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Enrique Reyes

Louisiana State University and Agricultural & Mechanical College

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**Ecosystem models of aquatic primary production and fish
migration in Laguna de Terminos, Mexico**

Reyes, Enrique, Ph.D.

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**ECOSYSTEM MODELS OF AQUATIC PRIMARY PRODUCTION AND FISH
MIGRATION IN LAGUNA DE TERMINOS, 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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ABSTRACT

Laguna de Terminos is Mexico's largest coastal lagoon. There is a high habitat diversity including open water, mangroves, seagrasses and marshes, which supports Mexico's most economically important fisheries. Understanding ecosystem processes is essential for effective management of the lagoon's resources. This research developed landscape-level models for aquatic primary production (LAPPTER model), and fish migration (ROE model) in Laguna de Terminos. The ROE model was developed first as a theoretical approach, and later integrated into the LAPPTER model as a submodule which utilizes simulated production as a food source. The ROE model includes behavioral rules for fish movement based on environmental tolerances and population parameters such as mortality and birth rates. LAPPTER describes landscape processes controlling aquatic primary production, and accounts spatially and temporally for fluxes and interactions among biotic and abiotic components in the water column. The output demonstrated patterns of production associated with rivers, rainfall and cloud cover. Modeled phytoplankton peaked during the maximum river discharge period (wet season). Seagrass production peaked when salinity and light were at a maximum (dry season). These patterns imply that phytoplankton are nutrient limited and benthic macrophytes are light limited. Spatial distribution of phytoplankton expanded with maximum river discharge, supporting the idea of nutrient limitation. The LAPPTER and ROE model combination examined spatial and biological population dynamics, giving a better analysis of fish behavior and habitat utilization. Spatial results for seasonal visitors into the lagoon indicated where ecological parameters combined "optimally". Modeled stenohaline visitors relied on presence of

marine waters inside the lagoon, never utilizing resources available near the deltas. Euryhaline visitors used the lagoon more fully, concentrating in the deltas. All migrations agreed with life history observations of prior studies. Finally, an interactive and user-friendly computer interface was developed to expedite organization and information transfer of research about Laguna de Terminos, providing assessment data for environmental policy makers and managers. This interface provides access to information on ecological functions and effects of human activities, including simulations of fish migrations and aquaculture scenarios. This system delivers capabilities and data from a desktop computer which were previously accessible only from mainframe computers.

**CHAPTER 1. LANDSCAPE ECOSYSTEM MODELING AND INFORMATION
TRANSFER FOR A TROPICAL COASTAL LAGOON**

INTRODUCTION

Studies on estuarine and coastal ecosystems during the past 20 years have been both intensive and extensive (Day *et al.* 1989a). Holistic analyses of coastal ecosystems have become more common in many areas, evolving from the seminal paper by Odum (1969) to more recent experiments (Patten 1971, 1972 and 1975, Day *et al.* 1973, 1989b, Odum 1983, Baker 1989). A valuable methodology for ecosystem analysis is simulation modeling. This mathematical approach facilitates holistic analysis due to the ease of scenario creation to provide insights into environmental mechanics (Jeffers 1978, Ulanowicz 1986). The use of computer simulations for understanding environmental processes at the ecosystem level has steadily increased in importance over the last decade, facilitating access to complex numerical calculations and subsequent analyses (Dame 1977, Day and Yáñez-Arancibia 1982, Costanza and Sklar 1985).

There have been several ecosystem level models designed for coastal areas, including the Delaware Estuary, New Jersey (Kelly and Spofford 1977); Narragansett Bay, Rhode Island (Kremer and Nixon 1978); Chesapeake Bay, Maryland (Baird and Ulanowicz 1986); Sapelo Island, Georgia (Wiegert *et al.* 1981, Wiegert and Pomeroy 1981); and Barataria Bay, Louisiana (Hopkinson and Day 1977, Conner and Day 1987, Costanza 1987). In tropical areas these efforts range in spatial scale from a mangrove ecosystem in South Florida (Lugo *et al.* 1976) to Campeche Sound, Mexico (Soberon 1987).

