 16.0 in November to 34.0 in February 1980 (Fig. 2.3).

The northern portion of the lagoon, adjacent to Carmen Island, has a more persistent marine influence with higher salinity and transparency. This area is called the inner littoral of Carmen Island (stations 6, 7, 12, 13, and 18). There was a pronounced seasonal salinity pattern. Surface salinities ranged from 14.2 (December) to 34.8 (June) and bottom salinities from 15.4 to 34.6 in the same months, respectively (Fig. 2.3).

Carmen Inlet (stations 1, 2 and 5) is a mixing zone influenced by fresh water from river discharge, marine water from the Gulf of Mexico, and brackish water from the lagoon. Therefore, the hydrology of this area is highly dynamic. Surface salinity fluctuated between 2.7 in November to 33.0 in May; while bottom salinity was from Fig 2.2 11.0 to 33.7 in the same months. In this area, water column stratification occurs as evidenced by higher salinities on the bottom (Fig. 2.3).

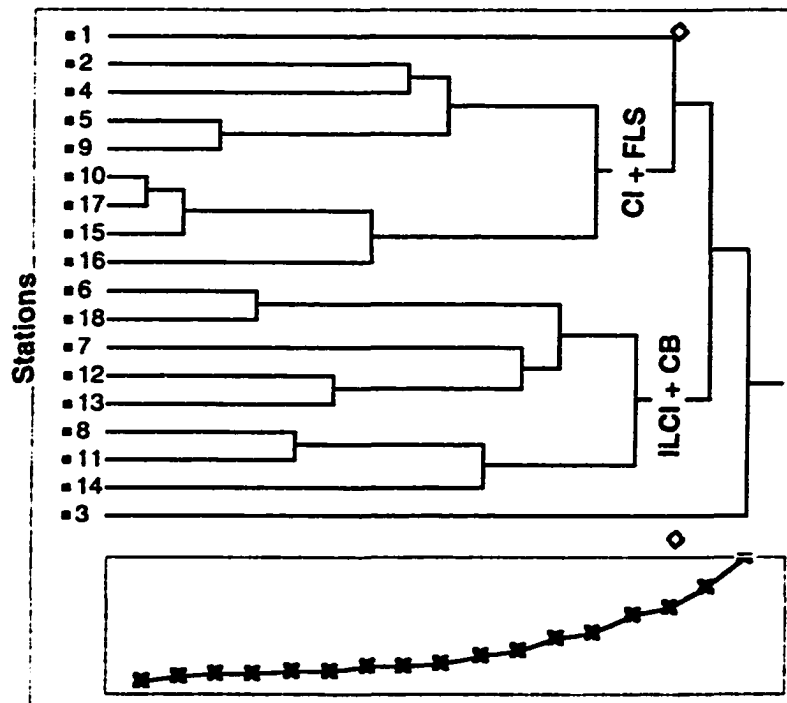


Fig. 2.2. Clustering dendrogram of the sampling stations based on physical parameters.

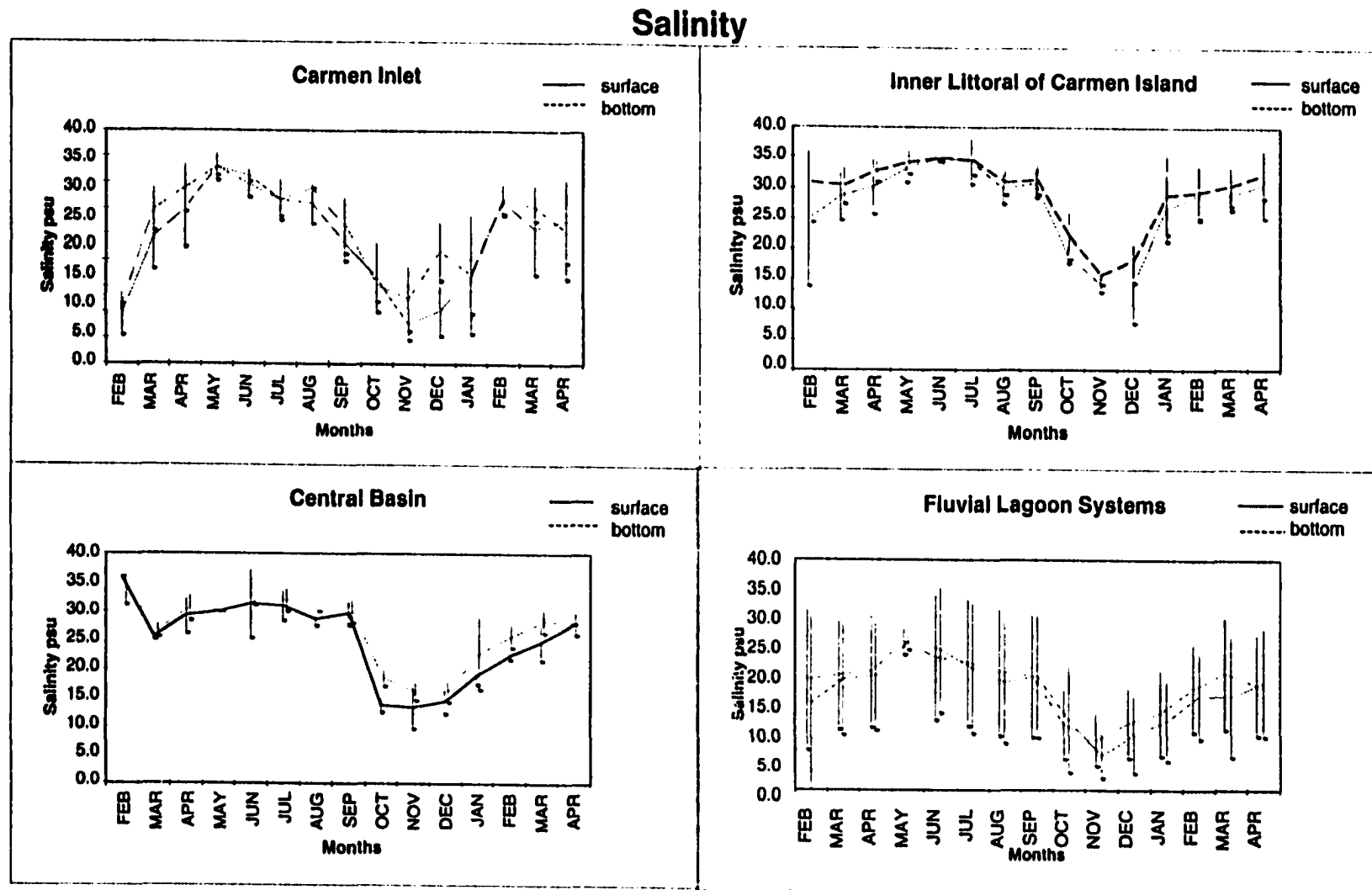


Fig. 2.3 Monthly surface salinity for each ecological subsystem during 1980-1981 during sampling period.

The tropical nature of Terminos Lagoon is seen in the relatively small annual variation in temperature. Lowest temperatures occurred in January with values between 21 and 23 °C while values between 30 and 31 °C occurred between April and June (Fig. 2.4). There were no pronounced differences between surface and bottom temperatures or between different areas of the lagoon.

Secchi depth and transparency were generally lowest in areas affected by riverine input waters (Secchi = 0.5-1.5 m, transparency = 14.3 - 70.6%). The readings were highest in the central and eastern parts of the lagoon which were more affected by clearer marine waters (Secchi = 0.6-3.5 m, transparency = 13.3-91.7%; Figs. 2.5 and 2.6). The lagoon waters tended to be clearer in the dry season. Because transparency is affected by a number of factors including river input, winds, depth and sediment type, there was considerable variation over the year. The mean annual Secchi depths were 0.9, 0.7, 1.2, and 1.3 in the fluvial lagoon systems, Carmen Inlet, the inner littoral of Carmen Island, and the central basin, respectively. The most turbid water (Secchi depth = 0 m) occurred in fluvial lagoon systems, while the clearest water (4.0 m, 100%) was in the central basin in February 1981.

The annual pattern of salinity and temperature related to the three climatic seasons. Mean salinity in the whole lagoon varied between 12 in November (during the norte season) and 29 in June (at the end of the dry season) and a similar pattern held for each ecological subsystem. The mean lagoon water temperature ranged from 21.8°C in January (end of the norte season) to 30.4°C in June (end of the dry season; Table 2.1 Appendix A and Fig. 2.7).

Temperature

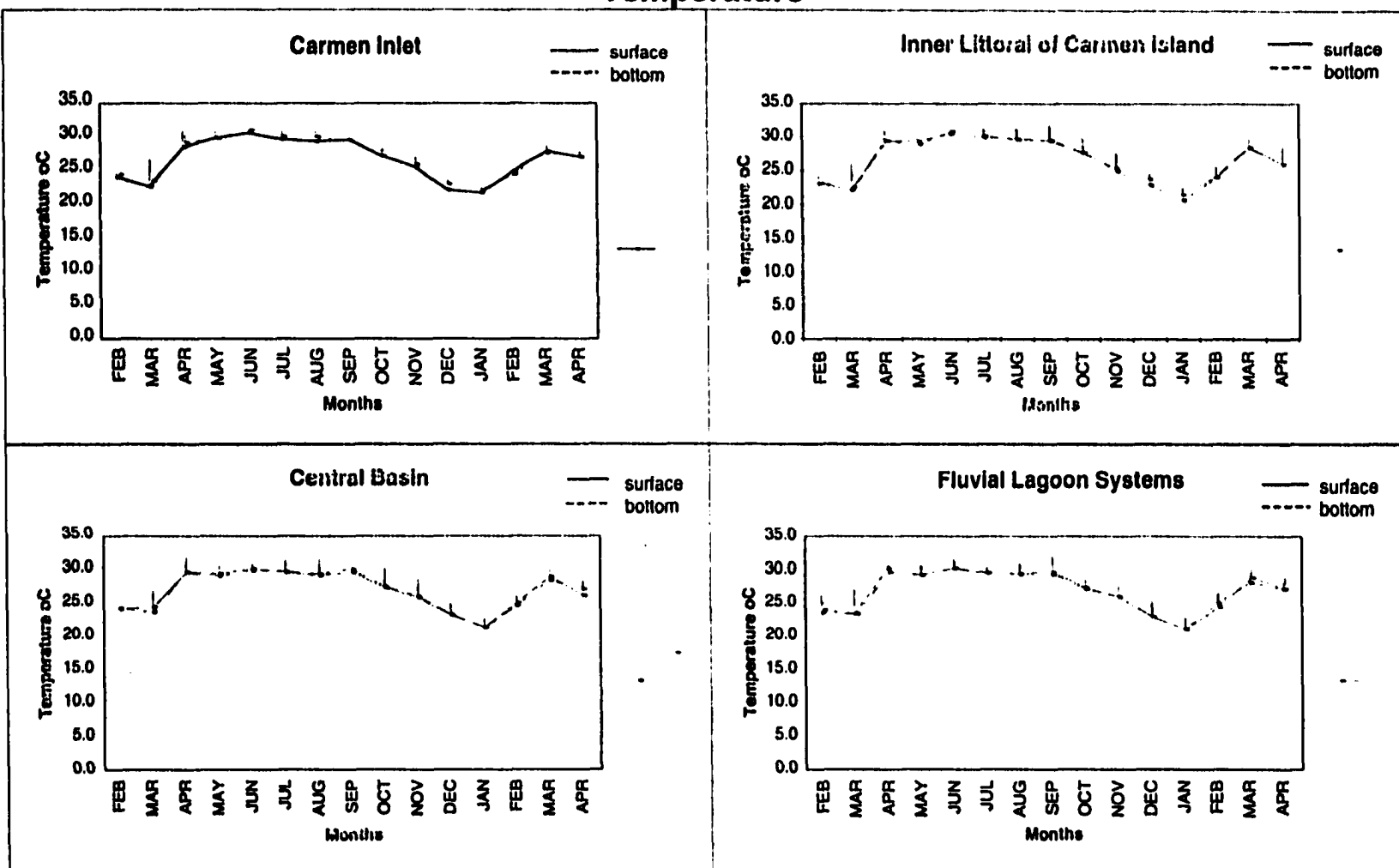


Fig. 2.4 Monthly surface and bottom temperature for each ecological subsystem during 1980-1981 the sampling period.

Secchi Depth

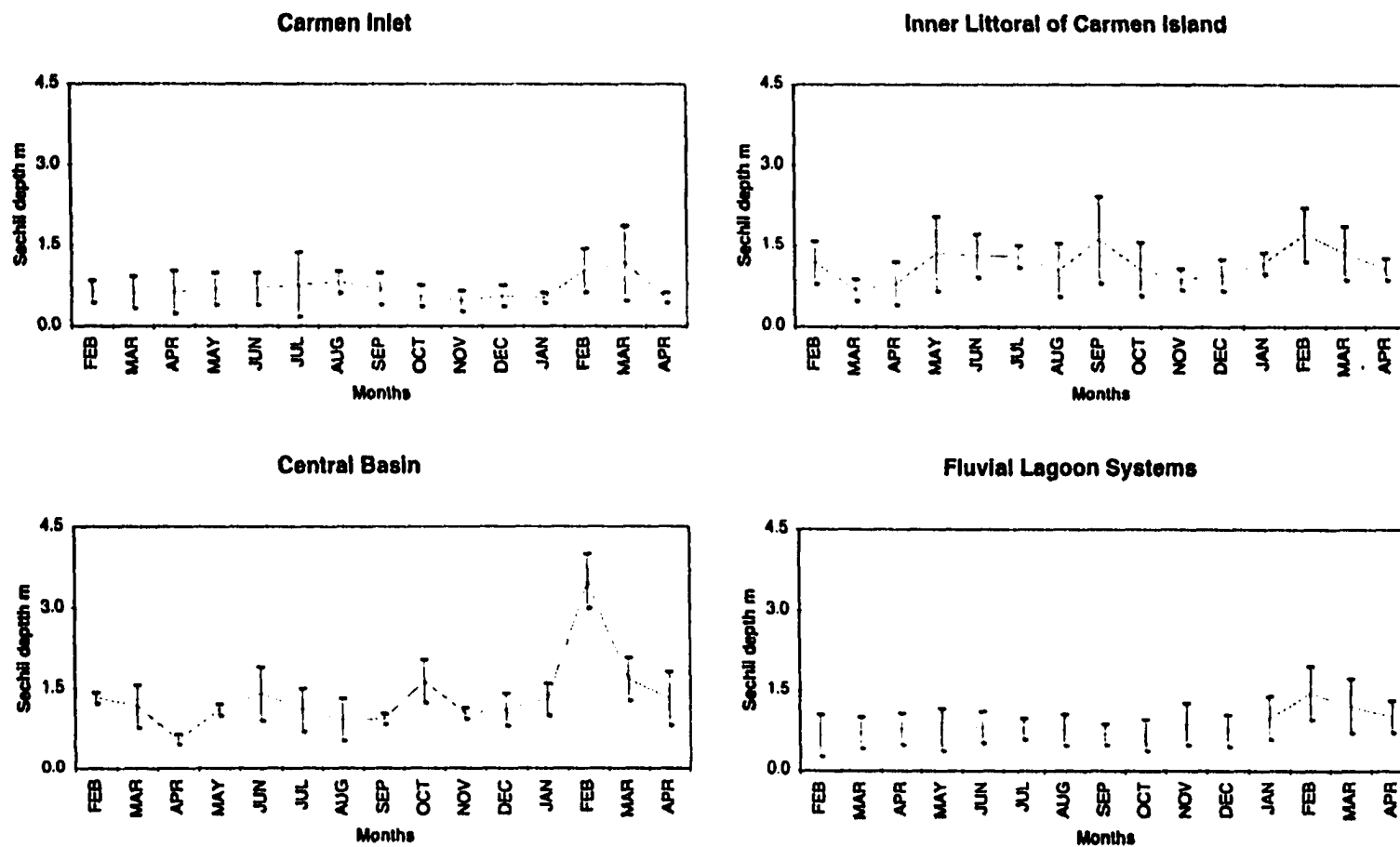


Fig. 2.5 Monthly Secchi disk depth records at each ecological subsystem during the 1980-1981 sampling period.

Transparency

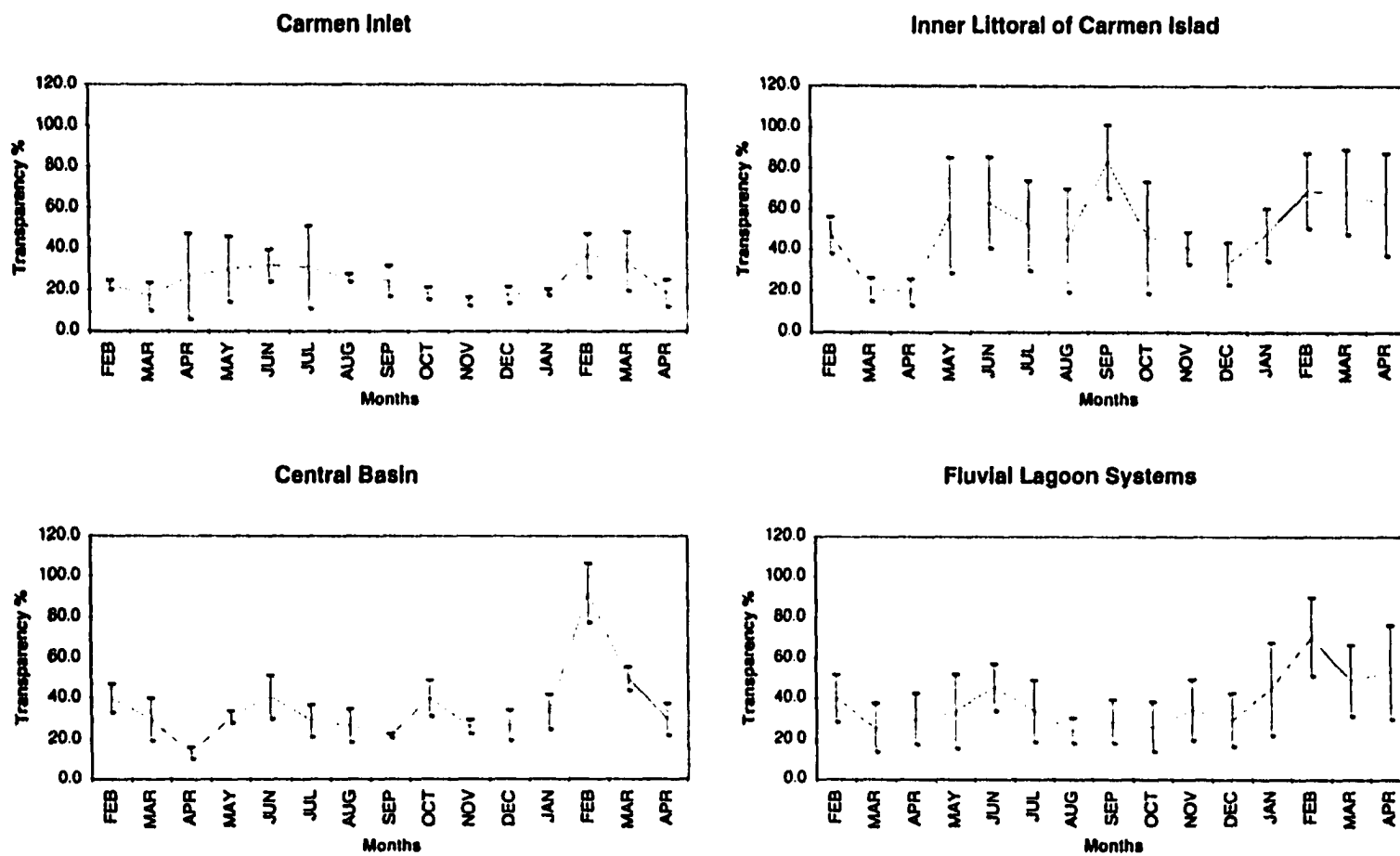


Fig. 2.6 Monthly transparency values at each ecological subsystem during the 1980-1981 sampling period.

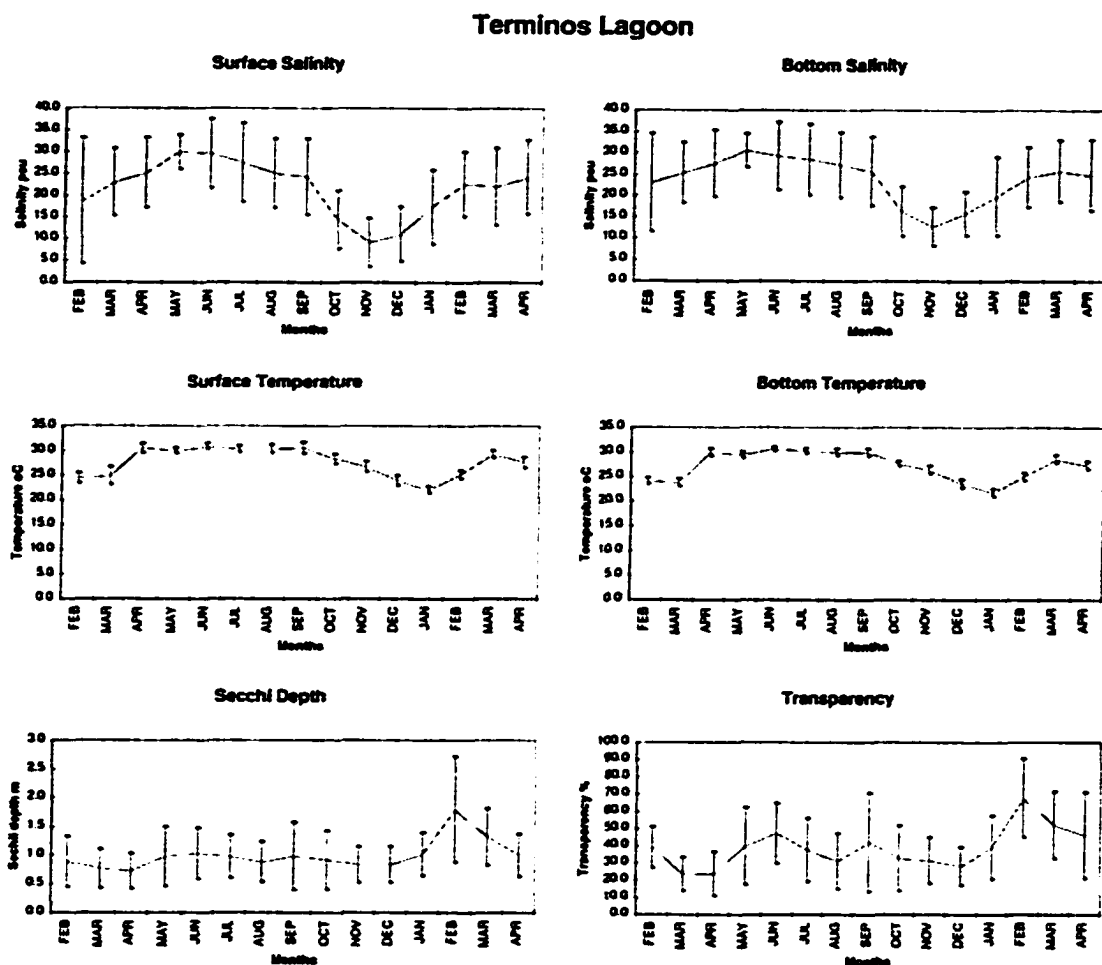


Fig. 2.7 Monthly variation of salinity and temperature of surface and bottom, secchi disk depth and transparency for the whole lagoon during the 1980-1981 sampling period.

The boundaries of each ecological subsystems were highly dynamic and varied depending on the season. During the dry season, there was a strong marine influence with similar temperature and salinity conditions prevailing in the inner littoral of Carmen Island, central basin and the eastern portion of the fluvial lagoon systems. During this season, these three subsystems cluster had similar high salinity values. During this period, Carmen Inlet and the western portion of the fluvial lagoon clusters were similar due to low salinity values caused by river discharge.

During the rainy season, salinity was more homogeneous in the lagoon and the inner littoral of Carmen Island, the central basin, the eastern portion of the fluvial lagoon and Carmen Inlet all cluster together. The western portion of the fluvial lagoon systems has lower salinity due to the high river discharge and forms a distinct cluster.

Finally, during the norte season, strong northerly winds associated with the cold fronts in combination with high river discharge leads to a high variation in salinity. The central basin and the fluvial lagoon systems clustered together. Carmen Inlet and station 17 (next to Puerto Real Inlet) had a marine influence, because the marine inflow through both inlets was caused by north winds. The pattern of distribution of physical parameters, particularly salinity, is highly dynamic in this season the lagoon and can strongly affect the distribution and abundance of fish species in each ecological subsystem, thus affecting patterns of diversity.

2.4.2 Community

The fish community consisted of 82 species. Over the 15 month sampling period 13,691 individuals were collected in 264 trawls (Table 2.2 Appendix A). *Cathorops spixii* (Mandamango sea catfish), *Sphoeroides testudineus* (Checkered puffer), *Bairdiella chrysoura* (Silver perch), *Ariopsis felis* (Hardhead sea catfish) and *Archosargus rhomboidalis* (Sea bream) were the most abundant species and

accounted for 63% of the total individuals. The 17 most abundant species accounted for 90% of all individuals and 25 species were represented by less than 5 individuals and 12 species were represented by a single individual.

Biomass and density had pulses in the rainy and norte seasons in Carmen Inlet, the inner littoral of Carmen Island and the fluvial lagoon systems, while in the central basin, the pulse of abundance was during the dry season. In general, these pulses are related to migratory movements of the different fish species. This reflects the fact that smaller individuals were captured in Carmen Inlet and the fluvial lagoon systems in low salinity waters while larger sizes were captured in the central basin and the inner littoral of Carmen Island in higher salinities. Therefore, Terminos Lagoon is a nursery for a number of species and a feeding ground for many marine species. They enter the lagoon through the inlets throughout the year, but mainly during the norte season when Carmen Inlet and the inner littoral of Carmen Island had a high density.

2.4.2.1 Community Structure

A total of 13,691 individuals were captured representing 82 fish species from 30 families (Table 2.2 Appendix A). For the whole lagoon, the number of fish species fluctuated monthly between 34 (March 1981) and 47 (November 1980) with little variation over the year (coefficient of variation = 8.74). The numbers of individuals captured ranged between 587 in February 1980 to 1637 in November. This seasonal pattern of abundance ranged from 0.019 to 0.052 individuals m^{-2} in February 1981 and November 1980, respectively. In a two-way analysis of variance examining habitat types and seasons and their interactions, there were significant differences in density and biomass (Table 3). Thus the density varied significantly by habitat types and season, while biomass varied only by habitat types (Table 3 and Fig. 2.8).

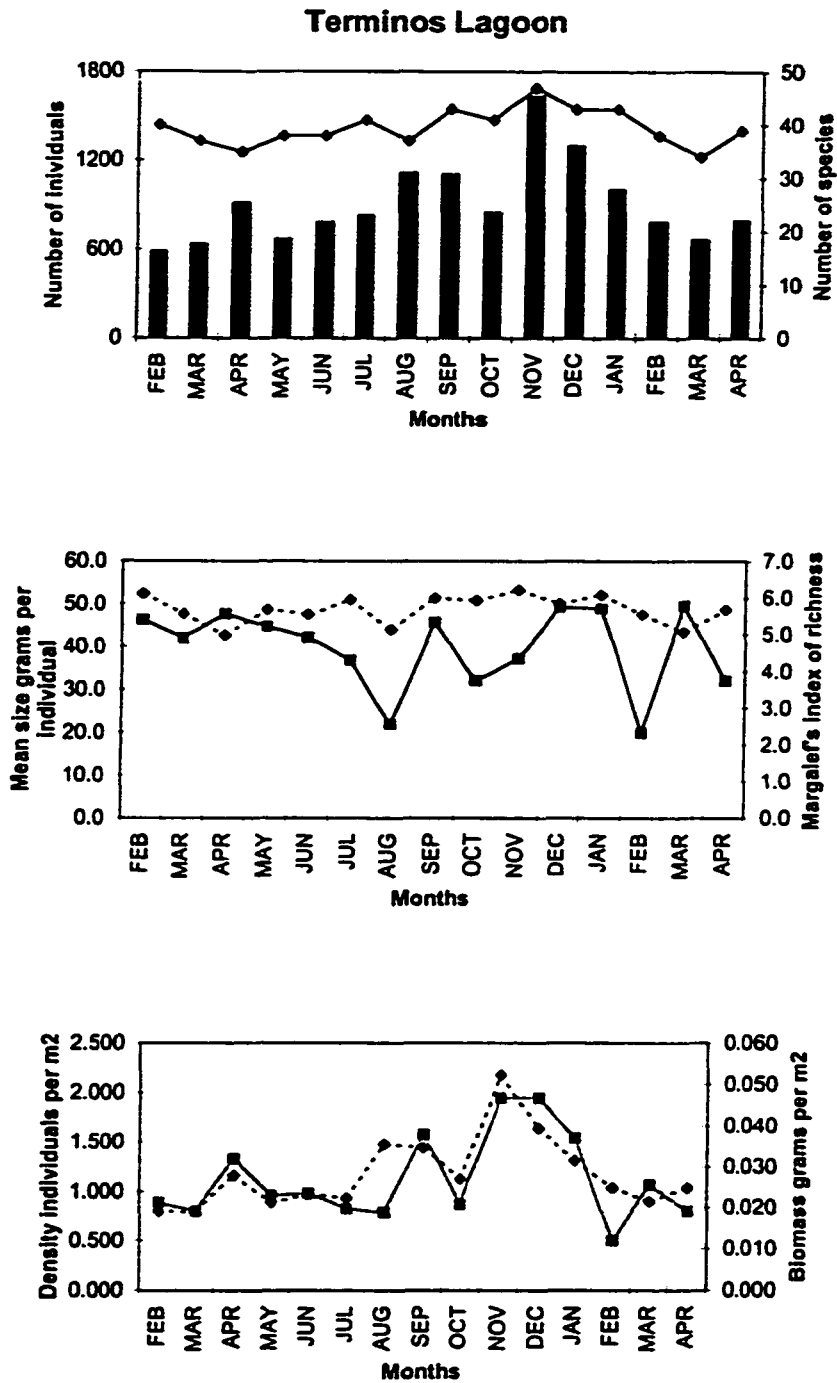


Fig. 2.8 Monthly variation of number of individuals, number of species, mean size in biomass, Margalef's index of richness, density and biomass for Terminos Lagoon during the 1980-1981 sampling period.

Spatially, the inner littoral of Carmen Island and fluvial lagoon systems had the higher number of species with 52 and 62, respectively, while the lowest number occurred in the Central Basin (34). The total number of individuals captured was highest in the inner littoral of Carmen Island (4928) and lowest in the Central Basin (777). The highest biomass also occurred in the inner littoral of Carmen Island (1.977 g per m²) with the lowest in Carmen Inlet (0.538 g m²). The contrast determined that density in the Carmen Inlet and the inner littoral of Carmen Island was significantly different ($p = 0.0020$), and inner littoral of Carmen island was significantly different in density with the central basin ($p = 0.0002$) and the fluvial lagoon systems ($p = 0.0054$) and the central basin with the fluvial lagoon systems ($p = 0.0402$). Seasonally, norte season was significantly different from the dry ($p = 0.0163$) and marginally different from the rainy season ($p = 0.0595$).

Biomass varied significantly by habitat types. The central basin was significantly different in biomass in contrasting with Carmen Inlet ($p = 0.398$), the inner littoral of Carmen Island ($p = 0.0175$) and the fluvial lagoon systems ($p = 0.308$). The highest biomass occurred in the inner littoral of Carmen Island, the subsystem with permanent marine influence. The lowest values for these parameters were in the central basin and Carmen Inlet which are areas of transition with high environmental variability (Table 2.4).

In general, there were seasonal variations in the number of species and the total number of individuals in each ecological subsystem which seems related to climatic factors. In Carmen Inlet, in the transition from the dry season to the rainy season, the number of species was at a minimum. Species numbers then increased during the rainy and north seasons. In the inner littoral of Carmen Island, there were pulses in the number of species in the dry season and at the end norte season. In the

fluvial lagoon systems the maximum number of species was in July during rainy season. While in the central basin, there were low values in the number of species throughout the year, with the lowest numbers in December 1980 to April 1981 (Fig. 2.9).

The number of individuals had a seasonal trend. In all the ecological subsystem the minimum number of individuals occurred during the dry season and the maximum during the nortes season. There were three periods of abundance in different subsystems. The first occurred in the western fluvial lagoon system in the fluvial-deltaic basin during the dry season. The second was in this same area at the end of the rainy season. The third period of abundance occurred during the nortes season; in the fluvial lagoon systems during November and the inner littoral of Carmen Island during December when the highest abundance occurred (Fig. 2.9).

Biomass and density varied significantly by habitat types, and density also significantly by season. The highest values of biomass were in Carmen Inlet during November and the inner littoral of Carmen Island during December; while the maximum values of density occurred in the inner littoral of Carmen Island during nortes season. In general, the Carmen Inlet had high density from the rainy to the dry season in 1981. The central basin had high values of both biomass and density during the dry season while in the other systems it was during the rainy and nortes season (Fig. 2.10).

In estuarine-lagoon ecosystems, most fish captured are juveniles and pre-adults (McHugh, 1967, 1985; Yáñez-Arancibia, 1985; Pauly, 1999). For the entire lagoon, the average fish size was small at 39.8 g per individual (range 20.0 in February 1981 to 49.3 in December; Table 2.4 Appendix A, Fig. 2.8). The spatial variation of this

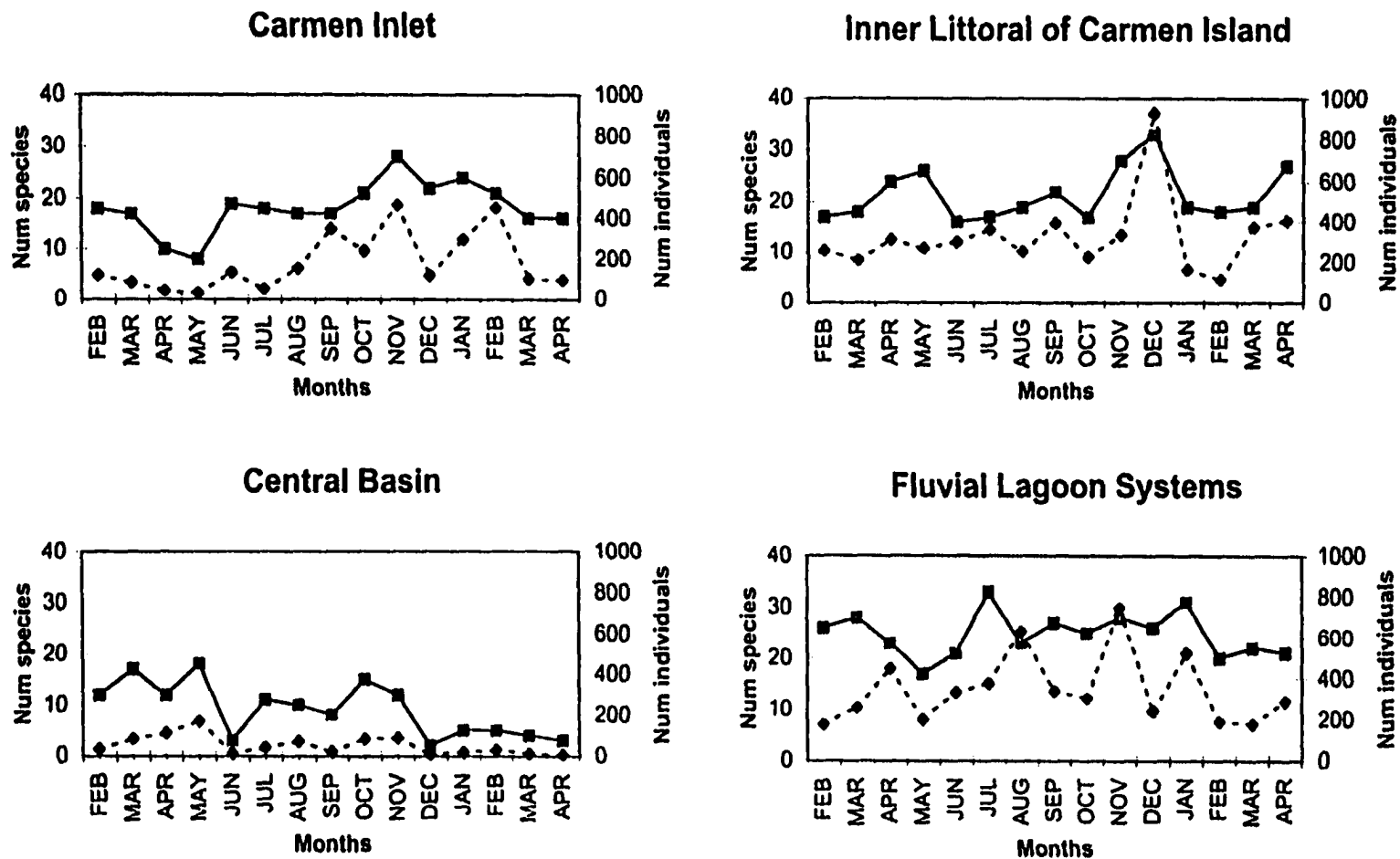


Fig. 2.9 Monthly values for number of individuals, number of species in each ecological subsystem during the 1980-1981 sampling period.

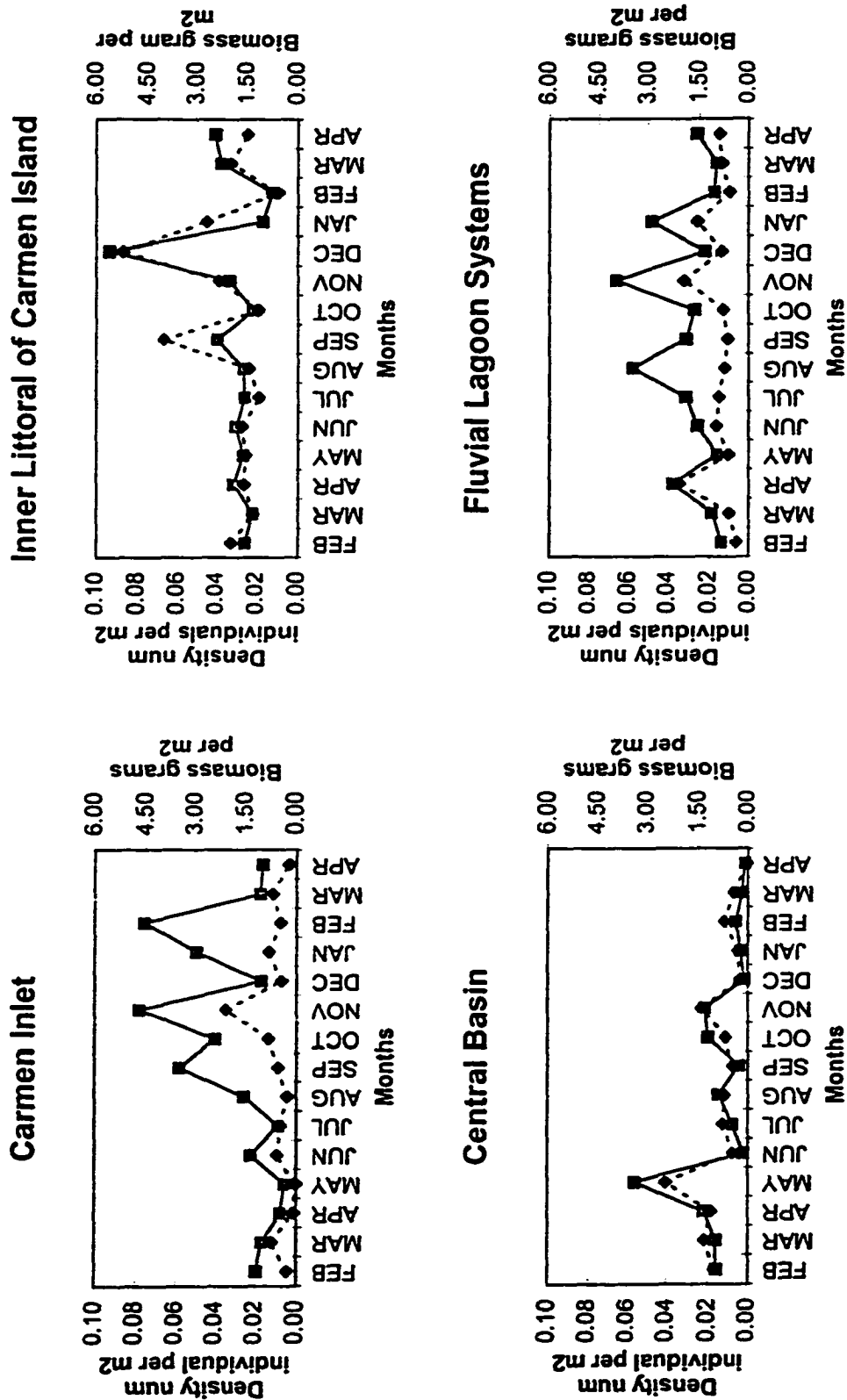
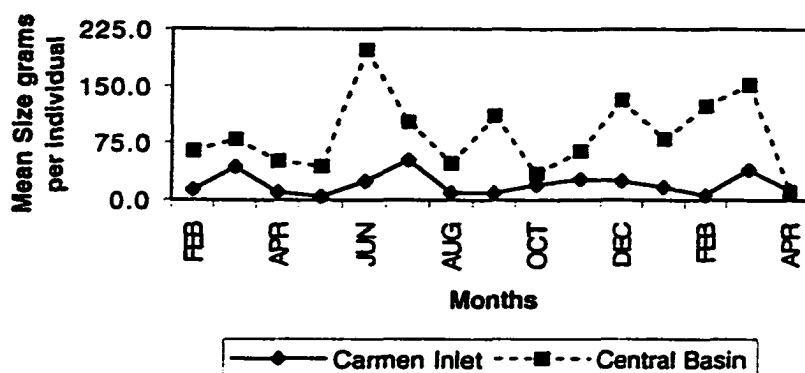


Fig. 2.10 Monthly fish density and biomass in each ecological subsystem during the 1980-1981 sampling period.

Carmen Inlet and Central Basin



Inner Littoral and Fluvial Lagoon S

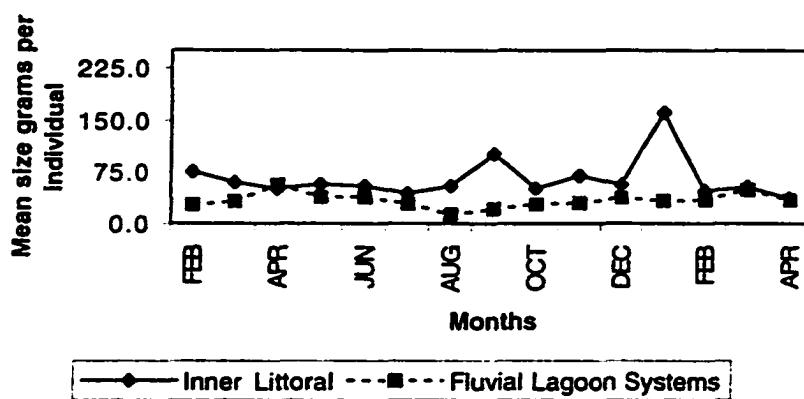


Fig. 2.11 Monthly mean size in biomass for ecological subsystem during the 1980-1981 sampling period.

parameter was related to salinity. The highest average sizes were in the Central Basin and inner littoral of Carmen Island (86.0 and 64.6 g per individual, respectively) where salinity values were also high. The smallest average sizes occurred in Carmen Inlet and the fluvial lagoon systems (20.4 and 32.9 g per individual, respectively), where the salinity was low (Table 2.4 Appendix A, Fig. 2.11).

The mean size varied significantly by season (Table 2.3). Nevertheless the residuals of this parameters did not conform the normality assumption. In the central basin, high average sizes occurred in the rainy (June and September), norte (December) and dry seasons (March, Fig. 2.11), while in the inner littoral of Carmen average size was highest in the rainy (September) and norte (January) seasons. Therefore, the seasonal changes in the average size in the community are related to seasonal salinity changes.

2.4.2.1.1 Species Richness

For the entire lagoon, the index of species richness ranged from 4.98 in April 1980 to 6.22 in November (Fig. 2.8). The Margalef's index of species richness did not have statistical significance by season and habitat types. The four subsystems had a relatively small coefficient of variation, which indicates that the richness of species was relatively constant over the year (Fig. 2.12). In general, the fluvial lagoon systems had the maximum richness and the minimum coefficient of variation (16.5%). Species richness ranged from 3.02 in May to 5.39 in July. The inner littoral of Carmen Island also had high species richness with a low annual CV (19.8%). Minimum species richness occurred in June (2.63), and the maximum in December (4.68). The central basin had the lowest species richness and the highest annual CV (48.3%). Species richness was highest in March 1980 (3.63) and lowest in December (0.45). Values stayed low during the dry season in 1981 (Fig. 2.12). Carmen Inlet had little change in

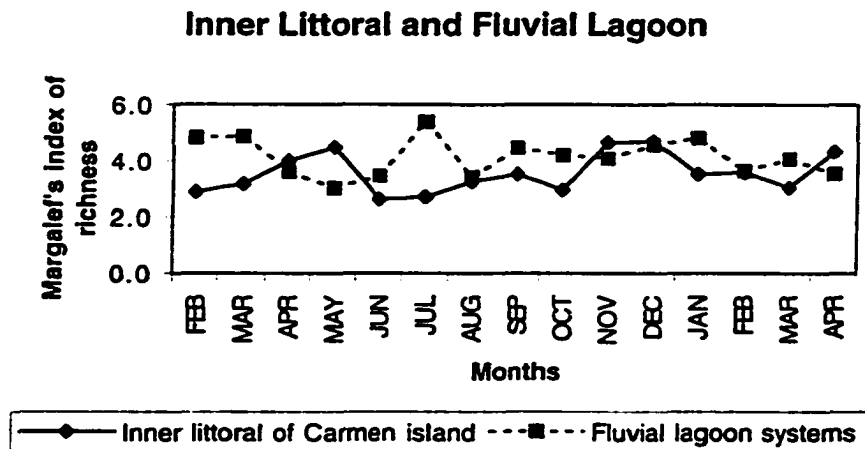
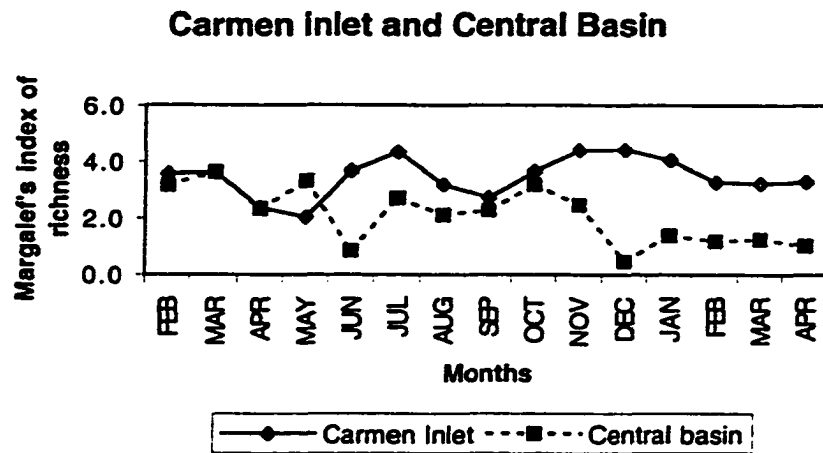


Fig. 2.12 Monthly Margalef's index of richness values for each ecological subsystem during the 1980-1981 sampling period.

species richness throughout the year with a CV value of 20.39. Minimum values were recorded at the end of dry season (2.02 in May) and maximum values occurred in December (4.40) and stayed high during the norte and dry seasons of 1981.

2.4.2.1.2 Species Abundance Models

In a comparison of the four models of species abundance with fish data from Terminos Lagoon, I found that only two of four models fit the data. For the logarithmic series and log normal distribution models, the fit was close and the null hypothesis could not be rejected. In Terminos Lagoon, the distribution of the fish species abundance, considered as the number of individuals, did not follow a geometric series model ($\chi^2_{df=81} = 139343.02 > \chi^2_{0.05(81)} = 103.01$). Therefore, the fish community in the lagoon and the different subsystems is not only characterized by dominant species (Table 2.5 Appendix A).

The logarithmic model had a good fit for fish communities in Carmen Inlet, the central basin as well as for the entire lagoon (Table 2.5 Appendix A, Fig. 2.13). For the inner littoral of Carmen Island, the model was fitted to $\chi^2_{[10]} = 21.9, < \chi^2_{[11]} = 23.209$. However, this model fit species abundance in the inner littoral better than the other models (Table 2.5 Appendix A and Fig. 2.13). This indicates that the ecology of the fish community in the inner littoral of Carmen Island is controlled by one or few factors that limit the pattern of diversity and abundance. The model fit was not significant for the fish community in the fluvial lagoon systems ($\chi^2_{[11]} = 73.3, > \chi^2_{0.05(11)} = 19.675$), indicating that community ecology may be affected by a number of factors, either acting directly or in combination, in these settings.

The implementation of lognormal model for fish communities in the lagoon generally yielded a good agreement between expected and observed numbers of

Log series Model

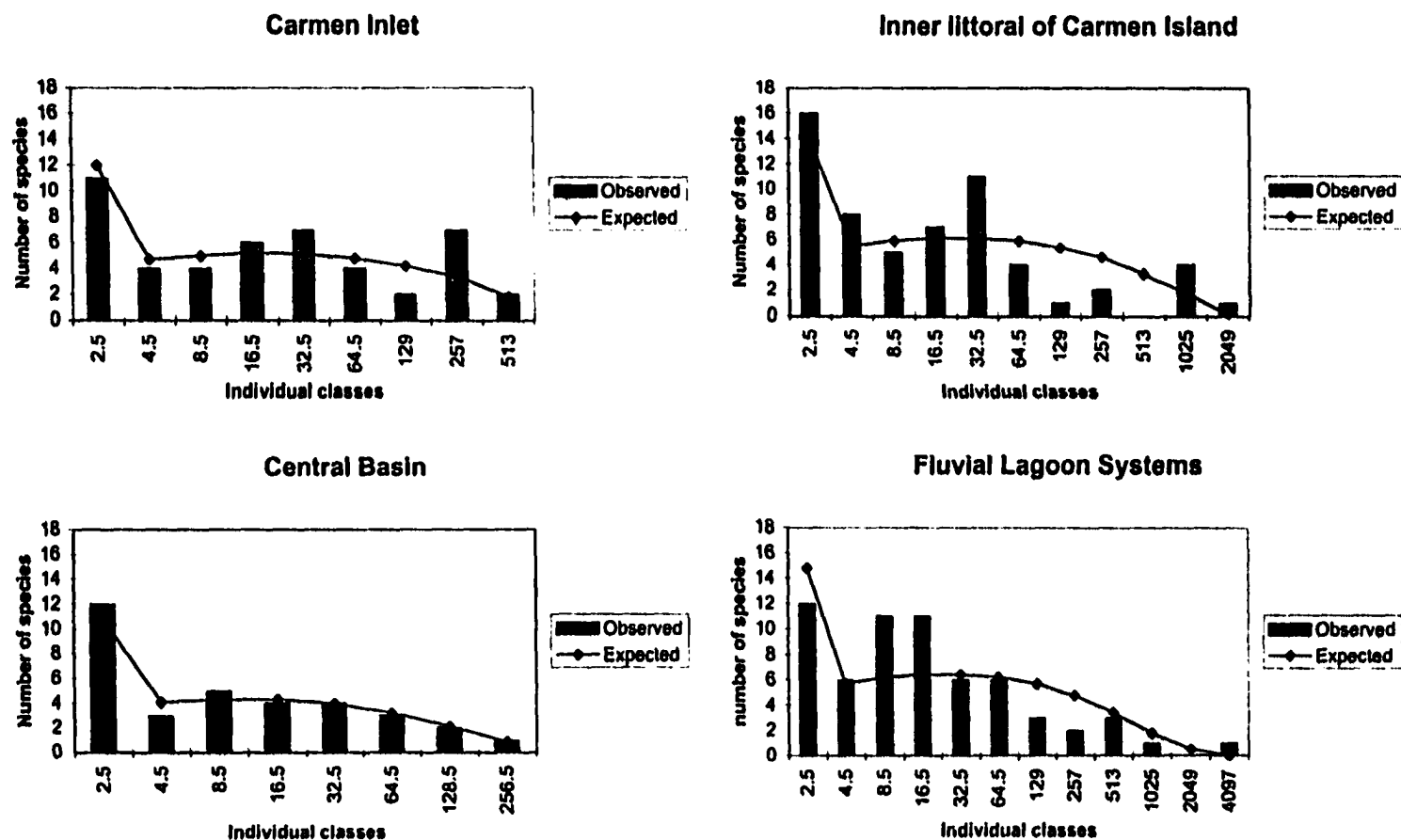


Fig. 2.13 Fish diversity. Log series distribution for each ecological subsystem. Classes of individuals are \log_2 , species abundance is expressed in terms of doubling of number of individuals. The observed and expected number of species for each ecological subsystem is also presented.