Ecosystem simulation and analysis provide insights into the mechanics of ecosystem physical-biological interactions. Understanding

ecosystem mechanics allows one to predict biological changes under different physical, chemical, and landscape scenarios. Traditional coastal research often focuses on a single taxonomic class or a physical and chemical set of variables. These studies in many instances, have created large data bases, a basic requirement for implementing sound resource management. Costanza and Sklar (1985) pointed out the need to consolidate this environmental information into a form accessible to both scientific and non-scientific users. Ecosystem simulation and analysis are holistic by nature, potentially underscoring interconnections in space and time. They inherently synthesizes large data bases, enhances basic ecological understanding, and emphasizes future research (Sklar *et al.* 1986). Modeling is a tool well suited for ecosystem analysis and for answering both basic and applied questions, because models synthesize existing knowledge (both structure and function) into the process of simulating or predicting (Burns, 1992). The predictive potential of simulation experiments can aid in resource management decisions (Mann 1982). The use of simulation models has led to a growing realization that ecosystem management must be a comprehensive, holistic process (Bahr *et al.* 1983, Craig and Day 1987, Day and Templet 1989, Day *et al.* 1989c, Gosselink 1984, Gosselink *et al.* 1989).

In this work, I first review landscape models and discuss the objectives of this dissertation (this chapter). Then I present a design for a spatially explicit model of fish migration (The Regional Organism Exchange model, ROE; Chapter 2). In chapter 3, I consider ecosystem-scale interactions, such as aquatic primary production (APP) and fish migration, among spatially defined heterogeneous habitats in Laguna de Terminos, a tropical coastal

lagoon in the southern Gulf of Mexico. Two models, one for Landscape Aquatic Primary Production of TERminos lagoon (LAPPTER model) and the ROE model (Regional Organism Exchange for TERminos lagoon, ROETER), are combined into a dynamic landscape simulation, that includes both primary producers and consumers (nekton). This model combination explored how landscape processes and patterns interact controlling the distribution of fish over long time scales and large geographic areas. Finally (Chapter 4), a bilingual (Spanish and English), interactive and user-friendly computer interface is developed to enhance information transfer from scientific research, and to provide assessment data for use as a predictive tool for environmental policy makers and resource managers.

Advances in Landscape Ecosystem Simulation.

Ecosystem simulation has become a major area of research made possible by both recent conceptual developments and new technologies (Hall and Day 1977, Naveh and Lieberman 1984, Wulff *et al.* 1989). Such advances include: (1) the advent of bigger and faster computers that reduce the need for expensive processing time; (2) the ease with which spatial data can be classified using geographic information systems (Quattrochi and Pelletier 1989); and, (3) dense data collection due to such technologies as satellite imagery and flow-through systems which allow more precise calibration and validation (Madden and Day 1992). These new technologies and a strong concern for environmental health have allowed the development of a new class of dynamic spatial ecosystem simulation model: the landscape ecosystem simulation (Costanza *et al.* 1990, Sklar and Costanza 1990, Merriam *et al.* 1990).

Sklar and Costanza (1990) discuss the potential of landscape models to: (1) map the flows of energy and matter; (2) designate source, sink and receptor areas (Szymer and Ulanowicz 1987); (3) predict succession in two and three dimensions; (4) determine cumulative thresholds for anthropogenic substances; and, (5) address questions of landscape scale (Forman and Godron 1986, Reiners 1988). This type of dynamic modeling has been characterized by the development and maintenance of spatial heterogeneity, including spatial and temporal interactions and exchanges across landscapes, and the ability to qualify and quantify the influences of heterogeneity on biotic and abiotic processes (Griffith and MacKinnon 1981, Risser *et al.* 1984). These dynamic ecosystem simulations integrate spatially discrete data over whole ecosystems, synthesize information, and examine ecological interactions.

Hierarchical Properties of Landscape Ecosystem Simulations.

The hierarchical properties of ecosystems have been discussed by Odum (1971), and the application of hierarchy theory to ecosystems by Webster (1979) and Allen and Starr (1982). A hierarchical conceptual approach to dynamic spatial simulations simplifies ecosystem-level analysis (Allen and Starr 1982, O'Neill *et al.* 1986). Moreover, the hierarchical structure proposed by Zonnoveld (1972) for landscape examination helps in the analysis of ecosystems at macroscales (thousands of km) and in postulating new ideas and concepts for the overall system. This analysis is done by examining each landscape component and interactions at different scales and spatial structures. Table 1.1 describes this hierarchical approach and uses the models developed in this thesis to exemplify the different scales and spatial interactions. First, the *ecotope* is the smallest holistic landscape

Table 1.1

Spatial hierarchical levels for landscape models*

Ecotope is the smallest holistic landscape unit, usually characterized by homogeneity of at least one attribute of the ecosystem and without excessive variations in other attributes.

	<u>Main Attribute</u>	<u>Variations</u>	<u>Chapter</u>
Water Unit Model	Phytoplankton Productivity, Detritus	Mangrove and Seagrass Production	3
Population Unit Model	Nekton Biomass	Fish groups	2, 3

Land facet is a combination of ecotopes, forming a pattern of spatial relationships and being strongly related to properties of at least one land attribute.

	<u>Properties</u>	<u>Spatial Relationships</u>
Water Column Spatial Grid	Lagoon water	River discharge and Tidal flux on each inlet.
Fish Migration Grid	Population tolerance ranges	Migration through inlets and spatial specific birth and mortality rates.

Land system is a combination of land facets that form one convenient mapping unit on reconnaissance scale. These are the interactions that occur along the boundaries that define the studied ecosystem and its surroundings.

	<u>Land facets</u>	<u>Mapping unit</u>
LAPPTER model	Laguna de Terminos Basin	10 km ² cells
ROE Model	"Swimming organisms"	10 km ² cells

Main landscape is a combination of land systems in one geographical region.

*Modified from Zonnoveld (1972).

unit, characterized by one homogeneous main attribute of the ecosystem with variations according to attribute types. Examples of this landscape component are the fish population unit cell in the ROE model (Chapter 2) and the water-column unit model of the LAPPTER model (Chapter 3), in which the main attribute of the former is the fish population and of the latter the phytoplankton production, and the variations include the ecological tolerance ranges for each fish population and the contributions to the primary production by mangroves or seagrass beds, respectively. At the next level, the *land facet* is a combination of ecotopes forming a pattern of spatial relationships. This level implies a recognition of spatial interactions and fluxes. The spatial communication among contiguous unit models includes exchange of water and suspended materials fluxes (Chapter 3) and movement of fish from one habitat to the next according to population physiological tolerance (Chapters 2 and 3). At the third level is the *land system*; a combination of land facets that forms one mapping unit. In the LAPPTER simulation model, this mapping unit is exemplified by the spatial grid that represents Laguna de Terminos and the river discharge and tidal pumping as the variations that create a heterogeneous landscape (Chapter 3). Finally, there is a *main landscape*, where a combination of land systems is connected into one geographical region. As an example, aquatic landscapes might vary on scale from watersheds (10 to 1000's km²) to large marine ecosystems with areas > 200,000 km² (as defined by Sherman 1991).

Dynamics in Landscape Ecosystem Simulations.