Log normal Model

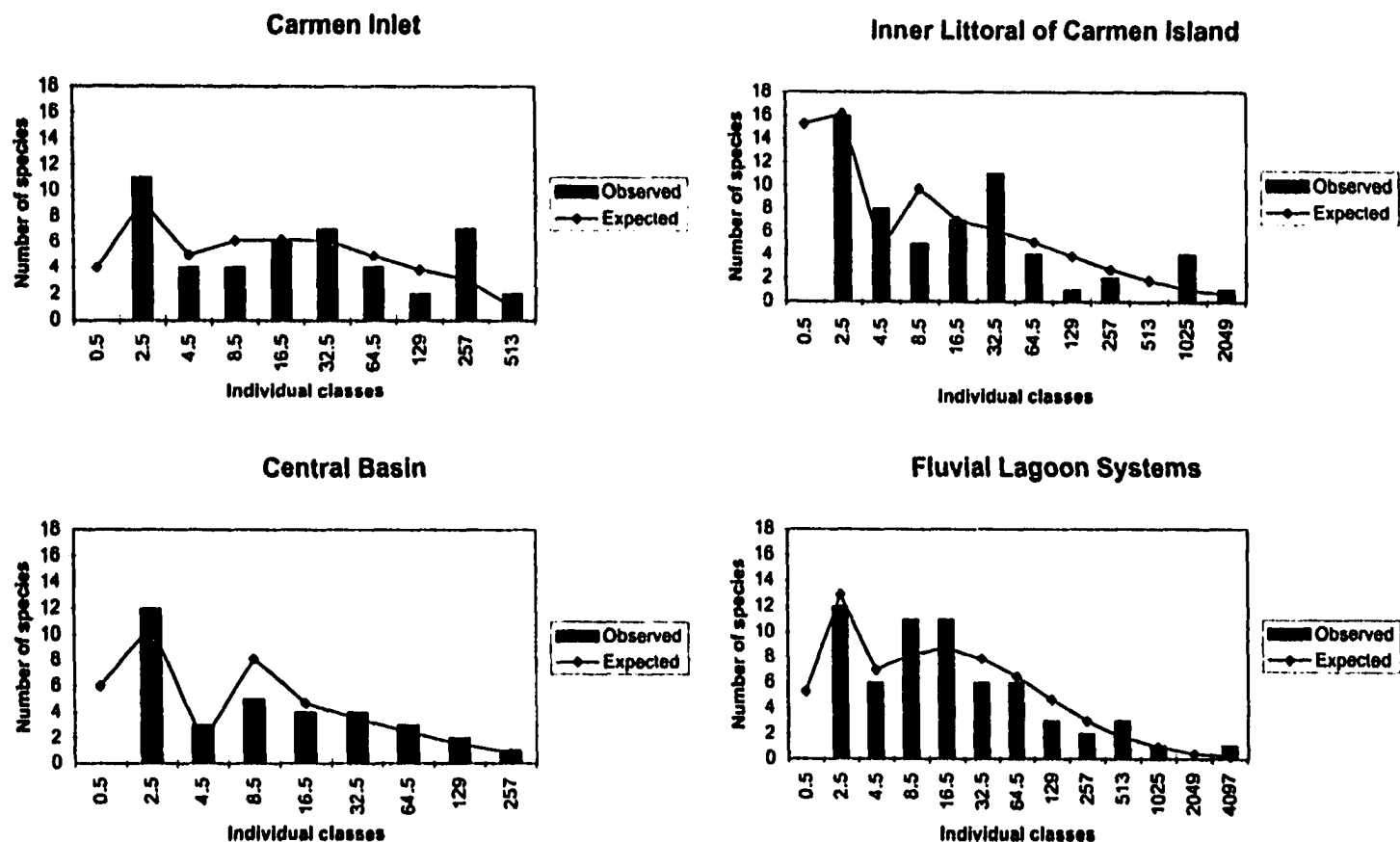


Fig. 2.14 Fish diversity. Classes of individuals are \log_2 . Species abundance is expressed in terms of doubling of number of individuals. It is presented in each subsystem the observed and predicted number of species by the log normal distribution (truncated).

species (Table 2.6 Appendix A, Fig. 2.14). In particular, this model had the best fit for the fish community of the fluvial lagoon systems. Therefore, this model suggests that the ecology of the fish community in this system is controlled by numerous factors that limit the pattern of diversity and abundance (May, 1975; Ugland and Gray, 1982; Magurran, 1988).

Table 2.7 Appendix A shows that the results of both log series and lognormal models for each system and are significant. Magurran (1988) suggests evaluating the fit of these results based on the degrees of freedom and the p obtained in each fit. In both cases, the values of p are clearly below the conventional level of 95%; nevertheless, based on the degree of freedom the values with an asterisk have a better fit with the model. The broken stick model did not result in a significant fit in any of the ecological subsystems (Table 2.8).

The Q statistic was high in the inner littoral of Carmen Island and the fluvial lagoon systems; and low in the Central basin and Carmen Inlet (Table 2.6 Appendix A).

Figures 2.15a-f show comparisons of k-dominance curves for the different subsystems in the lagoon. The fish assemblage in Carmen Inlet is more diverse than the other systems because the curve lies below the others. The curves for the inner littoral of Carmen Island and the fluvial lagoon systems were similar to each other and intermediate between the other subsystems indicating a shift in the relative dominance of these two systems. The fluvial lagoon systems had the smallest diversity relative to the other subsystems. These relationships are clearer when only two systems are plotted together in each figure. The inner littoral of Carmen Island has higher diversity associated with the dominant species while the central basin and the fluvial lagoon systems have higher diversity of fish species with intermediate abundance in comparison with the inner littoral of Carmen Island.

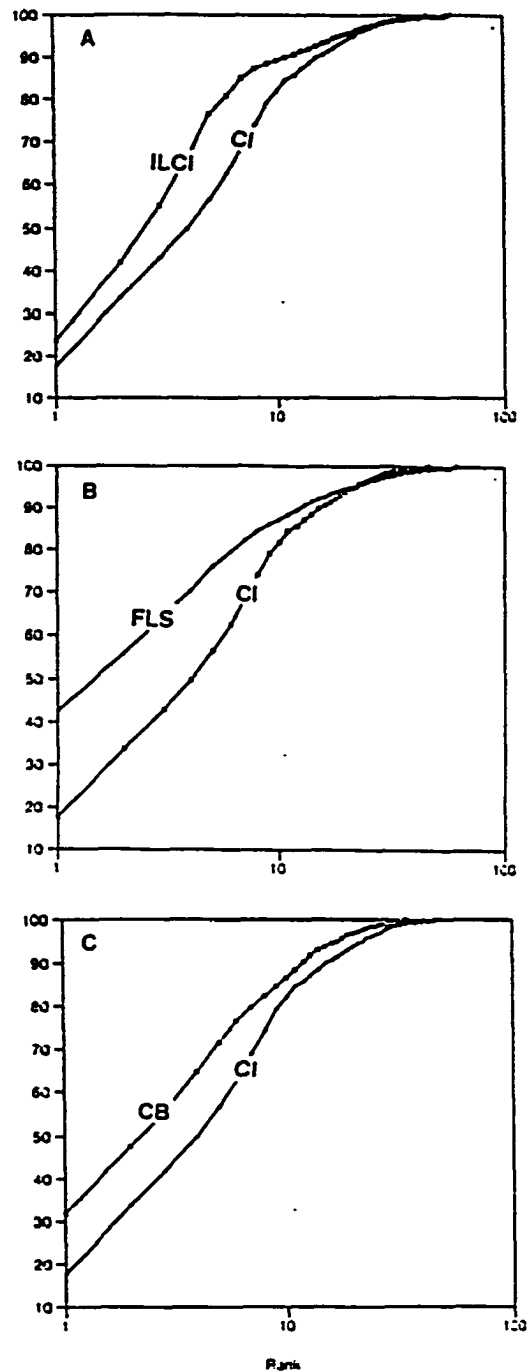


Fig. 2.15. K-dominance curves. A) Comparison between Carmen inlet and the inner littoral of Carmen Island. B) Comparison between fluvial lagoon systems and Carmen Inlet. C) Comparison between the central basin and Carmen inlet. D) Comparison between the fluvial lagoon systems and the inner littoral of Carmen Island. E) Comparison between the central basin and the inner littoral of Carmen Island. F) Comparison between the central basin and the fluvial lagoon systems.

(Figure continued)

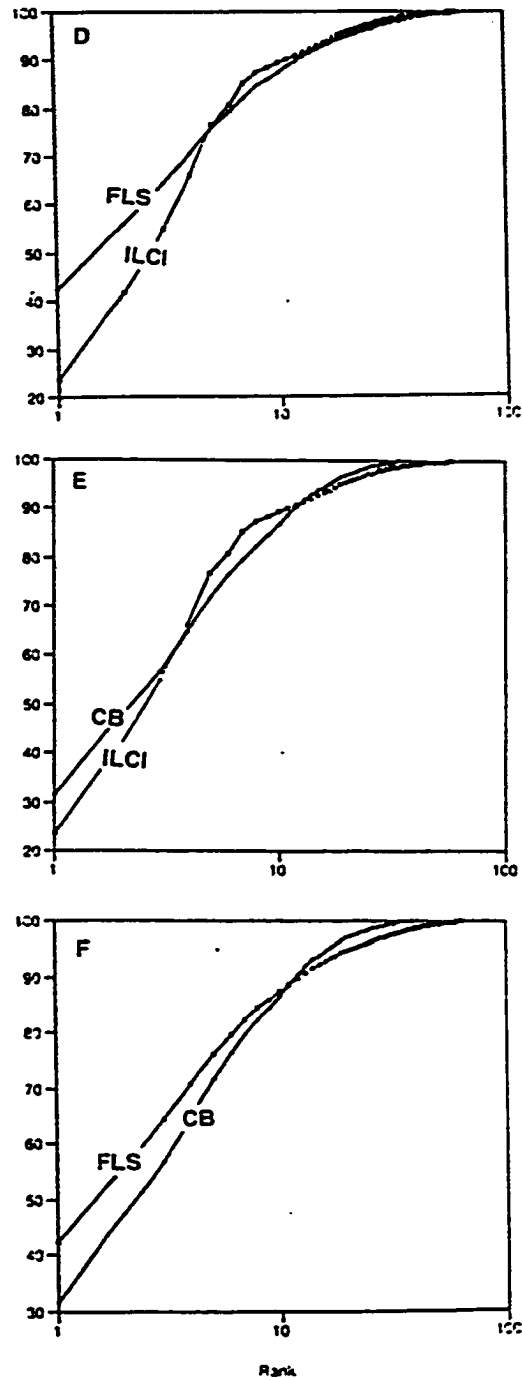


Fig. 2.15 (continued). K-dominance curves. D) Comparison between the central basin and Carmen inlet. E) Comparison between the fluvial lagoon systems and the inner littoral of Carmen Island. F) Comparison between the central basin and the inner littoral of Carmen Island. G) Comparison between the central basin and the fluvial lagoon systems.

2.4.2.1.3 Indices Based on the Proportional Abundance

The Shannon index for Carmen Inlet varied from 1.42 (February of 1980) and 2.79 in December and the Whilm (1968) index ranged from 1.29 (September) and 2.41 (April of 1981; Fig. 2.16). The Shannon index varied significantly by season and habitat types (Table 2.3 Appendix A). There were two peaks in this index during the rainy and norte seasons. By the analysis of contrast the norte season was significantly different from the dry and rainy seasons ($p = 0.0033$ and $p = 0.373$ respectively) and by habitat types the inner littoral of Carmen Island was significantly different from Carmen Inlet and the central basin. There was no significant differences by season and habitat types in the Whilm index and no detectable trend during the year ($F = 1.76$, $r^2 = 0.114$ $p = 0.17$). In general, fish species diversity in Carmen Inlet was best represented by the number of individuals than by biomass (Table 2.3 Appendix A, Fig. 2.16).

In the central basin, the Shannon index varied from 0.53 (December) to 2.07 (May), while the Whilm index ranged from 0.875 in April (0.86) to 2.28 in May (Fig. 2.16). Diversity by biomass was higher than for numerical diversity. This was more evident during rainy and norte seasons (from August 1980 to March 1981; Fig. 2.16). This pattern is likely related to the main fish immigration patterns to the lagoon (e.g., Yáñez-Arancibia et al., 1980, 1982, and 1988a). The diversity by biomass had higher values than numeric diversity, suggesting that fish species diversity in this community is mainly due to fish species that are present as pre-adults and adults.

By contrast, the inner littoral of Carmen Island and the fluvial lagoon systems had higher values of numeric diversity than diversity by biomass. This suggests that in these two systems, the fish community is dominated by numerous individuals of small size. The variation of these parameters was not significant with either season or

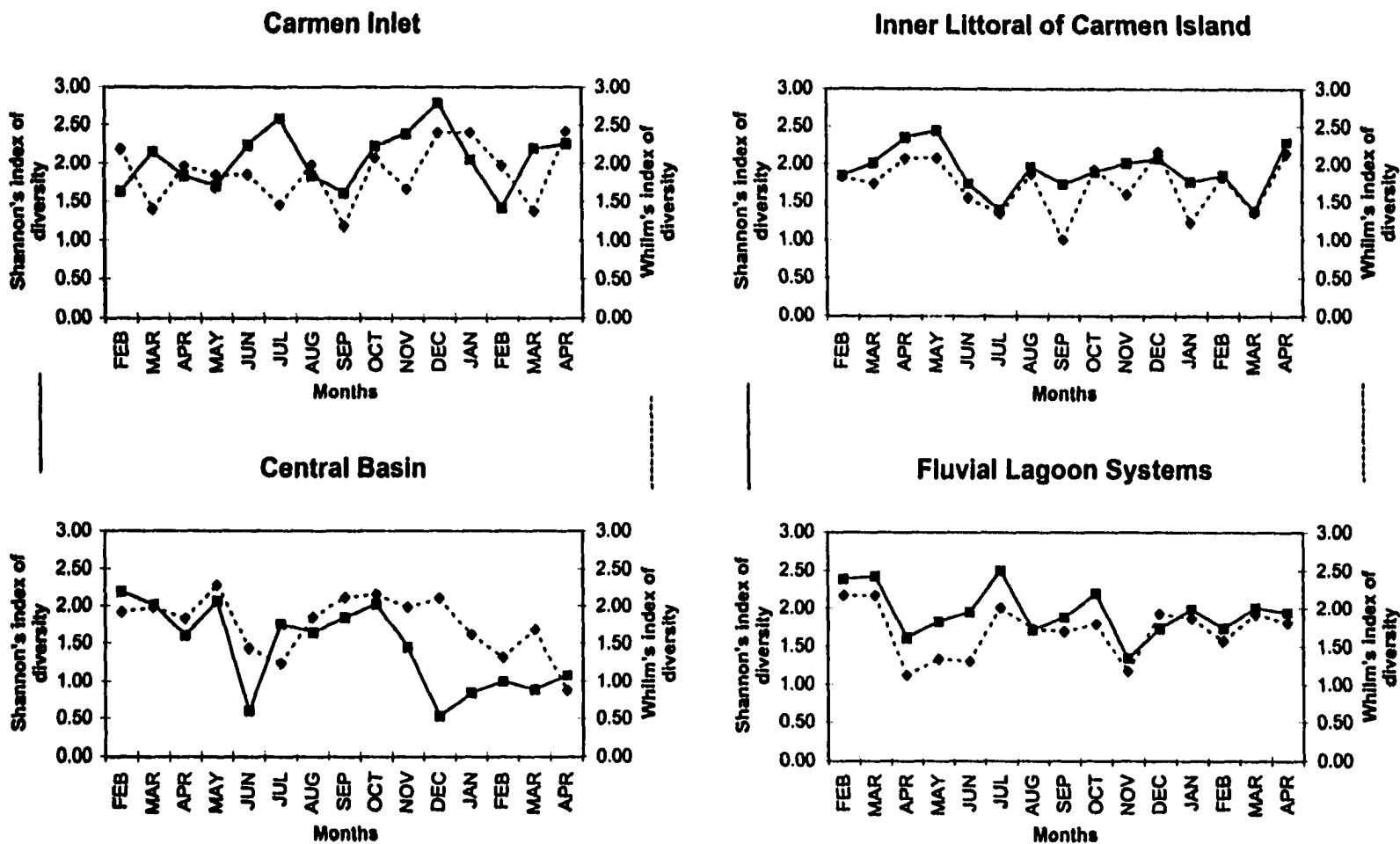


Fig. 2.16. Monthly Shannon and Whilm indices of diversity in each ecological subsystem during 1980-1981 sampling period.

months. However, inner littoral of Carmen Island had high numeric diversity during the dry season, while in the fluvial lagoon systems it was during the rainy season (Fig. 2.16).

In Terminos Lagoon overall, Simpson's Index varied from 0.76 (March of 1981) to 0.91 (October), while the evenness index (Pielou) ranged from 0.61 (March 1981) to 0.73 (April 1981). The Pielou index was not statistical significance by seasons or habitat types. But Simpson index varied significantly by season; nevertheless the residuals did not conform the assumption of normality. In Carmen Inlet, the Simpson Index ranged from 0.52 in February of 1981 to 0.93 in December 1980, while Pielou's index was from 0.47 and 0.90 during the same months. Both indices suggest to have similar annual patterns with high values in the dry season of 1980 and low values in the dry season of 1981. In the inner littoral of Carmen Island, Simpson's index ranged from 0.55 (March of 1981) to 0.87 (April of 1980), while the evenness index varied from 0.47 (March of 1981) and 0.75 (May 1980).

In the fluvial lagoon systems, Simpson's index was from 0.48 in November and 0.84 in July, while the evenness ranged from 0.40 in November to 0.73 in February 1980. There were high values in dry and norte seasons for the inner littoral, and for the fluvial lagoon systems at the beginning of the dry season and during the rainy season. During the dry season, the inner littoral of Carmen Island had high values of both indices during dry season while the fluvial lagoon was low. In July, the situation was the reverse with high values in the fluvial lagoon and low values in the inner littoral (Fig. 2.17).

Finally, the central basin had a marked evenness throughout the year. During the norte season and early dry season of 1981, this system had high evenness

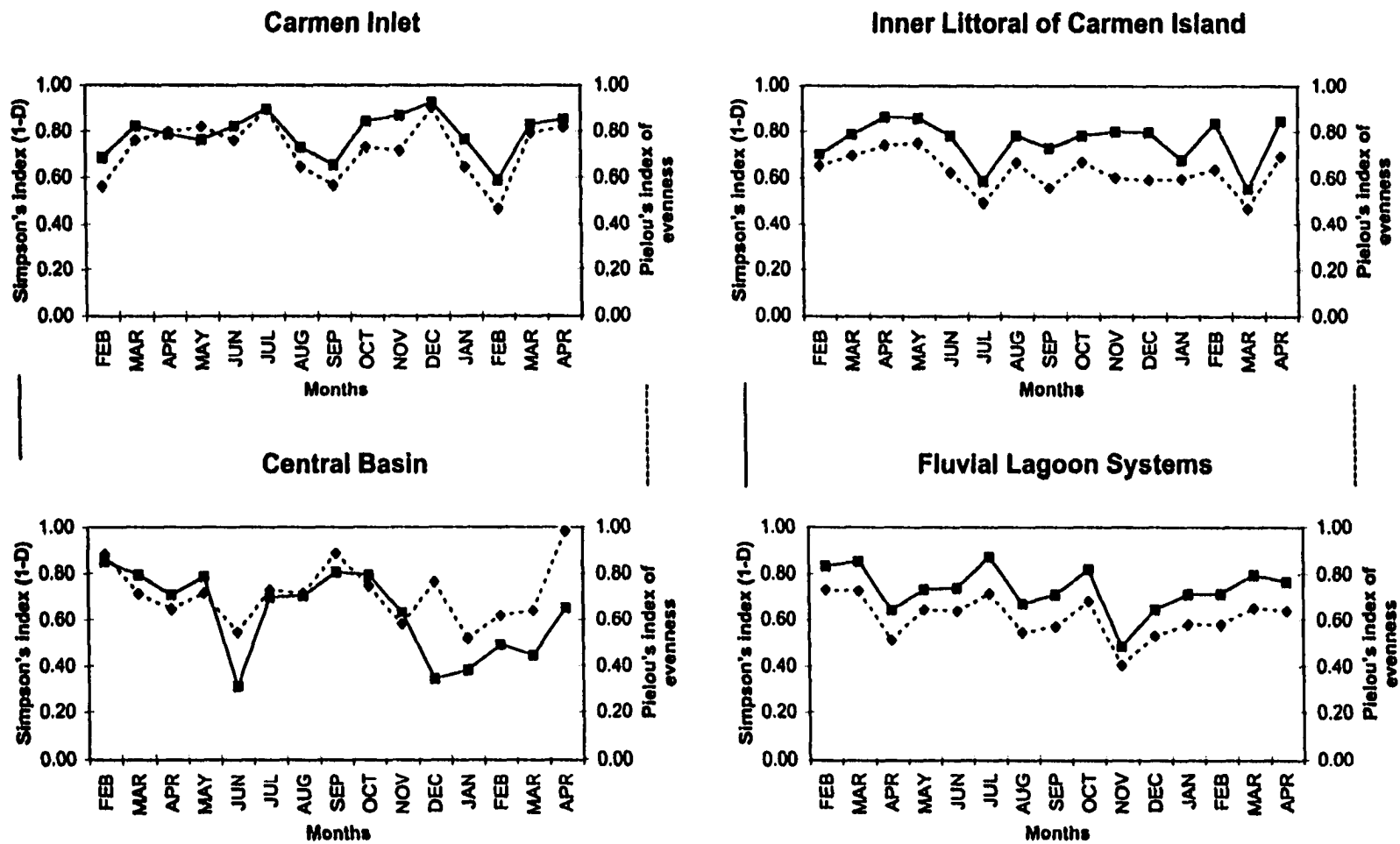


Fig. 2.17. Monthly Simpson and Pielou indices in each ecological subsystem during 1980-1981 sampling period.

values. Simpson's index was between 0.34 in June and 0.85 in February of 1980, while to the evenness fluctuated between 0.52 in January and 0.98 in April of 1981.

2.4.3 The Relation of Diversity Indices to Physical Parameters

In multiple regression analysis physical parameters did not predict very well the behavior of the diversity indices for both Terminos Lagoon as a whole and for individual subsystems: coefficients of determination adjusted for the number of terms in the model (partial r^2 values) varied between 0.06 to 0.37.

For the overall Lagoon, the relationship between the physical parameters and the number of individuals and mean biomass per individual was high ($p = 0.0006$ and $p = 0.0019$, respectively). Nevertheless, the partial correlation coefficients were not significant with number of individuals and average size. However, the stepwise analysis selected water transparency as significantly related to for mean biomass per individual ($r^2 = 0.0739$ and $p = 0.0001$). The stepwise analysis showed that the numbers of individuals was correlated to temperature, Secchi depth and transparency ($r^2 = 0.0095$, $p = 0.1124$; $r^2 = 0.0337$, $p = 0.0039$; $r^2 = 0.0289$, $p = 0.0068$ respectively) indicating that they should contribute to an optimum multiple regression model.

In Carmen Inlet, the number of species, Whilm's diversity index and average size was highly correlated with environmental parameters. The full model of multiple regression between number of species and physical parameters had a coefficient of determination of $r^2 = 0.3386$ and $p = 0.0416$, but it was not clear which physical variables had a significant partial correlation. The number of species had a good fit with salinity ($r^2 = 0.2397$ and $p = 0.0006$). Whilm's diversity index had a $r^2 = 0.3743$ and $p = 0.0198$ for the whole multiple regression model, with salinity having the highest partial correlation coefficient ($p = 0.0185$). Stepwise analysis selected surface temperature ($r^2 = 0.2253$, $p = 0.0010$), salinity ($r^2 = 0.0472$, $p = 0.1063$) and depth ($r^2 = 0.0473$, $p =$

0.0918). Finally, average size was highly correlated with physical parameters ($r^2 = 0.3595$, $p = 0.0272$) but the partial correlation coefficients were not significant. The stepwise analysis selected Secchi depth ($r^2 = 0.1341$ and $p = 0.0134$), temperature ($r^2 = 0.0700$, $p = 0.0444$) and salinity ($r^2 = 0.0470$, $p = 0.1282$). These physical parameters should produce a best fit with average size.

In the inner littoral of Carmen Island, only Shannon's diversity index ($r^2 = 0.2686$ and $p = 0.0104$) and Margalef's species richness index ($r^2 = 0.2490$ and $p = 0.0191$) were highly correlated with physical parameters. Secchi depth and transparency were significantly partially correlated with numerical diversity ($p = 0.0321$ and $p = 0.0294$, respectively) and with species richness ($p = 0.0211$ and $p = 0.0314$, respectively). The stepwise analysis showed that bottom temperature was highly correlated with both indices of diversity ($r^2 = 0.0779$, $p = 0.0150$ for the Shannon's index and of $r^2 = 0.0660$, $p = 0.0310$ for species richness).

The central basin was not significantly correlated with the physical parameters, and the stepwise analysis did not select physical parameters that should produce an optimum multiple regression model.

Finally, the physical variables in the fluvial lagoon systems were highly correlated with Whilm's index ($r^2 = 0.2629$, $p = 0.0005$), Margalef's index ($r^2 = 0.1713$, $p = 0.0274$) and average mass ($r^2 = 0.1791$, $p = 0.0202$). Both indices of diversity had highly partially correlated with salinity ($p = 0.0115$ for Whilm, $p = 0.0053$ for species richness). Whilm's diversity index was also highly partially correlated with the temperature. The stepwise technique for mean size selected salinity and Secchi depth ($r^2 = 0.0680$, $p = 0.0075$ and $r^2 = 0.0339$, $p = 0.0531$, respectively). In Margalef's index was chose salinity ($r^2 = 0.0554$, $p = 0.0196$) and temperature ($r^2 = 0.0412$, $p = 0.0346$).

For Whilm's index, the stepwise analysis selected salinity ($r^2 = 0.1263$, $p = 0.0003$), temperature ($r^2 = 0.0919$, $p = 0.0012$) and transparency ($r^2 = 0.0205$, $p = 0.1150$).

2.5 Discussion

Terminos Lagoon is an open system with permanent connections to the Gulf of Mexico and the rivers that discharge into the lagoon. These conditions maintain semi-permanent gradients in salinity, turbidity and sediment type which in turn influence the presence of different types of vegetated and un-vegetated habitats. The habitats and environmental gradients are important in determining the different fish assemblages comprised of changing species, which have different biological strategies for optimal use of the available resources across environmental gradients (Day and Yáñez-Arancibia, 1982; Yáñez-Arancibia and Day, 1982, 1988; Day et al., 1982; Yáñez-Arancibia et al., 1983)

The environmental parameters had similar seasonal patterns in all ecological subsystem. The end of the dry season was characterized by the highest salinity, temperature and Secchi depth. With the onset of rains and increasing river discharge, there was a progressive decrease in salinity, temperature, and transparency reaching the lowest values during the nortes season. Winter storms also intensified circulation in the lagoon (Fig. 2.3). Because of the gradient from marine influence in the northeast to riverine influence in the southwest, there are semi-permanent gradients in the environmental parameters across the lagoon. Thus, the ecological subsystem are characterized by definite seasonal and spatial patterns of physico-chemical parameters and well defined fish communities, which may migrate through all systems related to their biological strategies (Day and Yáñez-Arancibia, 1985; Yáñez-Arancibia and Day, 1982; Yáñez-Arancibia et al., 1983, Yáñez-Arancibia et al., 1980 and 1985b).

In Terminos Lagoon, 125 species of fish have been reported, including freshwater species associated with the fluvial lagoon systems and species associated with shallow tidal creeks (Yáñez-Arancibia et al., 1988a and 1988b; Vera Herrera et al., 1988). Also, detailed studies have been carried out in Puerto Real and Carmen Inlets and in the inner littoral of Carmen Island (Yáñez-Arancibia et al., 1982 and 1985a; Yáñez-Arancibia and Lara-Domínguez, 1983)

There were 28 species in common between the inner littoral of Carmen Island and the Central basin with 31 species occurring only in the inner littoral and 8, only in the central basin. This gives a similarity of 43% between these two ecological subsystem. Between Carmen Inlet and the inner littoral of Carmen Island, there was a coefficient of similarity of 47%, due to the presence of 34 common species, with 25 occurring only in the inner littoral and 13 only in the inlet. The coefficient of similarity was 59% between the inner littoral of Carmen Island and the fluvial lagoon systems with 45 species in common, 14 only in the inner littoral and 17 in the fluvial systems. Between the central basin and the fluvial lagoon systems, the coefficient of similarity was 50%, with 32 species in common, 30 species only in the fluvial systems and 2 in the central basin. Between Carmen Inlet and the fluvial lagoon systems, the coefficient was 60% with 41 species in common, 21 which only occurred in the fluvial systems and 6 in the inlet. Finally, between Carmen Inlet and the central basin, the coefficient of similarity was 45% with 25 species in common, 22 only in the inlet and 9 only in the central basin. The most similar ecological subsystems are: Carmen Inlet and fluvial lagoon systems, and the most different are the central basin and the inner littoral of Carmen Island (Table 2.8 Appendix A).

Yáñez-Arancibia et al. (1985b) analyzed fish-habitat affinities in Terminos Lagoon and established that there is a high level of significance between the estuary-

lagoon inlets and adjacent inner shelf. The fish communities reflect the typical characteristics of each system. Thus, they identified seven subsystems, 5 in Terminos lagoon (groups I, II, III and the two inlets), and two in the adjacent shelf.

The purpose of using the different diversity indices and models is to develop a clearer quantitative differentiation among the subsystems. For example, Kushland (1976) assessed environmental stability in relation to fish community diversity in the Everglades using Shannon's density index and Whilm's (1968) biomass index to evaluate fish community structure in relation to water level changes in a marsh habitat. He concluded that although Shannon's index explained some aspect of changes in community species diversity, this index alone was not sufficient to characterize total change in the community. This suggested that a more functional analysis could be achieved by characterizing species in the community on a functional basis and measuring diversity in additional ways such as biomass and productivity. Blanchard (2001), interpreted the dynamic patterns of demersal fish communities in the Bay of Biscay from species diversity indices in conjunction with k-curves and life strategy characteristics.

In Terminos lagoon, higher biomass, species numbers, and abundance and smaller size occurred during the transition from the rainy to the norte season. Higher nutrient levels, greater flushing of adjacent wetlands, and high river discharge lead to higher lagoon productivity during this period (Yáñez-Arancibia and Day, 1982; Day et al., 1982 and 1998b; Rivera-Monroy et al, 1995 and 1998; Rojas Galaviz et al., 1992). This time of year is also the period when immigration of juvenile estuarine-dependent fish is facilitated by the prevailing current patterns (Yáñez-Arancibia et al., 1982; Chavance et al., 1986). Yáñez-Arancibia et al. (1980) concluded that this fish immigration was related to the high lagoon productivity during this period. During

October, there were high values of the Shannon, Whilm and Pielou indices indicating a high diversity of species as adults with numerous individuals (Fig. 2.16).

During the dry season, high values of the Shannon and Whilm indices in the inner littoral of Carmen Island indicated high species diversity with larger pre-adult individuals (Figs. 2.11 and 2.16). This high diversity is likely related to the high levels of primary productivity during this season as a result of higher water clarity (Fig. 2.5; Day et al., 1982; Moore and Wetzel, 1988). The inner littoral of Carmen Island has abundant seagrass meadows of *Thalassia testudinum* and mangrove swamps. During November there was a peak of the Shannon index in Carmen Inlet that indicated a high species diversity of small individuals. This high diversity in Carmen Inlet should be related to fish immigration to the lagoon (Figs. 2.11 and 2.16).

For the Mississippi River deltaic plain, Deegan and Thompson (1985) reported that species per sample, number of individuals per square meter, species diversity and species richness were different among the different sub-estuaries. However, these parameters did not change significantly over the course of the year because the migration patterns resulted in 'species compensation' or sequential replacement of species (Louis et al., 1995). Taken together, this sequential replacement results in four major migration patterns of fishes in Louisiana estuaries. This is likely the case in Terminos Lagoon because there were no pronounced diversity changes during the year. Thus, the Shannon and Whilm indices ranged from 1.35 to 2.79 and from 1.01 to 2.42, respectively.

The four ecological systems had different relationships to the species abundance models. Carmen Inlet, the central basin and the inner littoral of Carmen Island were better described by the log series model while the fluvial lagoon systems were best described by the log normal distribution. In both models, species with

intermediate abundance are important in fish diversity in the lagoon. The difference between the two models reflects the factors that dominate the ecology of the fish communities. When the log series model better describes a community, one or a few environmental factors dominate the ecology of the community. For example, the multiple regression model selected salinity as an important environmental factor which was linearly related to Whilm's index for Carmen Inlet. This should suggest that salinity could be the most significant factor that controls the abundance and diversity of the fish community in Carmen Inlet. The multiple regression model was significant for Secchi depth which was linearly related to Shannon's index, Margalef's index and Simpson's index in the inner littoral of Carmen Island. May be, Secchi depth could be an indicator of water clarity and high productivity in the seagrass habitat. Therefore, this suggests that this factor could be important in the ecology of the fish community in the inner littoral of Carmen Island. For the fluvial lagoon systems, salinity and temperature were significant in the multiple regression model. Both salinity and temperature were linearly related the Shannon's index, and they should be important cues to the presence or absence of fish species and their abundance.

Species abundance models have not been used very often for aquatic ecosystems (Washington, 1984) probably because of the necessity of collecting such large amounts of data. In Terminos lagoon overall and for the different subsystems, the log series and log-normal models fit well (Table 2.9 Appendix A). These abundance models fit the distribution of the fish community and describe the abundance of individuals for each species. This indicates that the species diversity in abundance in the different subsystems was determined mainly by species of intermediate abundance. This pattern was verified by the Q-statistic, which showed that between 50 and 76% of the species in the community were of intermediate abundance. These

models verify that the fish community in Terminos Lagoon is made up of a few dominant species, a relatively large number of species of intermediate abundance and an intermediate number of rare species. Therefore, both the inner littoral of Carmen Island and the fluvial lagoon systems have fish communities where most of the species are of intermediate abundance. This is also true for the entire lagoon.

The k-dominance curves indicated that the Carmen Inlet assemblage is more diverse than the other subsystems, though it did not have the greatest number of species. This is because the evenness of the community was higher in the highly dynamic system. For the other systems, the k-dominance curves cross indicating a shift between a community with few species with high values of relative abundance to a fish community with more species but with similar abundance. The Living Marine Resources Panel of the Global Ocean Observing System recommended this methodology (GOOS, 2000) as an indicator of changes in the community structure of living marine resources and in the function of ecosystems.

Although there is overlap in species utilization of different estuarine subsystems, it is clear that each may serve as the primary nursery for different suites of species (Weinstein, et al., 1980; Yáñez-Arancibia et al., 1988c, 1993). Combined with considerations of seasonality, physiological limitations, and other factors, I find that the fish community in Terminos is highly programmed, where available resources are partitioned to maximize production of individual species. This is also reflected in the whole community, which maintains relative high and constant diversity as a result of this seasonal programming.

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CHAPTER 3. ECOLOGY OF DOMINANT FISH POPULATIONS, ENVIRONMENTAL FACTORS REGULATING BIOLOGICAL STRATEGIES IN A TROPICAL LAGOON

3.1 Introduction

Coastal lagoon systems are highly productive environments with high habitat diversity (seagrass meadows, mangrove swamps, tidal freshwater environments, etc.) that support a high diversity of fauna and flora. They serve as nurseries, feeding grounds and refuges for a wide variety of fish species, typically during their first year. This ecological role is best appreciated when one considers that more than 75% of commercially-important species have estuarine-dependent life cycles or are estuarine related (McHugh, 1985; Yáñez-Arancibia, 1985; Yáñez-Arancibia et al., 1988; Yáñez-Arancibia et al., 1994; Arrivillaga and Baltz, 1999; Chesney et al., 2000).

These systems have high ecological and economic value in terms of such factors as fish production, wetland health, wildlife habitat, protected areas, water quality improvement, freshwater storage, agriculture and tourism (Reyes et al., 1993; Day et al., 1999; Yáñez-Arancibia 2000; Chesney et al., 2000). Despite these important values, there are serious environmental problems in many lagoon-estuarine ecosystems. The most important are: subsidence due to drainage, habitat destruction, reduced accretion, salinity intrusion, water quality deterioration, and decreased biological production (Boesch et al., 1994; Day et al., 1995, 1997; Coleman et al., 1998). These problems are often the result of reclamation for agricultural, urban, and industrial uses (Diegues, 1999), reduction in the influence of pulsing events such as storms and river floods resulting in reduce freshwater input (Botero and Salzwedel, 1999; Day et al., 1995) and reduced biological production (Windevoixhel et al., 1999; Mendelssohn and McKee, 1988; Day et al., 1997). Fishery scientists and managers have become increasingly aware and concerned about the direct, indirect and

cumulative impacts of habitat change on commercial and recreational fisheries, and conversely the effects of these fisheries in an ecosystem context (Fluharty, 2000).

Fish communities in tropical and subtropical areas often have high species diversity, with very complex interactions between individuals, species and populations. These relationships between different fish species and the environment in tropical regions are often subtle, and frequently it is difficult to detect changes and determine accurately the nature of the relationships (Yáñez-Arancibia and Pauly, 1986; Pauly, 1998).

The dominant fish species characteristic of temperate and cold-temperate latitudes are generally defined by their numeric abundance. By contrast, in tropical and subtropical latitudes, the situation is much more complex because the high number of species leads to a high complexity of interactions. The concept of dominant species in low latitude coastal areas includes a number of characteristics of adult fishes including: 1) numeric abundance, 2) biomass abundance, 3) a wide distribution in the system, and 4) a high frequency of capture (Yáñez-Arancibia et al., 1985; Pauly, 1998; Sanchez-Gil and Yáñez-Arancibia, 1997).

3.1.1 Background

In Terminos Lagoon (the largest tropical coastal lagoon in Mexico), numerous studies have addressed the ecological role of the fish communities in the system. It has been shown that fish communities are seasonally related, through structural parameters of biomass and diversity, to the different estuarine habitats. Reflecting this, the dominant species, as indicators of these relationships, are related to the different habitats and climatic periods during different periods of their life cycles in the lagoon (Yáñez-Arancibia et al., 1980, 1985a, 1988a, 1993, 1994; Yáñez-Arancibia and Day, 1982; Yáñez-Arancibia and Lara-Domínguez, 1988).

There is a sequence between the maximum and minimum values of the structural parameters of the fish populations for each habitat (Yáñez-Arancibia et al., 1980, 1985a, and 1988a). The seasonality of these changes is related to the biological adaptations of the different fish species to changes in environmental parameters during the year (Yáñez-Arancibia et al., 1993). Adaptations and tolerances to certain physical and biological parameters determine fish species diversity and distribution. Different fish life history stages occur along spatial and temporal gradients that should reflect optimum conditions (physical, chemical and biological) for each stage (Baltz et al., 1993).

An understanding of the diversity, behavior and microhabitat requirements of estuarine-dependent fishes is important for the conservation of the nursery function of coastal wetlands (Baltz, et al., 1993). Enhanced survival and growth of early life history stages in nursery habitats are known to increase recruitment success. It is not clearly known how environmental factors influence survival and growth in estuaries, nor the extent to which habitat preferences affects recruitment success for many estuarine-dependent fishes.

Baltz (1990) defined the microhabitat of an individual fish as the site that it occupies at a given point in time. This site is presumably selected by the fish in response to proximate factors to optimize net energy gain while avoiding predators and minimizing interactions with competitors. Baltz et al. (1993) approached the question of habitat preferences by fine scale studies of distribution and abundance at the microhabitat level. To begin to understand the linkages between fish habitat preferences and recruitment (which interrelate microhabitat use), prey selection and daily growth are needed.

Several authors have discussed habitat requirements for fish in their early life-history stages. Blaber and Blaber (1980) studied how physical factors affect the distribution of juvenile estuarine and inshore fish. Boehlert and Mundy (1988) discussed the role of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Pinto (1987) related environmental factors to the occurrence of juvenile fish in mangroves in Pagbilao, Philippines. Weinstein (1985) studied the role of the distribution ecology of fishes inhabiting warm-temperate and tropical estuaries on community relationships.

The abundance and importance of some fish species and families in coastal lagoons and estuaries have been studied particularly well because of their commercial importance. A number of studies have been carried out in Terminos Lagoon. The family Ariidae, for example, is common in many temperate, tropical and subtropical coastal ecosystems. In Terminos Lagoon, Lara-Dominguez et al. (1981) and Yáñez-Arancibia and Lara-Domínguez (1988) studied the biological strategies and abundance patterns of three species of sea catfish. Also, Yáñez-Arancibia et al. (1985a) reported on the environmental factors that regulate biological strategies and production of dominant fish populations. Several authors (Diaz et al., 1982; Aguirre Leon et al., 1982; Mallarad Colmenero et al., 1982; Aguirre Leon and Yáñez-Arancibia, 1986) reported on the families Pomadasidae, Gerreidae and Tetraodontidae, which are also commercially important. Chavance et al. (1984 and 1986) studied the population dynamics of *Bairdiella chrysoura* and *Archosargus rhomboidalis*.

Habitat and primary production are important determinants controlling fish community structure and distribution. For example, Yáñez-Arancibia et al. (1988a) related fish abundance patterns in to aquatic primary productivity in Terminos Lagoon. A number have shown that mangroves are important nursery sites. Pinto (1988)

studied the population dynamics and community structure of fish in mangroves in Pagbilao, Philippines and Lewis et al. (1985) related mangrove habitat to fishery resources in Florida. Other studies documenting the importance of mangroves include comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia (Robertson and Duke, 1987), the utilization of red mangrove prop root habitat by fishes in South Florida (Thayer et al., 1987), the relationship of fish trophic dynamics to mangrove ecosystems in the north littoral of the Yucatan (Vega Cendejas, 1998), the coupling of primary and secondary production in mangrove and seagrass habitats in Terminos Lagoon (Yáñez-Arancibia et al., 1993)

Seagrasses and salt marshes have also been shown to be important habitat for fishes. For example, Arrivillaga and Baltz (1999) documented the nursery value of seagrasses to fishes and macroinvertebrates on the Atlantic coast of Guatemala. Bell and Pollar (1989) also related the ecology of fish assemblages and fisheries with seagrass. Other studies have documented the importance of seagrass habitats including: the role of habitat complexity, competition and predation in structuring fish and motile macroinvertebrates assemblages (Heck and Orth, 1980), the trophic organization of fish in coastal seagrass systems (Livingston, 1982), the response of the organization of fishes in coastal seagrass system to stress (Livingston, 1985). Food, density, and microhabitat relationships have also been studied for salt marshes. Examples include factors affecting the growth and recruitment potential of juvenile saltmarsh fishes (Baltz et al., 1998), microhabitat use by marsh-edge fishes in a Louisiana estuary (Baltz et al., 1993), the role of food and refuge on the dependence of fishery species on salt marshes (Boesch and Turner, 1984), shallow marsh habitats as primary nurseries for fish and shellfish in the Cape Fear River, North Carolina

(Weinstein, 1979), and the ecology of fish communities in the Mississippi River deltaic plain (Deegan and Thompson, 1985).

3.1.2 Objectives

In this chapter, I assess the ecological function of the different ecological subsystems of the lagoon for dominant species using measures of biomass, density, and frequency of capture as they are related to biological strategies.

- **General Objectives**

For each major ecological subsystems in Terminos Lagoon, To determine the dominant species unique to that habitat and the dominant species shared with other habitats.

To establish the linkages among habitats with respect to different biological strategies of habitat utilization.

To define quantitatively which environmental parameters are associated with each pattern.

To describe the ecological linkages among the dominant fish species in different habitats and describe their seasonal programming.

- **Specific Objectives**

To use data on abundance, frequency and distribution to identify dominant species in each ecological subsystem.

To determine the abundance patterns and mean size for each dominant species and establish the relationship to environmental factors

To determine the population structure for some dominant fish species in relation to each habitat and / or season of the year.

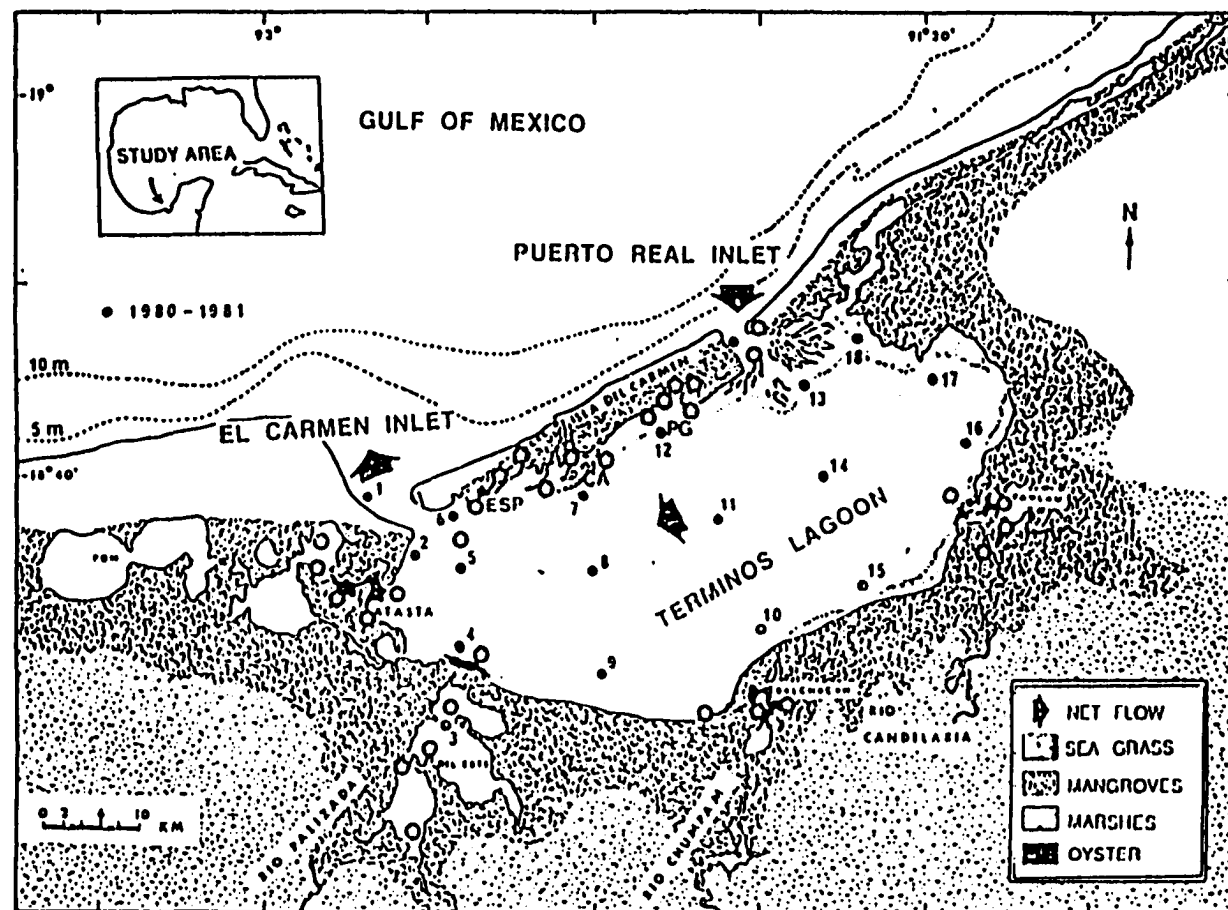
To establish the sequential occurrence of the dominant fish species in the different ecological subsystems in Terminos Lagoon.

3.2 Study Area

Terminos Lagoon is a large (about 1700 km² for the lagoon surface area surrounded by about 2500 km² of mangroves and freshwater wetlands), shallow (mean depth 3.5 m) coastal lagoon located at the base of the Yucatan Peninsula in the state of Campeche, Mexico (Fig. 3.1). The lagoon is separated from the Gulf of Mexico by Isla del Carmen and water exchange with the Gulf occurs through two deep inlets. There is a mixed diurnal tide with a range of about 0.5 m. Trade winds induce a net inflow into the lagoon through the eastern inlet at Puerto Real, and a net outflow through the western inlet at Carmen (Mancilla and Vargas, 1980; Graham et al., 1981). This net flow has resulted in the formation of a flood-tide delta in the lagoon at Puerto Real inlet and an ebb-tide delta in the Gulf at Carmen Inlet (Phleger and Ayala Castañares, 1971; Coll de Hurtado, 1975; Gutierrez Estrada and Castro del Rio, 1988; Kjerfve et al., 1988).

Climatically, this tropical area is characterized by three seasons with distinct patterns in precipitation, river discharge, winds and temperature (Yáñez-Arancibia and Day, 1982): the dry season from February to May, the rainy season from June to September, and the "Nortes" season from October to January. Rainfall is very low during the dry season (66.1 mm/month), occurs during afternoon and evening thunder showers in the rainy season (289.0 mm/month) and is associated with frontal systems during the norte season (175.2 mm/month).

The same rainfall pattern occurs over the drainage basin of the lagoon resulting in a similar pattern of river discharge with peak discharge in the months of September, October and November. Three main rivers discharge to the lagoon: the Candelaria, the



3.1 Location of study area. Terminos Lagoon in the Southern Gulf of Mexico. Sampling stations are indicated

Chumpan and the Palizada (is a distributary of the Usumacinta River) (Phleger and Ayala-Castañares, 1971; Amezcua Linares and Yáñez-Arancibia, 1980; Vera Herrera et al., 1988). The Palizada has the highest discharge resulting in a pronounced lowering of salinity in the western part of the lagoon.

Seagrass beds occur in shallow areas along shallow shorelines in the eastern end of the lagoon (Moore and Wetzel, 1988). *Thalassia testudinum* (turtle grass) is the most abundant species, but *Diplantera wrightii* (shoal grass) and *Syringodium filiforme* (manatee grass) also occur. Extensive mangrove swamps dominated by *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove) and *Laguncularia racemosa* (white mangrove) surround the lagoon (Day et al., 1982, 1988, and 1996).