A process-based landscape model includes the mechanics of the ecological processes on a spatial structure and function. The dynamics for

such models are produced by: (1) compartmentalizing the landscape into some geometric design (generally set by local geomorphology or geography); (2) implementing the interactions within compartments (Ulanowicz 1972); and, (3) defining the spatial fluxes among compartments according to location-specific algorithms (Sklar and Costanza 1990). The incorporation of feedback loops, neighborhood influences, and spatial exports and imports is made spatially explicit to reflect actual landscape interactions. Examples of spatially articulate models range from global weather circulation models (Pielke 1984), wetland models (Sklar *et al.* 1985, Costanza *et al.* 1986, Kladec and Hammer 1988, Boumans and Sklar 1990), oceanic plankton models (Show 1979), and coral reef growth models (Maguire and Porter 1977). These models simulate flows of materials over large areas and describe the transport of materials as a function of mass balance in combination with diverse climatic forcing functions.

Laguna de Terminos Landscape Simulation Model.

Laguna de Terminos (Figure 1.1) is a diverse ecological system. Controlling influences include ocean-river interactions, mangrove runoff, seagrass/water interactions, and human modifications (both within and among landscape components). This lagoon is well suited for landscape simulation studies and spatially dynamic fish migratory predictions because it is a regional ecosystem with significant physical and biological gradients, and research in this basin has created a large data base that contains more than 15 years of environmental and biological data (summarized in Yáñez-Arancibia and Day 1988). In addition, specific and urgent management issues must be addressed in this area such as creation of aquaculture farms,