3.3 Material and Methods

3.3.1 Field and Laboratory Measurements

Fish were collected with a 5 m shrimp otter trawl (2.5 m mouth with a 19 mm mesh). Tows lasted 10 to 12 min at 2 to 2.5 knots and covered an area of 1500 to 2000 m². Sampling depth varied but never exceeded 3.5 m. Samples were collected monthly at 18 stations from March 1980 to April 1981 (Fig. 3.1). Specimens were fixed in neutralized 10% formalin. Temperature (thermometer), salinity (temperature-compensated refractometer), Sechii depth and total depth, sediment type, presence of submerged vegetation, air temperature and wind direction were also measured at each sampling station. In the laboratory, individuals were identified to species, counted and measured to the nearest millimeter total length.

3.3.2 Analysis of Dominant Species Population Structure

For each subsystem, the dominant fish species were determined based on the frequency (percentage occurrence), broad distribution, biomass and numerical abundance. Biomass, density and mean fish size per m² were calculated monthly for

each dominant species by subsystem and for the entire lagoon. Mean fish size by species was calculated monthly by dividing total biomass by density. Data are presented as means and standard errors.

To determine which environmental factors were most important in determining the temporal and spatial distribution of the dominant species in the lagoon, I conducted the following statistical analyses: I conducted an ANOVA to determine relationships of density to both stations and months. A similar model was used for biomass. The dependent variables (density and biomass) were log-transformed to conform to the assumptions of normality.

A multiple regression was used to fit two regression models relating the log transformed variables, density and biomass, to surface and bottom salinity, surface and bottom temperature, secchi depth, transparency, depth. For some species, month and station were included as independent variables to improve model fit. The diagnostic options used included VIF, COLLIN, and INFLUENCE. Stepwise selection was also used to determine the most efficient model (SAS Institute, 1999).

I examined variation of the fifteen most abundant fish species in Terminos lagoon within the four ecological subsystems in a principal component analysis with seven environmental variables based on the correlation matrix (SAS Institute, 1999). Environmental variables without missing data were used to calculate variable loading and generate principal component scores for each sample. Principal component scores for each sample were then used to calculate species' centroids.

Seven dominant species were analyzed by size class distribution (total length in mm) related to the season of the year. An index of seasonal abundance was used to follow changes in these dominant species (Roger and Herke, 1985; Yáñez-Arancibia et al., 1988a, 1993). The monthly index for each species was calculated as the mean

catch per month divided by the highest monthly mean catch of the species, multiplied by 100. Thus the highest monthly catch for each species had an index of 100.

Dominant fish populations were defined on the basis of frequency (percent of occurrence), broad distribution, biomass and numerical abundance.

3.4 Results

Terminos Lagoon has a high diversity of ecological subsystems. We grouped the 18 stations based on all sampling environmental records using cluster analysis as follows: Carmen Inlet (stations 1, 2 and 5), fluvial lagoon systems (stations 3, 4, 9, 10, 15, 16 and 17), the inner littoral of Carmen Island with persistent marine influence and seagrass meadows (stations 6, 7, 12, 13 and 18) and the central basin (stations 8, 11 and 14). During the study period 1980-1981, we captured 82 species of fish in the lagoon. For each ecological subsystem, the following numbers of species were captured: Carmen Inlet, 47; the central basin, 34; the fluvial lagoon systems, 62, and the inner littoral of Carmen Island, 59. They are described in detail in Chapter 2.

For the whole lagoon, 17 species accounted for 90% of all individuals. There were 14 dominant species in Carmen Inlet, 10 in the central basin, 11 in the fluvial lagoon systems and 9 in the inner littoral of Carmen Island. These species represented 89% of the total numbers of fish captured and between 74 and 91% of the capture by mass for the individual subsystems. Therefore, there were 21 fish dominant species in total that represented 26% of the total number of species reported for the whole lagoon. I carried out a detailed analysis of the 15 most dominant species. These 15 species were either dominant in all four ecological subsystems or they were very common but limited to less than four subsystems (Table 3.1 Appendix B).

Five species (33%) of the 15 selected dominant occurred in all ecological systems of Terminos Lagoon. These are *Cathorops spixii* (mandamango sea catfish) *Sphoeroides testudineus* (checkered puffer), *Bairdiella chrysoura* (silver perch), *Ariopsis felis* (hardhead sea catfish) and *Eucinostomus gula* (silver jenny).

Three of the dominant species (20%) each occurred in at least three ecological subsystems. *Archosargus rhomboidalis* (sea bream) was distributed mainly in areas with persistent marine influence. It was a dominant member of the fish community in the inner littoral of Carmen Island, in the eastern part of the fluvial lagoon systems, and in the central basin. *Anchoa mitchilli* (bay anchovy) and *Chaetodipterus faber* (Atlantic spadefish) were captured in all ecological subsystems in the lagoon. However, they were mainly found associated with areas affected by river discharge. These two species were dominant in the Carmen Inlet, the fluvial lagoon systems, and in the central basin of the lagoon.

The remainder species had limited distributions and were dominant in only one or two of the ecological subsystems (Table 3.1 Appendix B). *Diapterus rhombeus* (caitipa mojarra) occurred in all subsystems, however, it was important in terms of abundance and frequency only in the fluvial lagoon systems and the central basin. *Orthopristis chrysoptera* (pigfish) had a limited distribution, being captured mainly in the inner littoral of Carmen Island, and to a lesser extent in the central basin and fluvial lagoon systems. *Cynoscion arenarius* (sand seatrout) was dominant in Carmen Inlet and the inner littoral of Carmen Island and occurred to a lesser extent in the fluvial lagoon systems.

Stellifer lanceolatus (star drum) and *Cetengraulis edentulus* (anchoveta) occurred in Carmen Inlet and the western region of the fluvial lagoon systems but were

dominant in Carmen Inlet. *Citharichthys spilopterus* (bay whiff) occurred in these two subsystems and the inner littoral of Carmen Island. It was dominant, however, only in Carmen Inlet. Finally, *Cyclichthys schoepfi* (stripe burrfish) is a marine species typically associated with coral reef and sea grasses. In Terminos Lagoon, it is a dominant in the inner littoral of Carmen Island but occurs to a lesser extent in the central basin and fluvial lagoon systems.

This spatial distribution of the dominant fish species reflects the affinity of to specific ecological subsystem as a result of the limitation of one or several environmental or biological factors. The description of the results will be presented for each species, from the most abundant with wide distribution to the less abundant with limited distribution in the lagoon.

3.4.1 *Cathorops spixii* (mandamango sea catfish)

This species is the most abundant fish in the lagoon. By number of individuals, 71% were captured in the fluvial lagoon systems, 16% in the inner littoral of Carmen Island, and 10% in Carmen inlet. This species was first in number and mass in the fluvial lagoon systems, second in Carmen Inlet and third for numerical capture and fourth for mass in both the central basin and the inner littoral of Carmen Island (Table 3.1 Appendix B). This species had a strong affinity to station 3 (the lower Palizada River) in contrast to the other stations. Table 3.2 Appendix B shows the ranges of the total number of individuals and biomass, mean size in grams, density, biomass per unit area, and environmental characteristics. This species occurred over a wide range of salinities, temperatures and water clarity, but 52% of the individuals were captured in salinity between 0-10 (Table 3.2 Appendix B).

The biomass model for this species was significant ($p = 0.0015$), and station was significant ($p = 0.0001$). Mandamango sea catfish had high mean density through the year in the fluvial lagoon systems. In the fluvial lagoon systems, there were three density peaks in April (0.057 ± 0.049 indiv/m²), November (0.046 ± 0.027 indiv/m²) and February (0.037 ± 0.037 indiv/m²). In the inner littoral of Carmen Island, there were density peaks in December (0.074 ± 0.073 indiv/m²) and March 1981 (0.061 ± 0.033 indiv/m²). The lowest values occurred in the central basin. Biomass per unit area was high in the fluvial lagoon systems through the year with peaks in April (7.002 ± 3.209 g/m²), June (1.605 ± 0.7 g/m²), November (2.298 ± 0.771 g/m²) and February 1981 (2.651 ± 31.3 g/m²; Fig. 3.2).

The multiple regression models for both for density and biomass had a significant coefficient of determination. The full model for *Cathorops spixii* was significant at $p < 0.0001$ for both models ($r^2 = 0.2364$ for density, and $r^2 = 0.2478$ for biomass). The individual analysis showed that salinity and temperature were significant for density and biomass at the 0.05α level (Type I error). This indicates that temperature and salinity affect the biomass of *C. spixii*. The model of density found that salinity and Secchi disk depth were significant with negative coefficients. This indicates that the density of this species was associated with low salinity, turbid waters.

The smaller mean mass per individual sizes occurred in Carmen inlet from August to November of 1980. The smaller individuals occurred in salinities from 5 to 10, while heavier individuals occurred between 15 to 20. Large individuals occurred mainly in the inner littoral of Carmen island from February to May 1980 (Fig. 3.3). Individuals with intermediate mass occurred in the central basin and fluvial lagoon systems. The full multiple regression mass model for this species was significant ($r^2 =$

Cathorops spixii

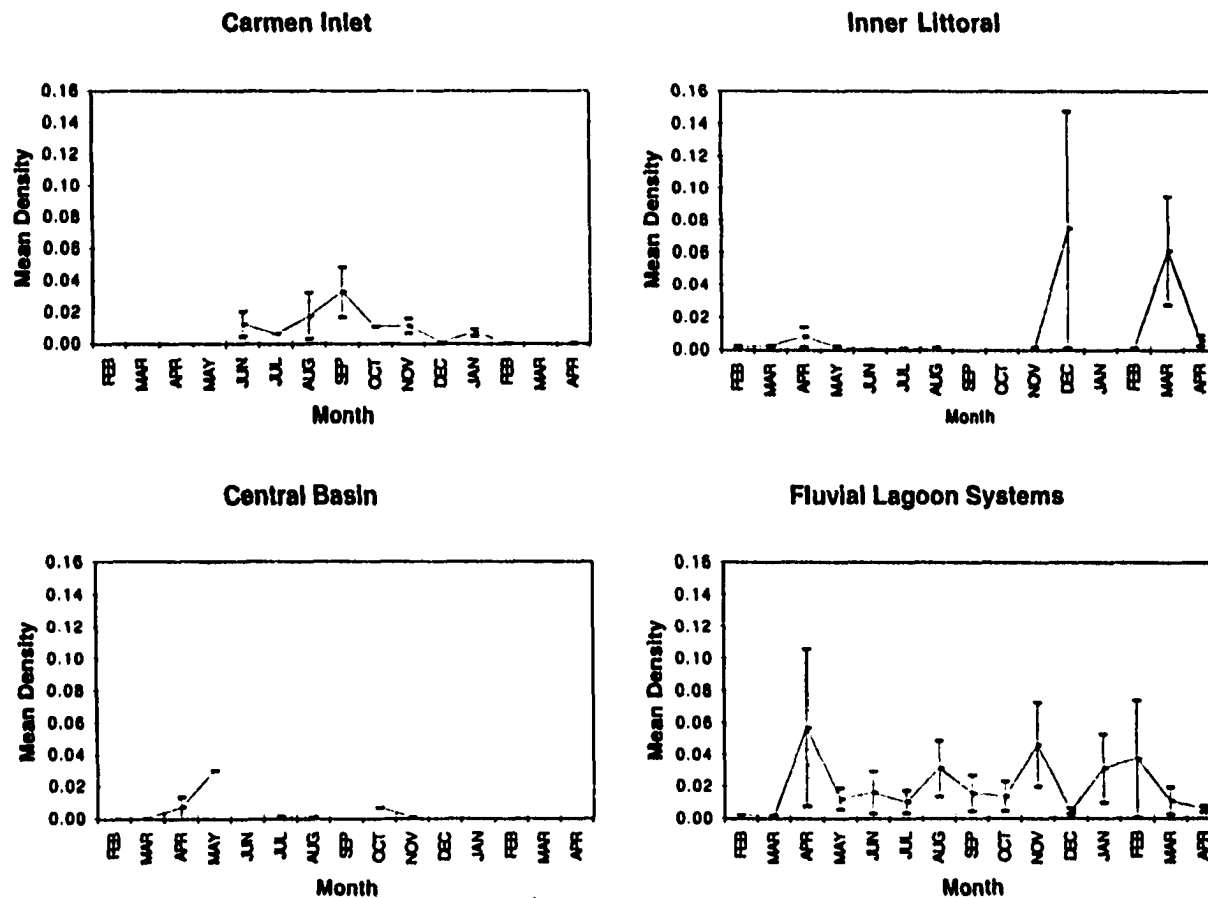


Fig. 3.2 Seasonal patterns of mean density (indiv/m²) in each ecological sybsystem of Terminos Lagoon for *Cathorops spixii* (mandamango sea catfish).

Cathorops spixii

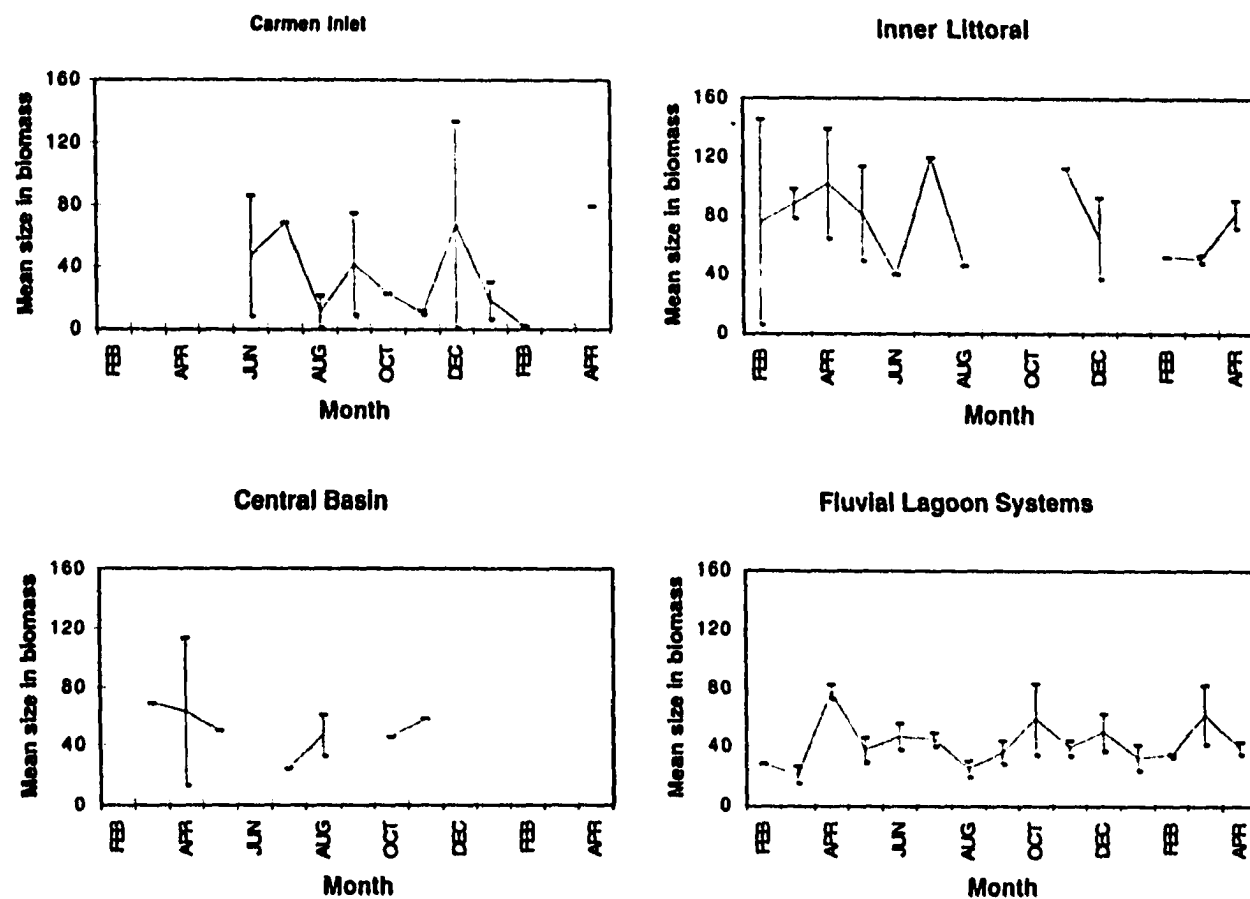


Fig. 3.3 Seasonal variation of mean biomass per individual (gr/indiv) in each ecological subsystem of Terminos Lagoon for *Cathorops spixii* (mandamango sea catfish).

0.1345, $p = 0.0019$), and showed that Secchi depth ($p = 0.0014$) and temperature ($p = 0.0123$) were significant.

3.4.2 *Sphoeroides testudineus* (checkered puffer)

This was the second most abundant species in Terminos Lagoon. Sixty-three percent of the total catch was from the inner littoral of Carmen Island, 25% from the fluvial lagoon systems, and 9% from Carmen Inlet, and the rest from the central basin. Table 3, Appendix B shows the ranges of the total number of individuals and weight, mean size in grams, density, biomass per unit area, and environmental characteristics related to this species in Terminos Lagoon. This species is the first by number and second by mass in the inner littoral of Carmen Island, third by number and second by mass in the fluvial lagoon systems, sixth by number and fifth by mass in the central basin, and seventh by number and first by mass in Carmen Inlet (Table 3.1 Appendix B). This species also occurred over a wide range of environmental conditions, but 52% of the individuals were captured in salinity between 5-20 (Table 3.3 Appendix B).

The checkered puffer had significant differences in biomass among stations ($p = 0.0001$), and for the density both stations ($p = 0.0001$) and months ($p = 0.0297$). The biomass model for *Sphoeroides testudineus* (checkered puffer) was significant ($p = 0.0001$). For *Sphoeroides testudineus* (checkered puffer), both station and month were significant ($p = 0.0001$ and 0.0502 respectively).

The highest density was in the inner littoral of Carmen Island in relation where four peaks in density occurred; February of 1980 (0.017 ± 0.007 indiv/m²), July (0.021 ± 0.013 indiv/m²), November (0.013 ± 0.008 indiv/m²) and March of 1981 (0.011 ± 0.004 indiv/m²). The fluvial lagoon systems and Carmen inlet registered intermediate values of density. In Carmen inlet, there were density peaks in November

(0.023 ± 0.0001 indiv/m²) and March of 1980 (0.015 indiv/m²; Fig. 3.4). While peak density in the fluvial lagoon systems was in July (0.011 ± 0.005 indiv/m²). The minimum values occurred in the central basin (Fig. 3.4). The highest biomass was in the inner littoral of Carmen Island and Carmen inlet with peaks in December (1.280 ± 0.828 g/m²), July (0.931 ± 0.397 g/m²), and February 1980 (0.726 ± 0.277 g/m²). In Carmen inlet there were peaks in November (1.869 ± 1.232 g/m²) and March 1980 (1.050 g/m²). Intermediate biomass occurred in the fluvial lagoon and the lowest was in the central basin (Fig. 3.4).

For *Sphoeroides testudineus* (checkered puffer) the multiple regression models for both for density and biomass had a significant coefficient of determination. The full model of Ln(density) for *Sphoeroides testudineus* was significant ($p = 0.0004$, $r^2 = 0.1245$). Analysis of individual variables in the density model showed that both temperature and Secchi depth were significant ($p = 0.0002$ and $p = 0.0017$, respectively). The temperature relationship was positive while the Secchi relationship was negative.

The mean mass per station for *Sphoeroides testudineus* (checkered puffer) ranged from 8.0 to 187.2 g/indiv (63.55 ± 2.95 g/indiv). The smaller sizes occurred in salinities of 5 to 10 while heavier individuals occurred between 15 and 40 with a homogeneous size distribution along the salinity gradient. Large individuals were captured mainly in the inner littoral of Carmen Island from December 1980 to February 1981 (Fig. 3.5). Small sizes occurred in the fluvial lagoon systems from July to October. Carmen inlet had both large (August and December) and small (October) sizes. In general, the central basin had small to intermediate sizes. The multiple regression model was significant ($r^2 = 0.1018$, $p = 0.0025$). Analysis of individual

Sphoeroides testudineus

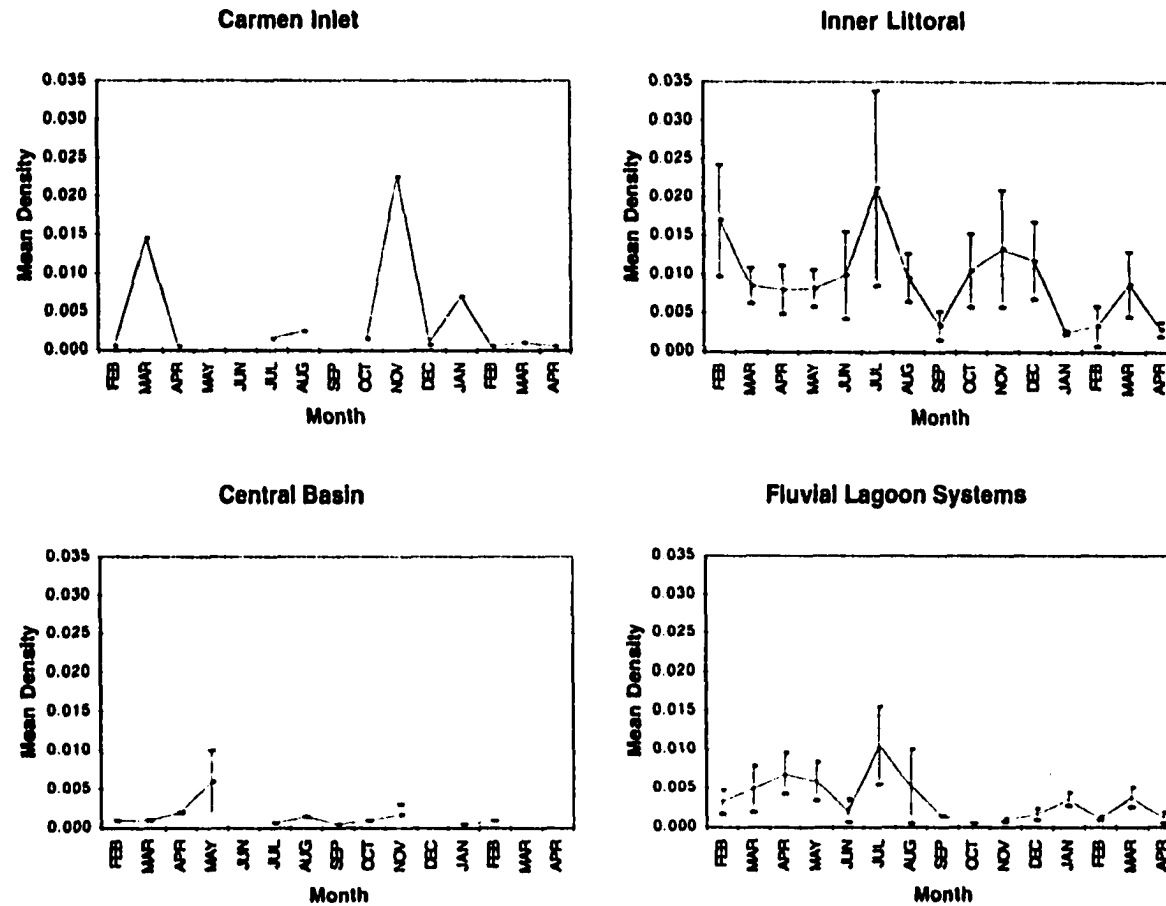


Fig. 3.4 Seasonal patterns of mean density (indiv/m²) in each ecological sybsystem of Terminos Lagoon for *Sphoeroides testudineus* (checkered puffer).

Sphoeroides testudineus

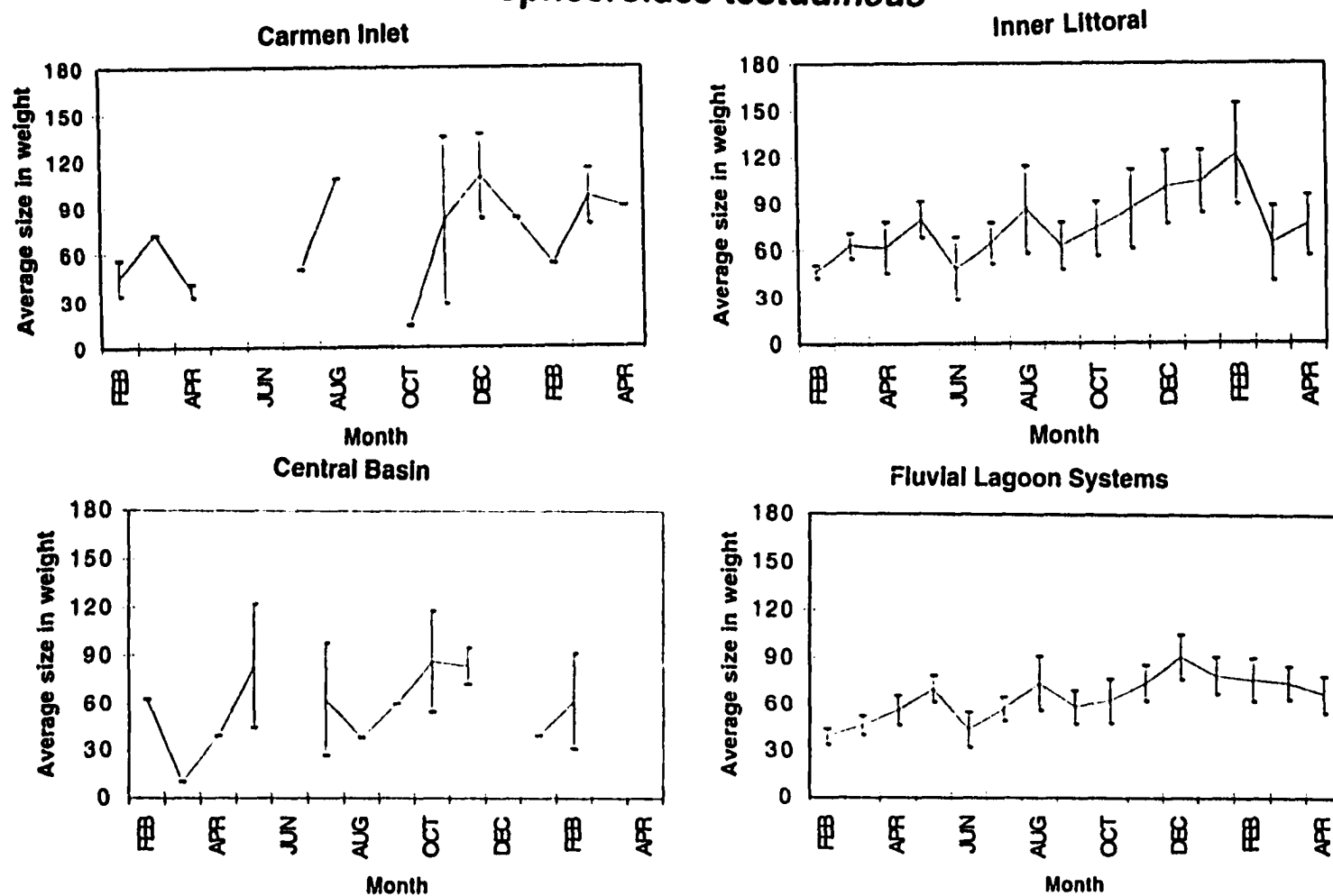


Fig. 3.5 Seasonal variation of mean biomass per individual (gr/indiv) in each ecological subsystem of Terminos Lagoon for *Sphoeroides testudineus* (checkered puffer).

variables showed that depth ($p = 0.0175$) and Secchi depth ($p = 0.0067$) were significant.

3.4.3 *Bairdiella chrysoura* (silver perch)

This species was the third most common species in terms of numerical catch (1197) and the fifth in terms of mass (29,134.6 grams). Fifty-eight percent of the individuals were from the fluvial lagoon systems, 24% from the central basin, 14% from the inner littoral of Carmen Island and the remainder from Carmen Inlet. This species was the first in numerical abundance and mass for the central basin, second in number and third in mass from the fluvial lagoon systems, seventh in number and in mass for the inner littoral of Carmen Island; and thirteenth in number and ninth in mass in Carmen Inlet (Table 3.1 Appendix B). Table 3.4, Appendix B shows the ranges of the total number of individuals and weight, mean size in grams, density, biomass per unit area, and environmental characteristics related to this species in Terminos Lagoon. This species occurred over a wide range of environmental conditions, but 46% of the individuals were captured in salinities between 15-25 (Table 3.4 Appendix B). Significant differences among sampling stations were evident in density of *Bairdiella chrysoura* (silver perch; $p = 0.0501$).

Density was highest in the central basin and the inner littoral of Carmen Island. In the central basin, there were density peaks in July (0.016 indiv/m^2), October ($0.015 \pm 0.002 \text{ indiv/m}^2$), and January (0.014 indiv/m^2 ; Fig. 3.6). Three peaks of mean density occurred in inner littoral of Carmen Island occurred in December (0.027 indiv/m^2), April 1981 (0.021 indiv/m^2) and April 1980 (0.017 indiv/m^2). The highest mean biomass for this species was in the inner littoral of Carmen Island with a peak in December (1.028 g/m^2). Intermediate biomass occurred in the central basin and the

Bairdiella chrysoura

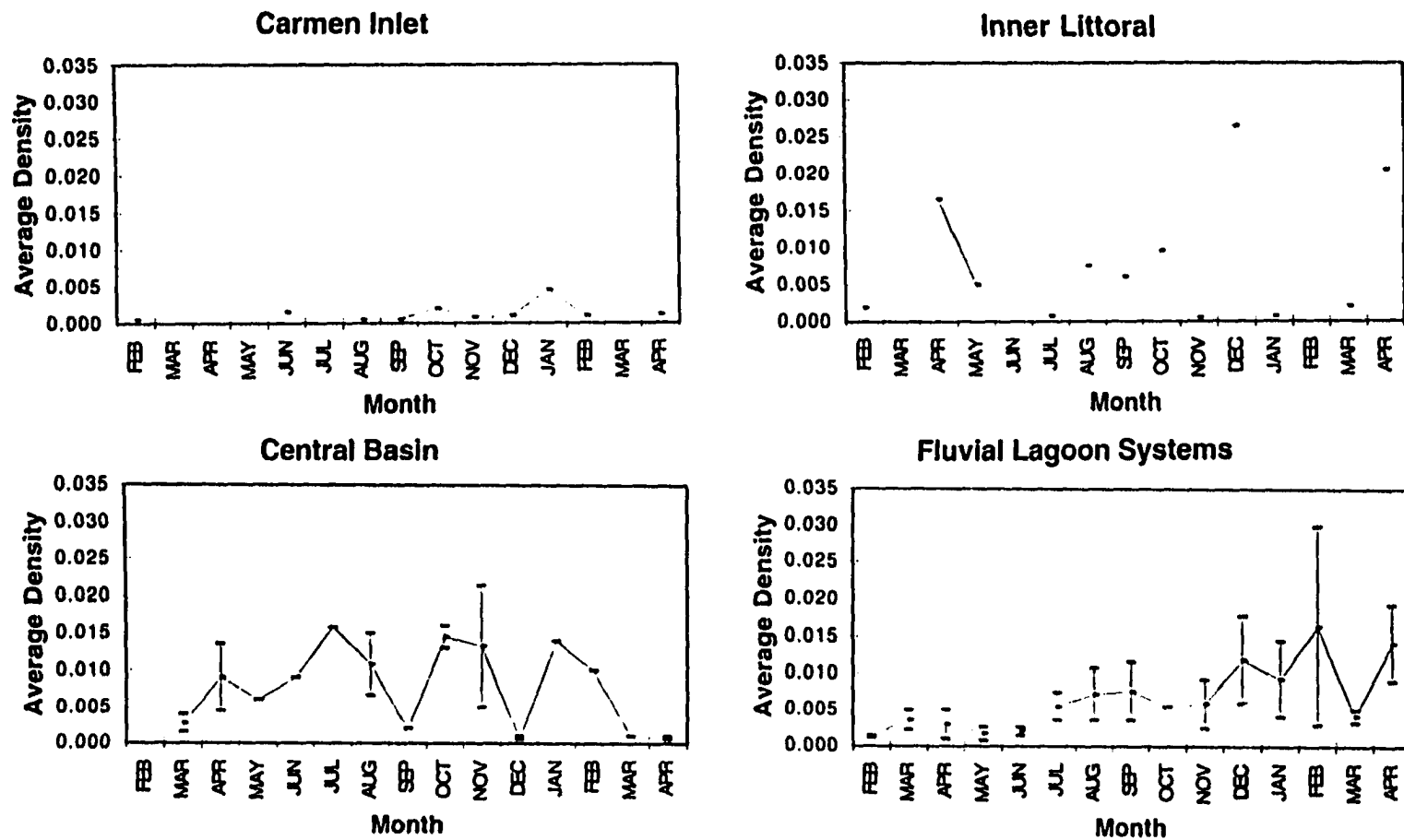


Fig. 3.6 Seasonal patterns of mean density (indiv/m²) in each ecological sybsystem of Terminos Lagoon for *Bairdiella chrysoura* (silver perch).

fluvial lagoon systems (Fig. 3.6). The lowest biomass was in Carmen inlet with a peak in January (0.117 g/m^2).

The density and biomass multiple regression models for *Bairdiella chrysoura* (silver perch) included station as an independent variable. The full model for $\text{Ln}(\text{density})$ was significant ($r^2 = 0.1887$ $p = 0.0004$) and *analysis of individual variables* showed that station ($p = 0.0001$) was significant.. The $\text{Ln}(\text{biomass})$ model was significant value ($r^2 = 0.1776$ $p = 0.0007$) and in the analysis of individual variables, station ($p = 0.0001$) was significant.

Small sizes occurred in low salinity between 0 and 5 and large sizes occurred over the entire salinity gradient. Intermediate sizes occurred in all subsystems. During January 1981, there were large sizes in the inner littoral of Carmen Island, and small sizes in Carmen Inlet from August to October, and in the central basin during March 1980 (Fig. 3.7). The full model of multiple regression for this species was significant ($r^2 = 0.1074$ and $p = 0.0155$). Analysis of individual variables showed that negative temperature ($p = 0.0012$) was significant.

3.4.4 *Ariopsis felis* (hardhead sea catfish)

This species was the fourth most abundant species in number (1184) and mass (60,631.3 grams) in Terminos lagoon. Forty-two percent of the individuals were captured in the inner littoral of Carmen Island, 27% in the fluvial lagoon systems, 16% in the central basin and 15% in Carmen inlet. This species was second in both numbers and mass in the central basin and fourth (numerically) in the inner littoral of Carmen Island, the fluvial lagoon systems and Carmen inlet. By mass, this species was third in the inner littoral of Carmen Island and Carmen inlet and fourth in the fluvial

Bairdiella chrysoura

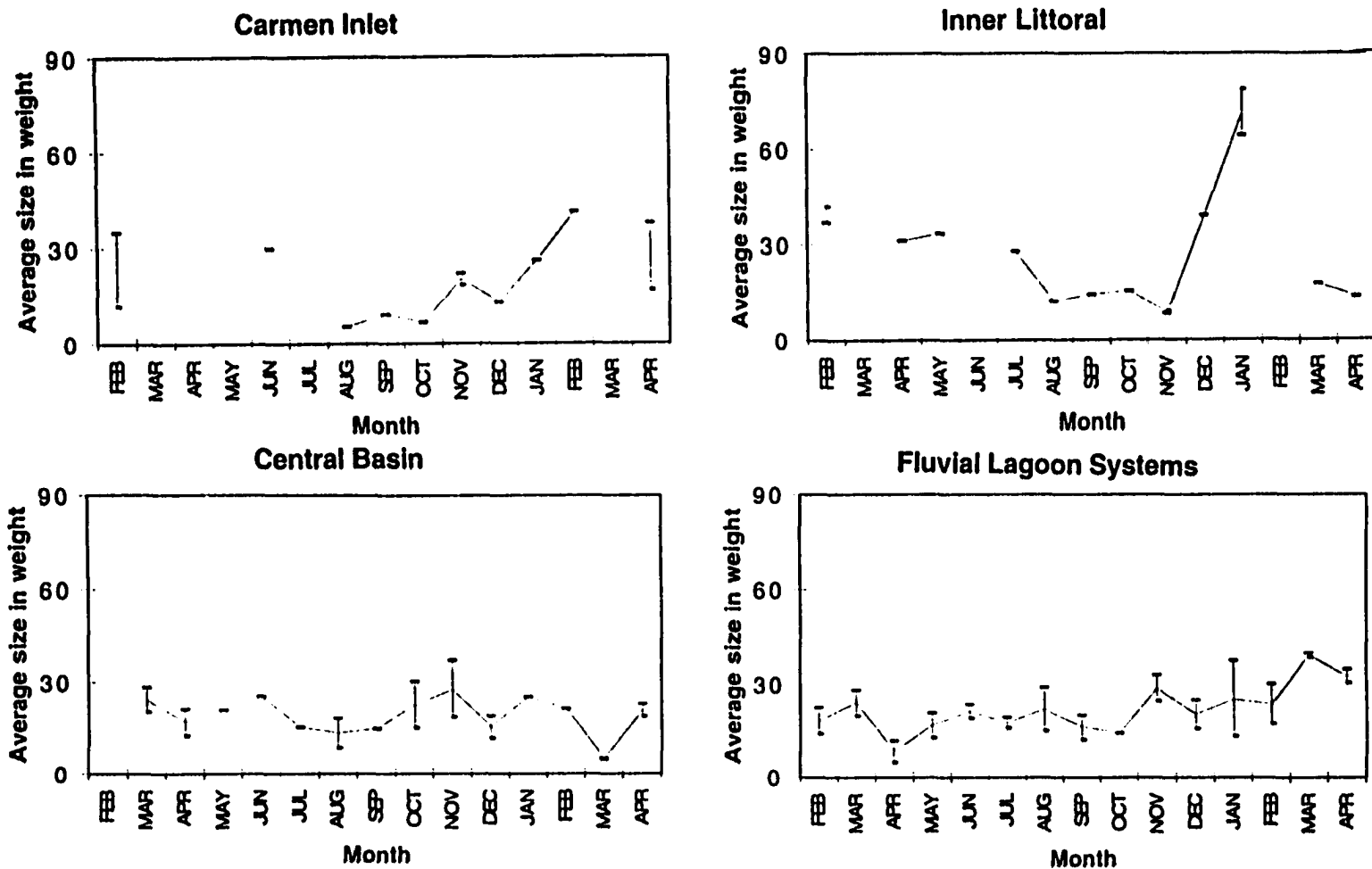


Fig. 3.7 Seasonal variation of mean biomass per individual (gr/indiv) in each ecological subsystem of Terminos Lagoon for *Bairdiella chrysoura* (silver perch).

lagoon systems (Table 3.1 Appendix B). Table 3.5, Appendix B shows the ranges of the total number of individuals and weight, mean size in grams, density, biomass per unit area and environmental characteristics related to this species in Terminos Lagoon. This species occurred over a wide range of environmental condition but 50% individuals were captured from 10-25 (Table 3.5 Appendix B). The biomass model for *Ariopsis felis* (hardhead sea catfish), was significant ($p = 0.0347$), and stations were significantly different in the biomass model ($p = 0.0061$).

The highest density occurred in the inner littoral of Carmen Island with peak density (0.033 indiv/m^2) in December and between 0.001 and 0.010 indiv/m^2 for the rest of the year. Density was similar in the central basin and Carmen inlet (Fig. 3.8). Biomass was higher in the inner littoral of Carmen Island with peaks in June ($0.868 \pm 0.079 \text{ g/m}^2$) and December ($1.312 \pm 0.888 \text{ g/m}^2$). Biomass peaks occurred in May ($0.575 \pm 0.375 \text{ g/m}^2$) in the central basin and in November ($0.438 \pm 0.000 \text{ g/m}^2$) in Carmen inlet. In the fluvial lagoon systems, there was low density and biomass.

The multiple regression model of $\text{Ln}(\text{density})$ for *Ariopsis felis* (hardhead sea catfish) included months and stations, and was weighted with month. The model of $\text{Ln}(\text{biomass})$ was weighted with Secchi depth. Analysis of individual variables in $\text{Ln}(\text{density})$ model showed that only depth ($p = 0.0568$) was significant. The $\text{Ln}(\text{biomass})$ model showed that temperature and Secchi disk depth were the significant variables at the 0.05 level.

Large sizes were caught in low and high salinity (between 0 to 5 and 35 to 38, respectively). Small sizes occurred in intermediate salinity, (15 to 25). Small individuals occurred in Carmen inlet from September 1980 to February 1981, in the fluvial lagoon

Ariopsis felis

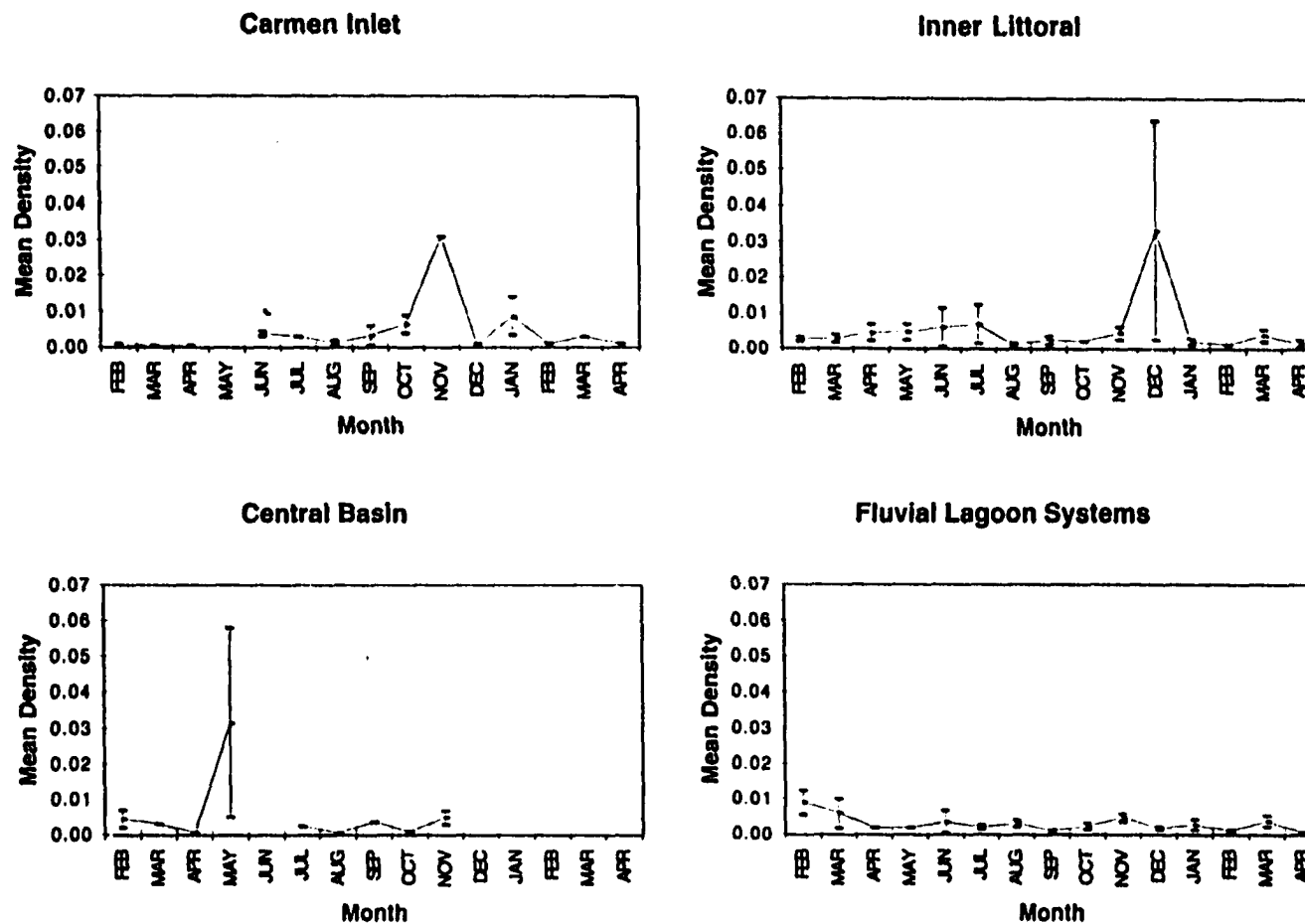


Fig. 3. 8 Seasonal patterns of mean density (indiv/m²) in each ecological sybsystem of Terminos Lagoon for *Ariopsis felis* (hardhead sea catfish).

systems in April and May, and in the central basin during April and August. In general, large sizes occurred in the inner littoral of Carmen Island through the year. There were large sizes in Carmen in March and April (Fig. 3.9). The full multiple regression model approached significance ($r^2 = 0.0600$, $p = 0.0878$). The analysis of individual variables showed that water column depth ($p = 0.0240$) and temperature ($p = 0.0762$) were significant.

3.4.5 *Archosargus rhomboidalis* (sea bream)

This species was limited to the areas with strong marine influence. It was the fifth most abundant species numerically (1055 individuals) and the third by mass (96,747.8 grams) in the lagoon. Eighty-two percent of its numerical capture was in the inner littoral of Carmen Island, 12% in the fluvial lagoon systems, mainly in the western region, and the rest (6%) in the central basin. This species was the second numerically and the first by mass in the inner littoral of Carmen Island, the fifth numerically and third by mass in the central basin, and the eighth numerically and seventh by mass in the fluvial lagoon systems (Table 3.1 Appendix B). Table 3.6, Appendix B shows the ranges of the total number of individuals and weight, mean size in grams, density, biomass per unit area, and environmental characteristics related to this species in Terminos Lagoon. This species tended to occur in medium to higher salinity water with 53% individuals captured from 25–40 (Table 3.6 Appendix B).

The density and biomass models were significant for *Archosargus rhomboidalis* (sea bream). The density model was significant for *Archosargus rhomboidalis* (sea bream; $p = 0.0375$) which was significantly different only for station ($p = 0.0588$). The biomass model was significant ($p = 0.0137$), and stations were significantly different $p = 0.0085$.

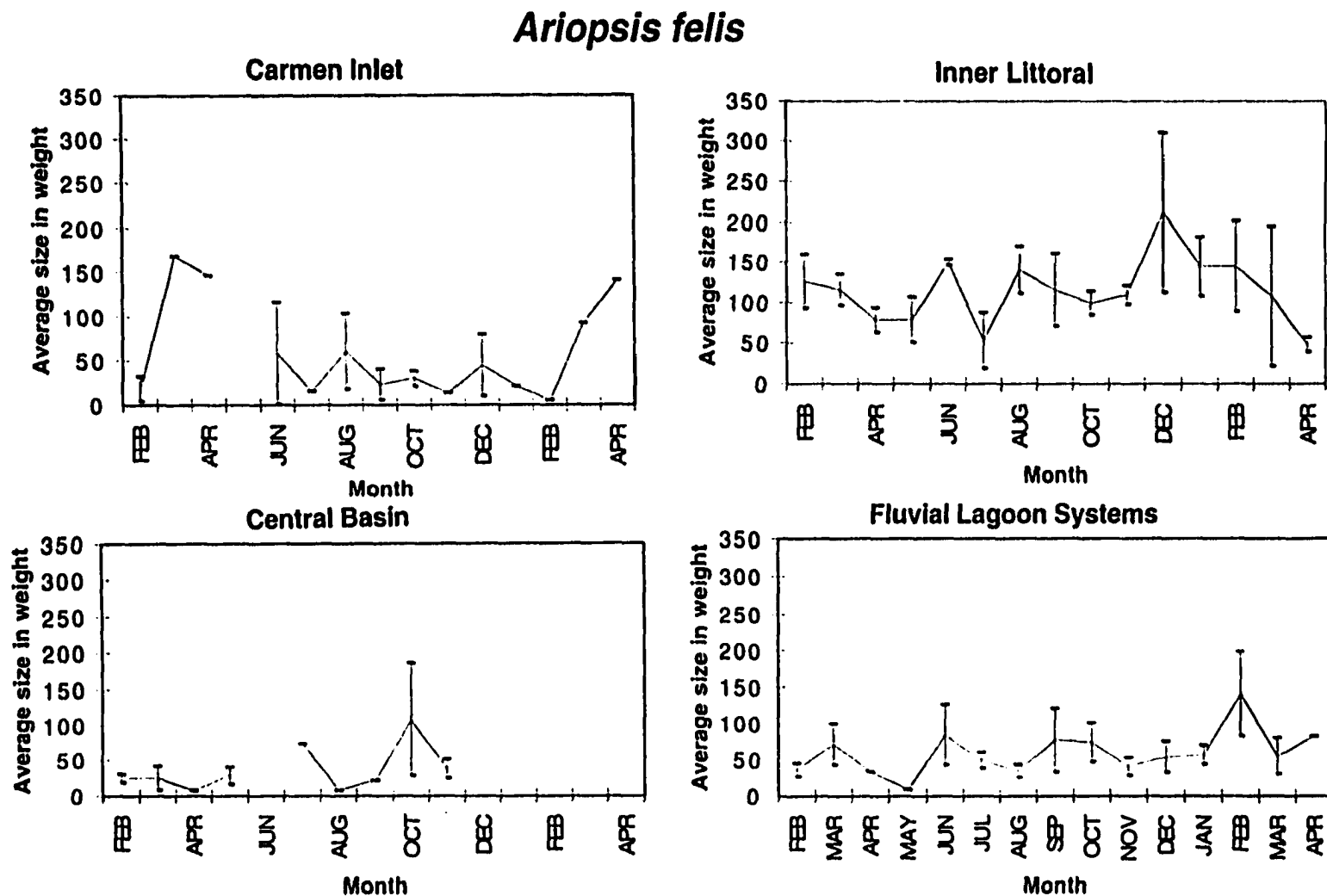


Fig. 3.9 Seasonal variation of mean biomass per individual (gr/indiv) in each ecological subsystem of Terminos Lagoon for *Ariopsis felis* (mardhead sea catfish).

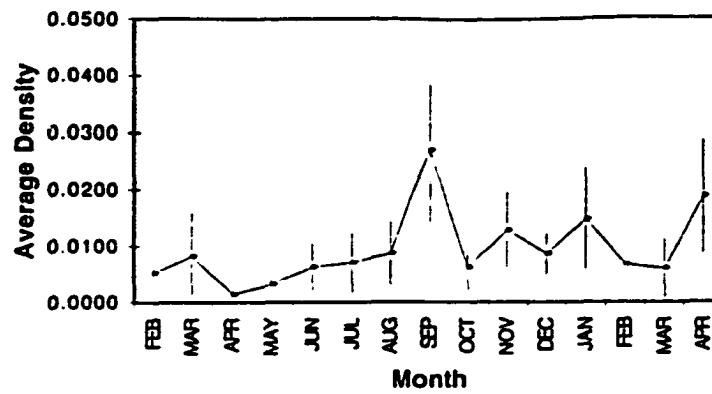
Sea bream was most common in the inner littoral of Carmen Island with density ranging from 0.0004 to 0.053 indiv/m² (mean = 0.006±0.001) and biomass from 0.006 to 14.999 g/m² (mean = 0.563±0.20). There were density peaks in September (0.027±0.013 indiv/m²) and April 1981 (0.019±0.010 indiv/m²). This species was common in the fluvial lagoon systems in September but reached 0.027 indiv/m² in October. There were low densities in the central basin during the dry and norté seasons but this species did not occur in Carmen inlet. Biomass was high in the inner littoral of Carmen Island in September (5.21±4.894 g/m²) and low in the central basin (Fig. 3.10).