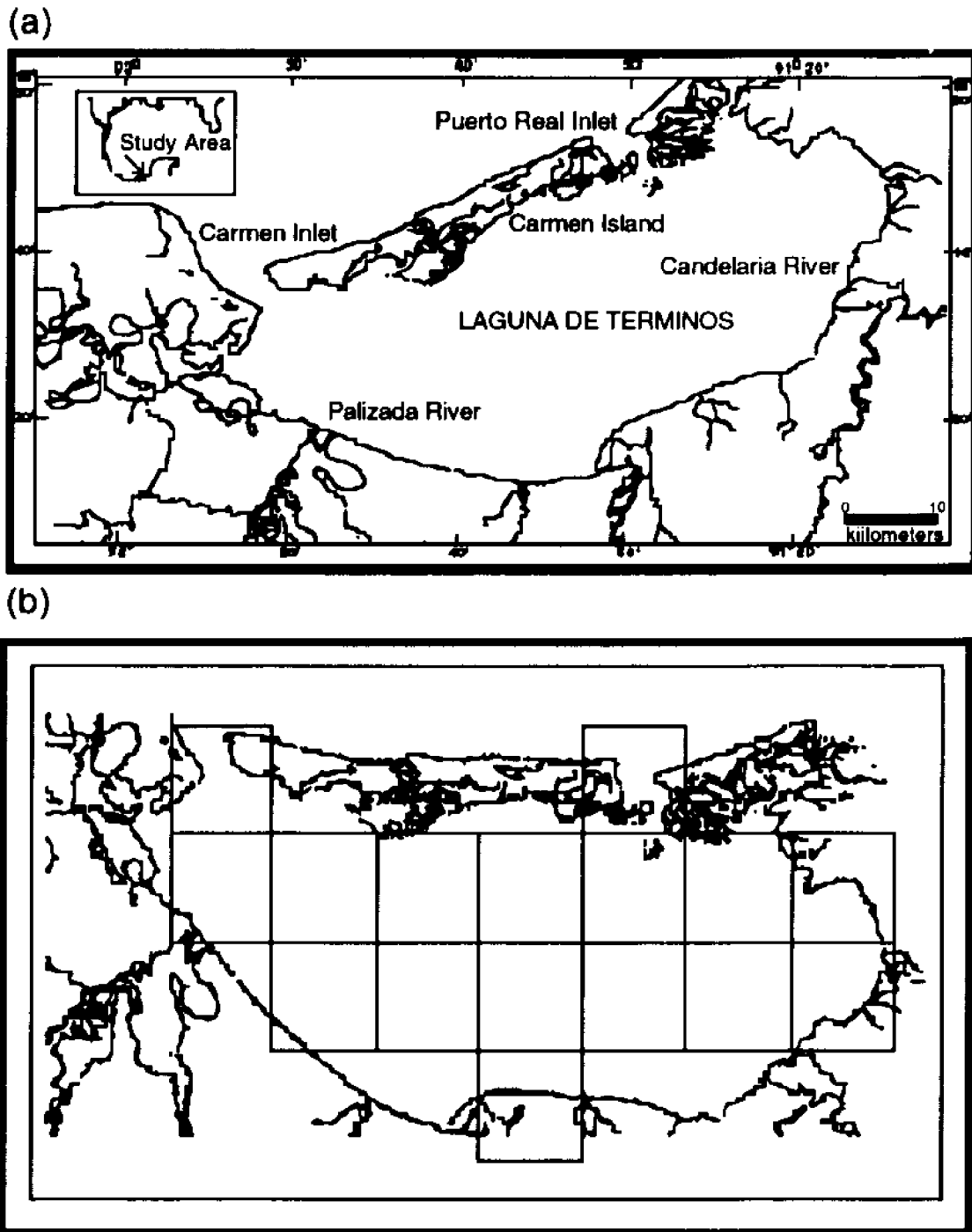


Figure 1.1 - Geographical location of Laguna de Terminos. (a) Names of inlets and associated fluvial systems, and (b) grid for landscape aquatic primary production and fish migration models. Each cell is 10 km².

wetland diversion for agriculture, and the extensive petroleum explorations and drilling that is now occurring.

Laguna de Terminos is Mexico's largest coastal lagoon, with an area of 2500 km² including open water and the adjacent mangroves and marshes (Figure 1.1). This lagoon receives discharge from a distributary of the Grijalva-Usumacinta River, the largest river system in Mexico and the second largest discharge to the Gulf of Mexico (after the combined Mississippi and Atchafalaya Rivers). Diverse marine and estuarine organisms use its various habitats as nursery grounds (Yáñez-Arancibia and Day 1982, 1988). As a result, the highly productive waters of Laguna de Terminos support Mexico's largest and most economically important fishery for brown shrimp Panaeus aztecus (Yáñez-Arancibia and Aguirre-León 1988). An understanding of ecosystem processes in the lagoon for both predicting and preventing the potential negative impacts of development on the system can be gained by using dynamic simulation. Ecosystem and landscape modeling is a critical tool for ecological and economic analyses in Mexico, as it is in other developing countries that lack the resources to generate broad scale monitoring programs and intensive sustained research.

Generally the best resource management plans are those based on a thorough understanding of basic environmental processes. Lessons from economic development in both industrialized and developing countries have shown that development relies crucially on natural resources and on the productivity of natural ecosystems (Loewinger 1983). It is apparent that in the future, economic plans will have to be tied to the realities of natural ecosystem processes (Savory 1991).

OBJECTIVES

This research develops and tests landscape-level models of aquatic primary production and its interaction with nektonic consumers in Laguna de Terminos, Mexico. The main objectives are to: (1) develop an aquatic, primary production, process-model of the dominant habitat (open water); (2) develop a dynamic, spatial population model for migratory species of fish; (3) combine these two models to simulate seasonal variability of nutrients, phytoplankton, organic matter and fish biomass; and, (4) integrate results of this work and past studies into a computer interface to facilitate information transfer to resource managers.