The density model of multiple regression for *Archosargus rhomboidalis* (sea bream) included months as an independent variable, and it was weighted with this variable. The biomass model was weighted with Secchi depth. Analysis of individual variables in the density model showed that salinity was significant ($p = 0.0051$). The analysis of individual variables in the Ln(biomass) model showed that salinity ($p = 0.0011$) and temperature ($p = 0.0222$) were significant. The full model was significant ($p = 0.0106$, $r^2 = 0.1482$).

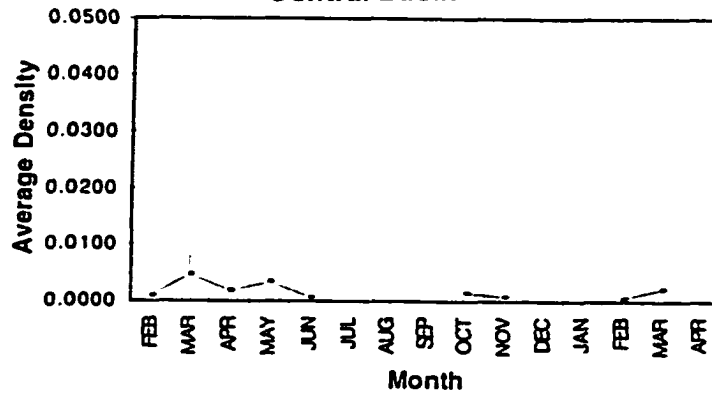
The mean mass of this species ranged from 6.30 to 439.8 g/indiv (80.36±7.54 g/indiv; Table 3.6 Appendix B). Large sizes occurred in intermediate salinity while smaller individuals were in salinity between 10 and 30. In general, the large individuals were in the inner littoral of Carmen Island during all sampling periods, but mainly from November 1980 to February 1981. Small sizes were recorded in the fluvial lagoon systems (May, August, October 1980 and February 1981) and in the central basin during February 1980 (Fig. 3.11). The full multiple regression model approached was

Archosargus rhomboidalis

Inner Littoral



Central Basin



Fluvial Lagoon Systems

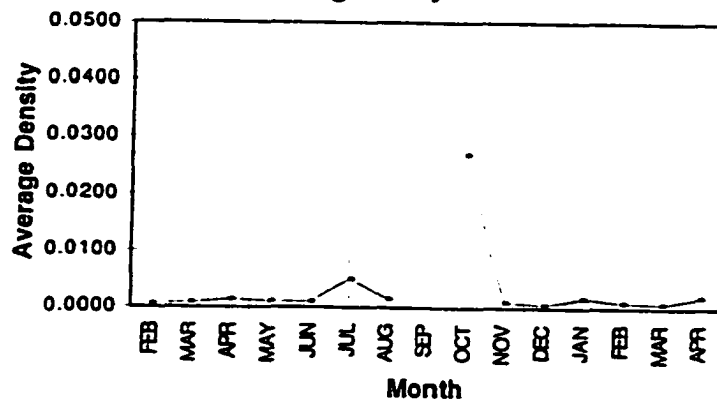
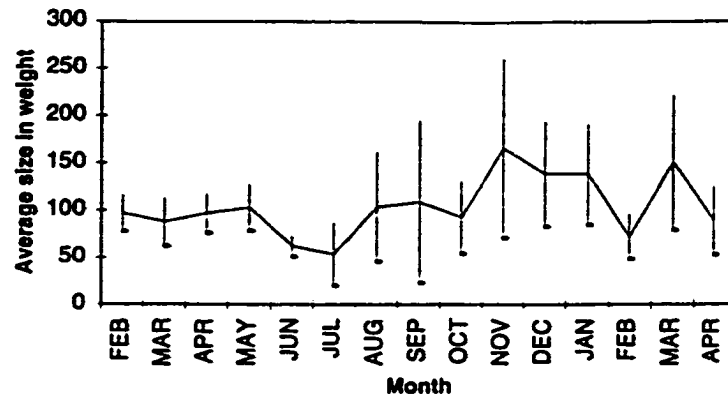


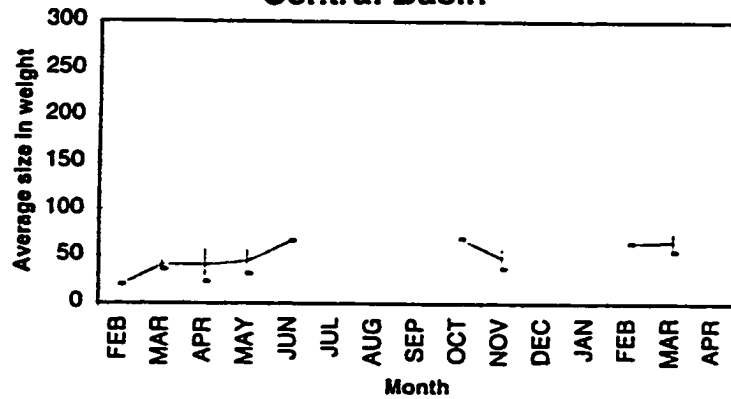
Fig. 3.10 Seasonal patterns of mean density (indiv/m²) in each ecological subsystem of Terminos Lagoon for *Archosargus rhomboidalis* (sea bream).

Archosargus rhomboidalis

Inner Littoral of Carmen Island



Central Basin



Fluvial Lagoon System

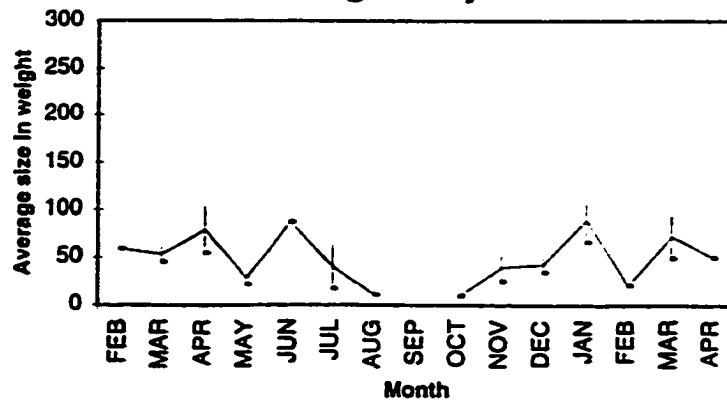


Fig. 3.11 Seasonal variation of mean biomass per individual (gr/indiv) in each ecological subsystem of Terminos Lagoon for *Archosargus rhomboidalis* (sea bream).

statistically significant ($r^2 = 0.0986$, $p = 0.0744$). Analysis of individual variables showed that temperature ($p = 0.0348$) and salinity ($p = 0.0253$) were significant.

3.4.6 *Eucinostomus gula* (silver jenny)

This species was the sixth most important species numerically (955 individuals) and the eighth by mass (8846.5 grams). Fifty-three percent were captured in the inner littoral of Carmen Island, 20% in both fluvial lagoon systems and Carmen inlet. This species was fourth numerically and seventh by mass in the central basin; fifth numerically for the inner littoral of Carmen Island and Carmen Inlet, and the sixth by mass in these two subsystems. Finally it was the sixth numerically and tenth by mass in the fluvial lagoon systems (Table 3.1 Appendix B). Table 3.7, Appendix B shows the ranges of the total number of individuals and weight, mean size in grams, density, biomass per unit area, and environmental characteristics related to this species in Terminos Lagoon. This species occurred over a wide range of environmental condition but 47% individuals were captured in salinities of 10-25 (Table 3.7 Appendix B).

This species had high density both in the inner littoral of Carmen Island and Carmen inlet. In the inner littoral there were peaks in June (0.016 ± 0.013 indiv/m²) and September (0.015 ± 0.006 indiv/m²). In Carmen inlet there was a peak in February 1980 (0.023 indiv/m²). Minimum density occurred in the central basin. Higher values of biomass occurred in the inner littoral of Carmen Island with a peak in June (0.414 ± 0.414 g/m²), with intermediate values in Carmen inlet with a peak in February 1980 (0.200 g/m²). The fluvial lagoon systems and the central basin had low biomass (Fig. 3.12).

Eucinostomus gula

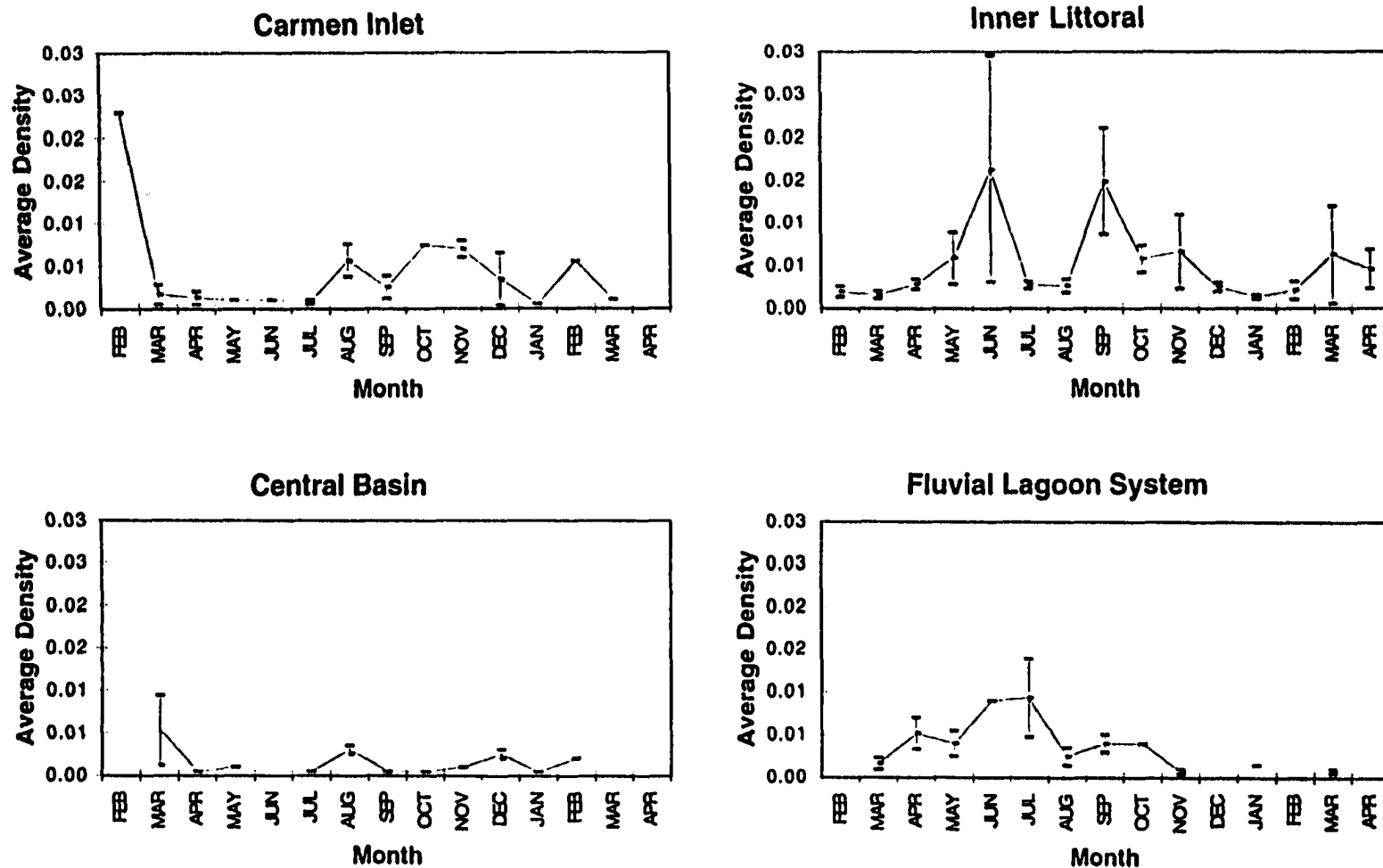


Fig. 3.12 Seasonal patterns of mean density (indiv/m²) in each ecological sybsystem of Terminos Lagoon for *Eucinostomus gula* (silver jenny).

Only the Ln(density) multiple regression model for the silver jenny was significant ($p = 0.0451$, $r^2 = 0.0812$). Analysis of individual variables showed that temperature was significant ($p = 0.0223$).

Eucinostomus gula (silver jenny) mean size ranged from 0.37 to 33.05 g/indiv (mean = 8.08 ± 0.51 g/indiv; Table 3.7 Appendix B). Small size organisms occurred mainly in low salinities while large sizes were in high salinity. Large sizes occurred in the inner littoral of Carmen island in March and June 1980, and in the central basin during January 1981. Small sizes occurred mainly recorded in the fluvial lagoon systems from June to October with intermediate sizes in Carmen inlet (Fig. 3.13). The full multiple regression model was significant ($r^2 = 0.1516$, $p = 0.0008$). Analysis of individual variables showed that both temperature ($p = 0.0001$) and salinity ($p = 0.041$) were significant. Temperature was negatively related to mean size.

3.4.7 *Anchoa mitchilli* (bay anchovy)

This species occurred mainly in areas with strong river influence. It was the seventh most abundant species numerically (503 individuals) and the fifteenth by mass (388.4 grams) in the lagoon (Table 3.1 Appendix B). Sixty percent of its numerical, capture was in the fluvial lagoon systems, 30% in Carmen inlet and the remainder in the inner littoral of Carmen Island (6%) and the central basin (4%). It was the fifth species numerically and eleventh by mass in the fluvial lagoon systems, the sixth numerically and the fourteenth mass in Carmen inlet, the ninth numerically and eleventh by mass in the central basin (Table 3.1 Appendix B). Table 3.8, Appendix B shows the ranges of the total number of individuals and weight, mean size in grams, density, biomass per unit area, and environmental characteristics related to this species in Terminos Lagoon. This species occurred over a wide range of

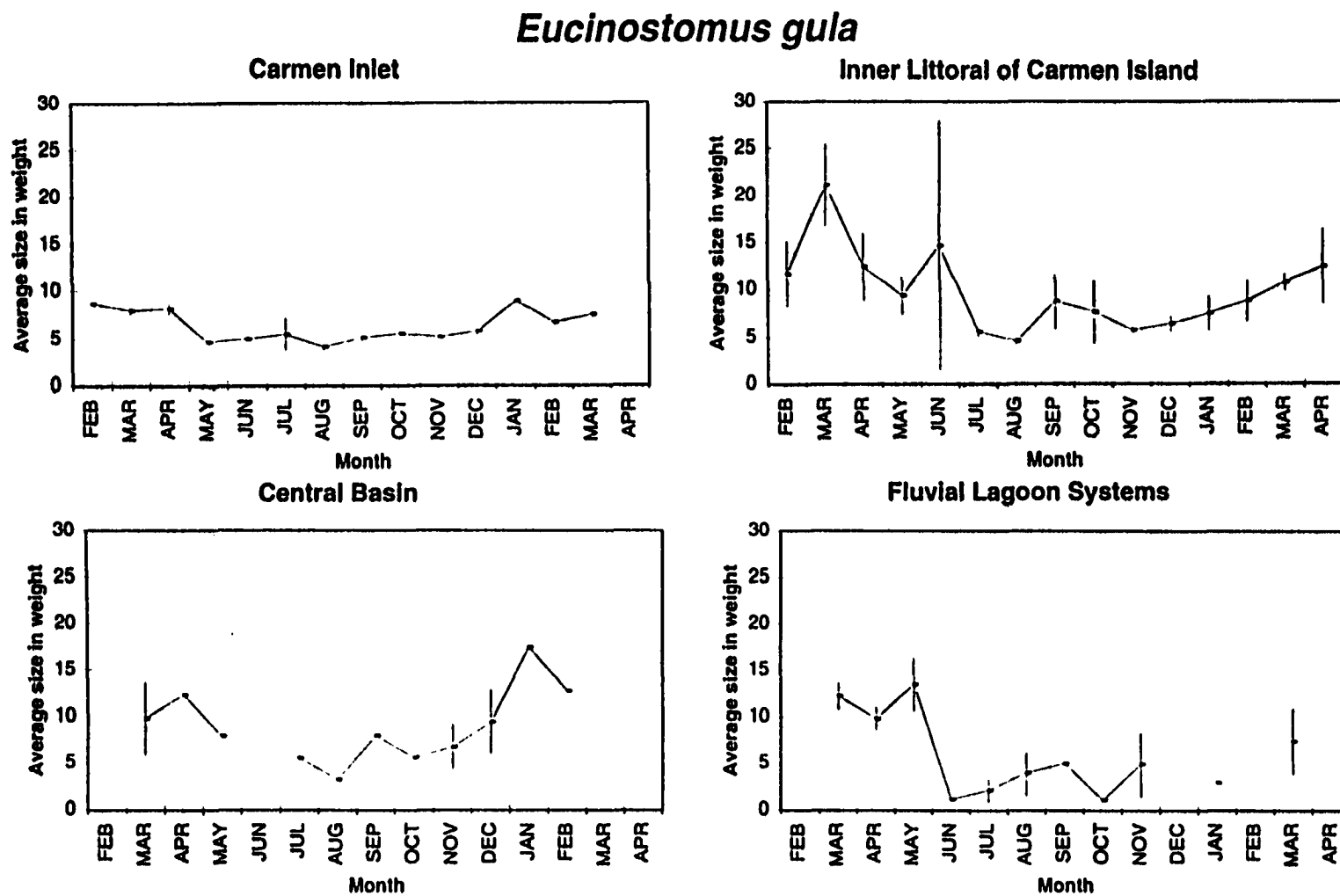


Fig. 3.13 Seasonal variation of mean biomass per individual (gr/indiv) in each ecological subsystem of Terminos Lagoon for *Eucinostomus gula* (silver jenny).

environmental conditions but 73% individuals were captured in salinities of 10-25 (Table 3.8 Appendix B).

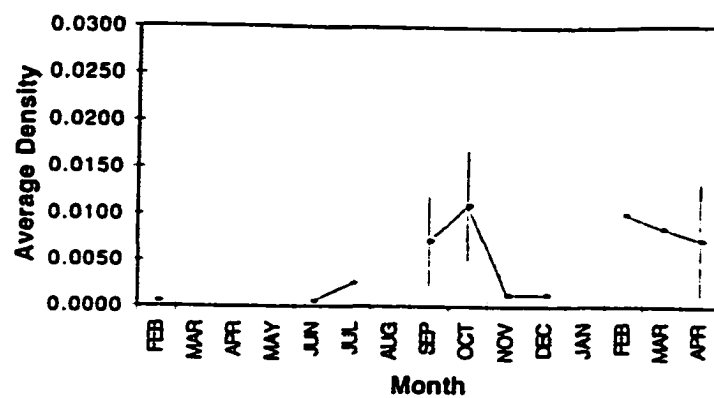
Anchoa mitchilli (bay anchovy) was captured mainly during the rainy and nortes season in the fluvial lagoon systems and Carmen inlet (Tables 1 and 8 Appendix B). Density was high in the fluvial lagoon systems in August and October (0.014 ± 0.010 indiv/m² for both months). Density was also relatively high in Carmen inlet in October (0.011 ± 0.006 indiv/m²) and February 1981 (0.010 indiv/m²) and in the inner littoral of Carmen Island in February 1981 (0.012 indiv/m²). Maximum biomass mean occurred in Carmen inlet during February 1980 (0.021 g/m², Fig. 3.14).

The multiple regression model of Ln(density) for the bay anchovy included station and months as independent variables, and it was weighted with stations. The full model was significant ($r^2 = 0.2990$ $p = 0.0122$), and the analysis of individual variables showed that temperature ($p = 0.0430$) and stations ($p = 0.0055$) were significant.

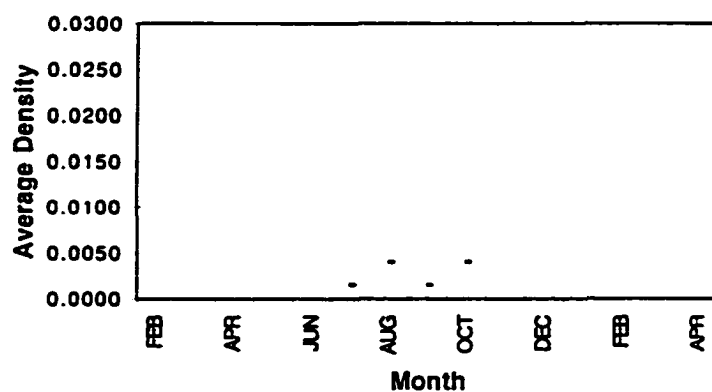
Anchoa mitchilli (bay anchovy) ranged in mass from 0.015 to 9.20 g/indiv (mean $= 1.17 \pm 0.20$). Small individuals occurred over the salinity gradient but predominantly in salinities of 30 to 35 while larger individuals occurred mainly between 5 and 15. Large sizes occurred mainly in Carmen inlet in February and June 1980 with small sizes in the fluvial lagoon systems from June to September (Fig. 3.15). The full model of multiple regression for this species was significant ($r^2 = 0.4226$, $p = 0.0001$). Analysis of individual variables showed that temperature ($p = 0.0001$) and Secchi depth ($p = 0.0404$) were significant with a negative relationship.

Anchoa mitchilli

Carmen Inlet



Central Basin



Fluvial Lagoon Systems

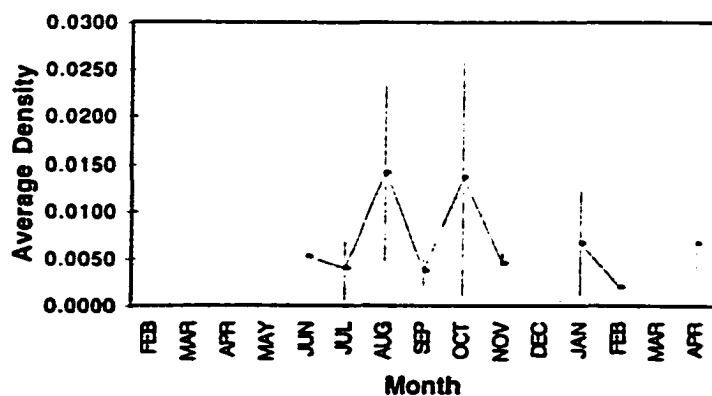


Fig. 3.14 Seasonal patterns of mean density (indiv/m²) in each ecological sybsystem of Terminos Lagoon for *Anchoa mitchilli* (bay anchovy).

Anchoa mitchilli

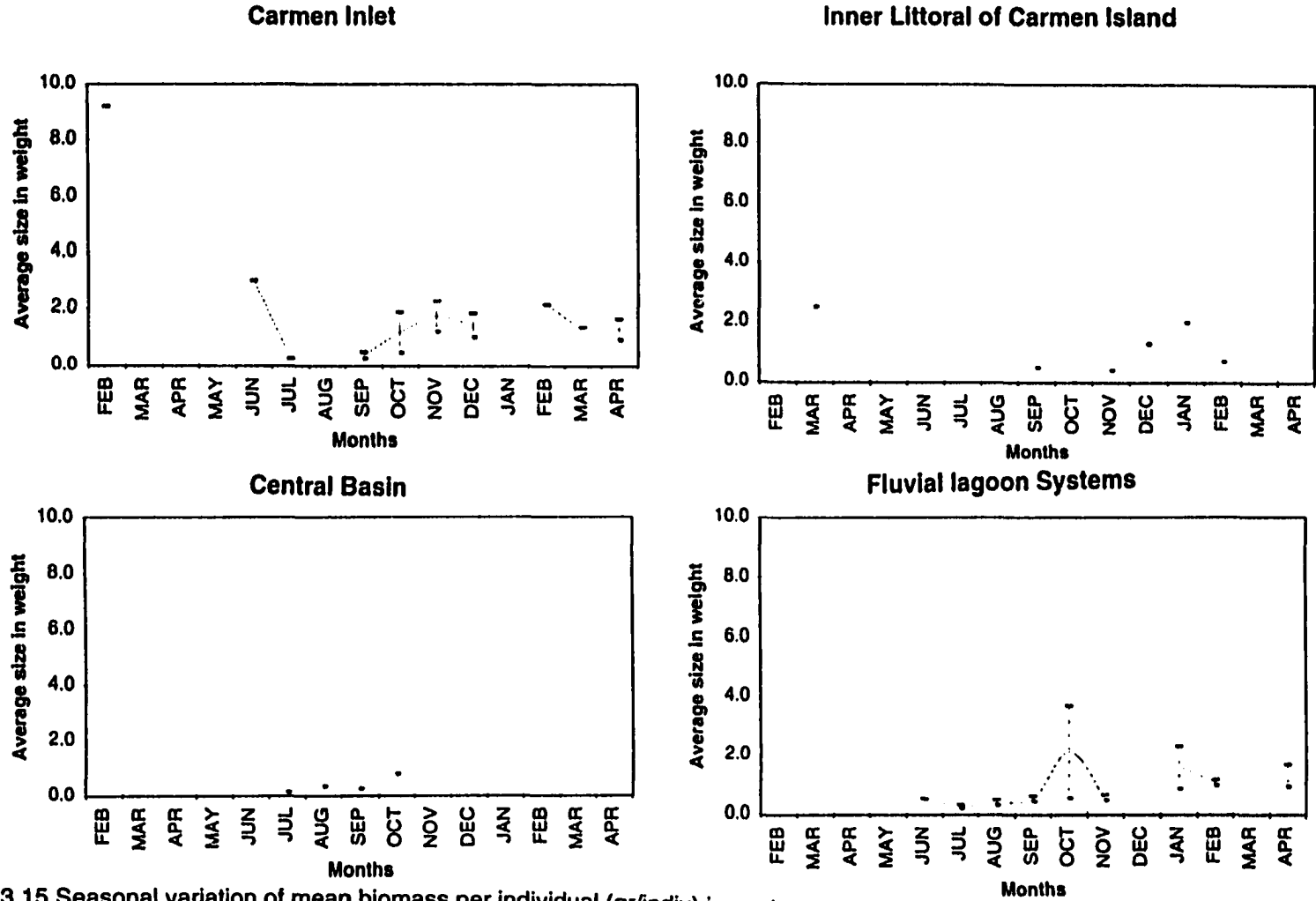


Fig. 3.15 Seasonal variation of mean biomass per individual (gr/indiv) in each ecological subsystem of Terminos Lagoon for *Anchoa mitchilli* (bay anchovy).

3.4.8 *Chaetodipterus faber* (Atlantic spadefish)

This species was the fourteenth most abundant species numerically (163 individuals) and the seventh by mass (15,109.5 grams) in the lagoon. Forty-nine percent of the individuals were from the fluvial lagoon systems, 19% from Carmen inlet, 18% from the central basin and 14% from the inner littoral of Carmen Island. This species was eighth numerically and sixth by mass in the central basin of the lagoon, ninth by mass and fifth numerically in the fluvial lagoon systems, and fourteenth numerically and fourth by mass in Carmen inlet (Table 3.1 Appendix B). Table 3.9, Appendix B shows the ranges of the total number of individuals and weight, mean size in grams, density, biomass per unit area and environmental characteristics related to this species in Terminos Lagoon. This species tended to occur at medium salinities with 53% individuals captured from 20-35 (Table 3.9 Appendix B).

Chaetodipterus faber (Atlantic spadefish) was captured during the rainy and norte seasons mainly in the fluvial lagoon systems and Carmen inlet. In general, this species had low density in relation to the other species that were dominant in three ecological subsystems. The highest density occurred in the central basin in May (0.007 indiv/m²) and January 1981 (0.006 indiv/m²). Biomass was higher in the inner littoral of Carmen island and Carmen inlet during the norte season (0.653 g/m² in Carmen Inlet in October and 0.635 g/m² in the inner littoral of Carmen island in January 1981). Biomass was high in the dry season in the fluvial lagoon systems (0.296 g/m² in April 1981) and the central basin (0.243 g/m² May; Fig. 3.16).

Chaetodipterus faber

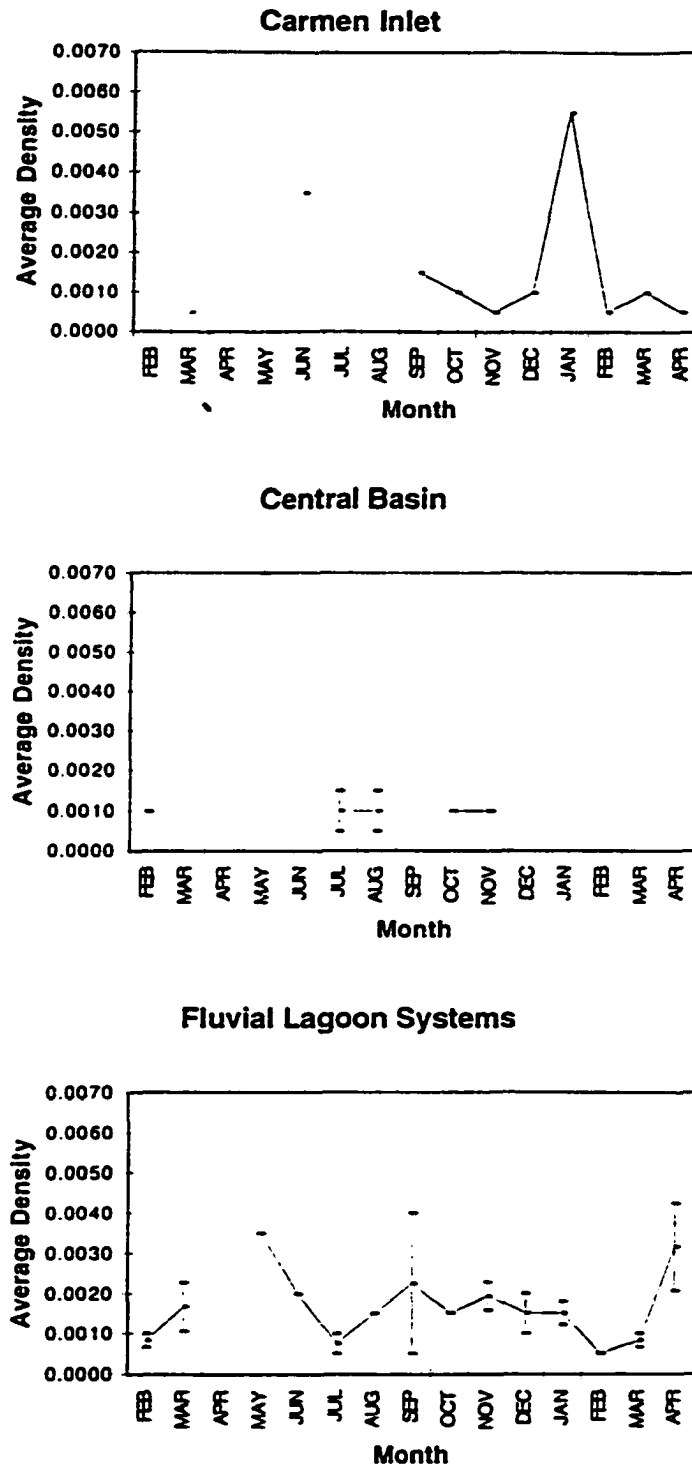


Fig. 3.16 Seasonal patterns of mean density (indiv/m²) in each ecological sybsystem of Terminos Lagoon for *Chaetodipterus faber* (Atlantic spadefish).

The multiple regression model of $\ln(\text{biomass})$ for this species included stations and months as independent variables, and was weighted with stations. The full model was significant ($r^2 = 0.1805$, $p = 0.0550$). Analysis of individual variables showed that month ($p = 0.0010$) was significant.

The small sizes of this species occurred in salinities between 15 and 35, while larger individuals were in marine salinity. Large individuals occurred in the inner littoral of Carmen island (November 1980 and January and April 1981) and in Carmen inlet (October 1980; Fig. 3.17). In general, the small sizes occurred in the fluvial lagoon systems (February, March, May and June 1980) and in Carmen inlet (November 1980 to January 1981). For this species, the multiple regression was not significant.

3.4.9 *Cynoscion arenarius* (sand seatrout)

This species was the ninth most abundant species numerically (357 individuals) and the eleventh by mass (2238.8 grams) in the lagoon (Table 3.1 Appendix B). Sixty-seven percent of the numerical capture was in Carmen inlet, 19% in the fluvial lagoon systems and 14% in the inner littoral of Carmen Island (Table 3.1 Appendix B). It was a dominant species in Carmen inlet and the inner littoral of Carmen Island. It was third numerically and fifth by mass in the former and ninth both numerically and by mass in the latter. Table 3.10, Appendix B shows the ranges of the total number of individuals and weight, mean size in grams, density, biomass per unit area, and environmental characteristics related to this species in Terminos Lagoon. This species occurred in a wide range of environmental conditions with 50% individuals captured in salinities of 0-20 (Table 3.10 Appendix B).

Cynoscion arenarius (sand seatrout) occurred mainly both in the inner littoral of Carmen Island and Carmen inlet the norte and dry seasons. Peak density was in

Chaetodipterus faber

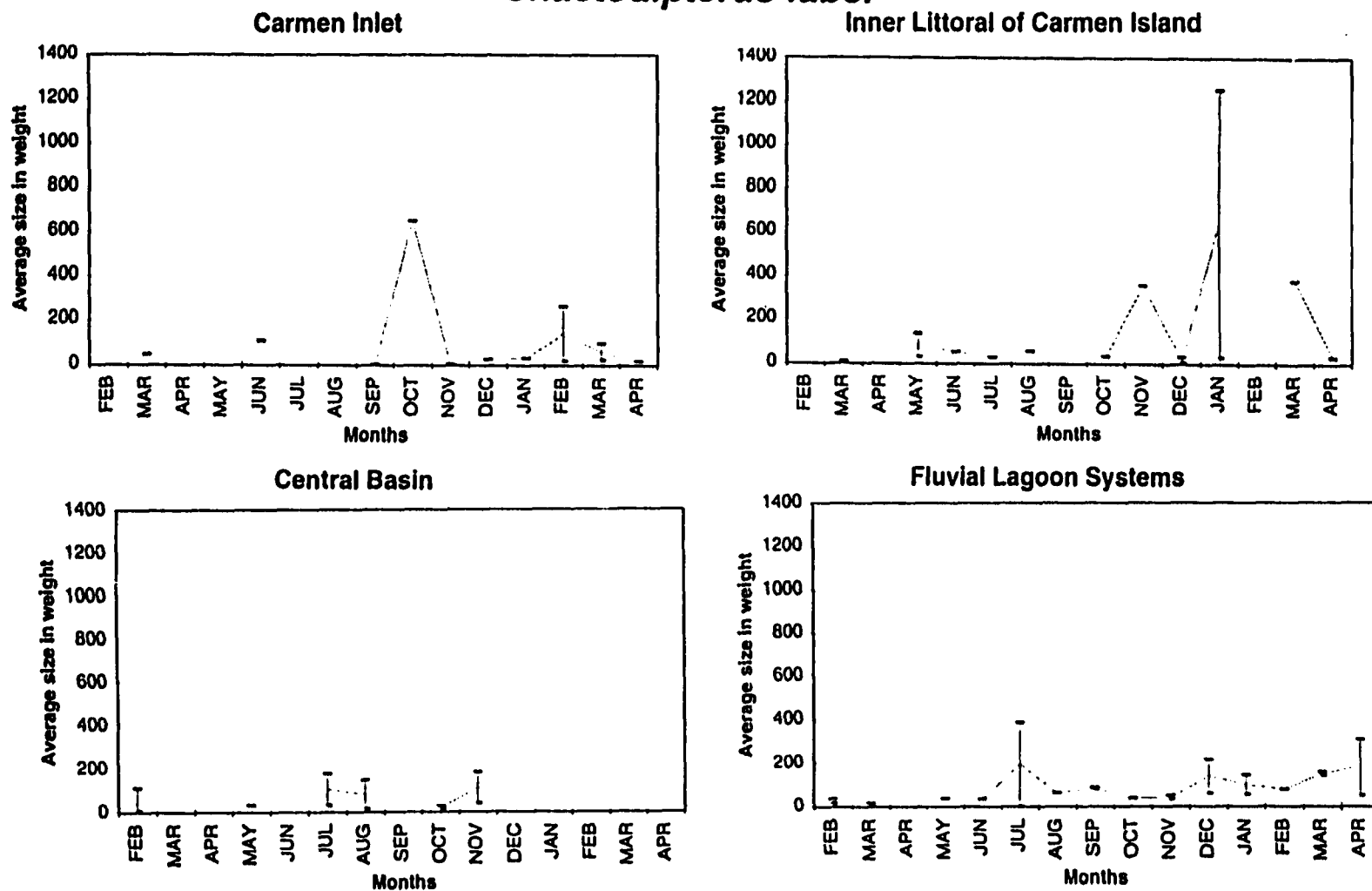


Fig. 3.17 Seasonal variation of mean biomass per individual (gr/indiv) in each ecological subsystem of Terminos Lagoon for *Chaetodipterus faber* (Atlantic spadefish).

December in both the inner littoral of Carmen Island (0.023 indiv/m^2) and in Carmen inlet ($0.018 \pm 0.008 \text{ indiv/m}^2$). Biomass had peaks in December (0.167 g/m^2) in the inner littoral of Carmen Island and in November ($0.094 \pm 0.062 \text{ g/m}^2$) in Carmen Inlet (Fig. 3.18).

The multiple regression model for the sand seatrout was modified. The $\text{Ln}(\text{density})$ model was weighted with salinity. The full model was significant ($r^2 = 0.2316$, $p = 0.0404$). Analysis of individual variables showed that salinity and Secchi depth had significant negative relationships ($p = 0.0396$ and $p = 0.0571$, respectively). The $\text{Ln}(\text{biomass})$ model included station as an independent variable and was weighted with station. The full model was significant ($r^2 = 0.3010$, $p = 0.0172$). Analysis of individual variables showed a negative relation with temperature ($p = -0.0195$) and directly relation with water column depth ($p = 0.0181$).

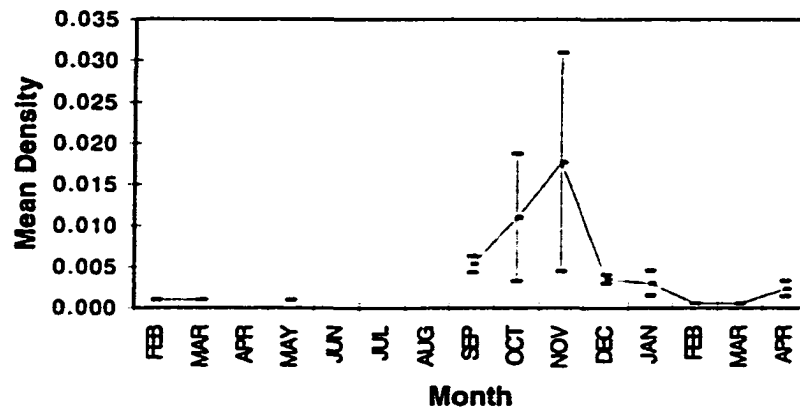
The mean size in mass of this species ranged from 0.30 to 36.95 g/indiv (mean = $8.10 \pm 1.25 \text{ g/indiv}$). Small sizes occurred mainly between 5 and 10 and large sizes occurred in marine salinity. Large individuals occurred in the fluvial lagoon systems in March 1981 while small sizes were in Carmen Inlet mainly in September and October 1980 (Fig. 3.19). The full model of multiple regression was significant ($r^2 = 0.3395$, $p = 0.0028$). Analysis of individual variables showed that temperature ($p = -0.0035$) and Secchi depth ($p = 0.0358$) were significant. Temperature was inversely related to size.

3.4.10 *Orthopristis chrysoptera* (pigfish)

This species was the tenth most abundant species numerically (233 individuals) and the ninth by mass (3693.7 grams) in the lagoon. 89% of the individuals were caught in the inner littoral of Carmen Island, 9% in the central basin and the rest in the fluvial lagoon systems (Table 3.1 Appendix B). This species was dominant for the inner

Cynoscion arenarius

Carmen Inlet



Inner Littoral

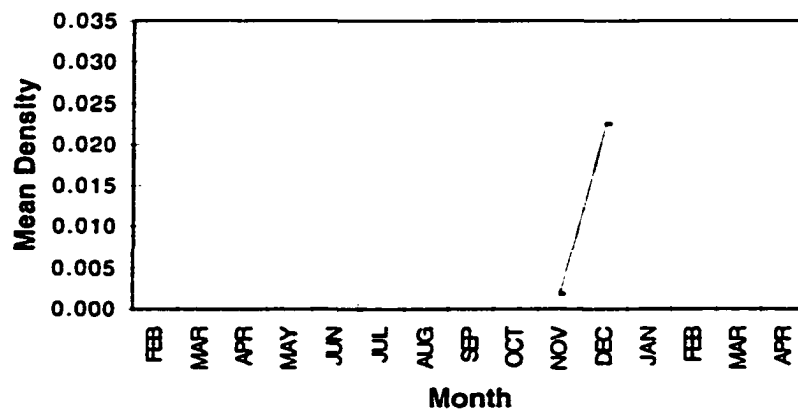
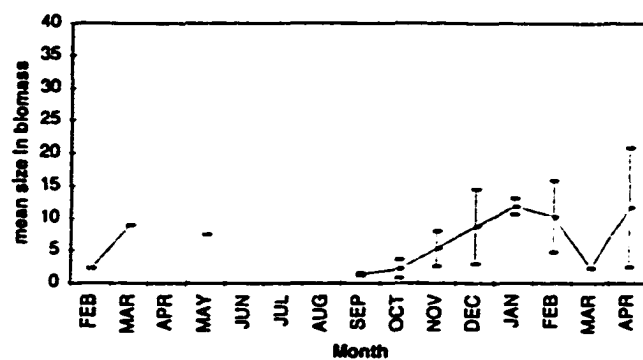


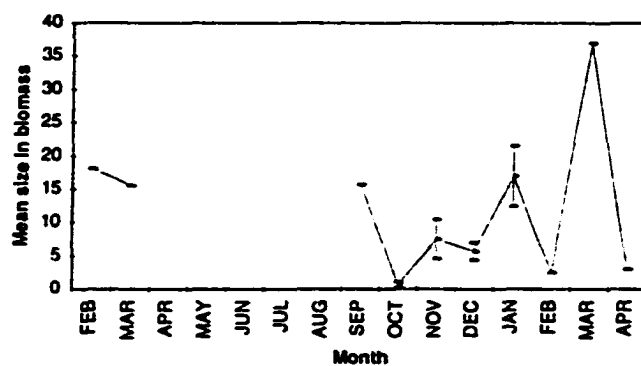
Fig. 3.18 Seasonal patterns of mean density (indiv/m²) in each ecological sybsystem of Terminos Lagoon for *Cynoscion arenarius* (sand seatrout).

Cynoscion arenarius

Carmen Inlet



Fluvial Lagoon Systems



Inner Littoral of Carmen Island

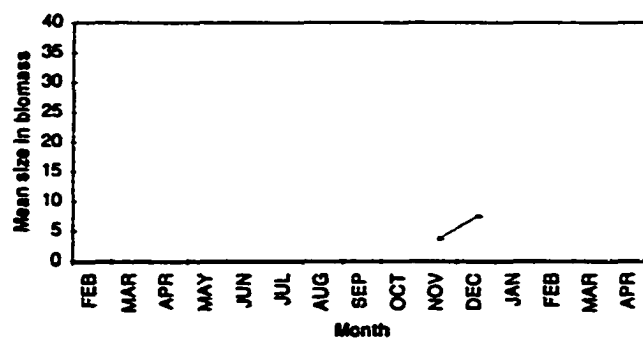


Fig. 3.19 Seasonal variation of mean biomass per individual (gr/indiv) in each ecological subsystem of Terminos Lagoon for *Cynoscion arenarius* (sand seatrout).

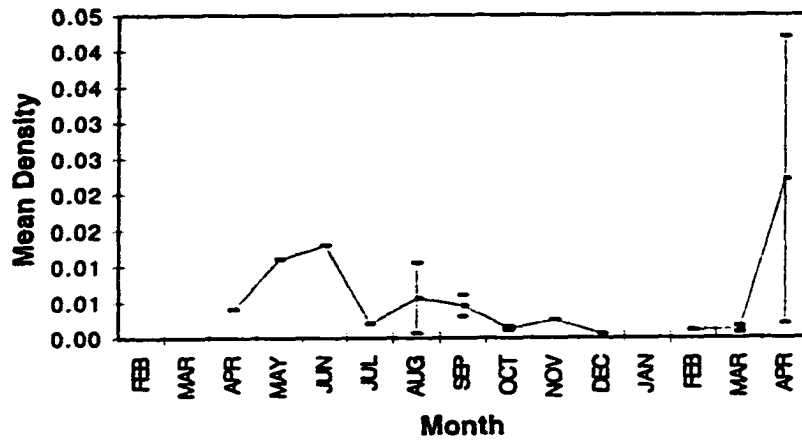
littoral of Carmen Island where it was sixth numerically and the ninth by mass. It was the eleventh most abundant species numerically and the tenth by mass in the Central Basin. Table 3.11, Appendix B shows the ranges of the total number of individuals and weight, mean size in grams, density, biomass per unit area, and environmental characteristics related to this species in Terminos Lagoon. This species tended to occur at higher salinities with 75% individuals captured from 25-35 (Table 3.11 Appendix B).

This species was captured during the rainy and nortes season in the inner littoral of Carmen island and during the dry season in the central basin. Higher density occurred in the inner littoral of Carmen Island in April 1981 (0.022 ± 0.020 indiv/m²) and June (0.011 indiv/m²). Density was low in the central basin and the fluvial lagoon systems. Biomass had peaks in the inner littoral of Carmen Island in September (0.338 ± 0.334 g/m²), May and June (0.136 and 0.134 g/m² respectively). Low values occurred in the other ecological subsystems (Fig. 3.20). For the pigfish, neither of the models of multiple regression was significant.

Orthopristis chrysoptera (pigfish) ranged in mass from 0.30 and 67.83 g/indiv (14.25 ± 3.88 g/indiv). Large sizes of this species occurred in salinities between 20 and 25. This was a typical species in the inner littoral of Carmen island, where large sizes occurred between July and November and small from February to April 1981 (Fig. 3.21). In both the central basin and fluvial lagoon systems, there were small sizes. The multiple regression model was not significant.

Orthopristis chrysoptera

Inner Littoral



Central Basin

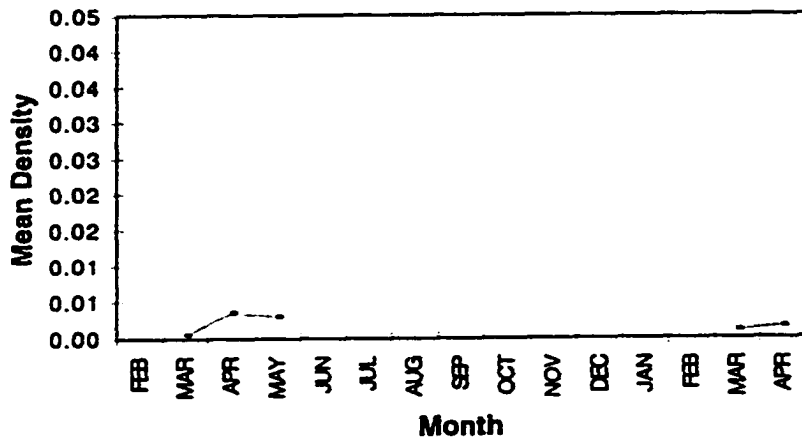
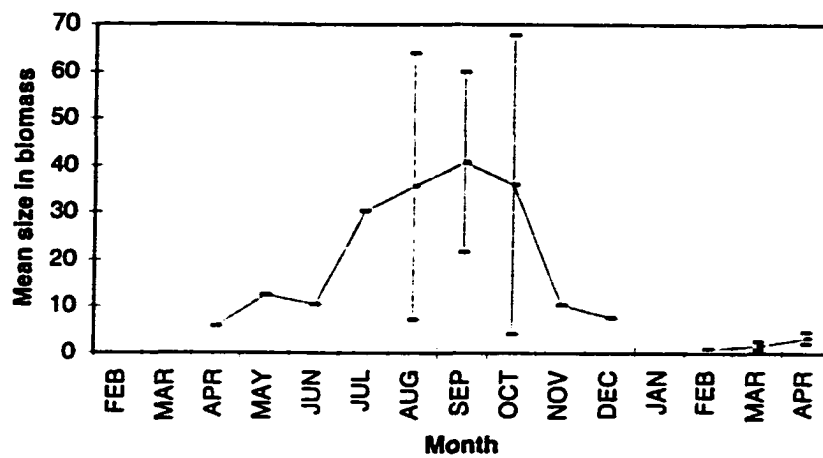


Fig. 3.20 Seasonal patterns of mean density (indiv/m²) in each ecological sybssystem of Terminos Lagoon for *Orthopristis chrysoptera* (pigfish).

Orthopristis chrysoptera

Inner Littoral of Carmen Inlet



Central Basin

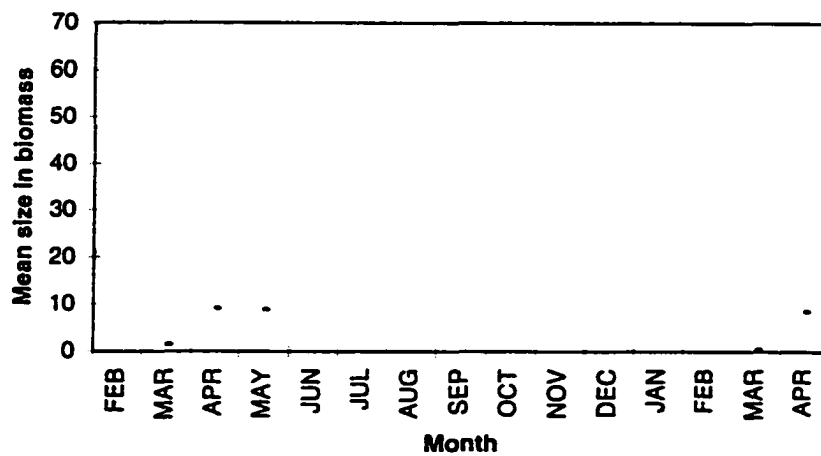


Fig. 3.21 Seasonal variation of mean biomass per individual (gr/indiv) in each ecological subsystem of Terminos Lagoon for *Orthopristis chrysoptera* (pigfish).

3.4.11 *Diapterus rhombeus* (caitipa mojarra)

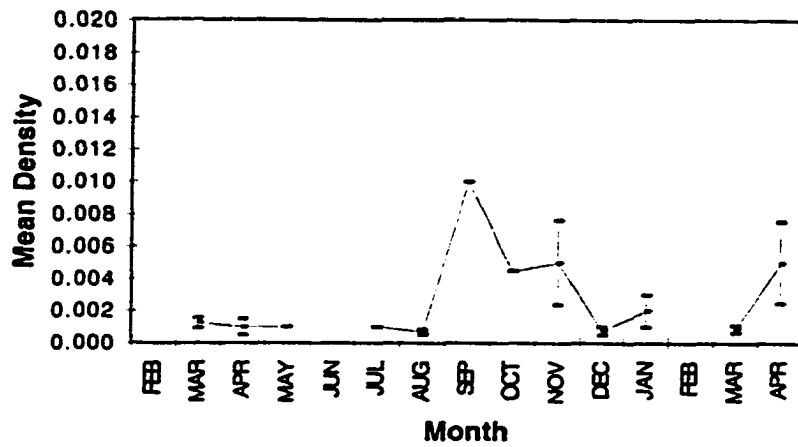
This mojarra was the twelfth most abundant species numerically (201 individuals) and the tenth by mass (3070.3 grams) in the lagoon (Table 3.1 Appendix B). Sixty-three percent of the catch numerically was from the fluvial lagoon systems, 19% from the central basin of the lagoon and 12% from the inner littoral of Carmen Island. This species as seventh numerically and the ninth by mass in the fluvial lagoon systems and the central basin (Table 3.1 Appendix B). Table 3.12, Appendix B shows the ranges of the total number of individuals and weight, mean size in grams, density, biomass per unit area, and environmental characteristics related to this species in Terminos Lagoon. This species tended to occur at somewhat lower salinities with 60% individuals captured from 10-25 (Table 3.12 Appendix B).

This species occurred mainly during the rainy and norte seasons in the fluvial lagoon systems. Catches in other subsystems and in the dry season were low. Density was highest in September at 0.010 indiv/m² (Fig. 3.22). The multiple regression model of Ln(biomass) was significant ($r^2 = 0.2676$, $p = 0.0073$), and analysis of individual variables showed that Secchi depth ($p = 0.0071$), water column depth ($p = 0.0257$) and negative temperature ($p = -0.0558$) were significant.

The small individuals of this species occurred mainly in low salinity (between 0 to 20) while large sizes were in marine salinities (between 20 to 35). Correspondingly, large sizes occurred in the inner littoral of Carmen island in April 1981 and in the fluvial lagoon systems in May. Small individuals occurred from July to January in all ecological subsystems (Fig. 3.23). The multiple regression model was significant ($r^2 = 0.3055$, $p = 0.0025$) and the analysis of individual variables showed that temperature ($p = 0.0420$) and Secchi depth ($p = 0.0583$) were significant.

Diapterus rhombeus

Fluvial Lagoon System



Central Basin

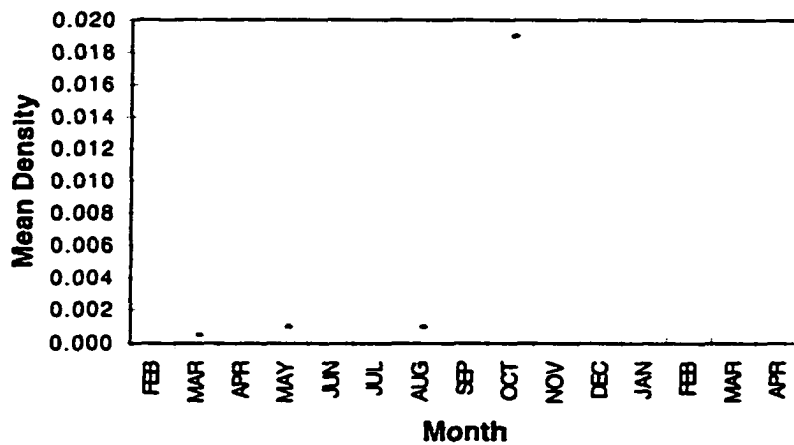
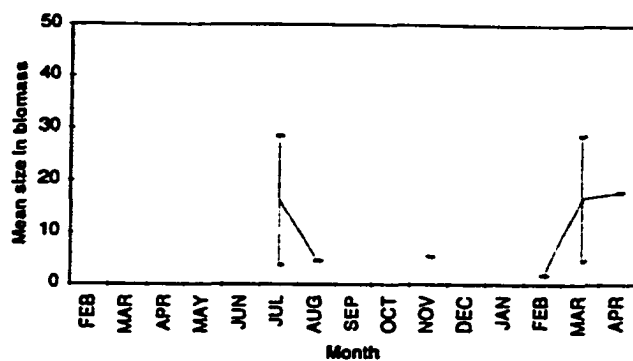


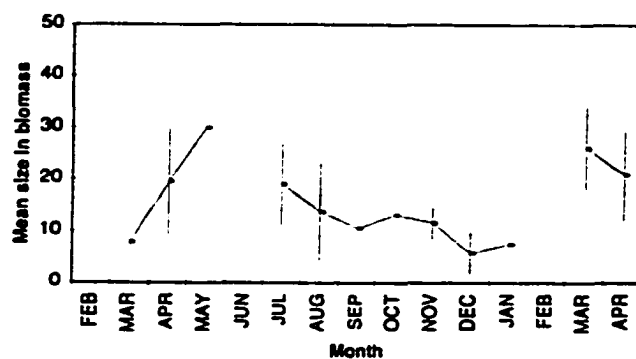
Fig. 3.22 Seasonal patterns of mean density (indiv/m²) in each ecological sybsystem of Terminos Lagoon for *Diapterus rhombeus* (caitipa mojarra).

Diapterus rhombeus

Carmen Inlet



Fluvial Lagoon Systems



Inner Littoral of Carmen Island

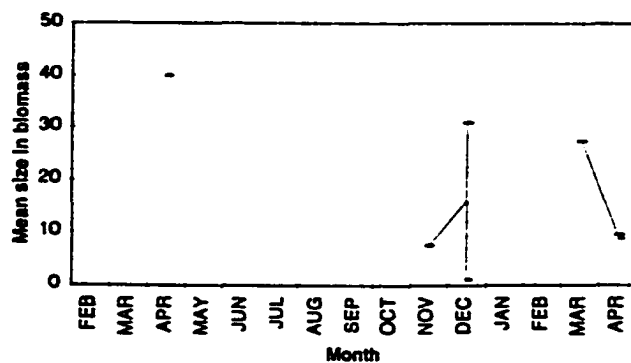


Fig. 3.23 Seasonal variation of mean biomass per individual (gr/indiv) in each ecological subsystem of Terminos Lagoon for *Diapterus rhombeus* (caitipa mojarra).

3.4.12 *Stellifer lanceolatus* (star drum)

The star drum was the eighth most abundant species numerically (503 individuals) and the twelfth by mass (1918.5 grams; Table 3.1 Appendix B). Ninety-six percent of its catch numerically was from Carmen inlet with the remainder from in the fluvial lagoon systems. This species was dominant in the Carmen inlet where it was first numerically and the sixth by mass. Table 3.13, Appendix B shows the ranges of the total number of individuals and weight, mean size in grams, density, biomass per unit area and environmental characteristics related to this species in Terminos Lagoon. This species tended to occur in a wide range of salinities 69% individuals captured from 20-35, but in more turbid waters (Table 3.13 Appendix B).

Stellifer lanceolatus (star drum) was captured during whole the year in Carmen inlet and to a much lesser extent in the fluvial lagoon systems. Peak density (0.068 ± 0.067 indiv/m²) and biomass (0.189 ± 0.188 g/m²) occurred in February 1980 (Fig. 3.24).

The multiple regression model for this species was necessary to include stations as an independent variable and to weigh them with station to obtain a better fit. The full Ln(biomass) model was significant ($r^2 = 0.4078$, $p = 0.0109$). Analysis of individual variables showed that station was significant ($p = 0.0183$).

The star drum ranged from 0.50 to 38.60 g/indiv (mean = 9.33 ± 1.65 g/indiv; Table 3.13 Appendix B). Small sizes occurred in both low and high salinity but large sizes were restricted to 10 to 25. There were large sizes in Carmen inlet and the fluvial lagoon systems in February 1980 and smaller sizes for the remainder of the year in these two ecological subsystems (Fig. 3.25). The multiple regression model was not significant.

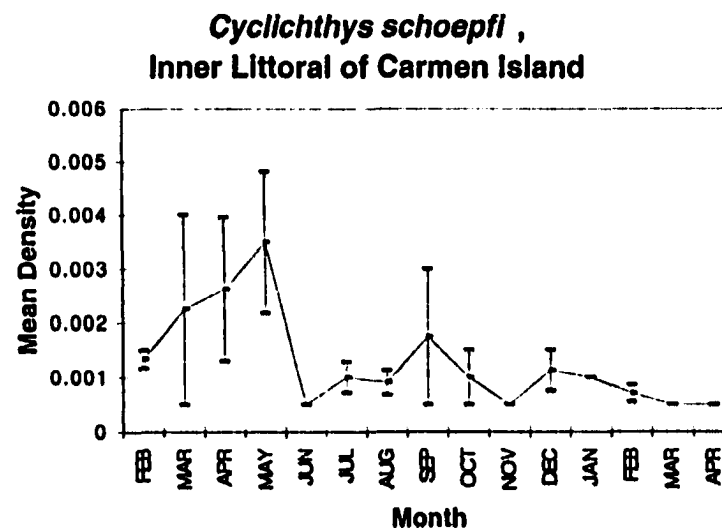
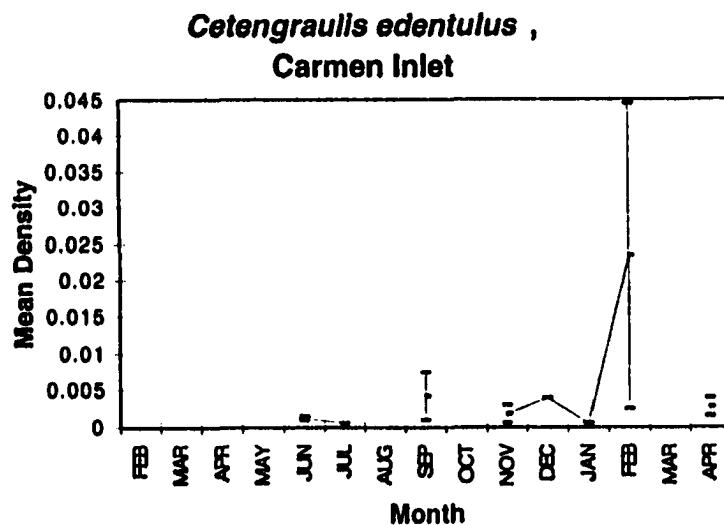
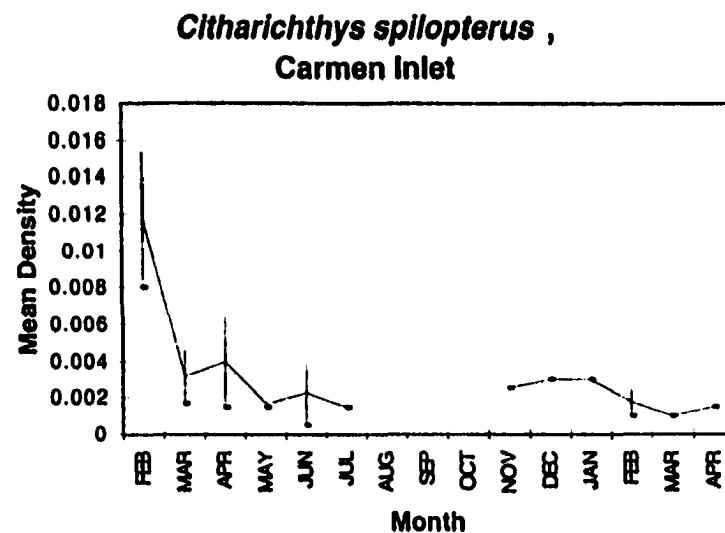
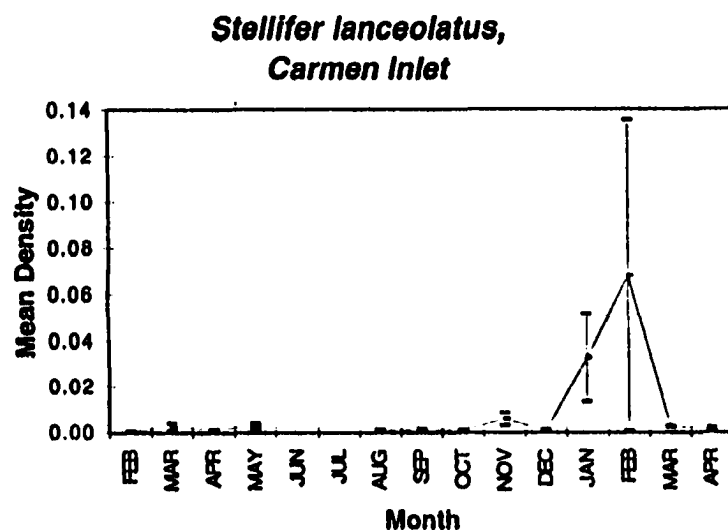


Fig. 3.24 Seasonal patterns of mean density (indiv/m²) in each ecological subsystem of Terminos Lagoon for *Stellifer lanceolatus* (star drum), *Citharichthys spilopterus* (bay whiff), *Cetengraulis edentulus* (Atlantic anchoveta) and *Cyclichthys schoepfi* (striped burrfish).

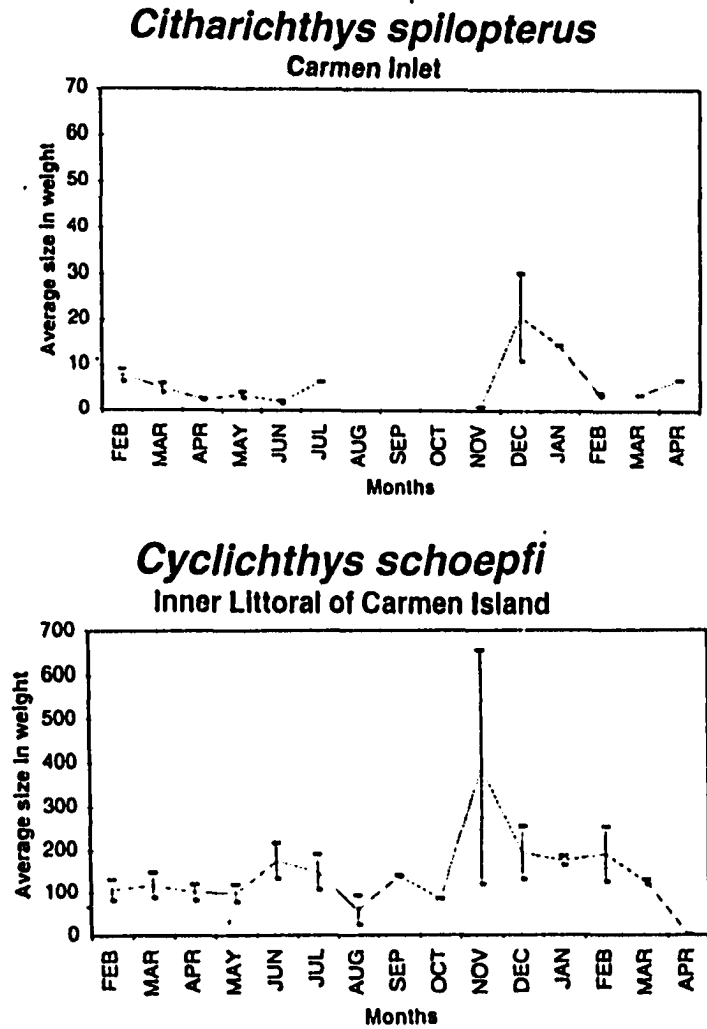
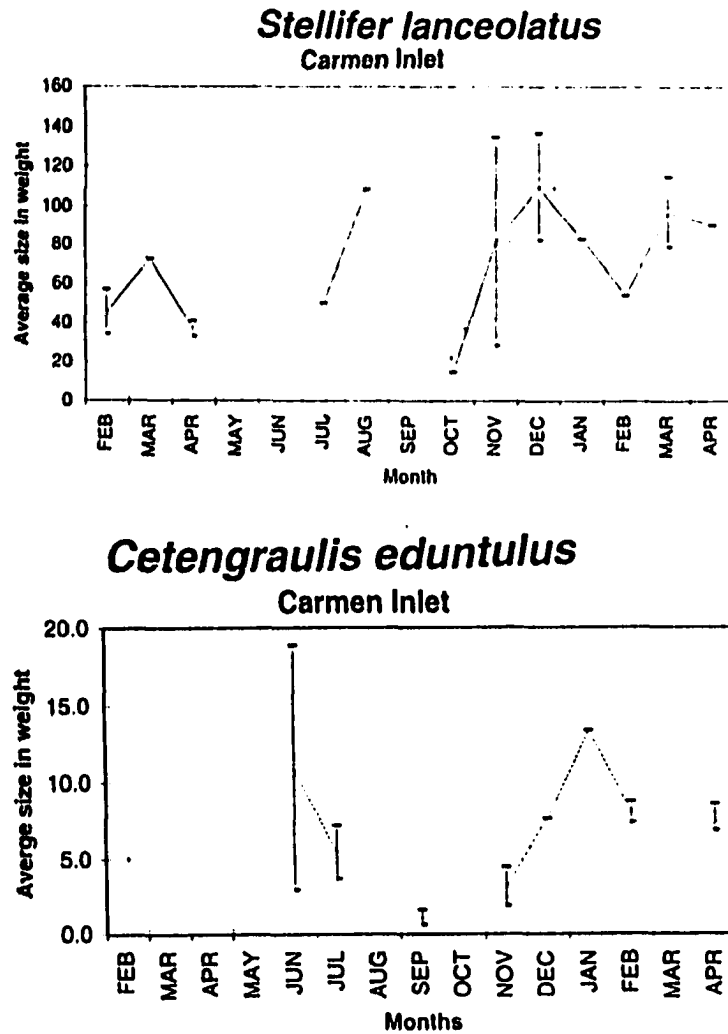


Fig. 3.25 Seasonal variation of mean biomass per individual (gr/indiv) in each ecological subsystem of Terminos Lagoon for *Stellifer lanceolatus* (star drum), *Citharichthys spilopterus* (bay whiff), *Cetengraulis eduntulus* (Atlantic anchoveta) and *Cyclichthys schoepfi* (striped burrfish).

3.4.13 *Citharichthys spilopterus* (bay whiff)

The bay whiff was the eleventh most species numerically (216 individuals) and the thirteenth by mass (1703.7 grams) for the lagoon (Table 3.1 Appendix B). Sixty-one percent of numerical capture was in Carmen inlet and 19% was in the fluvial lagoon systems and the inner littoral of Carmen Island. This species was dominant in Carmen inlet where it was the ninth numerically and the eighth by mass. Table 3.14, Appendix B shows the ranges of the total number of individuals and weight, mean size in grams, density, biomass per unit area and environmental characteristics related to this species in Terminos Lagoon. This species tended to occur at lower to medium salinities with 58% individuals captured from 10-25 and in more turbid waters (Table 3.14 Appendix B). This species was most abundant in Carmen Inlet. Peak density (0.012 ± 0.004 indiv/m²) and biomass (0.097 ± 0.046 g/m²) occurred in February 1980 in Carmen Inlet. Lesser periods of abundance occurred in the fluvial lagoon systems in November (0.065 g/m²) and January (0.050 g/m²; Fig. 3.24).

The transformed multiple regression model for density was significant ($r^2 = 0.1888$, $p = 0.0196$). Analysis of individual variables showed that Secchi depth ($p = 0.0552$) was significant. The mean size in mass ranged from 0.78 to 65.10 g/indiv (mean = 9.01 ± 1.35 g/indiv; Table 3.14 Appendix B). Large individuals occurred mainly in intermediate salinity (10 to 20) while small sizes were in high salinities. There were small sizes from February to July 1980 in all ecological subsystems while large sizes were present in the fluvial lagoon systems in November 1980 and January 1981 (Fig. 3.25). The multiple regression model was not significant.

3.4.14 *Cetengraulis edentulus* (Atlantic anchoveta)

This anchoveta was the thirteenth most abundant species numerically (178 individuals) and the fourteenth by mass (1299.0 grams) for the lagoon (Table 3.1 Appendix B). Eighty percent of its catch was in Carmen inlet and 17% in the fluvial lagoon systems. This species was characterized as dominant in Carmen inlet where it was the eighth numerically and seventh by mass. Table 3.15, Appendix B shows the range of the total number and weight, mean size in grams, density, biomass per unit area and related environmental characteristics. This species had a wide range of environmental conditions with 61% of individuals in salinities of 30-35 (Table 3.15 Appendix B).

Cetengraulis edentulus (Atlantic anchoveta) was restricted to the fluvial lagoon systems and Carmen inlet. In Carmen Inlet, density (0.024 ± 0.021 indiv/m²) and biomass (0.0206 ± 0.187 g/m²) were highest in February 1981 (Fig. 3.24). Neither of the multiple regression models was significant.

Mean size for the anchoveta was between 0.60 and 40.20 g/indiv (mean = 7.03 ± 1.46 g/indiv; Table 3.15 Appendix B). There were small sizes in low salinity (5 to 20) and large sizes in marine salinities (30 to 35). Small sizes occurred mainly in the fluvial lagoon systems and Carmen inlet from September 1980 to February 1981 (Fig. 3.25). There were large sizes in the central basin only in November. The multiple regression model was not significant.

3.4.15 *Cylichthys schoepfi* (striped burrfish)

Striped burrfish was the fifteenth most abundant species numerically (142 individuals) and the sixth by mass (17026.7 grams) in the lagoon (Table 3.1 Appendix

B). Seventy-five percent of catch was from the inner littoral of Carmen Island, 13% in the fluvial lagoon systems, and 11% in the central basin and the remainder in Carmen inlet. This species was dominant in Carmen Island where it was eighth numerically and fifth by mass. Table 3.16, Appendix B shows the range for total number of individuals, weight, mean size in grams, density, biomass per unit area and environmental characteristics related to this species in Terminos Lagoon. This species occurred at medium salinities with 52% individuals captured in salinities 30–40 (Table 3.16 Appendix B).

This species had a limited distribution, mainly in areas with permanent marine influence of Carmen Island. High density (0.004 ± 0.001 indiv/m²) and biomass (0.295 ± 0.086 g/m²) occurred in May in the inner littoral of Carmen Island. Lower biomass peaks occurred in September (0.243 ± 0.172 g/m²) and November (0.194 ± 0.133 g/m²). Maximum biomass, however occurred in the fluvial lagoon systems during December (0.460 g/m²; Fig. 3.24).

The multiple regression for the striped burrfish was significant ($r^2 = 0.1833$, $p = 0.0251$). Analysis of individual variables showed salinity ($p = 0.0347$) was significant. The Ln(biomass) model was weighted with Secchi depth and the full model was significant ($r^2 = 0.1651$, $p = 0.0451$). Analysis of individual variables showed that Secchi depth ($p = 0.0309$) was significant.

The mean size of this species ranged from 1.50 to 654.4 g/indiv (mean = 139.08 ± 13.66 g/indiv; Table 3.16 Appendix B). Both large and small sized individuals occurred in lower salinities (10 to 20). Large sizes appeared in the central basin (June), inner littoral of Carmen island (November) and the fluvial lagoon systems (January 1981). Small sizes occurred from February to October 1980 in the inner littoral of

Carmen island, fluvial lagoon systems and central basin (Fig. 3.25). The smallest sizes occurred in November (fluvial lagoon systems) and April 1981 (inner littoral of Carmen island). The multiple regression model was not significant.

3.4.16 Factor Analysis

The first three factors had eigenvalues ≥ 1 and explained 81.5% of the variance (Table 3.17 Appendix B). Factor One is related to temperature and explains 32.9% of the total variance. Factor Two is related to salinity and explains 31.8% of the variance. Factor Three is related to depth and explains 16.8% of the total variance (Fig. 3.26). Thus, Factors one and two are related to seasonally while Factor three is related to habitat. The centroids for season show that the main separation is for Factor One indicating that the rainy season has high temperature and low salinity.

In the factor analysis, the species that characterized Carmen inlet such as *Stellifer lanceolatus* (star drum), *Cynoscion arenarius* (sand seatrout) and *Cetengraulis edentulus* (Atlantic anchoveta) were located in the areas of high salinity and low temperature (Fig. 3.26). By contrast, *Cathorops spixii* (mandamango sea catfish) characteristic of the fluvial lagoon systems, was located in the low salinity, high temperature region (Fig. 3.26).

The factor analysis identified relationships among seasons and the different assemblages. The dry season was characterized by marine species (*Orthopristis chrysoptera* - pigfish and *Archosargus rhomboidalis* - sea bream), in the inlets to the lagoon. In the rainy season, the fish assemblage was characterized by immigration of fish species more tolerant of fresher water (*Eucinostomus gula* - silver jenny), *Diapterus rhombeus* - caitipa mojarra and *Anchoa mitchilli* - bay anchovy).

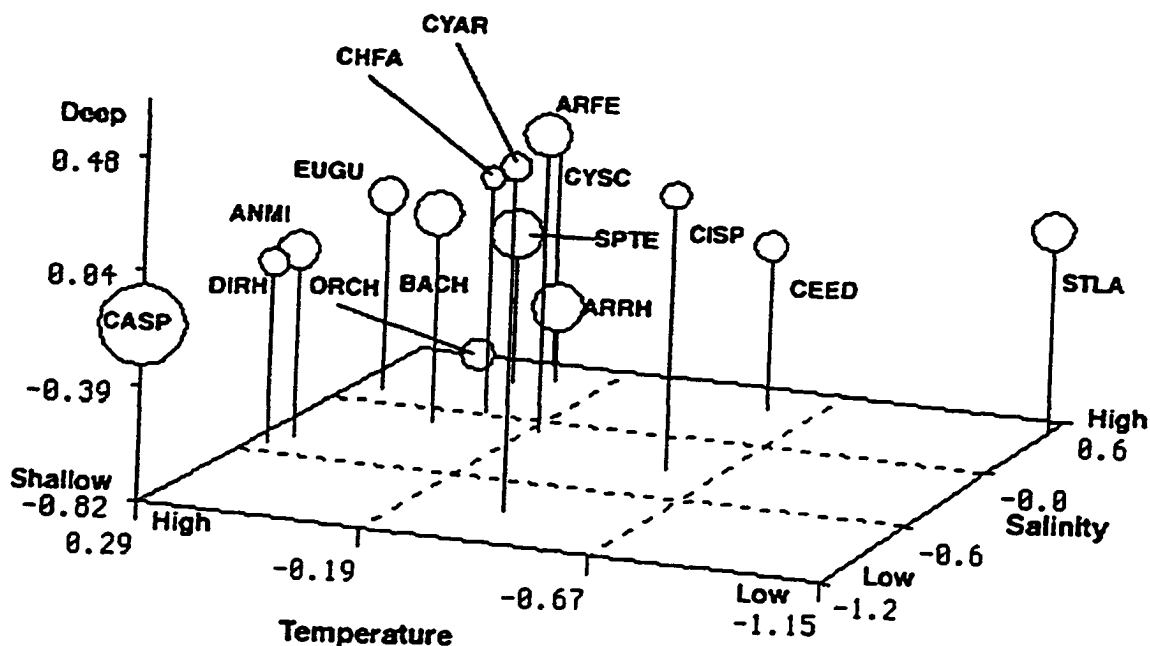


Fig. 3.26 Factor analysis relating environmental parameters to the 15 dominant fish species in Terminos Lagoon. The location of centroids for each species are plotted in three dimensional factor space with the radius of each circle representing one standard deviation about the mean. Each factor represents the weighted linear combination of the original set of six environmental variables. ANMI = *Anchoa mitchilli* (Bay anchovy); ARFE = *Ariopsis felis* (Hardhead sea catfish); CASP = *Cathorops spixii* (Mandamango sea catfish); ARRH = *Archosargus rhomboidalis* (Sea bream); BACH = *Bairdiella chrysoura* (Silver perch); CEED = *Cetengraulis edentulus* (Atlantic anchoveta); CHFA = *Chaetodipterus faber* (Atlantic spadefish); CHSC = *Cyclichthys schoepfi* (Striped burrfish); CISP = *Citharichthys spilopterus* (Bay whiff); CYAR = *Cynoscion arenarius* (Sand seatrout); DIRH = *Diapterus rhombeus* (Caitipa mojarra); EUGU = *Eucinostomus gula* (Silver jenny); ORCH = *Orthopristis chrysoptera* (Pigfish); SPTE = *Sphoeroides testudineus* (Checkered puffer) and STLA = *Stellifer lanceolatus* (Star drum).

3.5 Discussion

The discussion will characterize the life history strategies of the fish community based on available literature and will relate this information to the timing of use of each ecological subsystem. The data are based exclusively on trawl-caught fish.

It is important to emphasize the role of migration during fish life histories in how habitat is utilized. The dominant fish species have biological and ecological strategies that are highly adapted to the ecological subsystems of Terminos lagoon. Therefore, fish abundance in each subsystem at any given time is the result of a biological strategy such as feeding and growth, maturation, or reproduction. These factors define the pattern of habitat use for species along environmental and temporal gradients.

I used a classification based on the criteria of McHugh (1967) as modified by Yáñez-Arancibia and Nugent (1977) who took in account the species frequency in catches. Yáñez-Arancibia and Nugent (1977) defined a) occasional visitors with frequency of 1 to 30%, 2) seasonal or cyclical species with a frequency between 31 and 70%, and 3) resident or typically estuarine species with a frequency between 71 and 100%.

These groups are further defined as follows. Fully estuarine species or permanent residents spend their whole history in the lagoon, growing to maturity and reproducing inside the lagoon. The seasonal visitors use the lagoon seasonally as a nursery ground. Generally, these species spawn and spend much of their adult life at sea but enter to the lagoon as juveniles and return to the sea as pre-adults or adults. Finally the occasional visitors use the lagoon irregularly for protection and/or feeding (McHugh, 1967; Pauly, 1975; Yáñez-Arancibia and Nugent, 1977; Yáñez-Arancibia et al., 1994). The discussion is structured based on this classification, taking into

consideration the ecological role of each species in the community and the different biological strategies of species life history.

3.5.1 Residents or Typical Estuarine Species.

These species generally occur throughout the year in all habitats of the lagoon, and are dominant species in the four ecological subsystems. These include *Cathorops spixii* (mandamango sea catfish) which had a frequency of 75% in the fish catches, *Sphoeroides testudineus* (checkered puffer) with 82% and *Ariopsis felis* (hardhead catfish) with 80% frequency. These were classified as residents or typically estuarine. *Bairdiella chrysoura* (silver perch) and *Eucinostomus gula* (silver jenny) were cyclical or seasonal visitors because their frequency of capture was 63 and 66%, respectively.

This group of species, however, has different patterns of distribution related to their life histories. There is a habitat separation as, a function of their biological strategies resulting in two patterns for these species: 1) typically estuarine species with reproduction in Terminos lagoon such as *Cathorops spixii* (mandamango sea catfish) and *Bairdiella chrysoura* (silver perch); and 2) typically estuarine species with spawning areas located in the inner shelf which are, therefore, estuarine dependent. This latter group includes *Sphoeroides testudineus* (checkered puffer), *Ariopsis felis* (hardhead sea catfish) and *Eucinostomus gula* (silver jenny).

3.5.1.1 *Cathorops spixii* (mandamango sea catfish)

This species reproduces in Terminos Lagoon, particularly in the fluvial lagoon systems. The juvenile feeding area is in the highly turbid waters of Carmen inlet. The maturation and feeding areas of post-reproductive and pre-adults are the inner littoral of Carmen Island (Lara-Dominguez et al., 1981; Yáñez-Arancibia et al., 1985a; Yáñez-

Arancibia and Lara-Domínguez, 1988). Mandamango sea catfish had a greater affinity for the highly turbid waters associated with the Palizada River in the western part of the region.

Figure 3.27 shows the index of relative abundance (Roger and Herk, 1985) of this species in the different subsystems. Each peak in each subsystem during the year indicates a high density of the species. This is related to the different stages of the life history based on the population size structure. Thus, it is possible to infer the functional use of each subsystem related to life history.

Cathorops spixii (mandamango sea catfish) peaked in April 1980 in the fluvial lagoon systems, which was related to pre-adults and adults in phase III of gonadic maturation (Nikolsky, 1963) indicating recruitment to the reproductive population in this subsystem. During the reproduction season from April to September (Yáñez-Arancibia and Lara-Dominguez 1988) there was a reduction in relative abundance values in all the subsystems (Fig. 3.2). Then there was a peak in September in Carmen inlet related to the size distribution of this species (Fig. 3.3). This peak was associated with juveniles that were arriving after parental care, which is characteristic of this species. The peak in November in the fluvial lagoon systems was related to post-reproductive individuals that moved from the fluvial lagoon systems to the feeding and recovery areas. This stage can relate to the peaks observed in December of 1980 and March of 1981 in the inner littoral of Carmen Island. Yáñez-Arancibia and Lara-Domínguez (1980) made a detailed description of the life history of the species of Family Ariidae in Terminos lagoon, and particularly for *Cathorops spixii* (= *Arius melanopus*). Lara-Domínguez et al. (1980) reported that salinity and temperature determined the pattern of habitat use by this species.

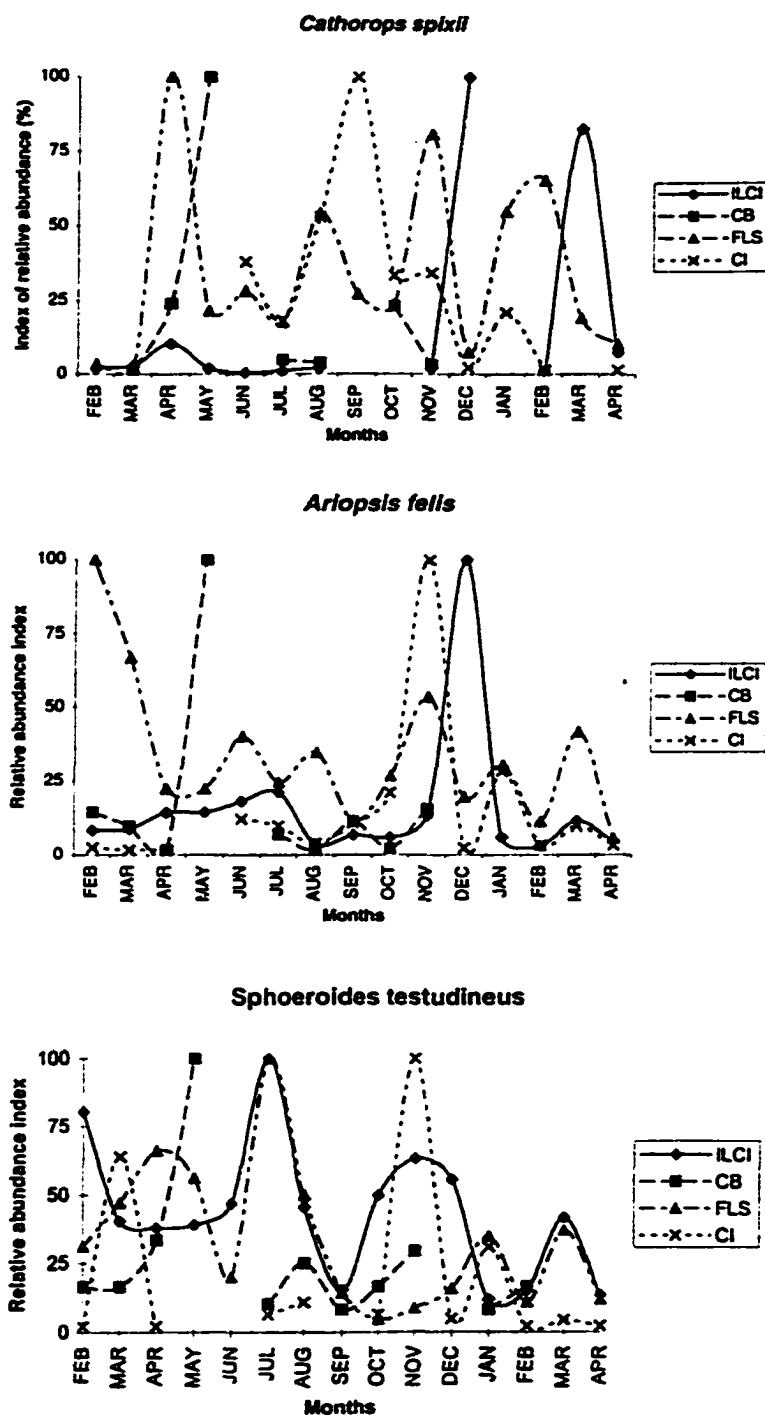


Fig. 3.27 Temporal variation in relative abundance of the resident or typical estuarine species in each ecological subsystem in Terminos Lagoon. ILCI = Inner littoral of Carmen island, CB = Central Basin, FLS = Fluvial lagoon systems and CI = Carmen inlet. *Cathorops spixii* (mandamango sea catfish), *Sphoeroides testudineus* (checkered puffer), *Ariopsis felis* (hardhead sea catfish). (Figure continued)

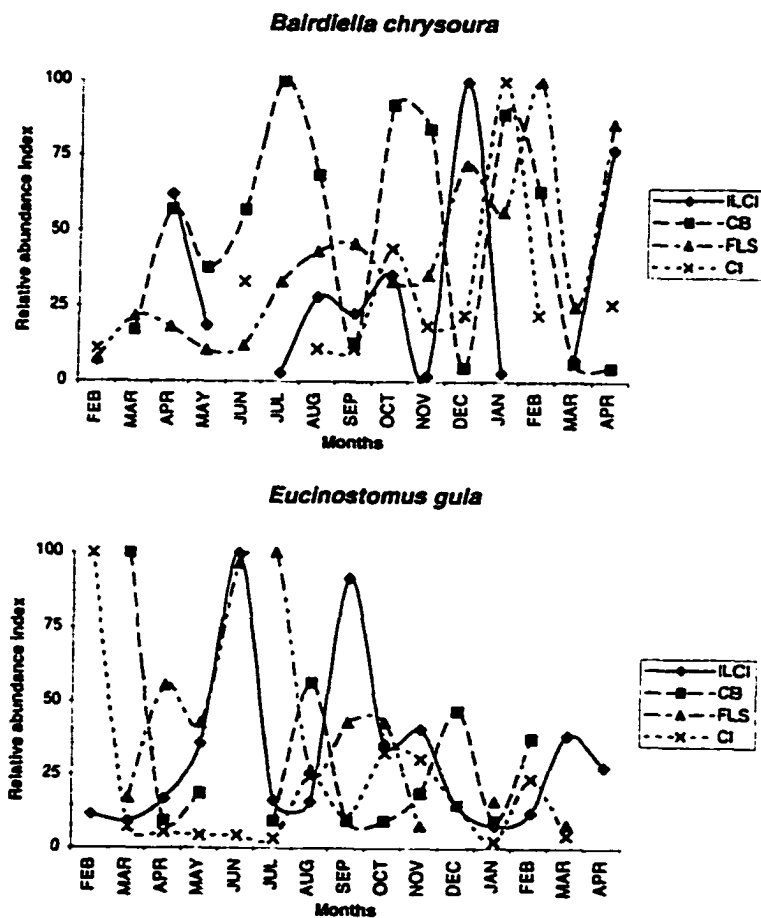


Fig. 3.27 (continued) Temporal variation in relative abundance of the resident or typical estuarine species in each ecological subsystem in Terminos Lagoon. ICLI = Inner littoral of Carmen island, CB = Central Basin, FLS = Fluvial lagoon systems and CI = Carmen inlet. *Bairdiella chrysoura* (silver perch) and *Eucinostomus gula* (silver jenny).

3.5.1.2 *Sphoeroides testudineus* (checkered puffer)

Checkered puffer was the most common species in all of the ecological subsystems in the lagoon, therefore it is considered as typically estuarine. Its abundance was positively correlated with salinity. This species has been also reported in open sea (Mallard Colmenero et al., 1982; Yáñez-Arancibia and Sanchez Gil, 1986). The highest abundance was in waters with higher transparency and sea grass meadows (Fig. 3.4). This pattern has been reported by Yáñez-Arancibia et al. (1980, 1982, 1985a, 1985b, 1985c, 1988) Mallard Colmenero et al. (1982), and Yáñez-Arancibia and Lara-Domínguez (1983) for the same subsystem. This species spawns, however, in clear, shallow coastal areas near Puerto Real inlet during the dry season, while maturation occurred inside the lagoon throughout the year (Mallard Colmenero et al., 1982; Yáñez-Arancibia et al., 1985a). This reproduction pattern indicates that it is an estuarine dependent species.

The relative abundance index of this species in the ecological subsystems (Fig. 3.27) together with bibliographical information and the analysis of mean mass allows a characterization the different life history stages of this species. The largest peaks were in the inner littoral of Carmen Island. In February 1980 there was a peak of pre-adults averaging 46.6 g per individual and 115 mm LT. These peaks were associated with the migration of pre-adults to the inner littoral of Carmen Island that was a maturation and feeding area for adults and pre-adults. Small sizes occurred in the fluvial lagoon systems (Fig. 3.5). Mallard Colmenero et al. (1982) determined that there was little variation in the ranges of sizes by subsystem and season of the year. Moreover, the population in the inner littoral of Carmen Island was larger than in the fluvial lagoon systems during the dry and rainy seasons. Therefore, they concluded that the fluvial

lagoon systems were nursery areas and the inner littoral of Carmen Island was a maturation area for pre-adult feeding and maturation (Yáñez-Arancibia et al., 1985a and 1985c).

Yáñez-Arancibia et al. (1985a) developed a conceptual model of the life history of *Spherooides testudineus* in Terminos lagoon. This species matured during the dry season in areas with permanent marine influence. Then it recruited to the adjacent continental shelf through both inlets, where it reproduced in shallow coastal areas with seagrass meadows. During the rainy season, larvae and juvenile recruited to the lagoon to areas with sea grass meadows and mangroves in the inner littoral of Carmen Island and to the fluvial lagoon systems.

3.5.1.3 *Bairdiella chrysoura* (silver perch)

This species has a similar pattern to *Cathorops spixii*. Chavance et al. (1984) carried out a detailed study of its autoecology, and established that this species reproduces inside the fluvial lagoon systems, particularly in Candelaria-Panlau. The silver perch occurred in the eastern part of the region in the Candelaria River. Lower turbidity and the presence of seagrass meadows (Moore and Wetzel, 1988) characterize this area.

The annual pattern of the relative abundance index (Roger and Herke, 1985) in each of the ecological subsystems is shown in figure 3.27. In April 1980, there was a peak in the central basin (Figs. 3.6 and 3.7). Chavance et al. (1984) pointed out that this species recruited to the fluvial lagoon systems as adults to reproduce when females had reached the gonadic maturity. There was a peak during July in the central basin made up of juvenile that left the fluvial lagoon systems to be recruited to the lagoon through the central basin. Chavance et al. (1984) established that the species

had a marked recruitment season from July to October. They pointed out a general pattern of recruitment with adult migration to the fluvial lagoon systems during the dry season. During the norte season, the adults left this subsystem and migrated to the lagoon. The juveniles migrated from the fluvial lagoon systems to the lagoon during the dry and rainy seasons. These patterns are shown in figure 3.27 with peaks in the different ecological subsystems during different months of the year.

Thus, these two species with wide distribution in the lagoon have adapted their reproductive strategies to the fluvial lagoon systems in salinity less than 15. As part of their life histories, they carry out trophic migration to other subsystems.

3.5.1.4 *Ariopsis felis* (hardhead sea catfish)

This species is an estuarine species that has permanent migration patterns between Terminos lagoon and the adjacent continental shelf. Yáñez-Arancibia and Lara-Dominguez (1988) established that the population was made up of mainly juveniles and pre-adults with an mean size of 160.1 mm TL. Small sizes occurred at the end of the rainy season and the beginning of the norte season while larger individuals were at the end of the norte season and beginning of the dry season. Figure 3.27 shows two peaks that correspond to these observations of the life history of this species. The first, in Carmen inlet during November, was mainly juveniles, and the second peak in December in the inner littoral of Carmen Island was juveniles and adults.

Yáñez-Arancibia and Lara-Dominguez (1988) established two criteria to determine the seasonality and area of reproduction for the family Ariidae in Terminos Lagoon: the number and developmental state of eggs state in the male's mouth, and the maturation phase of the female gonads. The reproduction season of this species

was from June to September in the inner littoral of Carmen Island, the northeast region of the lagoon (in the Sabancuy estuary) as well as in the adjacent inner continental shelf. The inner littoral of Carmen Island was a reproduction area . However, there was also a large spawning in the adjacent inner shelf and, as a result, a peak was observed in December in the inner littoral of Carmen Island corresponding to post-reproductive organisms. Therefore, this area is also a feeding ground. The peak in Carmen inlet was made up of juvenile organisms.

3.5.1.5 *Eucinostomus gula* (silver jenny)

This species is a typical estuarine species with reproduction areas in the adjacent continental shelf. Similar to *Ariopsis felis*, the silver jenny had continuous migratory movement during the year between the lagoon and the shelf for feeding and reproduction purposes (Yáñez-Arancibia et al., 1985a; Yáñez-Arancibia and Sanchez-Gil, 1986). This species occurred in all subsystems of the Terminos lagoon, mainly in the inner littoral of Carmen Island and the eastern region of the lagoon (near Sabancuy and the Candelaria-Panlau river; Fig. 3.12). These areas were used for nursery, maturation and feeding grounds. Reproduction occurred along the shoreline in sea grass meadows near Puerto Real inlet.

Figure 3.27 shows the monthly variations of the relative abundance index (Roger and Herke, 1975). There were several peaks in the inner littoral of Carmen Island. In June, this was due to pre-adults and adults. The second in September was due to juvenile recruitment from the adjacent continental shelf to the lagoon. Aguirre León and Yáñez-Arancibia (1986) suggested that the fluvial lagoon systems were growth and feeding areas for immature individuals, while the inner littoral of Carmen Island was a maturation area for this species.

Therefore, *Sphoeroides testudineus* (checkered puffer), *Ariopsis felis* (hardhead sea catfish) and *Eucinostomus gula* (silver jenny) had wide distribution in the lagoon and use the fluvial lagoon systems for a nursery and for feeding and the inner littoral of Carmen Island for maturation in a wide range of salinity.

3.5.2 Seasonal or Cyclical Visitors

Species characterized as seasonal or cyclical visitors were occurred less frequently in the catches than estuarine residents. This is because their occurrence was limited to one to three subsystems due to their ecological affinities and physiological tolerances to environmental parameters. The frequency of capture in the lagoon was as follows. *Archosargus rhomboidalis* (47%) and *Chaetodipterus faber* (36%) were dominant in three subsystems and were characterized as cyclical or seasonal visitors of the lagoon. *Cyclichthys schoepfi* (37%) and *Citharichthys spilopterus* (32%) were dominant in one subsystem and were characterized as seasonal visitors.

3.5.2.1 *Archosargus rhomboidalis* (sea bream)

This species and *Chaetodipterus faber* (Atlantic spadefish) are marine species with estuarine dependence. The sea bream occurred in the lagoon in high salinity ecological subsystems mainly during early life history stages. Chavance et al. (1986) determined the early life history stages based on changes in teeth morphology with age. For individuals between 88 and 160 mm SL, the high diversity of epifauna on seagrass leaves are important trophic components and play an essential role in the growth of this species. This ontogenetic shift in the type of teeth is characteristic of this species (Chavance et al., 1986; Yáñez-Arancibia et al., 1985a). Figure 3.28 shows the behavior of the relative abundance index in the different ecological subsystems of the

lagoon. The peak in March of 1980 in the central basin was related to juvenile recruitment to the lagoon through Puerto Real Inlet which is enhanced by the net inflowing currents (Chavance et al., 1986). In the inner littoral of Carmen Island this species had low abundance during the dry and norte seasons (Fig. 3.10). This is the period when reproduction takes place in the adjacent inner shelf.

The distribution of *Archosargus rhomboidalis* (sea bream) is limited by salinity and it occurred mainly in areas with permanent marine influence. Therefore, it is a typical species of the fish communities in seagrass meadows in the lagoon. Yáñez-Arancibia et al. (1985b) reported that this species is a typical resident of the inner littoral of Carmen Island and central basin, and a seasonal visitor in the fluvial lagoon systems. This species is exploited in the lagoon by artisanal fishers. Thus, because of its abundance and distribution, this species has the potential to become a more important economic resource (Chavance et al., 1986).

The peak of relative abundance in September in the inner littoral area was related to juvenile recruitment from the inner shelf and associated with its distribution of size (Chavance et al., 1986; Yáñez-Arancibia et al., 1985a). Salinity is an important environmental that affecting recruitment. of this species.

3.5.2.2 *Chaetodipterus faber* (Atlantic spadefish)

This species used the lagoon as an adult for feeding. This species reproduces in the adjacent inner shelf. It is a dominant species around petroleum platforms mainly in about 20 m water depth (Stanley and Wilson, 1997 and 2000). Ditty et al. (1994) reported that the larvae of this species occur in coastal waters off the Mississippi delta. The low salinities led to this coastal area being suitable habitat mainly from June to

Seasonal or Cyclical Visitors

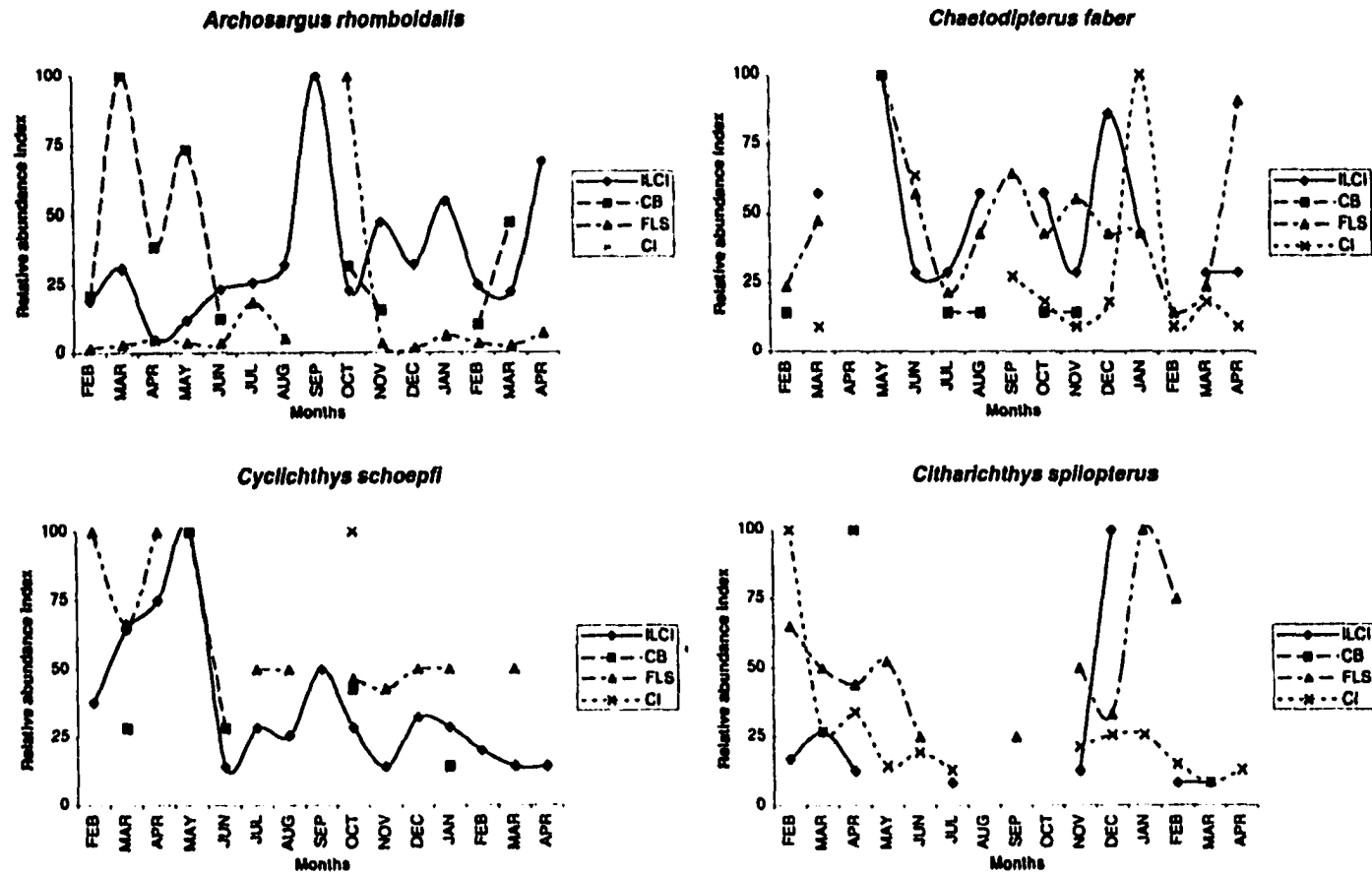


Fig. 3.28 Temporal variation in relative abundance of the seasonal or cyclical species in each ecological subsystem in Terminos Lagoon. ILCI = Inner littoral of Carmen island, CB = Central Basin, FLS = Fluvial lagoon systems and CI = Carmen inlet. *Archosargus rhomboidalis* (sea bream), *Chaetodipterus faber* (Atlantic spadefish), *Cyclichthys schoepfi* (striped burrfish) and *Citharichthys spilopterus* (bay whiff).