Two dynamic spatial models are developed at the landscape scale (1000's m²) for Laguna de Terminos using a 1/4 day time-step. Both are 2-dimensional, vertically-integrated, temporally- and spatially-articulated, finite-difference simulation models (after Sklar *et al.* 1985), one for aquatic primary production and nutrient dynamics (LAPPTER model), and the other for fish migratory patterns (ROE model). Environmental forcing functions such as solar radiation, temperature, river discharge, and tides drive both models. These models were designed to simulate vertically averaged distribution and fluxes for salinity, suspended sediments, total inorganic nitrogen concentration, chlorophyll, organic matter production, and fish standing stocks. The ROE model was first developed and tested against a hypothetical environment (Chapter 2) and then integrated into the LAPPTER model (Chapter 3) as a module that uses the output from the primary production model to stimulate fish migration behavior. Figure 1.2 depicts the hierarchical structure of the two models following the classification proposed by Zonnoveld (1972) and energy diagram notation by Odum (1972).

The following sections of this paper briefly describe specific objectives, methods and results from each of the simulation models. Each description is integrated as a chapter of this dissertation.

Chapter 2 - A Conceptual Design for Landscape Simulation of Fish Migration: the Regional Organism Exchange (ROE) model.

A spatially-explicit, grid-cell model was developed to understand how landscape processes and patterns may control migration of stenohaline fishes in Laguna de Terminos, Mexico. An interpolation model was used to spatially distribute environmental forcing functions. Behavioral rules for fish movement were based on environmental tolerance ranges and used to create a response matrix. Each cell of the landscape model was 10 km² in size, and included population parameters (i.e., mortality and birth rates), and plant-animal feedback mechanisms such as fish nutrient excretions. Daily maps of long-term spatial distributions of environmental and population parameters were compared to field data at four locations and were found to be realistic. Results indicate that mechanisms for fish migration are linked to regional biochemical processes. Sensitivity analyses evaluated the interrelations among food supply, birth rate, and changes in environmental and biological forcing functions. This theoretical approach to fish migration was transformed into a submodel of an aquatic primary production model for the same area (Chapter 3).

Chapter 3 - Landscape Ecosystem Model for Aquatic Primary Production and Fish Migration in Laguna de Terminos, Mexico.

A landscape model for aquatic primary production in Laguna de Terminos (LAPPTER) described water dynamics on a scale of 10's of km².