August. The Atlantic spadefish, by contrast, had high density in Puerto Real inlet, the central basin and the central part of the fluvial lagoon systems.

Figure 3.28 shows the variation of the index relative abundance in the different subsystems of the lagoon. The highest peak was in the central basin during May and in Carmen inlet during January 1981. This seems to be before and/or after the period of peak reproduction in the adjacent inner shelf. Therefore, this species used the ecological subsystems of the lagoon for feeding.

Chaetodipterus faber (Atlantic spadefish) has been reported as a dominant in the communities associated with oil rigs in depths of about 20 m (Stanley and Wilson, 1997). Larvae of this species occur in coastal waters, except near the Mississippi River delta, an area with a narrow shelf and rapidly increasing water depths. But delta waters may offer additional habitat suitable to Atlantic spadefish larvae because of lower salinity and high turbidity (Ditty et al., 1994). In Terminos Lagoon, *C. faber* is a permanent resident of the inner littoral of Carmen Island and fluvial lagoon systems and a cyclical visitor in the central basin (Yáñez-Arancibia et al., 1985b).

3.5.2.3 *Cylichthys schoepfi* (striped burrfish)

This species is a specialist feeding of hard-shelled prey (Ralston and Wainright, 1997). It is likely that it enters the lagoon as an adult for feeding. It was distributed mainly in the inner littoral of Carmen Island during the dry season (April and May, Figs. 3.16 and 3.28) and irregularly throughout the year in the fluvial lagoon systems, where there are important oyster banks.

Cylichthys schoepfi (striped burrfish) occurred as an adult in Terminos lagoon. It was distributed mainly in areas with seagrass meadows and persistent marine

influence. Yáñez-Arancibia et al. (1985b) characterized this species as typical resident in the inner littoral of Carmen Island, a seasonal or cyclical visitor in the central basin and fluvial lagoon systems and an occasional visitor in the fish community of Carmen inlet.

3.5.2.4 *Citharichthys spilopterus* (bay whiff)

This species occurred mainly in Carmen inlet and was characterized by its frequency in this subsystem as a seasonal or cyclical visitor (Fig. 3.24). *Citharichthys spilopterus* (bay whiff) occurred throughout in the whole lagoon. However, its highest density was in sea grasses of Sabancuy estuary near Puerto Real inlet and in influenced by outflow from Pom-Atasta and Palizada near Carmen inlet. In Mexico, this species occurs in Tampamachoco lagoon where smaller individuals use muddy substrate in the upper estuary and larger individuals use sand flats and channels in the lower estuary (Castillo Rivera, 2000). Toepfer and Fleeger (1995) utilized an exploratory regression model to examine the influence of marsh-edge characteristics on feeding by two size classes of juvenile bay whiff. Tidal creeks in the Duplin River, Georgia, are important nursery areas for this species (Reichert and Van der Veen, 1991). This species was classified in Terminos lagoon as a typical resident of the fish communities in Carmen inlet, a cyclical visitor in the inner littoral of Carmen Island and fluvial lagoon systems and an occasional visitor of the central basin (Yáñez-Arancibia et al., 1985b).

It had a maximum peak in February 1980. The population was made up mainly of juveniles ranging in total length between 43 and 190 mm (Table 3.14, Fig. 3.25). Smaller sizes occurred in areas of low salinity. This species used the high turbidity Carmen inlet as feeding and protection grounds (Fig. 3.28). Toepfer and Fleeger

(1995) studied the effects of marsh-edge habitat variability on feeding success by juveniles. They found that for small juveniles (less than 29 mm SL) salinity, current velocity, and median depth were the primary influences on feeding success. For larger juveniles (30 to 50 mm SL) time of capture and current velocity were significant variables affecting feeding.

This species has been object of study related to habitat utilization in a North Carolina estuary where there were ontogenetic shifts in habitat utilization. High densities of small bay whiff occurred in the upper estuary on muddy substrates and larger individuals utilized sand flats and channels in the lower estuary (Walsh et al., 1999). In Tampamachoco Lagoon, Mexico, Castillo Rivera et al. (2000) reported that larger individuals were almost entirely piscivorous and had a very narrow trophic niche. This species was very abundant in Barataria Bay and widely distribution over the salinity gradient. However, its abundance was concentrated in areas where offshore tonguefish was uncommon (Allen and Baltz, 1997).

3.5.3 Occasional Visitors

In general, the species dominant in only one or two subsystems were occasional visitors to the lagoon. This limited use of the lagoon was partly due to narrow physiological and habitat requirements. It is also partly due to the net selectivity. Fast swimmers and species that live in very shallow water are under-represented in trawl catches.

3.5.3.1 *Anchoa mitchilli* (bay anchovy)

The engraulids, which have an affinity for marine pelagic waters, are occasional visitors. *Anchoa mitchilli* (30% frequency) was dominant in three subsystems (Table

3.1 Appendix B). But because of its low frequency of captures over the whole lagoon, it was classified as an occasional visitor. However in the frequency analysis by subsystem, this species was a cyclical or seasonal visitor in Carmen inlet and occasional visitor in the other three subsystems. The bay anchovy occurred primarily in Carmen inlet and western part of the fluvial lagoon systems.

Figure 3.29 shows the variation of the relative abundance index of *A. mitchilli* in the different subsystems of the lagoon. The main peaks were in August and October in the fluvial lagoon systems and in Carmen inlet during September and October. These peaks were related to recruitment from the sea to feeding areas in the fluvial lagoon systems or from this subsystem to reproduction areas in the adjacent inner shelf. Therefore, Carmen inlet was a maturation ground (Ayala-Pérez et al., 1997). In the fish communities from the Mississippi delta, this species had highest abundance during August and September, coinciding with that for Terminos Lagoon (Deegan and Thompson, 1985).

A number of authors have reported on life history strategies of *Anchoa mitchilli* and showed, as in Terminos Lagoon, that this species occurs preferentially in to mid to lower salinities. Kimura et al. (2000) reported that *A. mitchilli* used the upper and middle part of Chesapeake Bay of Chesapeake during recruitment. Jordan et al. (2000) investigated spatial and temporal changes in growth rate and larval survival in the middle Hudson River estuary. They found significant spatial and temporal variation in growth rate. Larvae in the upper estuary tended to grow more slowly than in the middle estuary. Growth rate variation, probably governed by patches of zooplankton occurred on temporal scales of a week and spatial scales of 15 km.

Occasional Visitors

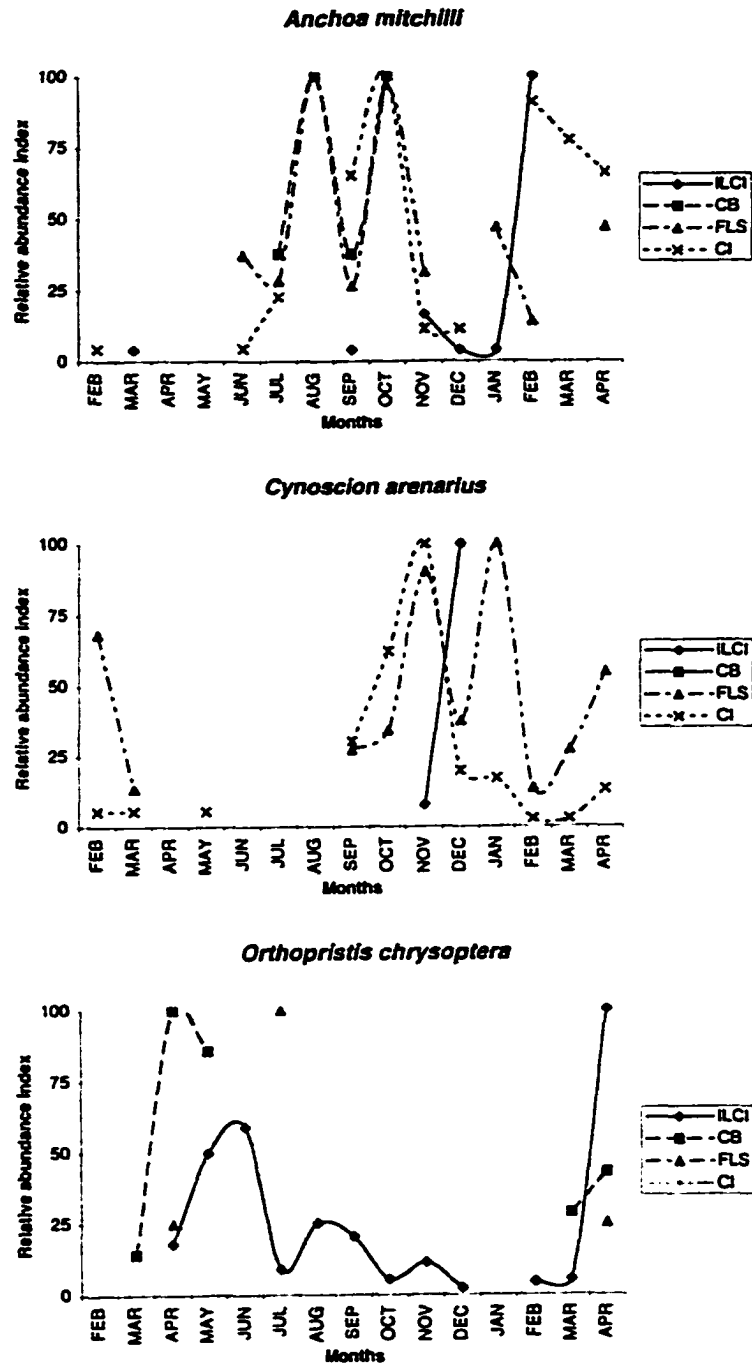


Fig. 3.29 Temporal variation in relative abundance of the occasional species in each ecological subsystem in Terminos Lagoon. ICLI = Inner littoral of Carmen island, CB = Central Basin, FLS = Fluvial lagoon systems and CI = Carmen inlet. *Anchoa mitchilli* (bay anchovy), *Cynoscion arenarius* (band seatrout) and *Orthopristis chrysoptera* (pigfish).

A. mitchilli (bay anchovy) is a cyclical visitor in all four ecological subsystems. Ayala Pérez et al. (1997) studied this species in the Palizada fluvial lagoon system in Terminos lagoon and reported that it was broadly distributed in the Palizada system, in Terminos Lagoon and on the continental shelf. They suggested that these three areas are used for feeding, maturation, and reproduction, respectively.

3.5.3.2 *Cynoscion arenarius* (sand seatrout)

This species was classified as a cyclical or seasonal visitor *in* Carmen inlet and an occasional visitor in the inner littoral of Carmen Island and fluvial lagoon systems. *Cynoscion arenarius* (sand seatrout) occurred primarily in the two inlets where it achieved a high density. In Terminos lagoon this species was reported as a typical resident of the Carmen inlet, a seasonal visitor in the fluvial lagoon systems and an occasional species both in the central basin and the inner littoral of Carmen Island (Yáñez-Arancibia et al., 1985b). It was also reported as common in the Candelaria-Panlau fluvial lagoon system (Ayala-Pérez et al., 1998).

The relative abundance index showed an important peak in Carmen inlet (Fig. 3.29), which is a nursery area with organisms between 30 and 173 mm TL. The spawning areas for *C. arenarius* is in the adjacent inner shelf during February-April and July-September and the alevins entered the lagoon for growth and protection (Yáñez-Arancibia and Sanchez Gil, 1986; Tapia Garcia et al., 1988). This species occurred in the lagoon during the rainy season and to a much less extent in the dry season (Figs. 3.18 and 3.19). *C. arenarius* occurs frequently in the demersal fish communities in the adjacent inner shelf. Seasonal variations in numerical and biomass distribution and abundance were not marked and it was captured regularly during the whole year in the continental shelf (Yáñez-Arancibia and Sanchez Gil, 1986; Tapia Garcia et al., 1988).

3.5.3.3 *Orthopristis chrysoptera* (pigfish)

This species had a low capture frequency in individual subsystems as well as in the whole lagoon. It was a cyclical visitor in the inner littoral of Carmen Island, central basin and fluvial lagoon systems. However, it is a typical species in areas of permanent marine influence with sea grass meadows (Fig. 3.20). *Orthopristis chrysoptera* (pigfish) was characteristic in areas with persistent marine influence with seagrass meadows in the inner littoral of Carmen Island and the east and southeast shore areas of the lagoon (Moore and Wetzel, 1988). This species was also reported as common in seagrass meadows of North Carolina (Petrik and Levin 2000). It had been categorized as typical resident species in the inner littoral of Carmen Island, a cyclical visitor in the central basin and an occasional visitor to the fluvial lagoon systems (Yáñez-Arancibia et al., 1985b)

The relative abundance index had two peaks in the inner littoral of Carmen Island in the dry season (Fig. 3.29). The first occurred from May to June and the second in April 1981. This area was a nursery and feeding area for small individuals (Fig. 3.21). The spawning area of this species is in the adjacent inner shelf, where it has been captured up to 269 mm TL (Yáñez-Arancibia et al., 1985a; Yáñez-Arancibia and Sanchez-Gil, 1986). Yáñez-Arancibia et al. (1985b) reported that *O. chrysoptera* enters the lagoon cyclically primarily in the inner littoral of Carmen Island through the Puerto Real inlet using shallow areas with *Thalassia testudinum* and *Rhizophora mangle* to complete part of its life history.

3.5.3.4 *Diapterus rhombeus* (caitipa mojarra)

This species was dominant in two ecological subsystems and an occasional visitor based on its frequency. *Diapterus rhombeus* (caitipa mojarra) occurred mainly in

the Candelaria-Panlau fluvial lagoon system where it had high mean density. Ayala-Pérez et al. (1998) characterized it as an ecological dominant in this system. This species has been classified as typical resident of the fluvial lagoon systems and seasonal visitor in the inner littoral of Carmen Island, Carmen inlet and the central basin (Yáñez-Arancibia et al., 1985b). This species occurs year-round in Sepetiba Bay, Brazil, where it uses the system as nursery and feeding grounds in various stages of its life history (Santos and Araujo, 1997).

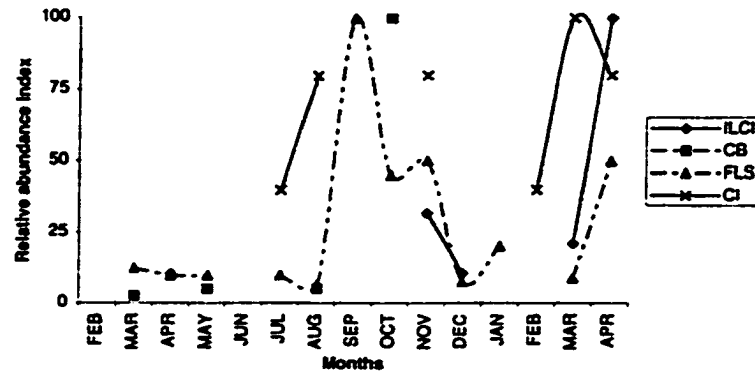
Figure 3.30 shows the variation of the relative abundance index in the ecological subsystems. There was a peak in the fluvial lagoon systems in September and March 1981 in Carmen inlet. The population consisted mainly of juveniles that used the lagoon for feeding and protection (Fig. 3.23). Aguirre León and Yáñez-Arancibia (1986) studied the family Gerreidae and reported that *D. rhombeus* was the second most abundant of the family. It uses the lagoon for feeding and nursery. In general the juveniles were in phase I and II of gonadic maturation with few individuals in phase III (Nikolsky, 1963). *D. rhombeus* is a cyclical visitor in the lagoon and it probably spawns in the adjacent continental shelf during spring to summer. It enters to the lagoon to grow, mature and feed and returning to the shelf to reproduce (Aguirre León and Yáñez-Arancibia, 1986).

3.5.3.5 *Stellifer lanceolatus* (star drum)

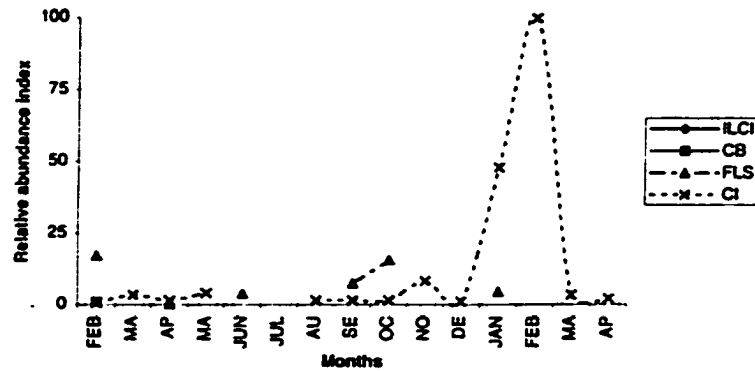
This species was restricted to areas with fluvial influence and Carmen inlet. *Stellifer lanceolatus* (star drum) was limited to the area Carmen inlet that is affected by river discharge. This species has been reported in estuarine sub-regions influenced by freshwater discharge of the Tomoka Basin/River near Ponce de León inlet, Florida (Paperno et al. 2001). In Terminos Lagoon, this species was classified as typical

Occasional Visitors

Diapterus rhombeus



Stellifer lanceolatus



Cetengraulis edentulus

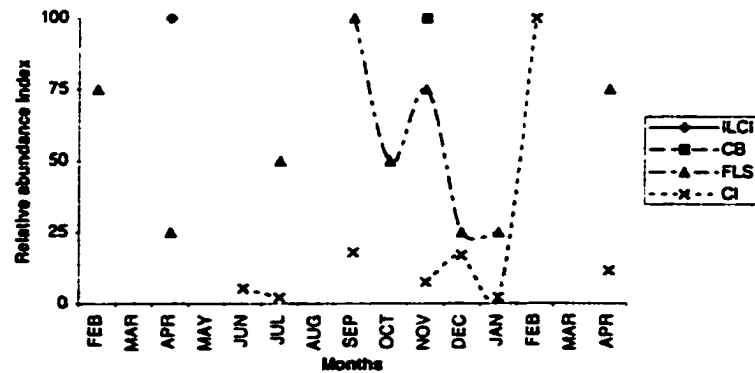


Fig. 3.30 Temporal variation in relative abundance of the occasional species in each ecological subsystem in Terminos Lagoon. ICLI = Inner littoral of Carmen island, CB = Central Basin, FLS = Fluvial lagoon systems and CI = Carmen inlet. *Diapterus rhombeus* (caitipa mojarra), *Stellifer lanceolatus* (star drum) and *Cetengraulis edentulus* (Atlantic anchoveta).

resident of Carmen inlet and an occasional visitor of the fluvial lagoon systems (Yáñez-Arancibia et al., 1985b).

The relative abundance index showed one peak at the end of the norte season and beginning the dry season in Carmen inlet (Figs. 3.24 and 3.30). This species used the lagoon as a nursery and feeding ground and its pattern was very similar to *Cynoscion arenarius* in the adjacent continental shelf (Yáñez-Arancibia and Sanchez Gil, 1986; Tapia Garcia et al., 1988). Therefore it is a marine species with estuarine dependent and an occasional visitor.

3.5.3.6 *Cetengraulis edentulus* (Atlantic anchoveta)

This species had an irregular behavior in the relative abundance index in the inner littoral of Carmen Island and central basin (Figs. 3.24 and 3.30). However, there were low numbers in the fluvial lagoon systems and Carmen inlet. During the rainy season, there was a peak in the fluvial lagoon systems and in February in Carmen inlet (Fig. 3.30). *Cetengraulis edentulus* (anchoveta) presented a distribution associated to the connection inlets in Terminos lagoon. However, it was characterized as resident species in the Carmen inlet and fluvial lagoon systems and occasional visitor of the fish communities in the inner littoral of Carmen Island and central basin (Yáñez-Arancibia et al., 1985b). This species occurs in marine waters in the adjacent continental shelf where it has been characterized as dominant (Yáñez-Arancibia and Sanchez Gil, 1986). It enters the lagoon infrequently during the dry and norte seasons. A similar behavior for this species was reported in the Orinoco delta, Venezuela (Cervigon, 1985). Therefore this is a marine species with estuarine dependence and an occasional visitor.

3.5.4 Population Structure

The size composition of fish populations in Terminos Lagoon is an indicator of the ecological role of these species in the lagoon. Species that are permanent residents have a wide range in size, from large adults to smaller pre-adults and juveniles, indicating that these species complete their entire life cycle in the lagoon. When species are represented by individuals of a small size, this indicates that they are pre-adults or juveniles that use lagoon habitats for protection of predators, as feeding grounds and nursery areas. When a species is represented only by large size individuals, it indicates that these individuals are adults that enter the lagoon as cyclical or occasional visitors to feed. These adults could also be in post or pre-reproductive stages.

The sequential use of different ecological subsystems during different stages of a species life history allows an optimal use of the resources and helps avoid factors as predation, inter and intra- specific competition, and cannibalism. The dominant fish species, which occurred widely in the four ecological subsystems, have a wide size distribution from juvenile organisms to adults. These include *Cathorops spixii* (mandamango catfish), *Sphoeroides testudineus* (checkered puffer), *Ariopsis felis* (hardhead sea catfish) and *Bairdiella chrysoura* (silver perch). *Eucinostomus gula* (silver jenny) occurred in all four subsystems but its population was made up mainly of juveniles.

The species that were dominant in three ecological subsystems are cyclical or occasional visitors. Some enter the lagoon as juveniles, for example *Archosargus rhomboidalis* (sea bream), and *Chaetodipterus faber* (Atlantic spadefish). *Anchoa mitchilli* (bay anchovy) by comparison had a very uniform size structure.

The fish that were dominant species in two ecological subsystems were mainly juveniles, such as *Cynoscion arenarius* (sand seatrout) and *Diapterus rhombeus* (caitipa mojarra). But *Orthopristis chrysoptera* (pigfish) was represented by some large individuals (up to 200 mm LT).

Finally the species dominant in a single ecological subsystem were generally juveniles, for example *Stellifer lanceolatus* (star drum), *Citharichthys spilopterus* (bay whiff) and *Cetengraulis edentulus* (Atlantic anchoveta), which were all associated with Carmen inlet. In contrast, *Cyclichthys schoepfi* (striped burrfish) occurred mainly as adults in the inner littoral of Carmen island.

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CHAPTER 4. ESTUARINE NEKTON ASSEMBLAGES COUPLED WITH HABITAT HETEROGENEITY: INTERACTIONS BETWEEN PRIMARY AND SECONDARY PRODUCTION

4.1 Introduction

In Chapters 2 and 3, I presented information on the Terminos Lagoon fish community. In this chapter, in order gain a better understanding of the details of how fishes use specific habitats, I present a more detailed descriptive analysis of fish use in two high salinity habitats seagrasses in Puerto Real Inlet and seagrasses and fringing mangroves in the inner littoral of Carmen Island.

Coastal areas are transition zones with strong interactions among the sea, low, wetland, terrestrial habitats, and rivers. These interactions strongly affect the dynamics of the environment and result in a high diversity of habitats. Each habitat is characterized by specific physical characteristics and biological assemblages (Nixon, 1982; Yáñez-Arancibia and Day, 1982, 1988a; Day and Yáñez-Arancibia, 1985; Yáñez-Arancibia, 1986; Day et al., 1989; Kjerfve, 1994). Coastal lagoons and estuaries are ecologically important and widespread types of coastal systems. These are open systems that are subsidized by physical processes (Odum, 1980). There is important exchange of biological and non-biological material with adjacent ecosystems, including water, salts, nutrients, sediment, and organisms (Childers et al., 2000).

There is a high degree of variability in coastal lagoons and estuaries. Salinity changes with tide and river flow, water levels fluctuate, the intertidal area is subject to wetting and drying and extremes of temperature, deltas grow and erode, and barrier island shift (Day et al., 1989 and 2000). But estuarine organisms have developed physiological and behavioral patterns to deal with this dynamic environment (Yáñez-Day and Arancibia, 1985; Day et al., 1989). These ecosystems have a high diversity of

habitats, which are used as feeding, reproduction or spawning grounds by many different species, especially fish. These factors lead to ecologically complex systems characterized by a high diversity of environmental factors, species, and habitats. There is also a high connectivity in food webs and high diversity of coupling both internally and with neighboring systems (Day and Yáñez-Arancibia, 1985).

Many tropical coastal nekton use coastal lagoons during part or all of their life history. Fish are the main component of nekton and they have different migration patterns related to their ecological strategies. Coastal wetlands serve as both seasonal residence and nursery habitats for many estuarine dependent fishes and invertebrates such as penaeid, drums, snappers, and many others (Weinstein, 1979, 1985; Blaber and Blaber, 1980; Herck and Orth, 1980; Yáñez-Arancibia et al., 1980; Day et al., 1982a; Livingston, 1982, 1985; Zimmerman and Minello 1984; Boesch and Turner, 1984; Deegan and Thompson, 1985; Lewis et al., 1985; Claridge et al., 1986; Pinto, 1987, 1988; Robertson and Duke, 1987; Thayer et al., 1987; Boehlert and Mundy 1988; Yáñez-Arancibia and Lara-Domínguez, 1988; Yáñez-Arancibia et al., 1988a, 1993, 1994, 1998; Bell and Pollar, 1989; Baltz et al., 1993, 1998; Sedberry and Carter, 1993; Chesney et al., 2000; Raposa and Oviatt, 2000).

Coastal lagoon estuarine systems have high ecological and economic value in terms of such factors as fish production, wetland health, wildlife natural protected areas, potential for water quality improvement and freshwater storage, agriculture and tourism (Reyes et al., 1993; Day et al., 1999; Chesney et al., 2000; Yáñez-Arancibia 2000). Despite these high values, there are serious environmental problems in many lagoon-estuarine ecosystems. The most important are: subsidence due to drainage, urban expansion, lowered freshwater input, which can lead to reduced accretion and high

salinity intrusion, water quality deterioration, and decreased biological production (Boesch et al., 1994; Day et al., 1995, 1997; Coleman et al., 1998). These problems are the result of habitat destruction in tropical coastal wetlands (Diegues, 1999), blocking the influence of pulsing events such as storms and river floods that lead to accretion (Botero and Salzwedel, 1999; Day et al., 2000), higher net biological production (Windevoixhel et al., 1999), and enhanced delta building (Mendelssohn and McKee, 1988; Day et al., 1997).

There appears to be an empirical correlation between primary production and fisheries yields in a great variety of marine systems, which is similar in slope to that found in large lakes. However, the yield of marine systems at any given level of primary production appears to be 10 – 20 times greater. The yield of lagoon fisheries per unit area is commonly as high or higher than that from the most productive coastal and offshore fisheries (Nixon, 1982).

Pollution, improper management, and the economics of large-scale offshore fishing often reduce, destroy, and degrade the fishery potential of coastal waters, which were once prized for their seafood. There is little, if any, evidence that the primary production of such lagoons has decreased during the past 100 years, and if coastal lagoons were more effectively managed they could continue to support important fisheries might (Nixon, 1982).

Day et al. (1982a) suggested that nekton species, especially larval and juvenile forms preferentially seek out shallow waters adjacent to wetlands such as marsh ponds, tidal creeks, and the marsh edge in general. Data from Barataria Bay and Lake Pontchartrain, LA shows that nekton biomass is 7 to 12 times higher in shallow water marsh areas as compared with open waters. Moreover, they stated that the evidence

from Barataria Bay suggests that wetlands enhance fisheries productivity. The picture is certainly not complete and we know that very few nekton species are absolutely dependent on estuaries or wetlands (Blaber, 1985). However, the available data do suggest specific ways that nekton use wetlands. It is probable that many nektonic species have evolved behavioral patterns that allow them to exploit wetlands as both food sources and habitat.

Stimulated by nutrients from the Mississippi River, the vast coastal wetlands of the river's past and present deltas interface with the Gulf of Mexico to form a complex and prolific coastal, ecosystem. This ecosystem has been heavily exploited and significantly altered over the years to meet the demands for coastal development, seafood production, navigation, oil exploitation, flood control, and other social, economic, and industrial activities (Chesney et al., 2000). Over the past 46 years, fisheries yields from Louisiana water have remained strong. Although quantitative data are lacking to examine more than a few decades of environmental changes, an analysis of fishery-independent trends for selected inshore species of nekton over a recent 21-yr period suggests that many species have been remarkably resilient to significant changes in their habitats and pressures from exploitation (Chesney et al., 2000).

Baltz et al. (1993) established that high density of fish larvae and juveniles near the marsh edge confirmed the importance of marsh edge ecotone as a nursery for many estuarine dependent fish. Orth (1992) provided a brief overview of some of the major factors regulating faunal abundance in seagrass meadows. Plant-animal interactions are related to the role of refuge and habitat complexity; habitat selection processes; hydrodynamics and larval supply; and chemical cues. Horn (1992) described the

feeding and digestive mechanisms in herbivorous fishes and reviewed recent studies of the consumption and digestion of benthic algae and seagrass in this group.

Benfield and Minello (1996) reported that elevated turbidity is a pervasive characteristic of shallow estuarine systems throughout the world. Studies on the effects of turbidity on predator-prey interactions have generally revolved around the influence of suspended sediments on a predator's reactive distance. Reactive distance has been defined as either the maximum distance at which visual predators can detect their prey or a maximum distance at which they will pursue their prey. This distance can be a function of many factors including predator size, prey size, prey movements and turbidity.

4.1.1 The Problem

The sequential use of habitats by migrating marine and estuarine fish is an important mechanism maintaining higher fisheries in tropical coastal lagoons. The specific mechanisms of how this takes place are often unclear. I will address this issue for high salinity and seagrass and mangrove habitats in Terminos Lagoon.

Terminos Lagoon is located in the southern Gulf of Mexico at 18° N. There are three climatic seasons: a rainy season from June to September, winter frontal storms (norte) from October to January/February, and a dry season, from February to May/June. Terminos Lagoon is the largest coastal waterbody associated with the Usumacinta Delta. The Usumacinta-Grijalva River has the second highest discharge in the Gulf of Mexico after the Mississippi/Atchafalaya system. The area is one of the world's best known tropical estuaries (e.g., Yáñez-Arancibia and Day, 1988b; Yáñez-Arancibia et al., 1988b, 1993; Vera Herrera et al. 1988; Rojas Galaviz et al., 1992). In terms of functional characterization, this area of 2500 km² can be divided into three regions (Fig. 4.1) following Kjerfve (1989, 1994) and Yáñez-Arancibia (1987): 1) A tidal

river zone in the fluvial-deltaic systems characterized by lack of ocean salinity, but subject to tides; 2) A mixing zone characterized by water mass mixing and the 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. The central basin of the lagoon is the most conspicuous part of this zone; and 3) a near shore turbid zone 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 near-shore marine components that are estuarine in character, and implicitly considers the five main habitats in the system as a whole (Yáñez-Arancibia and Day, 1982 and 1988b).

4.1.2 Habitat Diversity

Yáñez-Arancibia and Day (1988b) identified 7 main habitats in Terminos Lagoon located along the semi-permanent gradients from tidal wetlands to the estuarine plume on the inner shelf and adjacent sea (Fig. 4.1). These habitats formed the basis of the ecological subsystems used for the analyses described in chapters 2 and 3.

The Fluvial deltaic systems in the southern littoral zone of Terminos Lagoon have very low salinity, high turbidity, high nutrient concentrations, silt-clay sediments, *Crassostrea virginica* reefs, riverine mangrove forests, and in some areas of clear water, submerged fresh water vegetation. In chapters 2 and 3, the fluvial lagoon systems included the areas associated with the three main rivers, which enter the southern part of the lagoon. 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 central basin

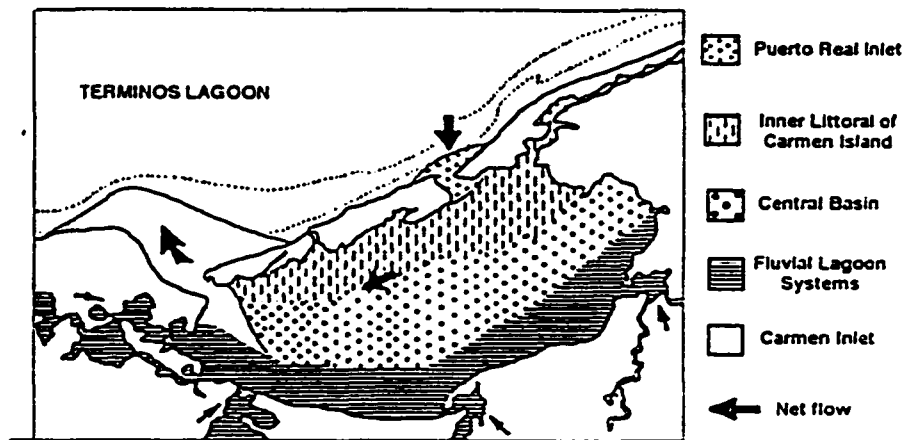


Fig. 4.1. Terminos Lagoon showing the distribution of different ecological subsystems. The lagoon consists of five major subsystems that are related to water circulation, river discharge, salinity and water depth.

was one of the four main ecological subsystems described in chapters 2 and 3. The inner littoral zone of Carmen Island is dominated by *Thalassia testudinum* and fringe mangrove habitat with near marine salinity, high water transparency, sandy sediments and a high diversity of both benthic and nektonic consumers. Puerto Real Inlet is characterized by calcium carbonate sediments, clear waters and extensive seagrass beds, where there is a net flow of Gulf water into the lagoon. Puerto Real was combined with the inner littoral area to form the inner littoral of Carmen Island subsystem. 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. This was the fourth ecological subsystem considered in chapters 2 and 3.

4.1.2.1. Functional Groups

Yáñez-Arancibia et al. (1998) described a number of important functional groups of primary producers and consumers in Terminos Lagoon. Primary producers include mangroves, seagrasses, phytoplankton, and macroalgae. Consumers include typical estuarine residents, seasonal visitors, and occasional visitors. 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. This suggest that consumers play an important ecological role by the coupling life-history strategies of their constituent species with the environmental variability and estuarine gradients.

4.1.2.1.1 Primary Producer Assemblage

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 structural habitats, such as mangrove swamps and submerged grass beds. The diversity of functional groups of primary producers can be high in estuarine ecosystems (Rojas Galaviz et al., 1992; Yáñez-Arancibia et al., 1998). Salinity gradients, turbidity, sediments, nutrients, and tidal range, control the distribution of primary producers, in the three above mentioned regions as follows:

1) The tidal freshwater deltaic areas have several important groups of primary producers including riverine mangrove swamps, submerged freshwater aquatic vegetation, and freshwater marshes. In this area, organic carbon in river input also provides an important additional food source. Phytoplankton production in this area is usually low due to high turbidity.

2) In the central basin with salinity ranges from 10 to 25, phytoplankton is the dominant primary producers. Benthic macroalgae can also be important.

3) Shallow intertidal and sub-tidal zones with high marine influence (salinity > 25) and clear waters support fringing mangroves and submerged seagrass beds.

These regions include the habitats in figure 4.1. Each region is dominated by specific primary producers, which form functional groups. The importance of these groups is that they represent a food source for estuarine and coastal consumers. They also act as a critical habitats for a great number of organisms during various life stages, and regulate important components of the estuarine chemical cycles (Odum, 1988; Day et al., 1989; Rojas Galaviz et al., 1992).

There is a clear seasonality of the pulses of abundance of different fish species and the productivity of different primary producer functional groups (Soberon Chavez et al., 1988, Rojas Galaviz et al. 1992; Yáñez-Arancibia et al., 1998). Primary production is

generally high during all year, but each functional group has a different seasonal pattern, related to the environmental parameters specific to each gradient. The main productivity peak of mangrove 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 norte seasons. Both marine and freshwater grasses start their productivity pulse at the end of the norte season. Maximal productivity of freshwater macrophytes occurs 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 level increase through the rainy season, reaching a peak during the beginning of the norte season from September until December. Aquatic primary productivity in mangrove bordered tidal channels is highest during the dry season. Day et al. (1982, 1988a, b) and Rivera-Monroy et al. (1998) showed that dissolved organic matter exported from mangroves stimulated aquatic primary productivity.

These results suggest that sequential pulses of different primary producers maintain a high year-round production in Terminos Lagoon but that the productivity peak occurs at different times for different functional groups. This seasonal programming is one of the functional processes sustaining high estuarine production.

4.1.2.1.2 Macro-Consumer Assemblages

I addressed the functioning of these fish assemblages generally in the lagoon in chapters 2 and 3. In this chapter, I will describe fish utilization in more detail for seagrass and mangrove systems in the high salinity area of the lagoon.

The primary producers discussed above and the dynamics of the ecological systems summarized in earlier sections, contribute to a high diversity of nektonic species, which was assessed by different abundance models and species diversity indices for each habitat in chapter 2. There seem to be clear fish-habitat relationships and a sequential use of the gradients in various time/space scales (Yáñez-Arancibia and Lara-Dominguez, 1988; Yáñez-Arancibia et al., 1988, 1993, 1998 chapters 2 and 3).

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 groups from Campeche Sound, i.e., the adjacent continental shelf (Yáñez-Arancibia et al., 1985 Sanchez-Gil and Yáñez-Arancibia, 1986). The widespread use of estuaries by larvae and juveniles of so many species has lead 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. Recruitment is defined 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; Yáñez-Arancibia et al., 1998; Velasco and Wolff, 2000).

The 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. 4.2) as was established in Chapter 3 on the dominant fish populations and discussed by Pauly and Yáñez-Arancibia (1993): 1) Resident or typical estuarine species: Those that spend their entire Life history within the system, 2)

Seasonal or cyclical visitors: Those that 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 that 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 that spend their entire life cycle on the inner sea shelf under the estuarine plume influence; and 5) Freshwater, estuarine-related species. Those that spend their entire life cycle in the fluvial-deltaic river zone, associated with the upper zone of the estuarine system.

One mechanism that probably allows high standing stock to be maintained in the lagoon-estuarine ecosystem is small-scale between-habitat migration. For example, a functional group that mainly exists in the fluvial-deltaic river zone of the estuary (Fig. 4.2) might utilize the estuarine system mainly as a feeding and nursery ground. This pattern is similar to that of some functional groups in the inner shelf. 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 (Yáñez-Arancibia et al., 1993, 1998).

For 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., 1994). Rather, seasonal variations of abiotic parameters such as temperature and salinity which were related to season coupled with fish migration (Chapter 3, factor analysis). Fishes adjust to the seasonal changes of primary production and of competitors through the phenomenon called "seasonal programming" (of consumers) which refers to the temporal and spatial sequence of lagoon-habitats used by juveniles and pre-adult fishes (Pauly and Yáñez-Arancibia, 1994). Fish

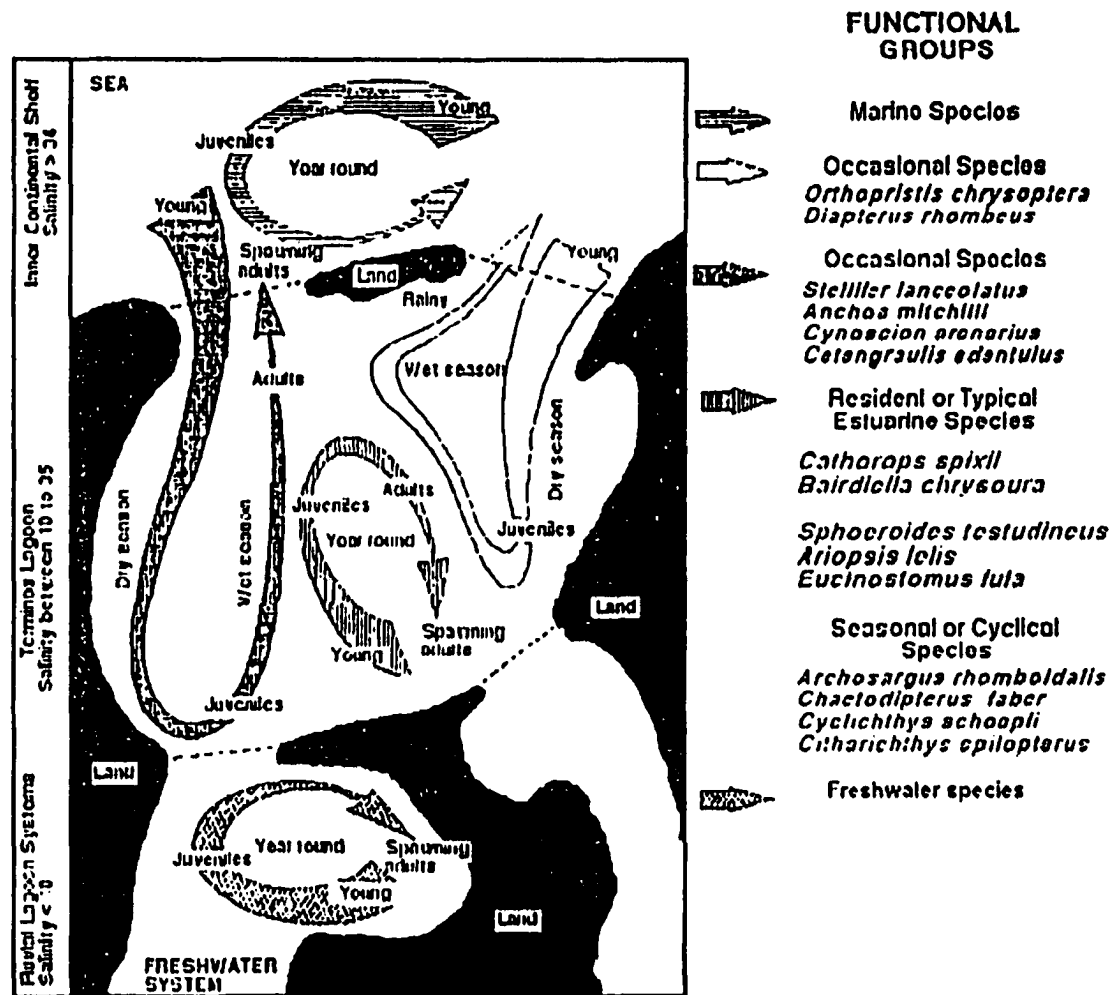


Fig. 4.2. Diagrammatic representation of functional groups of fishes with characteristic migration patterns and habitat utilization of Terminos Lagoon (modified from Pauly and Yáñez-Arancibia, 1994; Yáñez-Arancibia et al., 1998).

migration also allows optimum utilization of primary production. Fish tend to visit different habitats during periods of peak primary production (Yáñez-Arancibia et al., 1993, 1998; Laegdsgaard and Johnson, 2001). This ensures high food availability and thus high fish growth rates.

4.1.3 General Objective

Describe the seasonal biomass variation for each dominant fish species in each habitat and the relationships with patterns of primary production.

- **Specific Objectives**

To describe the importance of the relationship between Puerto Real Inlet and the inner littoral of Carmen island (Estero Pargo) in the dominant fish life history.

To describe the synchrony of habitat utilization through the year by the dominant fish life history and its relation to primary production. In chapters 2 and 3, I discussed broad patterns of fish community structure and habitat utilization. In this chapter, I address these patterns in a more detailed analysis of the utilization of mangrove and seagrass habitats in two marine influenced areas.

4.2 Study Area

Terminos Lagoon is a large (about 1700 km² for the lagoon surface area surrounded by about 2500 km² of mangroves and freshwater wetlands), shallow (mean depth 3.5 m) coastal lagoon located at the base of the Yucatan Peninsula in the state of Campeche, Mexico (Fig. 4.3). The lagoon is separated from the Gulf by Isla del Carmen and water exchange with the Gulf occurs through two deep inlets. There is a mixed diurnal tide with a range of about 0.5 m. Trade winds induce a net inflow into the lagoon through the eastern inlet at Puerto Real, and a net outflow through the western inlet at

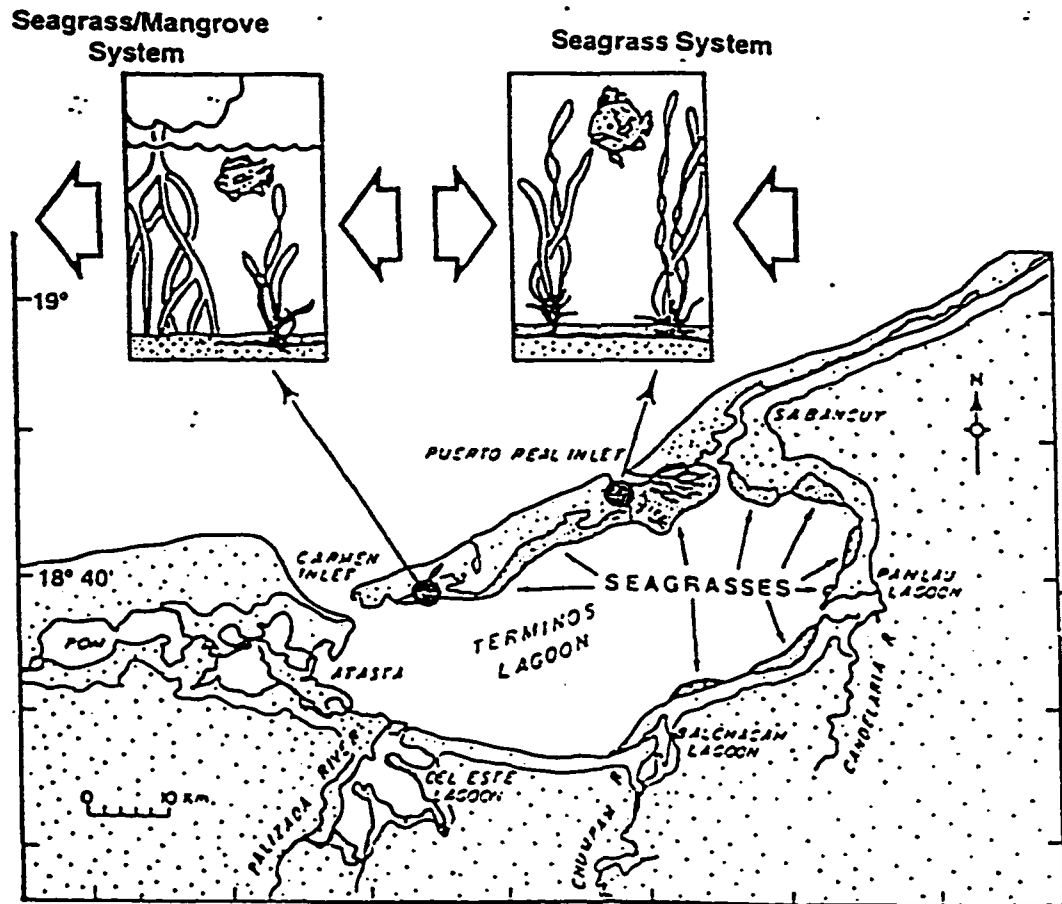


Fig. 4.3. Terminos Lagoon showing the locations of the seagrass system in Puerto Real inlet and the seagrass/mangrove system in Estero Pargo (modified from Yáñez-Arancibia et al., 1993).

Carmen (Mancilla and Vargas, 1980; Graham et al., 1981; Kjerfve et al., 1988). This net flow has resulted in the formation of a flood-tide delta in the lagoon at Puerto Real inlet and an ebb-tide delta in the Gulf at Carmen Inlet (Phleger and Ayala Castañares, 1971; Coll de Hurtado 1975; Gutierrez Estrada and Castro del Rio, 1988).

Climatically, this tropical area is characterized by three seasons with distinct patterns in precipitation, river discharge, winds and temperature (Yáñez-Arancibia and Day, 1982): the dry season from February to May, the rainy season from June to September, and the "Nortes" season from October to January. Rainfall is very low during the dry season (66.1 mm/month), occurs during afternoon and evening thunder showers in the rainy season (289.0 mm/month) and is associated with frontal systems during the norte season (175.2 mm/month).

The same rainfall pattern occurs over the drainage basin of the lagoon resulting in a similar pattern of river discharge with peak discharge in the months of September, October and November. Three main rivers discharge to the lagoon: the Candelaria, the Chumpan and the Palizada (a tributary of the Usumacinta River; Phleger and Ayala-Castañares, 1971; Amezcua Linares and Yáñez-Arancibia, 1980; Vera Herrera et al., 1988). The Palizada has the highest discharge resulting in a pronounced lowering of salinity in the western part of the lagoon.

Seagrass beds occur in shallow areas along shallow shorelines in the eastern end of the lagoon (Moore and Wetzel, 1988). *Thalassia testudinum* (turtle grass) is the most abundant species, but *Diplantera wrightii* and *Syringodium filiforme* (manatee grass) also occur. Extensive mangrove swamps dominated by *Rhizophora mangle* (red mangrove), *Avicennia germinans* (black mangrove) and *Laguncularia racemosa* (white mangrove) surround the lagoon (Day et al., 1982b, 1988b, and 1996).

Two seagrass areas were considered for this study (Fig. 4.3): Seagrass meadows in Puerto Real inlet without adjacent mangroves, and Estero Pargo with seagrass meadows adjacent to mangrove swamps in the inner littoral of Carmen island. Puerto Real inlet connects the lagoon to the Gulf. It is a clear water marine habitat with strong tidal currents and a net flow from the Gulf to the lagoon, sandy sediments, a salinity range from 30 (December) to 37 (June), and a temperature range from 24°C (December) to 31°C (June). The dominant plants are *Thalassia testudinum* (Yáñez-Arancibia et al. 1982, 1988). Estero Pargo is a more turbid, marine-estuarine habitat with moderate tidal currents ranges from 15 (November) to 36 (May), and a temperature range from 22°C (February) to 30°C (September). The dominant plant community are intermingled *Rhizophora mangle* fringing mangrove swamps and *Thalassia testudinum* meadows (Yáñez-Arancibia and Lara-Dominguez, 1983; Yáñez-Arancibia et al. 1985c, 1993, 1998).

4.3 Material and Methods

Fish were collected with a 5.0 m shrimp otter trawl (mouth opening while fishing was 2.5 m, 19 mm mesh) with tows of 10 to 12 min at 2.0 to 3.5 knots; individual trawls covered an area of 1500 to 2000 m². Depths sampled varied but never exceeded 3.0 m. Ninety trawl tows were made in bimonthly collections from February 1981 to January 1982 in Estero Pargo (seagrass meadows and adjacent to mangrove borders). During each sampling period, tows were made every two hours over a 24-h period. In this paper, all of the data were used to describe the overall behavior of the community rather than the diurnal variation. The diurnal variability is discussed in a different publication (Yáñez-Arancibia et al., 1982; Yáñez-Arancibia and Lara-Dominguez, 1983; Yáñez-Arancibia et al., 1985c). In Puerto Real inlet a total of 168 trawl tows were made over

24-h periods in bimonthly collections from August 1980 to July 1981. Specimens were fixed in neutralized 10% formalin.

In the laboratory, fish were identified, counted, weighed and measured. For each area with seagrass, the dominant fish species were determined based on the frequency (percentage occurrence), broad distribution, biomass and numerical abundance.

Biomass, density and average fish size per m² were calculated monthly for each dominant species by study area. Average fish size by species was calculated monthly by dividing total biomass by total density. An index of seasonal abundance was used to follow changes in these dominant species (Roger and Herke, 1985, Yáñez-Arancibia et al., 1988, 1993). The monthly index for each species was calculated as the average catch per month divided by the highest monthly average catch of the species, multiplied by 100. Thus the highest monthly catch for each species had an index of 100. Dominant fish populations were defined on the basis of frequency (percent of occurrence), broad distribution, weight and numerical abundance (Yáñez-Arancibia et al., 1988, 1993).