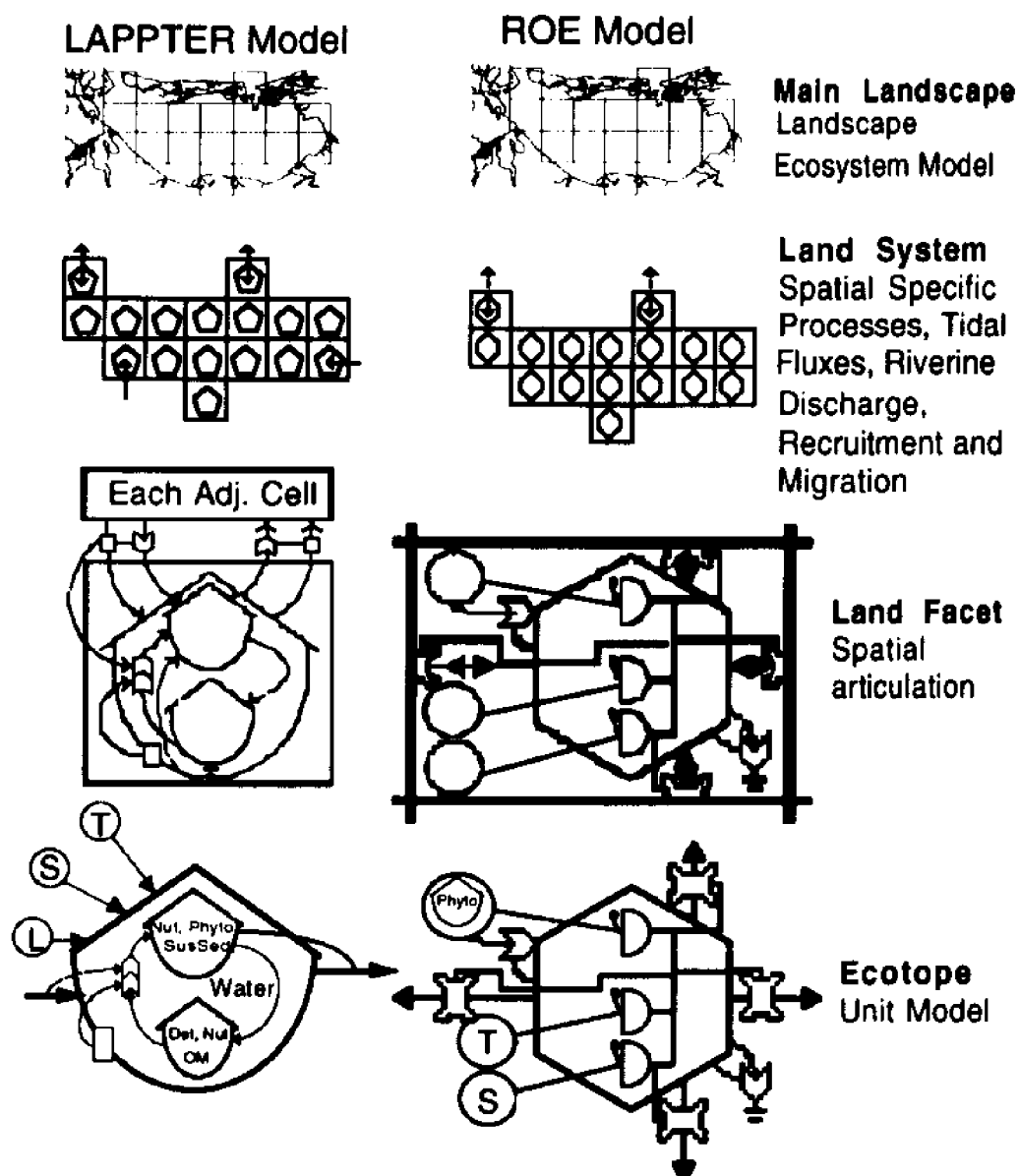


Figure 1.2 - Hierarchical structure for the landscape ecosystem models for Laguna de Terminos, Mexico. The naming convention follows the classification by Zonnoveld (1972) and identifies hierarchical processes. Forcing functions are S for salinity, T for temperature, and L for light, SusSed is suspended sediments, Nut is nutrients, OM is organic matter, Det is detritus, and Phyto is phytoplankton.

The model accounted, spatially and temporally, for fluxes and interactions among biotic (i.e., seagrasses and phytoplankton production, and detrital organic matter) and abiotic (i.e., nutrients, salinity) components in the water column. As a submodel of this simulation a ROE model was implemented to investigate trophic pathways. Forcing functions included mean annual solar irradiance, river discharge, tidal pumping, water temperature, and Secchi depth records. The model required these forcing functions to be spatially organized. Therefore, forcing functions with only temporal information were geometrically interpolated across space as a function of grid size and distance between actual data locations. Simulation output was presented either as synoptic tables or as maps. Maps allow examination of production figures according to site-specific controls, and identify critical habitats along a production gradient.

The landscape aquatic primary production (LAPPTER) model and the regional organism exchange (ROETER) model combination is an attempt to analyze how consumers interact with primary production at the landscape level. This primary producer and consumer coupling tests the interactions and contribution among the various habitats of Laguna de Terminos. Several migratory patterns have been identified in Laguna de Terminos in which spatial behavior seems to be related to the habitat utilization and physiological tolerance ranges of the different species (Yáñez-Arancibia *et al.* 1980, Díaz-Ruiz *et al.* 1982). Several fish species utilize the same areas and have similar feeding habits. This adaptation serves as the basis for grouping "functional groups". Species that have similar biological and environmental requirements exploit the diverse lagoon habitats similarly. The fish component of this migration model uses, as forcing functions, the output

from the LAPPTER model. Several feedback mechanisms are incorporated, such as nutrient supplementation as excretion from the fish population, and carrying capacity expressed as food availability. Spatial population dynamics, with the addition of biological dynamics such as birth and mortality rates, combined to produce a descriptive analysis of fish behavioral patterns and habitat utilization.