4.4 Results

In Estero Pargo, the total catch of fish was 14200 individuals from 70 species, while in Puerto Real inlet the catch was 7700 individuals from 58 species, with a total of 83 fish species for both areas. There were 45 (53%) common species in both areas, 25 (30%) were only captured in the seagrass/mangrove system and 13 (15%) only in the seagrass habitat. Among the common species which occurred in both areas were:

Harengula jaguana (scaled sardine), *Anchoa hepsetus* (striped anchovy), *Cetengraulis edentulus* (Atlantic anchoveta), *Synodus foetens* (inshore lizardfish), *Hippocampus hudsonius* (sea horse), *Prionotus carolinus* (northern searobin), *P. scitulus* (leopard searobin), *Chloroscombrus chrysurus* (Atlantic bumper), *Selene vomer* (lookdown),

Lutjanus synagris (lane snapper), *Eucinostomus argenteus* (spotfin mojarra), *Chaetodipterus faber* (Atlantic spadefish), *Chaetodon ocellatus* (spotfin butterflyfish), *Citharichthys spilopterus* (Bay whiff), *Etropus crossotus* (fringed flounder), *Aluterus schoepfi* (orange filefish), *Sphoeroides greeleyi* (green puffer), *S. spengleri* (bandtail puffer). There were a larger number of exclusive species in Estero Pargo (30%) than in Puerto Real inlet likely because more of the species in Puerto Real were marine and were only captured in this area. The greater number of exclusive species in the seagrass/mangrove system suggests that it had more species in common with the other ecological subsystems of the lagoon.

The dominant or typical species of each community were identified on the basis of abundance, biomass and high frequency (Table 1 and 2 Appendix C). At Puerto Real inlet there were 21 dominant species and at Estero Pargo system there were 18 dominant species. Only 39% of the dominant species occurred in both sites. This was related to species composition. At Puerto Real inlet 48% were marine species, 36% marine-estuarine, and 16% estuarine. At Estero Pargo system 6% were freshwater species 22% estuarine, 66% marine-estuarine and only 6% marine.

Figure 4.4A and B gives the index of seasonal abundance for seven dominant species common at both sites. In Puerto Real inlet there was a tendency of high abundance during the rainy and norte season (June to December, Fig. 4.4A), while in Estero Pargo system the trend was of higher species abundance late in the norte season and during the dry season (December to March, Fig. 4.4B). Non-dominant species also followed this tendency in the two systems.

4.5 Discussion

Seagrass and mangrove habitats in tropical and subtropical areas in the middle western Atlantic are used by many species of nekton and are generally characterized by high fish abundance and diversity. The literature on these two topics is broad and the reader is referred to Yáñez-Arancibia and Lara-Domínguez (1983), Livingston (1984) and Weinstein (1985), Baltz et al. (1993 and 1998), Sedberry and Carter (1993), Kuenen and Debrot (1995), Louis et al. (1995), Loneragan et al. (1997), Primavera (1997), Laegdsgaard and Johnson (1995 and 2001).

Overall patterns of biomass, density, number of species and size presented for the fish community in the results section suggest that this results as a function of the patterns of behavior of individual species. Pauly and Yáñez-Arancibia (1994) reported that when specific species is considered, it is apparent that the use of different habitats has strong seasonal programming.

In both areas, the results suggested that the sequential utilization of the two habitats by fishes is different. In general, fishes in the seagrass system in Puerto Real inlet were larger (mean size in biomass = 58.8 g per individual for all the community) while those captured in the seagrass/mangrove system at the inner littoral of Carmen island were smaller (mean size in biomass = 21.0 g per individual) (Yáñez-Arancibia et al., 1993; Laegdsgaard and Johnson, 1995). This reflects the predominance of juvenile and pre-adult fishes in the Estero Pargo area compared to mainly adult fishes at the Puerto Real inlet. This pattern is also seems evident when the index of relative seasonal abundance of individual dominant species is considered (Fig. 4.4). The dominant species captured in the seagrass system were found more often in the inlet during the end of wet season and all of the norte season. In the seagrass/mangrove system,

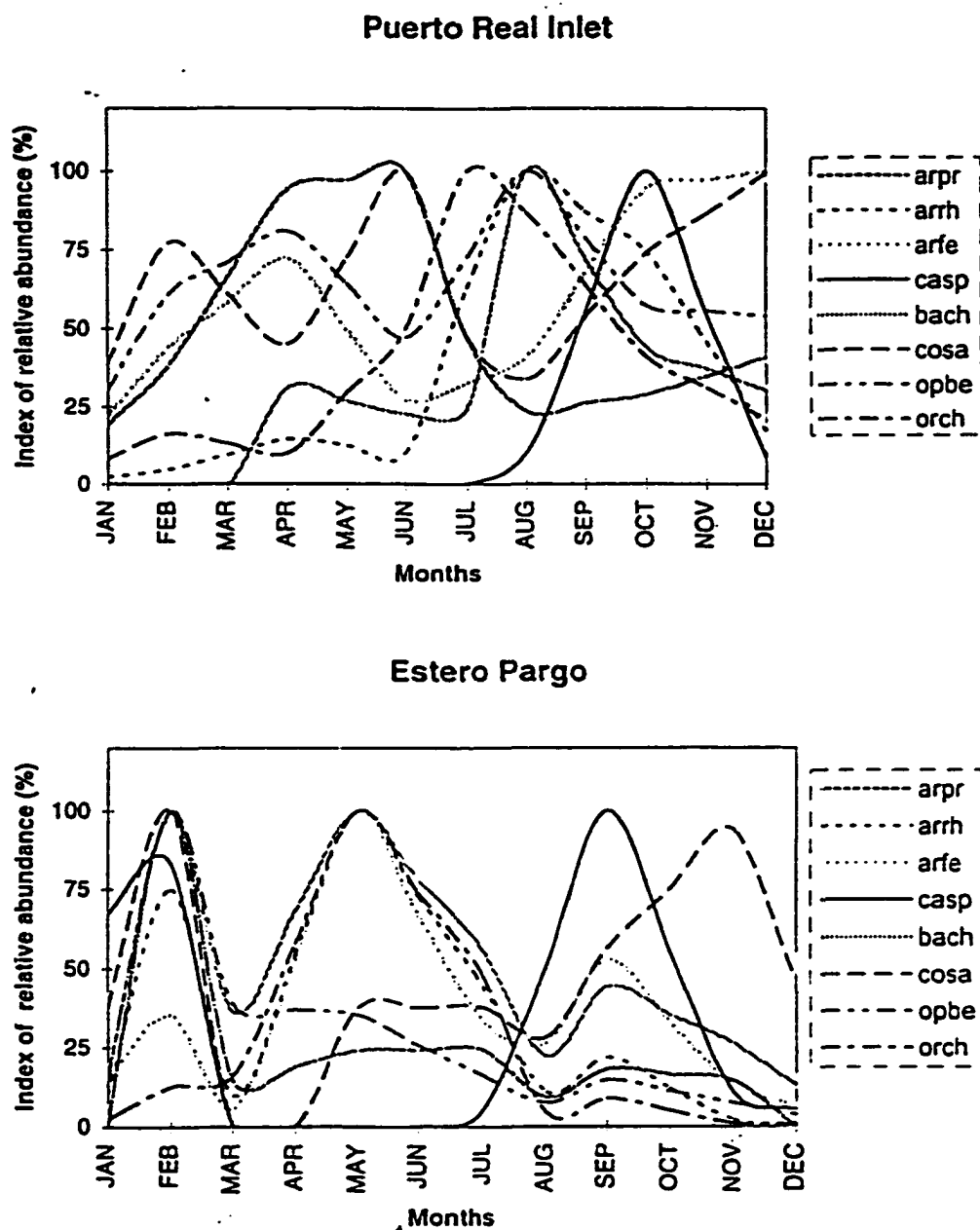


Fig. 4.4. Temporal variation in the index of seasonal abundance of dominant fish population assemblages from trawl catch in A) The seagrass system, and B) the seagrass/mangrove system. opbe = *Opsanus beta*, orch = *Orthopristis chrysoptera*, bach = *Bairdiella chrysoura*, cosa = *Corvula sanctae-luciae*, arrh = *Archosargus rhomboidalis*, arpr = *Archosargus probatocephalus*, casp = *Cathorops spixii*, arfe = *Ariopsis felis*.

relative abundance tended to be high for all the community at the end of the nortes and during the dry season. This suggests that larger fish captured in the inlet use the seagrass beds mainly as an area of transit. The movement into and through the inlet during the norte season is likely facilitated by the strong net inflow, especially during frontal passages (Kjerfve et al., 1988). The results in the seagrass/mangrove system of the inner littoral of Carmen Island suggest that is used mainly as a nursery. The combination of calm water, high organic matter content, mangrove and seagrass habitat, and high densities of invertebrates likely makes this a rich nursery area (Yáñez-Arancibia et al., 1991, 1993; Sedberry and Carter, 1993).

Similar patterns of the use of estuarine habitats by migratory nekton species has been shown for a wide variety of coastal systems (Boehlert and Mundy, 1988; Shaw et al., 1988). For Terminos Lagoon Chavance et al. (1986), and Yáñez-Arancibia and Lara-Dominguez (1988) have documented life history patterns for different dominant species. There are a number of advantages of using estuarine habitats including protection, calm waters, abundant food resources, and a diversity of habitats (Boehlert and Mundy, 1988; Shaw et al., 1988). Our results suggest that adult fish enter the lagoon through Puerto Real inlet in the fall during the wet and norte seasons and spawn near shore in the vicinity of the inlets or in the inlet itself. This indicates that eggs and larvae are swept into the lagoon and distributed widely by prevailing currents. Thus, my findings and reports in the literature, suggest that there are at least three patterns of use of the seagrass and mangrove habitats in Puerto Real inlet and the inner littoral of Carmen island: (I) There are marine species which spawn in or near the inlet and the eggs and larvae are transported into and distributed throughout the lagoon by the predominant currents. *Archosargus rhomboidalis* (sea bream) and *Orthopristis chrysoptera* (pigfish)

are two important species which follow this pattern. (2) There are estuarine-marine species that spawn in different habitats of the lagoon and migrate to the seagrass/mangrove system as a nursery area, e.g. *Bairdiella chrysoura* (silver perch), *Cathorops spixii* (mandamango sea catfish), and *Ariopsis felis* (hardhead sea catfish). (3) Finally, there are species that complete their life history in the inlet seagrass and seagrass/ mangrove systems, e.g. *Urolophus jamaicensis*, *Opsanus beta*. A number of these species use other habitats in the lagoon during their life histories as described in chapters 2 and 3. For example, *Sphoeroides testudineus* (checkered puffer) is a typical marine estuarine-dependent species which spawns in the adjacent inner shelf. It enters to the lagoon via the two inlets and uses the fluvial lagoon systems as nursery areas, while the inner littoral of Carmen Island is an area for pre-adult feeding and maturation (Mallard-Colmenero et al., 1982). A similar pattern is suggested that *Eucinostomus gula* (silver jenny) followed in the lagoon as was described in Chapter 3.

It seems clear that life history patterns have evolved to ensure the distribution, migration, biomass, and habitat use in an optimal manner (Blaber 1985, Velasco and Wolff 2000). But which factors have influenced the evolution of these patterns? It has been found that there is a strong relation between the life history patterns of migratory fish and the patterns of primary production (Yáñez-Arancibia et al. 1993, Fig. 4.5). In general, fish tend to use habitats during periods of high primary production (Reyes et al., 1993).

I illustrate this pattern with the index of relative abundance of the dominant fish species that use inlet seagrass meadows and the seagrass/mangrove systems in the inner littoral of Carmen Island. The index of seasonal abundance suggests that the period of greatest relative abundance of the species of the inlet area was during the

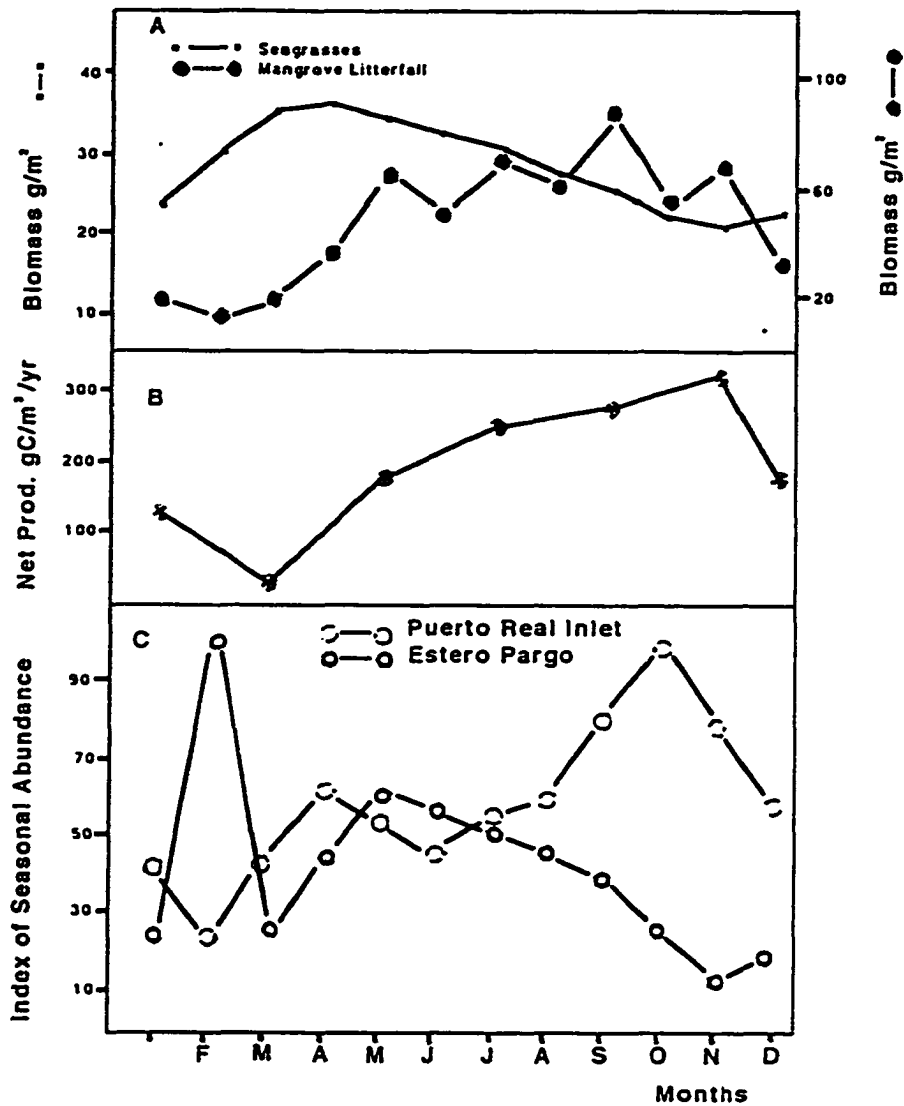


Fig. 4.5. A) Temporal variation of plant biomass in the seagrass and seagrass/mangrove systems. B) Temporal variation of total net primary productivity in Terminos Lagoon, C) Monthly index of seasonal abundance of fishes in seagrass and seagrass/mangrove systems. (Aquatic primary productivity data from: Day et al., 1982b and 1988a; seagrass productivity data from Day et al., 1982; Moore and Wetzel, 1988; and Soberon Chavez et al., 1988; mangrove productivity data from Day et al., 1982b; 1987, 1988b; modified from Yáñez-Arancibia et al., 1993).

rainy season, June to October (Fig. 4.5). The fish which occur there are mainly adults, many of which spawn in or near the inlet and the eggs and larvae are swept into the lagoon. These eggs and larvae arrive at a time when there is a high availability of organic matter in the central lagoon (Day et al., 1988a). This was due to high levels of phytoplankton productivity at that time as well as to high river input (Day et al., 1982, 1988a; Soberon-Chavez and Yáñez-Arancibia, 1985; Deegan et al., 1986, Rivera-Monroy et al. 1998). Thus it is likely that the young fish feed directly and indirectly on these sources of organic matter in the open waters of the lagoon.

With the end of the rainy season, river flow diminishes thus reducing river input of organic matter and nutrients (Day et al., 1982, 1988a). Aquatic primary productivity in the central lagoon is lowest during the dry season probably because of low nutrient input from the river (Day et al., 1988a). In contrast to the open lagoon waters, tidal creeks and shallow waters associated with seagrass beds and mangroves have the highest levels of aquatic primary productivity during the dry season (Fig. 4.5, Estero Pargo system). Studies have shown that this high level of production is at least partially the result of stimulation of primary production by water draining from mangroves (Day et al., 1987, 1988b; Rivera-Monroy 1995). In addition, the productivity of seagrasses is highest during the dry season as a result of higher water clarity (Fig. 4.5, Day, et al., 1982; More and Wetzel, 1988).

During the dry season, the density and biomass of fishes tended to be highest in the seagrass/mangrove area (Fig. 4.5). The great majority of these fishes were small juveniles and pre-adults. Many of these fish immigrate from the fluvial lagoon systems to other areas such as the inner littoral of Carmen island (e.g., *Eucinostomus gula*, silver jenny and *Sphoeroides testudineus*, checkered puffer; see chapter 3). Thus the data

suggest that these organisms use the seagrass/mangrove areas during the period of highest primary production and during the most rapid growth period of the life history. Also during this season, the inner littoral of Carmen island had high species diversity values as it was described in Chapter 2.

Manickhand-Heileman et al (1998) constructed an ecopath model of 20 compartments for Terminos Lagoon (Christensen and Pauly, 1995; Braid and Ulanowicz, 1989; Christian et al., 1996). They established that total system throughput was $3710 \text{ gm}^2 \text{ year}^{-1}$ and total net primary production $2611.6 \text{ gm}^2 \text{ year}^{-1}$. Of the latter, only about 4% ($101.6 \text{ m}^2 \text{ year}^{-1}$) is grazed by herbivores and the rest enters the detrital food chain. These authors determined that the proportion of net primary production that is harvested as fisheries catch was 0.04%. The trophic flow originating from detritus was $466 \text{ gm}^2 \text{ year}^{-1}$, resulting in a detritivory:herbivory ratio of 4.6:1, a Finn cycling index of 7.0 and an average path length of 10.

Therefore, Manickhand-Heileman et al., (1998) established that the main trophic pathway in Terminos lagoon appears to be detritus → detritivores → primary carnivores → secondary carnivores. This happens in the seagrass/mangrove and seagrass systems where fish communities are highly diverse and abundant (see Chapter 2).

In relation to secondary production, they pointed out that little of the biomass produced by benthic autotrophs is consumed directly with most of the production entering the detritus food chain (Manickhand-Heileman et al. 1998). There was an intense use of detritus as a food source in the lower part of the trophic web. Among invertebrates, meiofauna and polychaetes had the highest food consumption (Yáñez-Arancibia et al., 1985b and 1986; Ayala Perez et al., 1997; Manickchand-Heileman et al., 1998), while among fish groups, the highest consumption is by Engraulidae (e.g. *Anchoa*

mitchilli, Bay anchovy) followed by Ariidae (e.g. *Cathorops spixii*, mandamango sea catfish and *Ariopsis felis*, hardhead sea catfish, Manickhand-Heileman et al. 1998). Thus, the seagrass ecosystem played important ecological roles as nursery, feeding and maturation grounds for many of the dominant species analysed in Chapter 3.

In summary, for nekton species using seagrass and mangrove habitats in Terminos Lagoon, the pattern of migration seems to be strongly coupled to patterns of primary production in the lagoon. The idea of migratory nekton species using coastal habitats because of high productivity is a generally accepted tenant of estuarine ecology (Yáñez-Arancibia, 1985, Yáñez-Arancibia et al., 1988, 1991; Day et al., 1989; Pinto 1988) but here I described specifically some mechanisms of how this occurs in Terminos Lagoon.

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CHAPTER 5. SUMMARY

In Terminos Lagoon (the largest tropical coastal lagoon in Mexico), numerous studies have addressed the ecological role of the fish community. It has been determined that fish communities are seasonally related, through structural parameters of biomass and diversity, to the different estuarine habitats. Reflecting this, the dominant species, as indicators of these relationships, are coupled to the different habitats and climatic periods during different periods of their life cycles in the lagoon. Terminos lagoon has at least 5 different ecological subsystems defined by their physical characteristics that determine the presence of different types of vegetative communities that provide habitat to fish species. They are: 1) the *fluvial lagoon systems* located in the southern area of the lagoon. This area is characterized by a permanent influence of the rivers discharging to the lagoon. This region has low salinity, high turbidity, high concentrations of nutrients, silty-clay sediments, oyster reefs and in the inner lagoons of each river, there is submerged freshwater vegetation. These areas are bordered by riverine and fringe mangrove swamps.

The *central basin* is a transition area between marine conditions and the areas directly affected by river discharge. This area has intermediate salinity, highly variable transparency, with silty-clay with mixed sand sediments. Primary production in this area is mostly by estuarine phytoplankton, but there are also important macroalgae beds located mainly in the eastern region of the lagoon. Water depth is 3-4 m.

Inner littoral of Carmen Island, is an area characterized by strong marine influence, high transparency, silt and mixed sand sediments and there are extensive seagrass meadows. The intertidal zone is covered with fringing mangrove swamps.

Two permanent inlets connect the lagoon with the adjacent continental shelf. *Carmen inlet* is typically estuarine with a net water transport toward the shelf,

producing an extensive estuarine plume mainly during rainy and norte seasons. It is characterized by high turbidity, silty clay sediment and the absence of submerged aquatic vegetation.

Puerto Real inlet is characterized by a net inflow of waters from the Gulf of Mexico toward the lagoon. Sediments are mixed sands with a high calcium carbonate high content. There is high transparency and extensive seagrass meadows. There is a dynamic exchange of fish species among the different ecological subsystems of the lagoon throughout the year. This maintains high species diversity in these subsystems.

In the chapter 2, I studied the ecological structure of the fish community in Terminos lagoon using different indices. Several diversity indices based on the proportional abundance of species, which are widely used in the literature, were used are which. Four models of species abundance were used in the analysis: the Geometric model (Motomura, 1932), the logarithmic series model (Fisher, 1943), the log normal distribution model (Preston 1948), the broken stick model (MacArthur, 1957), k-dominance curves (Platt et al., 1984) and the Q statistic (Kempton and Taylor, 1976, 1978).

Biomass and density peaked in the rainy and norte seasons in Carmen inlet, the inner littoral of Carmen island and the fluvial lagoon systems, while in the central basin, peak abundance occurred during the dry season. In general, these pulses were related to the migratory movements of the different fish species. Small individuals were captured in Carmen inlet and the fluvial lagoon systems associated with low salinity, and larger sizes occurred in the central basin and the inner littoral of Carmen island, where there is high salinity. Therefore, Terminos Lagoon is a nursery and feeding ground for many marine species. They immigrate into the lagoon through the inlets

throughout the year, but mainly during the norte season when Carmen inlet and the inner littoral of Carmen Island had high numbers of individuals and density.

The diversity values in the lagoon are similar to those reported in other coastal ecosystems. The diversity indices based on the proportional abundance of species had seasonal variations related to the movements of different fish species between the lagoon and the adjacent inner shelf. However, these variations were not extreme and were between 1.35 and 2.79 for Shannon and of 1.01 at 2.42 for Whilm. The central basin generally had the lowest values for these indexes.

Carmen inlet is a highly dynamic subsystem because of its connection function between the lagoon and the Gulf of Mexico. It had high values of diversity indices, comparable to the fluvial lagoon systems and the inner littoral of Carmen island. This high diversity can be related to fish movements and high turbidity in the inlet with. This environmental feature enhances the presence of a great number of fish species of small size. Since the turbid water offers them protection from predators, their survival probability is increased.

The central basin is an area of low diversity. This area functions as a transit zone between the inlets and high salinity environments and the fluvial lagoon systems. The fish communities in this area are permanently in transit between the different ecological subsystems.

The inner littoral of Carmen Island and fluvial lagoon systems had higher values of diversity. The community in the seagrass area was generally made up of individuals of large size compared to the fluvial lagoon systems. The community in this area composed of fish species typical of clear waters with seagrass meadows. The community in the fluvial lagoon systems, by contrast, is composed of fish species typical of turbid and brackish waters.

The logarithmic series and log normal abundance distribution models produced the best fits and best explained the species distribution abundance in each ecological subsystem. The fish communities of each subsystem are composed of numerous species with intermediate abundance (among 50 and 76% of the total of species in each ecological subsystem), a few rare species, and a few with high relative abundance. Salinity was the environmental factor that most controlled the ecological diversity of the fish community in Carmen inlet, while secchi depth was the factor that best explained the ecological diversity in the inner littoral of Carmen island. In the fluvial lagoon systems, the log normal distribution model better fit the abundance distribution. Therefore, in this ecological subsystem many processes affect the ecological diversity. The multiple regression model indicated that diversity in this subsystem is influenced by salinity, temperature and probably the high concentrations of nutrients introduced in river water.

In conclusion, the fish communities are mainly composed of numerous species with intermediate abundance. This means that species diversity in the lagoon is reflected in both abundance and variety. The diversity is comparable to that in other similar ecosystems.

In chapter 3, I defined dominant fish species using at least three parameters, abundance by weight and number and frequency of capture. Nevertheless, the autoecology studies of these species were important in correlating life history stages in the different ecological subsystems. Therefore, the dominant fish species were characterized by different distribution patterns in the lagoon as related to their physiological tolerances and biological strategies. These patterns are described in the following paragraphs.

Species with wide distribution in the lagoon. These are residents or typical estuarine species, such as *Cathorops spixii* (Mandamango sea catfish) and *Bairdiella chrysoura* (Silver perch). They were present as adult and juveniles with a predictable seasonal programming of use of the different ecological subsystems of the lagoon.

Marine species with wide distribution in the lagoon. These were captured mainly as juvenile or pre-adults in the lagoon with their reproduction areas located in the adjacent inner shelf. Species in this group were *Sphoeroides testudineus* (Checkered puffer) and *Eucinostomus gula* (Silver jenny). The ecological subsystems are used for protection, nursery and maturation areas. Finally, *Ariopsis felis* (Hardhead sea catfish) occurred as adults and juveniles in all areas of the lagoon where the different habitats served as maturation areas for adults and as nursery grounds for juveniles. These three species used the adjacent inner continental shelf for spawning, probably in seagrass meadows between 10 m and 3.5 m (the average depth of the lagoon). Therefore, these species use the lagoon in a predictable way during the year.

There are several dominant fish species that have a limited distribution in the Lagoon. *Archosargus rhomboidalis* (sea bream) and *Orthopristis chrysoptera* (pigfish) are dominant in environments with permanent marine influence with seagrass meadows. *Stellifer lanceolatus* (start drum), *Cetengraulis edentulus* (anchoveta) and *Cynoscion arenarius* (sand seatrout) are typical species in the brackish, high turbidity waters of Carmen inlet. *Anchoa mitchilli* (Bay anchovy) and *Diapterus rhombeus* (Caitipa mojarra) are typical species in the fluvial lagoon systems. All these species are marine estuarine-dependents with a defined pattern of use in at least one ecological subsystem. They were captured mainly as juveniles that use the lagoon as protection and nursery grounds. They were considered as seasonal or cyclical species.

Chaetodipterus faber (Atlantic spadefish), *Citharichthys spilopterus* (bay whiff) and *Cyclichthys schoepfi* (Stripe burrfish) are marine species that enter to the lagoon seasonally. They are mainly adults and/or juveniles which use the lagoon for feeding purposes and their distribution is restricted to certain ecological subsystems. Nevertheless, these species had low frequency in the captures, they could be classified as seasonal or cyclical species in the lagoon.

It is important to emphasize the role of migration during fish life histories in how habitat is utilized. The dominant fish species with wide or restricted distribution have biological and ecological strategies highly adapted to the ecological subsystems of Terminos lagoon. Therefore, the pulses of fish abundance in each subsystem are the result of fish's biological strategies such as feeding, growth, maturation, or reproduction. These factors define the pattern of habitat use for species on spatial and temporal scales.

There were two types of habitat use for the different fish species. The first is a sequential use of the ecological subsystems by individual species. This means that there is a separation of different biological stages of a single species in different habitats. This tends to diminish cannibalism and intra-specific competition for prey. The second type of habitat use is the occurrence of high peaks of abundance at different time among different species as a result of the affinity or physiological limits for the physical-chemical characteristics of each habitat. Therefore, these different species diminish inter-specific competition and this suggests an even utilization of Terminos Lagoon throughout the year.

Because there are seasonal variations of abiotic parameters and of food supplies and to reduce competition, there is a strong seasonal programming. This is

the temporal and spatial sequential use of lagoon habitats by juvenile and in some species also by adults.

In Chapter 4, I examined in a more detailed way the relation between fish use of Puerto Real inlet and the inner littoral of Carmen Island, particularly Estero Pargo. Both locations are characterized by permanent marine influence, and extensive seagrass meadows. The main differences between the two habitats are that Estero Pargo is bordered by fringe mangroves and is located approximately in the middle of the inner littoral of Carmen Island. Puerto Real inlet is a dynamic connection pathway between the lagoon and the adjacent inner shelf. This inlet has a net inflow of marine towards the lagoon.

The two habitats are used differently by fishes. Fishes in Puerto Real inlet were larger and fewer in number while those captured in Estero Pargo were smaller and more abundant. The dominant species were more abundant in the inlet during the end of wet season and all of the norte season, while in the estero area, dominant species were more abundant at the end of the norte and during the dry season. This means that larger fish use the seagrass beds in the inlet mainly as an area of transit. The movement into and through the inlet during the norte season is facilitated by the strong net inflow, especially during frontal passages. The seagrass/mangrove system of the inner littoral of Carmen island is used mainly as a nursery.

These results indicate that adult fish enter the lagoon through Puerto Real inlet in the fall during the wet and norte seasons. These fish often spawn near shore in the vicinity of the inlets or in the inlet itself. This ensures that eggs and larvae are swept into the lagoon and distributed widely by prevailing currents. Therefore, there are at least three main patterns of use of the seagrasses in Puerto Real inlet and the seagrass-mangrove areas in the inner littoral of Carmen island: (I) There are marine

species which spawn in or near the inlet and the eggs and larvae are transported into and distributed throughout the lagoon by the predominant currents. (e.g. *Archosargus rhomboidalis* sea bream and *Orthopristis chrysoptera* pigfish). (2) There are estuarine-marine species that spawn in different habitats of the lagoon and use Estero Pargo as a nursery area, e.g. *Bairdiella chrysoura* (Silver perch), *Cathorops spixii* (Mandamango sea catfish), and *Ariopsis felis* (Hardhead sea catfish). (3) Finally, there are species that complete their life history in the inlet seagrass and seagrass/ mangrove systems, e.g. *Urolophus jamaicensis* and *Opsanus beta*.

There is a strong correlation between the life history patterns of migratory fish and the patterns of primary production. In general fish tend to use habitats during periods of high primary production. During the rainy season, June to October, the fish occur mainly adults, many of which spawn in or near the inlet and the eggs and larvae are swept into the lagoon. These eggs and larvae arrive at a time when there is a high availability of organic matter in the central lagoon. At the end of the rainy season, river flow diminishes thus reducing river input of organic matter and nutrients. During the dry season aquatic primary productivity in the central lagoon is lowest due to low nutrients, and the tidal creeks and shallow waters associated with seagrass beds and mangroves have the highest levels of aquatic primary productivity. In this season, density and biomass of fishes is highest in the inner littoral and Estero Pargo areas. The great majority of these fishes are small juveniles and pre-adults. Thus, these organisms use the seagrass/mangrove areas during the period of highest primary production and during the most rapid growth period of the life history.

APPENDIX A: DATA TABLES FOR CHAPTER 2

Table 2.1. Monthly average of the environmental parameters at each ecological subsystem in Terminos Lagoon Period 1980-1981. CI = Carmen Inlet, CB = Central Basin, FLS = Fluvial Lagoon Systems ILCI = Inner Littoral of Carmen Island

a) Surface salinity

Months	CI		CB		FLS		ILCI		TTL	
1980-1981	Avg.	±STD	Avg.	±STD	Avg.	±STD	Avg.	±STD	Avg.	±STD
FEB	4.7	4.2	36.0	0.0	15.1	15.2	25.0	11.1	18.6	14.6
MAR	19.3	6.1	25.7	0.6	19.3	9.7	28.6	4.0	22.9	7.8
APR	25.0	7.5	29.3	3.1	19.9	9.4	30.2	4.5	25.2	8.1
MAY	33.0	2.6	30.0	0.0	25.8	1.5	33.2	2.3	30.0	3.9
JUN	31.3	1.2	31.3	6.0	24.4	11.0	34.8	0.4	29.6	7.9
JUL	26.7	3.1	31.0	2.6	21.3	11.4	34.4	3.8	27.4	9.1
AUG	26.0	4.0	28.7	1.2	18.8	10.6	30.0	2.5	25.1	8.0
SEP	18.3	3.5	29.7	2.1	19.9	10.7	30.8	2.3	24.3	8.7
OCT	11.7	6.7	13.7	1.2	12.3	9.3	19.0	1.4	14.3	6.7
NOV	2.7	3.1	13.3	3.8	6.1	4.1	14.4	1.5	9.1	5.6
DEC	5.3	4.9	14.3	2.1	9.7	6.8	14.2	6.5	11.0	6.4
JAN	12.0	7.2	19.0	1.7	12.1	7.1	26.8	5.6	17.3	8.6
FEB	26.7	2.9	22.3	0.6	16.4	7.5	29.0	4.3	22.6	7.5
MAR	21.0	8.7	24.7	3.2	16.3	10.5	29.0	2.5	22.0	9.0
APR	22.7	8.1	28.0	0.0	18.7	9.4	30.6	5.5	24.2	8.6

b) Bottom salinity

FEB	10.0	0.0	34.0	2.8	20.0	11.9	30.6	6.7	23.0	11.6
MAR	26.3	3.8	26.7	1.2	20.9	9.3	30.2	3.1	25.3	7.1
APR	30.0	4.0	30.7	2.3	21.4	9.5	32.6	1.9	27.5	7.8
MAY	33.7	1.5	30.0	0.0	26.5	2.3	34.0	1.9	30.6	3.9
JUN	30.7	2.3	31.7	0.6	23.9	10.7	34.6	0.5	29.3	7.9
JUL	28.0	3.5	32.0	2.0	23.0	10.8	34.4	2.5	28.5	8.4
AUG	30.0	0.0	30.0	0.0	21.3	10.9	30.8	2.2	27.2	7.6
SEP	23.7	4.9	30.0	2.0	20.7	10.4	31.2	2.6	25.7	8.1
OCT	13.7	3.2	18.3	1.5	12.6	6.0	21.8	4.0	16.3	5.9
NOV	11.0	5.6	16.0	1.7	9.9	4.5	15.4	1.7	12.6	4.4
DEC	19.3	5.1	16.0	2.0	12.7	6.0	17.8	3.8	15.8	5.2
JAN	15.3	10.3	22.7	6.4	14.4	7.3	28.6	6.7	19.9	9.3
FEB	28.3	2.5	25.7	2.1	18.6	7.5	29.2	4.5	24.3	7.1
MAR	27.0	2.6	28.3	2.1	21.1	9.6	30.2	3.3	25.8	7.2
APR	22.7	8.1	28.0	2.0	19.1	8.6	32.2	4.0	24.8	8.3

(Table continued)

c) Surface temperature (°C)

FEB	24.4	0.4	24.4	0.2	25.0	1.4	23.8	0.7	24.5	1.1
MAR	24.6	2.0	25.7	1.3	25.3	1.9	24.2	2.0	24.9	1.8
APR	29.7	1.2	30.8	1.1	31.0	0.7	30.4	1.0	30.6	1.0
MAY	30.3	0.6	30.1	0.6	30.1	0.7	29.8	0.4	30.0	0.6
JUN	31.0	0.5	30.6	0.4	31.1	0.8	30.8	0.4	30.9	0.6
JUL	30.3	0.7	30.6	0.9	30.1	0.4	30.7	0.8	30.4	0.6
AUG	30.1	0.8	30.5	1.2	30.4	0.8	30.6	0.9	30.4	0.8
SEP	29.6	0.1	30.4	0.7	31.0	1.2	30.7	1.3	30.6	1.1
OCT	27.6	0.5	28.8	1.5	28.2	0.8	28.9	1.2	28.4	1.0
NOV	26.2	0.7	27.3	1.5	26.9	0.9	26.6	1.2	26.8	1.1
DEC	23.0	0.9	24.1	0.9	24.2	1.2	24.3	0.4	24.0	1.0
JAN	22.3	0.6	22.1	0.7	21.9	0.9	22.0	0.5	22.0	0.7
FEB	25.0	0.0	25.5	0.5	25.6	1.2	24.9	0.7	25.3	0.9
MAR	28.7	0.8	29.6	0.6	29.6	0.7	29.2	0.7	29.3	0.7
APR	27.4	0.4	27.4	1.2	28.1	0.9	27.4	1.4	27.7	1.0

d) Bottom temperature (°C)

Months	CI		CB		FLS		ILCI		TTL	
1980-1981	Avg.	±STD	Avg.	±STD	Avg.	±STD	Avg.	±STD	Avg.	±STD
FEB	24.0	0.0	24.2	0.1	24.6	0.7	23.6	0.5	24.1	0.7
MAR	23.5	0.5	23.8	0.4	24.1	0.8	23.6	1.1	23.8	0.8
APR	29.3	0.6	29.9	0.6	30.4	0.8	30.0	0.7	30.0	0.8
MAY	29.7	0.3	29.0	0.1	29.9	0.7	29.1	0.2	29.5	0.6
JUN	30.9	0.3	30.1	0.4	30.8	0.5	30.9	0.2	30.7	0.4
JUL	30.0	0.4	30.2	0.7	30.1	0.4	30.5	0.5	30.2	0.5
AUG	29.8	0.3	29.8	0.6	30.1	0.8	30.3	0.7	30.1	0.7
SEP	29.4	0.4	29.9	0.1	30.1	0.8	30.4	0.9	30.0	0.7
OCT	27.4	0.6	27.8	0.5	27.6	0.5	28.1	0.5	27.7	0.5
NOV	26.1	0.6	26.6	0.7	26.6	0.7	26.1	1.2	26.4	0.8
DEC	22.8	0.2	23.9	0.8	23.9	1.0	23.7	0.8	23.7	0.9
JAN	21.9	0.1	21.7	0.6	21.9	0.9	21.7	1.1	21.8	0.8
FEB	24.3	0.3	25.2	0.8	25.6	0.7	24.8	0.8	25.1	0.8
MAR	27.6	0.5	28.5	0.3	28.9	0.8	29.0	0.7	28.6	0.8
APR	27.2	0.5	27.4	0.5	27.6	0.5	27.3	1.4	27.4	0.8

(Table continued)

e) Secchi depth (m)

FEB	0.6	0.2	1.3	0.1	0.7	0.4	1.2	0.4	0.9	0.4
MAR	0.6	0.3	1.2	0.4	0.7	0.3	0.7	0.2	0.8	0.3
APR	0.6	0.4	0.6	0.1	0.8	0.3	0.8	0.4	0.7	0.3
MAY	0.7	0.3	1.1	0.1	0.8	0.4	1.4	0.7	1.0	0.5
JUN	0.7	0.3	1.4	0.5	0.8	0.3	1.3	0.4	1.0	0.4
JUL	0.8	0.6	1.1	0.4	0.8	0.2	1.3	0.2	1.0	0.4
AUG	0.8	0.2	0.9	0.4	0.8	0.3	1.1	0.5	0.9	0.3
SEP	0.7	0.3	0.9	0.1	0.7	0.2	1.6	0.8	1.0	0.6
OCT	0.6	0.2	1.6	0.4	0.7	0.3	1.1	0.5	0.9	0.5
NOV	0.5	0.2	1.0	0.1	0.9	0.4	0.9	0.2	0.8	0.3
DEC	0.6	0.2	1.1	0.3	0.7	0.3	1.0	0.3	0.8	0.3
JAN	0.5	0.1	1.3	0.3	1.0	0.4	1.2	0.2	1.0	0.4
FEB	1.0	0.4	3.5	0.5	1.5	0.5	1.7	0.5	1.8	0.9
MAR	1.2	0.7	1.7	0.4	1.2	0.5	1.4	0.5	1.3	0.5
APR	0.5	0.1	1.3	0.5	1.0	0.3	1.1	0.2	1.0	0.4

f) Transparency (%)

FEB	22.7	2.3	40.0	7.1	40.3	11.6	47.0	9.2	39.1	12.1
MAR	17.0	6.9	29.7	10.4	25.7	12.0	20.8	5.8	23.6	9.7
APR	26.7	20.8	13.3	2.9	30.1	12.5	19.4	6.5	23.8	12.7
MAY	30.0	15.9	31.0	2.8	33.8	18.2	57.0	28.2	40.0	22.3
JUN	31.7	7.6	40.7	10.7	45.7	11.5	63.2	22.5	47.4	17.7
JUL	31.0	20.1	29.0	7.8	34.0	15.1	52.0	22.1	37.7	18.4
AUG	26.0	2.0	26.7	8.0	24.5	6.4	44.6	25.3	31.1	16.2
SEP	24.3	7.5	22.0	1.0	28.9	10.6	83.4	17.7	42.1	28.7
OCT	18.3	3.1	40.0	8.7	26.3	12.2	46.2	27.4	32.8	18.9
NOV	14.3	2.1	26.3	3.5	34.6	14.8	40.8	7.7	31.6	13.4
DEC	17.7	4.0	26.7	7.4	29.6	13.1	33.2	10.3	28.1	11.0
JAN	19.0	1.7	33.3	8.4	45.0	22.9	47.6	12.8	39.4	18.6
FEB	37.0	10.5	91.7	14.4	70.6	19.4	68.8	18.6	68.0	22.9
MAR	34.0	14.2	49.7	5.8	49.1	17.5	68.2	20.9	52.0	19.4
APR	18.7	6.7	29.7	7.6	53.3	23.1	62.4	25.1	46.1	25.1

(Table continued)

g) Water depth (m)

FEB	2.8	0.6	3.4	0.9	1.9	0.5	2.5	0.6	2.4	0.7
MAR	3.7	0.5	4.0	0.0	2.9	0.8	3.4	0.8	3.4	0.8
APR	2.7	0.6	4.1	0.1	2.7	0.5	3.1	1.2	3.0	0.9
MAY	2.5	0.4	3.6	0.8	2.6	0.5	2.3	0.4	2.6	0.6
JUN	2.2	0.3	3.4	0.6	1.8	0.3	2.1	0.3	2.2	0.7
JUL	2.6	0.2	3.8	0.3	2.4	0.7	2.8	1.0	2.8	0.8
AUG	3.1	0.5	3.4	1.0	3.1	0.4	2.7	1.2	3.0	0.8
SEP	2.8	0.3	4.2	0.4	2.5	0.7	2.0	0.9	2.7	1.0
OCT	3.0	0.9	4.1	0.4	2.5	0.5	2.5	0.6	2.9	0.8
NOV	3.2	0.8	4.0	0.3	2.5	0.3	2.2	0.4	2.8	0.7
DEC	3.2	0.8	4.2	0.1	2.6	0.3	3.0	0.5	3.0	0.7
JAN	2.8	0.3	3.9	0.1	2.3	0.5	2.7	0.9	2.8	0.8
FEB	2.8	0.2	3.8	0.3	2.0	0.3	2.5	0.5	2.6	0.7
MAR	3.4	0.7	3.3	0.4	2.5	0.5	2.1	0.7	2.6	0.7
APR	3.0	0.7	4.3	0.6	2.0	0.4	2.0	0.9	2.5	1.1

Table 2.2. Fish species in Terminos Lagoon caught during 1980-1981.

	Number		Mass		Freq. of capture	
	Total	%	Total	%	Total	%
<i>Cathorops spixii</i>	3405	24.9	120296.0	22.2	122	46
<i>Sphoeroides testudineus</i>	1845	13.5	109142.4	20.1	157	59
<i>Bairdiella chrysoura</i>	1197	8.7	29134.6	5.4	114	43
<i>Arius felis</i>	1184	8.6	60631.3	11.2	135	51
<i>Archosargus rhomboidalis</i>	1055	7.7	96747.8	17.8	86	33
<i>Eucinostomus gula</i>	955	7.0	8846.5	1.6	119	45
<i>Stellifer lanceolatus</i>	503	3.7	1918.5	0.4	33	13
<i>Anchoa mitchilli</i>	503	3.7	388.4	0.1	51	19
<i>Cynoscion arenarius</i>	357	2.6	2238.8	0.4	43	16
<i>Orthopristis chrysoptera</i>	233	1.7	3693.7	0.7	26	10
<i>Citharichthys spilopterus</i>	216	1.6	1703.7	0.3	60	23
<i>Diapterus rhombeus</i>	201	1.5	3070.3	0.6	49	19
<i>Cetengraulis edentulus</i>	178	1.3	1299.0	0.2	28	11
<i>Chaetodipterus faber</i>	163	1.2	15109.5	2.8	67	25
<i>Cyclichthys schoepfi</i>	142	1.0	17026.7	3.1	59	22
<i>Micropogon undulatus</i>	129	0.9	776.5	0.1	43	16
<i>Bagre marinus</i>	116	0.8	1336.5	0.2	32	12
<i>Cynoscion nebulosus</i>	103	0.8	6597.5	1.2	54	20

(Table continued)

<i>Bairdiella ronchus</i>	96	0.7	3928.0	0.7	30	11
<i>Achirus lineatus</i>	80	0.6	1072.6	0.2	48	18
<i>Sphoeroides nephelus</i>	68	0.5	939.2	0.2	32	12
<i>Synodus foetens</i>	59	0.4	2093.5	0.4	35	13
<i>Etropus crossotus</i>	54	0.4	444.5	0.1	28	11
<i>Symphurs plagiusa</i>	53	0.4	305.7	0.1	17	6
<i>Prionotus carolinus</i>	50	0.4	1080.0	0.2	21	8
<i>Acanthostracion</i>	48	0.4	3730.9	0.7	27	10
<i>quadricornis</i>						
<i>Chloroscombrus</i>	48	0.4	592.5	0.1	24	9
<i>chrysurus</i>						
<i>Harengula jaguana</i>	45	0.3	396.0	0.1	11	4
<i>Archosargus</i>	43	0.3	9598.4	1.8	20	8
<i>probatocephalus</i>						
<i>Sphoeroides greeleyi</i>	42	0.3	204.5	0.0	18	7
<i>Lutjanus griseus</i>	41	0.3	2150.3	0.4	15	6
<i>Cichlasoma</i>	40	0.3	1602.4	0.3	5	2
<i>urophthalmus</i>						
<i>Menticirrhus saxatilis</i>	37	0.3	995.6	0.2	21	8
<i>Eugerres plumieri</i>	29	0.2	964.5	0.2	12	5
<i>Polynemus octonemus</i>	28	0.2	2229.0	0.4	12	5
<i>Selene vomer</i>	28	0.2	471.7	0.1	12	5
<i>Dasyatis sabina</i>	27	0.2	19532.9	3.6	21	8

(Table continued)

<i>Cynoscion nothus</i>	27	0.2	241.1	0.0	9	3
<i>Eucinostomus</i>	23	0.2	111	0.0	8	3
<i>argenteus</i>						
<i>Syngnathus scovelli</i>	22	0.2	5.5	0.0	12	5
<i>Trichurus lepturus</i>	19	0.1	378.4	0.1	15	6
<i>Opisthonema oglinum</i>	17	0.1	174.6	0.0	7	3
<i>Opsanus beta</i>	16	0.1	1611.6	0.3	12	5
<i>Lutjanus synagris</i>	15	0.1	1020.2	0.2	12	5
<i>Prionotus scitulus</i>	14	0.1	699.9	0.1	7	3
<i>Caranx hippos</i>	14	0.1	351.8	0.1	11	4
<i>Menticirrhus americanus</i>	10	0.1	1675.3	0.3	6	2
<i>Hippocampus hudsonius</i>	9	0.1	95.1	0.0	7	3
<i>Anchoa lamprotaenia</i>	9	0.1	85	0.0	7	3
<i>Monacanthus hispidus</i>	8	0.1	146.4	0.0	8	3
<i>Eucinostomus</i>	8	0.1	44.1	0.0	6	2
<i>melanopterus</i>						
<i>Scorpaena plumieri</i>	7	0.1	950.1	0.2	6	2
<i>Prionotus tribulus</i>	7	0.1	21.3	0.0	7	3
<i>Gobionellus oceanicus</i>	6	0.0	107.5	0.0	5	2
<i>Odontoscion dentex</i>	6	0.0	66.6	0.0	4	2
<i>Anchoa hepsetus</i>	6	0.0	37.8	0.0	4	2
<i>Haemulon plumieri</i>	5	0.0	175	0.0	5	2

(Table continued)

<i>Ancylosetta</i>	4	0.0	520.4	0.1	4	2
<i>quadrocellata</i>						
<i>Porichthys plectrodon</i>	4	0.0	119.9	0.0	4	2
<i>Syngnathus louisianae</i>	4	0.0	8.4	0.0	3	1
<i>Prionotus beani</i>	3	0.0	126.7	0.0	1	0
<i>Prionotus punctatus</i>	3	0.0	26.5	0.0	3	1
<i>Stellifer sp.</i>	3	0.0	22.9	0.0	1	0
<i>Ophichthys gomesii</i>	2	0.0	242.5	0.0	2	1
<i>Haemulon bonariense</i>	2	0.0	142.1	0.0	2	1
<i>Centropomus</i>	2	0.0	133.8	0.0	2	1
<i>undecimalis</i>						
<i>Prionotus sp.</i>	2	0.0	48.5	0.0	1	0
<i>Oligoplites saurus</i>	2	0.0	6.6	0.0	2	1
<i>Urolophus jamaicensis</i>	1	0.0	439.8	0.1	1	0
<i>Dasyatis hastata</i>	1	0.0	324.3	0.1	1	0
<i>Lagocephalus laevigatus</i>	1	0.0	72.6	0.0	1	0
<i>Nicholsina ustus</i>	1	0.0	27.9	0.0	1	0
<i>Lutjanus analis</i>	1	0.0	25.4	0.0	1	0
<i>Pomadasys crocro</i>	1	0.0	25	0.0	1	0
<i>Bothus ocellatus</i>	1	0.0	20.1	0.0	1	0
<i>Chriodorus atherinoides</i>	1	0.0	19.1	0.0	1	0
<i>Sphoeroides spengleri</i>	1	0.0	19.0	0.0	1	0

(Table continued)

<i>Alutera schoepfi</i>	1	0.0	18.7	0.0	1	0
<i>Albula vulpes</i>	1	0.0	3.2	0.0	1	0
<hr/>						
Total	13691		542681.6			

Table 2.3 Results of the comparisons of the community structure parameters and indices of diversity by using a two-way Anova with main effects habitat types and seasons and their interactions. Abbreviation: NDF = numerator of degrees of freedom, DDF = denominator of degrees of freedom, TYPE III sums of squares, F values.

Indices	Source	NDF	DDF	Type III F	Pr > F
Density	Habitats	3	14	14.50	0.0001
	Seasons	2	12	5.91	0.0164
	Habitats * Seasons	6	207	1.80	0.1000
Biomass	Habitats	3	14	4.62	0.0190
	Seasons	2	12	2.18	0.1552
	Habitats * Seasons	6	207	1.54	0.1656
Mean size	Habitats	3	14	1.01	0.4183
	Seasons	2	12	4.42	0.0366
	Habitats * Seasons	6	207	1.55	0.1622
Margalef	Habitats	3	14	0.86	0.4833
	Seasons	2	12	2.21	0.1518
	Habitats * Seasons	6	207	0.94	0.4697
Shannon	Habitats	3	14	7.33	0.0034
	Seasons	2	12	9.03	0.0040
	Habitats * Seasons	6	207	0.52	0.7941
Whilm	Habitats	3	14	1.58	0.2378
	Seasons	2	12	3.46	0.0650
	Habitats * Seasons	6	207	1.81	0.0988
Pielou	Habitats	3	14	1.15	0.3643
	Seasons	2	12	3.39	0.0683
	Habitats * Seasons	6	207	1.81	0.0981
Simpson	Habitats	3	14	1.18	0.3542
	Seasons	2	12	5.10	0.0250
	Habitats * Seasons	6	207	0.76	0.6036

Table 2.4. Fish species and number of individuals in each ecological subsystem in Terminos Lagoon caught during 1980-1981 ordered overall abundance (see Table 2). CI = Carmen Inlet, CB = Central Basin, FLS = Fluvial Lagoon Systems ILCI = Inner Littoral of Carmen Island

Common name	Scientific name	CI	CB	FLS	ILCI
Scrawled cowfish	<i>Acanthostracion quadricornis</i>	1	9	2	36
Lined sole	<i>Achirus lineatus</i>	9	3	38	30
Bonefish	<i>Albula vulpes</i>				1
Orange filefish	<i>Aluterus schoepfi</i>				1
Striped anchovy	<i>Anchoa hepsetus</i>	1		5	
Bigeye anchovy	<i>Anchoa lamprotaenia</i>	2	1	5	1
Bay anchovy	<i>Anchoa mitchilli</i>	172	17	282	32
Ocellated flounder	<i>Ancylopsetta quadrocellata</i>				4
Sheepshead	<i>Archosargus probatocephalus</i>			11	32
Sea bream	<i>Archosargus rhomboidalis</i>		53	120	882
Hardhead catfish	<i>Ariopsis felis</i>	193	122	320	549
Gafftopsail catfish	<i>Bagre marinus</i>	76	5	35	
Silver perch	<i>Bairdiella chrysoura</i>	36	248	707	206
Ground croaker	<i>Bairdiella ronchus</i>	12	5	61	18
Eyed flounder	<i>Bothus ocellatus</i>			1	
Crevalle jack	<i>Caranx hippos</i>	4		9	1
Mandamango sea catfish	<i>Cathorops spixii</i>	441	73	2238	653
Snook	<i>Centropomus undecimalis</i>	2			

(Table continued)

Atlantic anchoveta	<i>Cetengraulis edentulus</i>	149	1	24	4
Atlantic spadefish	<i>Chaetodipterus faber</i>	35	21	79	28
Striped burrfish	<i>Cyclichthys schoepfi</i>	1	14	18	109
Atlantic bumper	<i>Chloroscombrus chrysurus</i>	21	5	16	6
Hardhead halfbeak	<i>Chriodorus atherinoides</i>				1
Mexican mojarra	<i>Cichlasoma urophthalmus</i>				40
Bay whiff	<i>Citharichthys spilopterus</i>	133	1	39	43
Sand seatrout	<i>Cynoscion arenarius</i>	253		52	52
Spotted seatrout	<i>Cynoscion nebulosus</i>	7	11	74	11
Silver seatrout	<i>Cynoscion nothus</i>	11		16	
Roughtail stingray	<i>Dasyatis hastata</i>				1
Atlantic stingray	<i>Dasyatis sabina</i>	7	3	6	11
Caitipa mojarra	<i>Diapterus rhombeus</i>	14	24	136	27
Fringed flounder	<i>Etropus crossotus</i>	23			31
Spotfin mojarra	<i>Eucinostomus argenteus</i>		6	14	3
Silver jenny	<i>Eucinostomus gula</i>	186	63	190	516
Flagfin mojarra	<i>Eucinostomus melanopterus</i>	3		4	1
No common name	<i>Eugerres plumieri</i>			24	5
Highfin goby	<i>Gobionellus oceanicus</i>	1		5	
Black grunt	<i>Haemulon bonariense</i>				2
White grunt	<i>Haemulon plumieri</i>			1	4
Scaled sardine	<i>Harengula jaguana</i>	34		7	4

(Table continued)

Lined seahorse	<i>Hippocampus erectus</i>				9
Smooth puffer	<i>Lagocephalus laevigatus</i>	1			
Mutton snapper	<i>Lutjanus analis</i>		1		
Gray snapper	<i>Lutjanus griseus</i>			23	18
Lane snapper	<i>Lutjanus synagris</i>		1	3	11
Southern kingfish	<i>Menticirrhus americanus</i>	5	1	4	
Northern kingfish	<i>Menticirrhus saxatilis</i>	21	2	12	2
Atlantic croaker	<i>Micropogon undulatus</i>	67	1	58	3
Planehead filefish	<i>Monacanthus hispidus</i>			2	6
Emerald parrotfish	<i>Nicholsina ustus</i>				1
Reef croaker	<i>Odontoscion dentex</i>	2		4	
Leatherjacket	<i>Oligoplites saurus</i>			2	
Shrimp eel	<i>Ophichthys gomesii</i>	2			
Atlantic thread herring	<i>Opisthonema oglinum</i>			17	
Gulf foadfish	<i>Opsanus beta</i>			2	14
Pigfish	<i>Orthopristis chysoptera</i>		15	6	212
Atlantic threadfin	<i>Polynemus octonemus</i>	12		5	11
Burro grunt	<i>Pomadasys crocro</i>			1	
Atlantic midshipman	<i>Porichthys plectrodon</i>	1		3	
Bean's searobin	<i>Prionotus beani</i>	3			
Northern searobin	<i>Prionotus carolinus</i>	4	17	11	18
Bluewing searobin	<i>Prionotus punctatus</i>	1		1	1

(Table continued)

Leopard searobin	<i>Prionotus scitulus</i>			2	12
	<i>Prionotus sp.</i>		2		
Bighead searobin	<i>Prionotus tribulus</i>	6			1
Spotted scorpionfish	<i>Scorpaena plumieri</i>			1	6
Lookdown	<i>Selene vomer</i>	17		5	6
Green puffer	<i>Sphoeroides greeleyi</i>	25	6	10	1
Southern puffer	<i>Sphoeroides nephelus</i>	18	2	23	25
Bandtail puffer	<i>Sphoeroides spengleri</i>				1
Checkered puffer	<i>Sphoeroides testudineus</i>	163	37	456	1189
Star drum	<i>Stellifer lanceolatus</i>	487		16	
	<i>Stellifer sp.</i>				3
Blackcheek tonguefish	<i>Symphurs plagiusa</i>	43		8	2
Chain piperfish	<i>Syngathus louisianae</i>		2	2	
Gulf piperfish	<i>Syngathus scovelli</i>		4	18	
Inshore lizardfish	<i>Synodus foetens</i>	21	1	7	30
Atlantic cutlassfish	<i>Trichurus lepturus</i>	14		5	
Yellow stingray	<i>Urolophus jamaicensis</i>				1
<hr/> Summary					
Total species		47	34	59	58
Total individuals		2740	777	5246	4928
Total biomass		0.538	0.744	0.939	1.977

Table 2.5. Average of the ecological parameters of fish community at each ecological subsystem in Terminos Lagoon. Period 1980-1981. (STD = Standard deviation, CV = Coefficient of variation).

Carmen Inlet, Stations 1,2,5 1980-1981											
Month	Num Species	Total Number	Total Weight	Density	Biomass	H'n	H'w	D	J'	1-D	Avg. size
1980-1981		Ind	gr	ind./m2	gr/m2	Shannon	Whilm	Margalef	Pielou	Simpson	gr./Ind
FEB	18	118	1495.7	0.02	0.25	1.63	2.19	3.56	0.56	0.69	12.7
MAR	17	84	3590.1	0.02	0.72	2.16	1.40	3.61	0.76	0.82	42.7
APR	10	44	417.9	0.01	0.07	1.84	1.96	2.38	0.80	0.79	9.5
MAY	8	32	141.3	0.01	0.02	1.71	1.84	2.02	0.82	0.76	4.4
JUN	19	134	3275.8	0.02	0.55	2.24	1.85	3.68	0.76	0.82	24.4
JUL	18	51	2653.1	0.01	0.44	2.58	1.46	4.32	0.89	0.90	52.0
AUG	17	154	1389.3	0.03	0.23	1.84	1.98	3.18	0.65	0.73	9.0
SEP	17	350	3016.8	0.06	0.50	1.61	1.19	2.73	0.57	0.66	8.6
OCT	21	240	4741.2	0.04	0.79	2.23	2.08	3.65	0.73	0.85	19.8
NOV	28	467	12403.9	0.08	2.07	2.39	1.66	4.39	0.72	0.87	26.6
DEC	22	118	2869.8	0.02	0.41	2.79	2.41	4.40	0.90	0.93	24.3
JAN	24	296	4682.9	0.05	0.78	2.05	2.41	4.04	0.65	0.77	15.8
FEB	21	453	2553	0.08	0.43	1.42	1.97	3.27	0.47	0.59	5.6
MAR	16	103	4003.7	0.02	0.67	2.20	1.37	3.24	0.79	0.83	38.9
APR	16	96	1168.9	0.02	0.19	2.27	2.42	3.29	0.82	0.85	12.2
Mean	18.13	182.67	3226.89	0.03	0.54	2.06	1.88	3.45	0.73	0.79	20.4
STD	4.97	144.54	2907.43	0.02	0.49	0.38	0.40	0.70	0.13	0.09	14.4
CV	27.40	79.13	90.10	79.05	90.09	18.62	21.12	20.39	17.25	11.70	70.7

(Table continued)

Central Basin, Stations 8, 11, 14 1980-1981

FEB	12	32	2034.1	0.02	1.02	2.19	1.92	3.17	0.88	0.85	63.6
MAR	17	82	6532.4	0.02	1.31	2.02	1.98	3.63	0.71	0.79	79.7
APR	12	110	5600.8	0.02	1.12	1.61	1.84	2.34	0.65	0.71	50.9
MAY	18	169	7328.9	0.06	2.44	2.07	2.28	3.31	0.71	0.79	43.4
JUN	3	11	2174.7	0.00	0.47	0.60	1.43	0.83	0.55	0.31	197.7
JUL	11	40	4093.1	0.01	0.77	1.75	1.24	2.71	0.73	0.70	102.3
AUG	10	71	3373	0.01	0.71	1.65	1.85	2.11	0.71	0.71	47.5
SEP	8	21	2328.5	0.00	0.47	1.84	2.12	2.30	0.89	0.81	110.9
OCT	15	80	2740	0.02	0.69	2.02	2.16	3.19	0.75	0.79	34.3
NOV	12	87	5536.2	0.02	1.38	1.45	1.99	2.46	0.58	0.63	63.6
DEC	2	9	1179.5	0.00	0.24	0.53	2.11	0.46	0.76	0.35	131.1
JAN	5	18	1433	0.00	0.29	0.84	1.61	1.38	0.52	0.38	79.6
FEB	5	29	3576.9	0.01	0.72	1.00	1.32	1.19	0.62	0.49	123.3
MAR	4	11	1664.4	0.00	0.42	0.89	1.68	1.25	0.64	0.45	151.3
APR	3	7	71.4	0.00	0.01	1.08	0.88	1.03	0.98	0.65	10.2
Mean	9.13	51.80	3311.13	0.01	0.80	1.43	1.76	2.09	0.71	0.63	86.0
STD	5.29	46.86	2119.49	0.01	0.60	0.57	0.40	1.01	0.13	0.18	50.1
CV	57.92	90.47	64.01	108.43	74.84	39.48	22.53	48.30	18.22	29.24	58.2

(Table continued)

Fluvial lagoon systems Stations 3, 4, 9, 10, 15, 16 and 17											
FEB	26	177	4727.4	0.01	0.37	2.39	2.17	4.83	0.73	0.83	26.7
MAR	28	260	8267.1	0.02	0.59	2.43	2.17	4.86	0.73	0.85	31.8
APR	23	451	25067.4	0.04	2.09	1.61	1.13	3.60	0.51	0.65	55.6
MAY	17	200	7539.5	0.02	0.60	1.83	1.34	3.02	0.64	0.73	37.7
JUN	21	335	12722.9	0.03	0.98	1.95	1.31	3.44	0.64	0.74	38.0
JUL	33	377	10732.9	0.03	0.89	2.50	2.01	5.39	0.72	0.87	28.5
AUG	23	634	8007.5	0.06	0.73	1.72	1.72	3.41	0.55	0.67	12.6
SEP	27	341	6898.1	0.03	0.63	1.88	1.69	4.46	0.57	0.71	20.2
OCT	25	304	8430.2	0.03	0.75	2.19	1.79	4.20	0.68	0.82	27.7
NOV	28	746	21808.3	0.07	1.92	1.35	1.18	4.08	0.40	0.48	29.2
DEC	26	242	9018.4	0.02	0.82	1.73	1.93	4.55	0.53	0.64	37.3
JAN	31	524	17032.6	0.05	1.55	1.99	1.86	4.79	0.58	0.71	32.5
FEB	20	190	6400.9	0.02	0.58	1.74	1.58	3.62	0.58	0.72	33.7
MAR	22	178	8677.1	0.02	0.79	2.01	1.92	4.05	0.65	0.80	48.7
APR	21	287	9623.5	0.03	0.87	1.95	1.81	3.53	0.64	0.77	33.5
Mean	24.73	349.73	10996.92	0.03	0.95	1.95	1.71	4.12	0.61	0.73	32.9
STD	4.32	171.64	5841.27	0.02	0.50	0.32	0.34	0.68	0.09	0.10	10.4
CV	17.45	49.08	53.12	51.91	53.40	16.38	19.81	16.50	14.82	13.57	31.5

(Table continued)

Inner Littoral of Carmen Island, Stations 6,7,12,13,18											
FEB	17	260	19664.5	0.03	1.97	1.85	1.83	2.88	0.65	0.70	75.6
MAR	18	212	12545.5	0.02	1.30	2.02	1.74	3.17	0.70	0.79	59.2
APR	24	313	15806.4	0.03	1.58	2.36	2.07	4.00	0.74	0.87	50.5
MAY	26	269	15332.7	0.03	1.53	2.45	2.08	4.47	0.75	0.86	57.0
JUN	16	303	16351.1	0.03	1.64	1.74	1.55	2.63	0.63	0.78	54.0
JUL	17	362	15756.5	0.03	1.13	1.40	1.35	2.72	0.49	0.59	43.5
AUG	19	256	13784.8	0.03	1.43	1.96	1.86	3.25	0.67	0.78	53.8
SEP	22	395	40026.1	0.04	4.00	1.73	1.01	3.51	0.56	0.73	101.3
OCT	17	226	11500.6	0.02	1.11	1.90	1.93	2.95	0.67	0.78	50.9
NOV	28	337	23262.8	0.03	2.33	2.01	1.59	4.64	0.60	0.80	69.0
DEC	33	931	52111	0.09	5.21	2.07	2.16	4.68	0.59	0.80	56.0
JAN	19	167	26950.6	0.02	2.70	1.76	1.22	3.52	0.60	0.68	161.4
FEB	18	116	5484.3	0.01	0.57	1.85	1.82	3.58	0.64	0.84	47.3
MAR	19	375	19752.4	0.04	1.98	1.38	1.36	3.04	0.47	0.55	52.7
APR	27	406	14741.2	0.04	1.47	2.29	2.14	4.33	0.70	0.85	36.3
Mean	21.33	328.53	20204.70	0.03	2.00	1.92	1.71	3.56	0.63	0.76	64.6
STD	5.11	186.41	11850.72	0.02	1.20	0.31	0.36	0.71	0.08	0.09	30.8
CV	23.95	56.74	58.65	57.82	60.11	15.97	20.81	19.85	12.83	12.33	47.8

(Table continued)

Terminhos Lagoon Total, 1980-1981

FEB	40	587	27161.9	0.02	0.89	2.53	2.25	6.12	0.69	0.85	46.3
MAR	37	638	26776	0.02	0.80	2.58	2.13	5.57	0.71	0.87	42.0
APR	35	918	43863.2	0.03	1.33	2.25	1.81	4.98	0.63	0.82	47.8
MAY	38	670	30000.2	0.02	0.95	2.61	2.26	5.69	0.72	0.88	44.8
JUN	38	783	33023.5	0.02	0.98	2.50	2.07	5.55	0.69	0.87	42.2
JUL	41	830	30634	0.02	0.82	2.34	2.00	5.95	0.63	0.82	36.9
AUG	37	1115	24590.1	0.04	0.78	2.28	2.34	5.13	0.63	0.82	22.1
SEP	43	1107	50532.5	0.03	1.58	2.35	1.56	5.99	0.63	0.83	45.6
OCT	41	850	27297.6	0.03	0.87	2.73	2.56	5.93	0.74	0.91	32.1
NOV	47	1637	61038	0.05	1.95	2.39	2.16	6.22	0.62	0.83	37.3
DEC	43	1300	64091.1	0.04	1.94	2.40	2.34	5.86	0.64	0.85	49.3
JAN	43	1005	49197.5	0.03	1.54	2.51	2.07	6.08	0.67	0.86	49.0
FEB	38	788	15788.9	0.02	0.50	2.33	2.53	5.55	0.64	0.83	20.0
MAR	34	667	33082.1	0.02	1.07	2.15	1.90	5.07	0.61	0.76	49.6
APR	39	796	25605	0.02	0.80	2.68	2.45	5.69	0.73	0.89	32.2
Mean	39.60	912.73	36178.77	0.03	1.12	2.44	2.16	5.69	0.66	0.85	39.8
STD	3.46	282.77	14219.08	0.01	0.44	0.17	0.27	0.39	0.04	0.04	9.6
CV	8.74	30.98	39.30	32.08	39.65	6.76	12.70	6.80	6.53	4.44	24.0

Table 2.6. a) A comparison of the different diversity indices for the four ecological subsystems and for the entire lagoon. b) Pattern of species abundance. n/s no significant.

	Carmen Inlet	Central Basin	Fluvial lagoon Sys	Inner Littoral	Terminos Lag.
a) Diversity					
Species richness	47	34	62	59	82
Individuals	2740	777	5246	4928	13691
Margalef	5.81	4.96	7.12	6.82	8.50
Pielou	0.73	0.69	0.55	0.60	0.63
Shannon	2.79	2.41	2.28	2.43	2.77
Whilm	2.62	2.42	1.98	2.18	2.43
Simpson (1-D)	0.91	0.85	0.78	0.86	0.89
Geom. series (k)	0.12	0.13	0.10	0.10	0.08
Log series (α)	8.06	7.26	9.92	9.48	11.59
Log normal (λ)	56.1	47.4	76.4	67.1	84.2
Q statistic	8.82	7.41	14.19	10.52	14.27
b) Fit of Models					
Geometric series	n/s	n/s	n/s	n/s	n/s
Log series	Yes	Yes	n/s	Yes	Yes
Log normal	Yes	Yes	Yes	n/s	Yes
Broken stick	n/s	n/s	n/s	n/s	n/s

Table 2.7. Values that it corresponds to χ^2 calculated with their degrees of freedom in each ecological system for the models of abundance in the Terminos Lagoon. (CI = Carmen inlet, CB = Central Basin, FLS = fluvial lagoon systems, ILCI = inner littoral of Carmen Island, TTL = Total Terminos Lagoon)

	CI	CB	FLS	ILCI	TTL
Log series	$\chi^2_{(8)} = 6.9^*$	$\chi^2_{(7)} = 0.6^*$	$\chi^2_{(11)} = 73.3$	$\chi^2_{(10)} = 21.9^*$	$\chi^2_{(11)} = 10.9^*$
	$\chi^2_{0.05(8)} =$	$\chi^2_{0.05(7)} =$	$\chi^2_{0.05(11)} =$	$\chi^2_{0.01(10)} =$	$\chi^2_{0.05(11)} =$
	15.507	14.067	19.675	23.209	19.675
Lognorm	$\chi^2_{(6)} = 8.5$	$\chi^2_{(5)} = 2.8$	$\chi^2_{(9)} = 8.97^*$	$\chi^2_{(8)} = 22.41$	$\chi^2_{(9)} = 9.18$
	$\chi^2_{0.05(6)} =$	$\chi^2_{0.05(5)} =$	$\chi^2_{0.05(9)} =$	$\chi^2_{0.05(8)} =$	$\chi^2_{0.05(9)} =$
	12.592	11.070	16.919	15.507	16.919

* highly significant

Table 2.8. The results of the broken stick model. The values presented correspond to χ^2 along with the degrees of freedom for each ecological subsystem in Terminos Lagoon (CI = Carmen inlet, CB = Central Basin, FLS = fluvial lagoon systems, ILCI = inner littoral of Carmen Island, TTL = Total Terminos Lagoon)

CI	CB	FLS	ILCI	TTL
$\chi^2_{(11)} = 80.6$	$\chi^2_{(9)} = 46.8$	$\chi^2_{(12)} = 156.2$	$\chi^2_{(12)} = 219.7$	$\chi^2_{(12)} = 6592.1$
$\chi^2_{0.05(11)} =$	$\chi^2_{0.05(9)} =$	$\chi^2_{0.05(12)} =$	$\chi^2_{0.05(12)} =$	$\chi^2_{0.05(12)} =$
19.675	16.919	21.026*	21.026*	21.026*
n/s	n/s	n/s	n/s	n/s
n/s no significant				

Table 2.9. Jaccard's coefficient reflects the similarity between ecological subsystems, based on common species. (CI = Carmen inlet, CB = Central Basin, FLS = fluvial lagoon systems, ILCI = inner littoral of Carmen Island, TTL = Total Terminos Lagoon)

	CI	CB	FLS	ILCI
CI	100			
CB	47 common = 25 45 34	100		
FLS	47 common = 41 60 62	34 common = 32 50 62	100	
ILCI	47 common = 34 47 34	34 common = 28 43 59	62 common = 45 45 59	100

Table 2.10 The 'fit' of the four models of species abundance for each ecological subsystems and its relation to the environmental parameters.

Habitat	Geometric Series	Logarithmic Series	Log normal model	Broken stick model	Conclusions
Carmen inlet		Best fit			One or few variables response for structure and diversity, temperature, salinity, and depth
Inner littoral of Carmen island		Best fit			One or few variables response for structure and diversity
Fluvial lagoon systems			Best fit		Temperature Numerous variables response for structure and diversity, temperature, salinity, Secchi depth and depth, and possibly others
Central basin		Best fit			One or few variables response for structure and diversity
Terminos Lagoon		Best fit			One or few variables response for structure and diversity

Table 3.1. Dominant fish species at each ecological subsystem in Terminos Lagoon). Total frequency, total number and total weight.

	Carmen Inlet			Central Basin			Fluvial lagoon systems			Inner littoral Carmen		
	Nu.	Wt.	Fr.	Nu.	Wt.	Fr.	Nu.	Wt.	Fr.	Nu.	Wt.	Fr.
<i>Cathorops spixii</i> (Mandamango sea catfish)	441	6024.0	38	73	2726.5	20	2238	80059.0	67	653	31486.5	26
<i>Sphoeroides testudineus</i> (checkered puffer)	163	12830.6	40	37	2337.7	35	456	21974.8	53	1189	71999.3	80
<i>Bairdiella chrysoura</i> (silver perch)	36	776.2	31	248	5568.7	48	707	17371.3	55	206	5415.4	20
<i>Ariopsis felis</i> (hardhead sea catfish)	193	5418.8	46	122	3510.0	35	320	12311.8	45	549	39390.7	59
<i>Archosargus rhomboidalis</i> (sea bream)				53	2829.2	33	120	3344.9	23	882	90573.7	58
<i>Eucinostomus gula</i> (silver jenny)	186	1162.3	52	63	661.0	35	190	1005.6	24	516	6017.6	65
<i>Anchoa mitchilli</i> (bay anchovy)	172	188.1	33	17	7.0	9	282	167.7	23			
<i>Chaetodipterus faber</i> (Atlantic spadefish)	35	3092.1	27	21	1510.3	24	79	5880.6	26			
<i>Cynoscion arenarius</i> (sand seatrout)	253	1262.1	46							52	363.7	4

(Table continued)

250

<i>Orthopristis chrysoptera</i> (pigfish)	15	117.7	11			212	3475.3	23
<i>Diapterus rhombeus</i> (Caitipa mojarra)	24	352.3	9	136	2252.4	27		
<i>Stellifer lanceolatus</i> (star drum)	487	1729.5	52					
<i>Citharichthys spilopterus</i> (bay whiff)	133	953.4	44					
<i>Cetengraulis edentulus</i> (anchoveta)	149	1124.1	29					
<i>Cyclichthys schoepfi</i> (stripe burrfish)						109	12691. 9	49
<i>Bagre marinus</i> (gafftopsail catfish)	76	658.7	31					
<i>Micropogonias</i> <i>undulatus</i> (Atlantic croaker)	67	197.3	35					
<i>Symphurus plagiusa</i> (blackcheek tonguefish)	43	238.0	23					
<i>Prionotus carolinus</i> (Northern searobin)	17	362.4	13					
<i>Cynoscion nebulosus</i> (spotted seatrout)				74	3550.6	30		
<i>Bairdiella ronchus</i>				61	2424.4	20		

Nu. = number of individuals, Wt. = wet mass (g), Fr. = Frequency in the catches

Table 3.2. Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Cathorops spixii</i> (Mandamango sea catfish)	Mean ± 1 SE	Range
Variables		
TOTAL number=3405		
Number	27.91 \pm 5.27	1 - 382
Mass (grams)	986.03 \pm 199.26	1.9 - 13.350
Total Length (mm)		36 - 258
Mean size in mass (grams per individual)	48.37 \pm 3.19	0.65 - 177.3
Biomass (grams per m ²)	0.647 \pm 0.15	0.001 - 13.350
Density (number of individuals per m ²)	0.017 \pm 0.003	0.001 - 0.204
Surface Salinity	18.09 \pm 0.98	0 - 35
Bottom Salinity	20.53 \pm 0.89	0 - 35
Surface Temperature (°C)	27.91 \pm 0.27	20 - 32.5
Bottom Temperature (°C)	27.42 \pm 0.27	20 - 31.5
Secchi depth (m)	0.79 \pm 0.03	0.2 - 1.8
Transparency (%)	32.61 \pm 1.52	10 - 92
Depth (m)	2.56 \pm 0.06	1.3 - 4.2

Table 3.3. Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Sphoeroides testudineus</i> (Checkered puffer). Variables	Mean ± 1 SE	Range
TOTAL number=1845		
Number	11.75 \pm 1.40	1 - 140
Mass (grams)	695.17 \pm 84.80	8 - 7451.2
Total Length (mm)		20 - 242
Mean size in mass (grams per individual)	63.55 \pm 2.96	8 - 187.2
Biomass (grams per m²)	0.352 \pm 0.04	0.004 - 3.726
Density (number of individuals per m²)	0.006 \pm 0.001	0.0003 - 0.070
Surface Salinity	21.99 \pm 0.80	0 - 38
Bottom Salinity	24.61 \pm 0.65	0 - 38
Surface Temperature (°C)	27.60 \pm 0.25	21.3 - 32.5
Bottom Temperature (°C)	27.12 \pm 0.25	20 - 32
Secchi depth (m)	1.03 \pm 0.04	0 - 3.5
Transparency (%)	42.27 \pm 1.80	10 - 100
Depth (m)	2.67 \pm 0.07	1 - 4.5

Table 3.4. Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Bairdiella chrysoura</i> (Silver perch)	Mean ± 1 SE	Range
Variables		
TOTAL number=1197		
Number	10.50 \pm 1.37	1 - 68
Mass (grams)	255.57 \pm 40.90	3 - 2256.6
Total Length (mm)		15 - 199
Mean size in mass (grams per individual)	22.58 \pm 1.25	1.5 - 78.6
Biomass (grams per m ²)	0.146 \pm 0.02	0.002 - 1.133
Density (number of individuals per m ²)	0.006 \pm 0.001	0.001 - 0.034
Surface Salinity	20.26 \pm 0.89	0 - 36
Bottom Salinity	22.33 \pm 0.72	0 - 36
Surface Temperature (°C)	27.67 \pm 0.29	21.5 - 32.5
Bottom Temperature (°C)	27.19 \pm 0.28	20 - 31.5
Secchi depth (m)	0.95 \pm 0.04	0.3 - 3.0
Transparency (%)	37.18 \pm 1.93	10 - 100
Depth (m)	2.76 \pm 0.08	1.3 - 5.0

Table 3.5. Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Ariopsis felis</i> (Hardhead sea catfish)	Mean \pm 1 SE	Range
Variables		
TOTAL number=1184		
Number	8.77 \pm 1.99	1 - 250
Mass (grams)	449.12 \pm 74.21	1.5 - 7900
Total Length (mm)		36 - 349
Mean size in mass (grams per individual)	77.48 \pm 5.99	0.88 - 490.7
Biomass (grams per m ²)	0.237 \pm 0.04	0.001 - 3.950
Density (number of individuals per m ²)	0.005 \pm 0.001	0.001 - 0.125
Surface Salinity	20.93 \pm 0.90	0 - 36
Bottom Salinity	23.56 \pm 0.75	0 - 38
Surface Temperature (°C)	27.59 \pm 0.27	21.5 - 32.5
Bottom Temperature (°C)	27.1 \pm 0.26	21.4 - 31.5
Secchi depth (m)	0.94 \pm 0.04	0.3 - 2.9
Transparency (%)	37.34 \pm 1.73	10 - 100
Depth (m)	2.74 \pm 0.07	1 - 4.5

Table 3.6.Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Archosargus rhomboidalis</i> (sea bream)	Mean ± 1 SE	Range
Variables		
TOTAL number=1055		
Number	12.27 \pm 2.11	10 - 106
Mass (grams)	1124.97 \pm 404.11	6.3 - 29998.4
Total Length (mm)		31-287
Mean size in mass (grams per individual)	80.36 \pm 7.58	6.3 - 439.8
Biomass (grams per m ²)	0.563 \pm 0.20	0.006 - 14.999
Density (number of individuals per m ²)	0.0054 \pm 0.001	0.0004 - 0.053
Surface Salinity	25.17 \pm 0.86	0 - 38
Bottom Salinity	26.71 \pm 0.76	10 - 38
Surface Temperature (°C)	28.04 \pm 0.31	21.5 - 32
Bottom Temperature (°C)	27.56 \pm 0.32	20 - 32
Secchi depth (m)	1.18 \pm 0.06	0.3 - 4.0
Transparency (%)	47.31 \pm 2.66	10 - 100
Depth (m)	2.69 \pm 0.10	1 - 4.5

Table 3.7. Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Eucinostomus gula</i> (silver jenny)	Mean ± 1 SE	Range
Variables		
TOTAL number=955		
Number	8.03 \pm 1.01	1 - 59
Mass (grams)	74.34 \pm 17.18	1.3 - 1650
Total Length (mm)		10 - 180
Mean size in mass (grams per individual)	8.08 \pm 0.51	0.37 - 33.05
Biomass (grams per m ²)	0.038 \pm 0.01	0.001 - 0.825
Density (number of individuals per m ²)	0.004 \pm 0.001	0.0003 - 0.030
Surface Salinity	22.66 \pm 0.81	0 - 38
Bottom Salinity	25.27 \pm 0.69	0 - 38
Surface Temperature (°C)	27.81 \pm 0.27	21.8 - 32.2
Bottom Temperature (°C)	27.34 \pm 0.27	22 - 32
Secchi depth (m)	1.00 \pm 0.04	0.2 - 3.0
Transparency (%)	37.46 \pm 1.9	12 - 100
Depth (m)	2.88 \pm 0.08	1.3 - 4.5

Table 3.8. Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Anchoa mitchilli</i> (Bay anchovy)	Mean ± 1 SE	Range
Variable		
TOTAL Number = 503		
Number	9.89 \pm 1.87	1 – 106
Mass (grams)	7.62 \pm 1.28	0.2 – 42.8
Total Length (mm)		9 – 96
Mean size in mass (grams per individual)	1.17 \pm 0.20	0.15 – 9.2
Biomass (grams per m ²)	0.0042 \pm 0.001	0.0001 – 0.0214
Density (number of individuals per m ²)	0.0054 \pm 0.001	0.0005 – 0.0325
Surface Salinity	17.69 \pm 1.34	0 – 35
Bottom Salinity	20.4 \pm 1.06	2 – 33
Surface Temperature (°C)	27.76 \pm 0.43	21.5 – 32.2
Bottom Temperature (°C)	27.39 \pm 0.40	21.5 – 31.5
Secchi depth (m)	0.75 \pm 0.04	0.3 – 1.6
Transparency (%)	30.78 \pm 2.33	11 – 83
Depth (m)	2.62 \pm 0.10	1.3 – 4.0

Table 3.9. Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Chaetodipterus faber</i> (Atlantic spadefish)	Mean ± 1 SE	Range
Variables		
TOTAL number=163		
Number	2.43 \pm 0.26	1 - 11
Mass (grams)	225.51 \pm 46.08	0.9 - 2510
Total Length (mm)		35-405
Mean size in mass (grams per individual)	107.4 \pm 22.89	0.9 - 1255.0
Biomass (grams per m ²)	0.130 \pm 0.02	0.005 - 1.255
Density (number of individuals per m ²)	0.001 \pm 0.0002	0.001 - 0.007
Surface Salinity	20.99 \pm 1.21	0 - 36
Bottom Salinity	23.73 \pm 0.91	10 - 38
Surface Temperature (°C)	27.35 \pm 0.36	21.5 - 31.9
Bottom Temperature (°C)	26.78 \pm 0.36	20 - 31.4
Secchi depth (m)	1.05 \pm 0.06	0 - 2.2
Transparency (%)	41.30 \pm 2.58	14 - 100
Depth (m)	2.79 \pm 0.10	1.2 - 4.5

Table 3.10. Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Cynoscion arenarius</i> (Sand seatrout)	Mean ± 1 SE	Range
Variables		
TOTAL number=357		
Number	8.30 \pm 2.48	1 - 88
Mass (grams)	52.07 \pm 13.86	0.3 - 426
Total Length (mm)		30 - 173
Mean size in mass (grams per individual)	8.10 \pm 1.26	0.3 - 36.95
Biomass (grams per m ²)	0.029 \pm 0.01	0.0002 - 0.213
Density (number of individuals per m ²)	0.004 \pm 0.001	0.0004 - 0.044
Surface Salinity	13.28 \pm 1.39	0 - 34
Bottom Salinity	16.81 \pm 1.14	0 - 32
Surface Temperature (°C)	26.08 \pm 0.41	20 - 31
Bottom Temperature (°C)	29.5 \pm 0.39	20 - 29.7
Secchi depth (m)	0.71 \pm 0.05	0.3 - 1.6
Transparency (%)	27.49 \pm 2.49	11 - 83
Depth (m)	2.79 \pm 0.10	1.8 - 4.0

Table 3.11. Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Orthopristis chrysoptera</i> (Pigfish)	Mean ± 1 SE	Range
Variables		
TOTAL number=233		
Number	8.96 \pm 3.36	1 - 84
Mass (grams)	142.07 \pm 54.97	0.3 - 1344.3
Total Length (mm)		24 - 215
Mean size in mass (grams per individual)	14.25 \pm 3.96	0.3 - 67.83
Biomass (grams per m ²)	0.069 \pm 0.03	0.0002 - 0.672
Density (number of individuals per m ²)	0.004 \pm 0.002	0.0005 - 0.042
Surface Salinity	27.42 \pm 1.14	15 - 35
Bottom Salinity	28.12 \pm 1.14	15 - 35
Surface Temperature (°C)	28.91 \pm 0.48	24 - 32
Bottom Temperature (°C)	28.38 \pm 0.46	22.8 - 31.5
Secchi depth (m)	1.29 \pm 0.10	0.4 - 2.9
Transparency (%)	56.81 \pm 5.30	10 - 100
Depth (m)	2.61 \pm 0.21	1.3 - 4.5

Table 3.12. Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Diapterus rhombeus</i> (Caitipa mojarra)	Mean ± 1 SE	Range
Variables		
TOTAL number=201		
Number	4.10 \pm 0.84	1 - 24
Mass (grams)	62.66 \pm 17.42	1.1 - 707.4
Total Length (mm)		40 - 148
Mean size in mass (grams per individual)	15.07 \pm 1.74	1.1 - 40
Biomass (grams per m ²)	0.035 \pm 0.01	0.001 - 0.354
Density (number of individuals per m ²)	0.002 \pm 0.001	0.001 - 0.019
Surface Salinity	19.63 \pm 1.30	0 - 31
Bottom Salinity	21.67 \pm 1.18	0 - 32
Surface Temperature (°C)	28.05 \pm 0.37	22.2 - 32
Bottom Temperature (°C)	27.53 \pm 0.37	21.4 - 32
Secchi depth (m)	0.91 \pm 0.05	0.2 - 2.0
Transparency (%)	36.04 \pm 2.57	12 - 83
Depth (m)	2.67 \pm 0.10	1.3 - 4.0

Table 3.13. Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Stellifer lanceolatus</i> (Star drum)	Mean ± 1 SE	Range
Variables		
TOTAL number=503		
Number	15.24 \pm 8.72	1 - 271
Mass (grams)	58.14 \pm 24.10	0.5 - 755
Total Length (mm)		30 - 143
Mean size in mass (grams per individual)	9.33 \pm 1.67	0.5 - 38.6
Biomass (grams per m ²)	0.030 \pm 0.01	0.0003 - 0.378
Density (number of individuals per m ²)	0.008 \pm 0.004	0.001 - 0.136
Surface Salinity	17.64 \pm 2.03	0 - 35
Bottom Salinity	20.64 \pm 1.62	0 - 35
Surface Temperature (°C)	26.73 \pm 0.56	20 - 31.9
Bottom Temperature (°C)	26.33 \pm 0.53	30 - 31
Secchi depth (m)	0.59 \pm 0.03	0.3 - 1.0
Transparency (%)	22.24 \pm 1.68	10 - 50
Depth (m)	2.80 \pm 0.11	1.3 - 4.0

Table 3.14. Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Citharichthys spilopterus</i>	Mean ± 1 SE	Range
Variables		
TOTAL number=216		
Number	3.60 \pm 0.63	1 - 31
Mass (grams)	28.40 \pm 6.00	1.4 - 285
Total Length (mm)		43 - 190
Mean size in mass (grams per individual)	9.01 \pm 1.36	0.78 - 65.1
Biomass (grams per m²)	0.015 \pm 0.003	0.001 - 0.143
Density (number of individuals per m²)	0.002 \pm 0.0003	0.001 - 0.016
Surface Salinity	20.28 \pm 1.42	0 - 36
Bottom Salinity	23.83 \pm 1.11	0 - 36
Surface Temperature (°C)	28.86 \pm 0.41	20 - 32.5
Bottom Temperature (°C)	26.36 \pm 0.40	20 - 32
Secchi depth (m)	0.77 \pm 0.05	0 - 2
Transparency (%)	30.10 \pm 2.00	10 - 67
Depth (m)	2.79 \pm 0.10	1.2 - 4.3

Table 3.15. Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Cetengraulis edentulus</i> (Atlantic anchoveta)	Mean ± 1 SE	Range
Variables		
TOTAL number=178		
Number	6.36 \pm 3.18	1 - 89
Mass (grams)	46.39 \pm 28.19	0.6 - 789
Total Length (mm)		36-163
Mean size in mass (grams per individual)	7.03 \pm 1.49	0.6 - 40.2
Biomass (grams per m²)	0.023 \pm 0.01	0.0003 - 0.393
Density (number of individuals per m²)	0.003 \pm 0.002	0.001 - 0.045
Surface Salinity	16.71 \pm 1.95	0 - 32
Bottom Salinity	20.36 \pm 1.42	5 - 32
Surface Temperature (°C)	27.61 \pm 0.54	22.3 - 31.9
Bottom Temperature (°C)	27.23 \pm 0.54	21.8 - 31.1
Secchi depth (m)	0.62 \pm 0.05	0.2 - 1.5
Transparency (%)	25.71 \pm 12.79	11 - 83
Depth (m)	2.56 \pm 0.11	1.8 - 4.3

Table 3.16. Means and ± 1 standard error and ranges for total number of individuals and mass, minimum and maximum Total Length caught, mean size in mass, density, biomass, and environmental characteristics.

<i>Cyclichthys schoepfi</i> (Striped burrfish)	Mean ± 1 SE	Range
Variables		
TOTAL number=142		
Number	2.41 \pm 0.33	1 - 13
Mass (grams)	288.59 \pm 35.35	2.4 - 1525
Total Length (mm)		28 - 2000(?)
Mean size in mass (grams per individual)	139.08 \pm 13.78	2.4 - 654.4
Biomass (grams per m ²)	0.146 \pm 0.02	0.001 - 0.763
Density (number of individuals per m ²)	0.001 \pm 0.0002	0.001 - 0.007
Surface Salinity	25.32 \pm 1.14	0 - 38
Bottom Salinity	26.76 \pm 0.94	15 - 36
Surface Temperature (°C)	27.5 \pm 0.42	23 - 32
Bottom Temperature (°C)	26.99 \pm 0.41	23 - 31.5
Secchi depth (m)	1.15 \pm 0.07	0 - 2.9
Transparency (%)	45.80 \pm 2.85	15 - 100
Depth (m)	2.72 \pm 0.11	1.2 - 4.5

Table 3.17. Rotated factor loadings (VARIMAX rotation over four axes) for six environmental variables measured in 264 samples at 18 station in Terminos Lagoon, between February 1980 and April 1981.

Variable	Factor 1	Factor 2	Factor 3	Factor 4
Surface salinity	0.19645	0.95244	0.00635	0.10784
Bottom salinity	0.15884	0.95074	0.08668	0.14173
Surface temperature	0.97962	0.16785	-0.01494	-0.00741
Bottom temperature	0.97445	0.18264	-0.07139	-0.00603
Secchi disk depth	-0.01493	0.17678	0.10366	0.97865
Depth	-0.06129	0.06257	0.99095	0.10007
Variance	1.977014	1.907734	1.005605	0.999567
% Cum. Var.	44.54	70.77	85.87	98.17

Table 4.1 Dominant fish species of seagrass system (Puerto Real Inlet, Terminos Lagoon), Monthly catch in number and weight, total frequency, total number and total weight.

Species	February		April		June		July		August		October		December		Total		
	wt	no	wt	no	wt	No	wt	No	wt	No	Wt	No	wt	No	wt	No	Freq
<i>Orthopristis chrysoptera</i>	227.4	24	550.1	44	3824.1	244	10279.5	520	11331	465	7537.4	242	1520.3	111	35269.8	1650	92
<i>Archosargus rhomboidalis</i>	3027.1	20	10031	74	4281	45	12047.3	274	16544.9	486	38754.7	435	11924.7	69	96610.7	1403	94
<i>Corvula sanctae-luciae</i>	2052.5	193	1599.4	117	2676.9	268	2008.8	136	1430.1	90	3063.5	237	5043.9	314	17875.1	1355	86
<i>Haemulon plumieri</i>	299.3	27	641.2	18	1080.4	20	857.6	38	1247.8	31	1830.2	113	1073	75	7029.5	322	86
<i>Cathorops spixii</i>									336.6	8	17301.8	232	884	13	18522.4	253	9
<i>Nicholsina usta</i>	1049.3	48	799.8	19	326.9	3	303.4	2			3442.6	138	872.5	42	6794.5	252	55
<i>Eucinostomus gula</i>			76.3	7	100.7	19	521.7	116	188.3	45	202.6	39	40.5	7	1130.1	233	58
<i>Cylichthys schoepfi</i>	1278.7	12	1876.2	9	1097.9	21	2173.8	38	2098.3	50	2591.8	35	1435	23	12551.7	188	68
<i>Diodon hystrix</i>	1514.1	25	1332.6	16	3401.7	27	2448.6	18	989.9	5	2816.4	54	1037.6	25	13540.9	170	68
<i>Ariopsis felis</i>	654.6	10	3294.9	37	824	5	144.3	2	438.7	10	1850.9	46	8057.9	59	15265.3	169	50
<i>Sphoeroides testudineus</i>	1928.3	15	2369.6	14	1627.3	12	1210.7	9	2303.3	27	4526.2	45	4812.8	44	18778.2	166	69

(Table continued)

268

<i>Bairdiella chrysoura</i>			219.5	8	42.8	6	143.7	12	1066.1	88	471.7	35	197.3	8	2141.1	157	45
<i>Stephanolepsis hispidus</i>	10.8	5	67.4	9	378.6	29	1666.6	62	1110.9	31	309.1	8			3543.4	144	53
<i>Haemulon bonariense</i>	408.5	5	628.3	10	909.6	10	220.6	7	144.5	21	1168.1	47	660.2	41	4139.8	141	55
<i>Lutjanus griseus</i>	523.8	8	764.7	7	731.8	4	114	1	3165.1	33	2693.6	37	2421.2	34	10414.2	124	54
<i>Anisotremus virginicus</i>	847.4	12	5470	21	2243	14	282.5	5	682.1	7	1289.4	37	1714.6	23	12529	119	56
<i>Opsanus beta</i>	656.5	9	854.6	16	310	7	2213.2	24	1571.6	24	1513.9	17	1006.2	19	8126	116	50
<i>Haemulon aurolineatum</i>					5.3	2	205.4	39	266.6	51	298.5	20	7.1	1	782.9	113	36
<i>Urolophus jamaicensis</i>	3985.8	7	3692.7	10	2882.8	7	4197.9	24	1255.8	8	5749.5	21	9773.4	27	31537.9	104	62
<i>Odontoscion dentex</i>	22.9	1	26.7	1							1230.5	74	394.7	23	1674.8	99	24
<i>Archosargus probatoccephalus</i>	461	3	23923.9	27	14248.3	17	2698.6	12	795.7	3	2507.2	11	4558	8	49192.7	81	49

Table 4.2 Dominant fish species of seagrass/mangroves system (Estero Pargo, Terminos Lagoon); monthly catch in number and weight (gr), total frequency, total number and total weight.

Species	Jan		Feb		Mar		May		Jul		Sep		Nov		Total		Freq.
	wt	no	wt	no	wt	no	wt	no	wt	no	wt	no	wt	no	wt	no	
<i>Orthopristis chrysoptera</i>	314.5	13	1228.1	174	1383.2	361	15047.6	2467	10636.9	1175	3841.8	199	120.7	6	32572.8	4395	74
<i>Eucinostomus gula</i>	408.2	83	1898.3	394	512.8	146	486	285	1983.4	960	316.5	189	1926	558	7531.2	2615	96
<i>Archosargus rhomboidalis</i>	2695.5	66	16470.5	488	3018.8	93	5837.1	1158	5724.3	514	8992.1	230	1608.5	14	44346.8	2563	83
<i>Bairdiella chrysoura</i>	508	46	5934.2	307	822.7	125	3163	413	1353.8	230	3061	163	726.6	54	15569.3	1338	88
<i>Anchoa mitchilli</i>	293.2	380	7	8	1.8	2					5.7	4	93.5	314	401.2	708	27
<i>Sphoeroides testudineus</i>	5432	44	18874.2	142	1666.7	11	9360.5	83	10558.3	78	4376.8	40	1079	7	51347.5	405	76
<i>Lutjanus griseus</i>	748.7	26	5195.6	135	1121	30	2600.6	52	924.5	12	550.1	22	87.1	3	11227.6	280	66
<i>Opsanus beta</i>	972.9	8	21810.7	123	6257.2	37	7793.9	53	2848.6	11	1155.9	10	725.4	3	41564.6	245	57
<i>Ariopsis felis</i>	1315.2	21	2088.5	38	125.2	1	784.2	8	1566.4	54	3400	104	158.5	7	9438	233	54
<i>Diapterus rhombeus</i>	40.4	11	26.7	8	2.6	1	23.1	4	0.7	1	10	2	211.1	184	314.6	211	34
<i>Cyclichthys schoepfi</i>	606	3	5233	51	3913.5	34	1571.4	22	1382.2	22	1692.8	15	2.2	1	14401.1	148	61
<i>Cathorops spixii</i>	3577.4	51	3501.1	71					86.3	1	800	19	302.7	4	8267.5	146	17

(Table continued)

<i>Cynoscion nebulosus</i>	74.5	2	1504.1	28	150.3	8	225.3	13	641.8	23	458.4	13	245	10	3299.4	97	60
<i>Archosargus probatocephalus</i>			3099.7	52	215.1	4	942.5	15	891.7	10	276.9	5	292.4	2	5718.3	88	43
<i>Acanthostracion quadricornis</i>	282.8	5	501.3	23	644.2	9	224.2	6	958.6	18	158.4	5	1.5	1	2771	67	46
<i>Bairdiella ronchus</i>			1503.7	22	20.5	1	609.7	16	38	16	44.8	2	3.4	2	2220.1	59	23
<i>Scorpaena plumieri</i>	847.3	6	1396.4	15	344.9	3	247.7	6	639.3	2	269	2	219.3	2	3963.9	36	26
<i>Cichlasoma urophthalmus</i>			404.7	11	364.7	14	270.8	5							1040.2	30	10

VITA

Ana Laura Lara Domínguez was born on September 28, 1955, in Mexico City. She is Scientist Research at the Instituto de Ecología, A.C. She has worked as a Research Assistant in the Laboratory of Ichthyology and Estuarine Ecology, Institute of Marine Sciences and Limnology, UNAM, and as a Research Scientist and Professor at the Centro EPOMEX, Universidad Autónoma de Campeche. She is part of the Advance Studies in Leadership for Environmental and Development. LEAD-Mexico Program. She has experience in ecology of coastal lagoons, estuaries, and coastal waters; ecology of mangrove and seagrass systems; ecology of estuarine communities; and ecological management of tropical estuaries. She has extensive research and teaching experience in coastal ecology and management of estuarine communities and coastal lagoons, and estuarine ecology in the Gulf of Mexico and Caribbean. She was coordinator of the international day of clean up coastal from 1991-1999. She is also a Consultant for Lara y Lara Asociados S.C.; and ECOPALS S.C. She was awarded the Gabino Barreda Medal for her Master Sciences Studies at UNAM, and she has been Member of the National Researchers System Mexico (SNI). 1987-1993.

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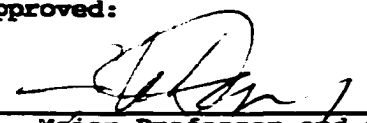
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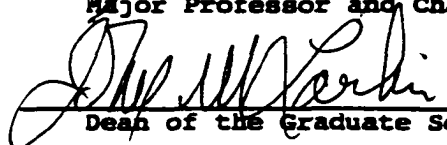
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Title of Dissertation: Ecological Structure of Estuarine Fish Communities:
Habitat Linkages Among Dominant Species Groups in
Terminos Lagoon, Mexico

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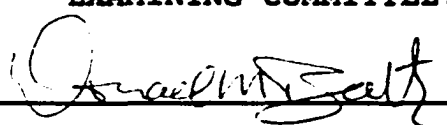


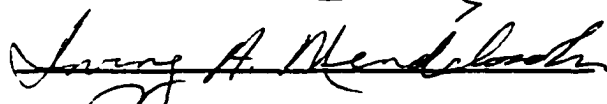
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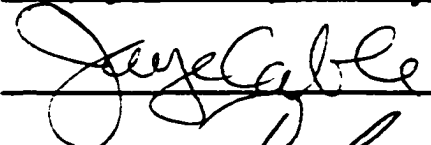
Dean of the Graduate School

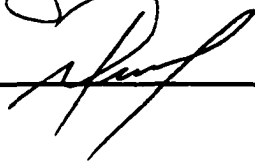
EXAMINING COMMITTEE:











Date of Examination:

June 4, 2001