Chapter 4 - Ecological and Resource Management Information Transfer for Laguna de Terminos, Mexico: a computerized interface.

A user-friendly information system to expedite the organization and transfer of research findings about Laguna de Terminos was developed. This system was designed to facilitate the transfer of research data and results to environmental managers, and built in a manner that simplified the addition of information modules as they are developed. Use of this graphically oriented interface allows the user access to a wide range of scientific information presented as maps, graphs, and computer simulations (Chapter 3). The program includes animation of fish migrations (Chapters 2 and 3) and predictions for shrimp aquaculture scenarios. This chapter discusses recent developments in microcomputer technology that make it possible to deliver to the desktop computer of the researcher or manager a wide range of capabilities and data that previously could only be accessed on expensive and user-unfriendly mainframe computers.

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**CHAPTER 2. A CONCEPTUAL DESIGN FOR LANDSCAPE SIMULATION OF
FISH MIGRATION: THE REGIONAL ORGANISM EXCHANGE (ROE) MODEL.**

INTRODUCTION

We have created a theoretical modeling framework for the spatial simulation of processes that control Regional Organism Exchange (ROE) in order to understand how changing land use patterns, hydrology, and climate alter renewable natural resources. Specifically, we want to develop an understanding of the mechanics or "rules" of fish behavior in relation to water quality. We will show that a spatially-articulate ROE model of organism behavior and response to its environment produces a better understanding of migration in relation to man-made and natural environmental variability than more "traditional" spatially-averaged population models. Our modeling framework quantifies organism response and directs future research. This research will show how to integrate landscape-scale (10-100 km²) simulations of migratory fish populations with process-based ecological models.

Previous mechanical facsimiles and cybernetic models of animal movement focused on force and counterforce movements in relation to muscle and body structure (DeAngelis and Yeh 1984). These models tend to be expensive to run and often do not predict the movement of an entire population or trophic group within a heterogeneous environment. A more expedient, less expensive approach to simulate population movement is to describe it in dynamic numerical terms and to include non-linear "rules" for behavior, similar to what has been done in the field of dynamic spatial landscape models (Sklar and Costanza 1990). We believe that animal motility can be described as vectors and consequently, analyzed using differential or finite-difference equations (Rohlf and Davenport 1969, Okubo

1980). By defining population density as a function of spatial and temporal position, we simulate movement as a flux across spatial coordinates as suggested by Nisbet and Gurney (1982).

As a first approximation to a process-oriented ROE model of fish migration, we develop the algorithms and basic ecological and behavioral rules for one of several fish assemblages in a Mexican tropical lagoon. These rules, used to control fish migration patterns, were based on population threshold responses and their nonlinear relationship to physical, chemical, and biological parameters (e.g., salinity, food availability, birth and death rates) in the water column.

The objective of this paper is to describe the conceptual development of a ROE model. Specifically, we will discuss: (1) simulation of annual fish migration patterns for an idealized lagoon landscape; (2) interpolation of spatial data bases for model initialization; (3) construction of rules for fish growth, mortality, and movement; and, (4) model sensitivity to physical and biological parameters.

STUDY AREA

Notable among tropical coastal lagoons with available long-term environmental and biological data is Laguna de Terminos, at the base of the Yucatan Peninsula (Figure 2.1; summarized in Yáñez-Arancibia and Day 1988). Laguna de Terminos is Mexico's largest coastal lagoon. It is shallow (mean depth 3.5 m) with an area of approximately 2500 km² including open water, mangroves, and freshwater marshes. Laguna de Terminos support Mexico's largest and most economically important shrimp fishery (Yáñez-Arancibia and Aguirre-Leon 1988). Diverse marine organisms use the

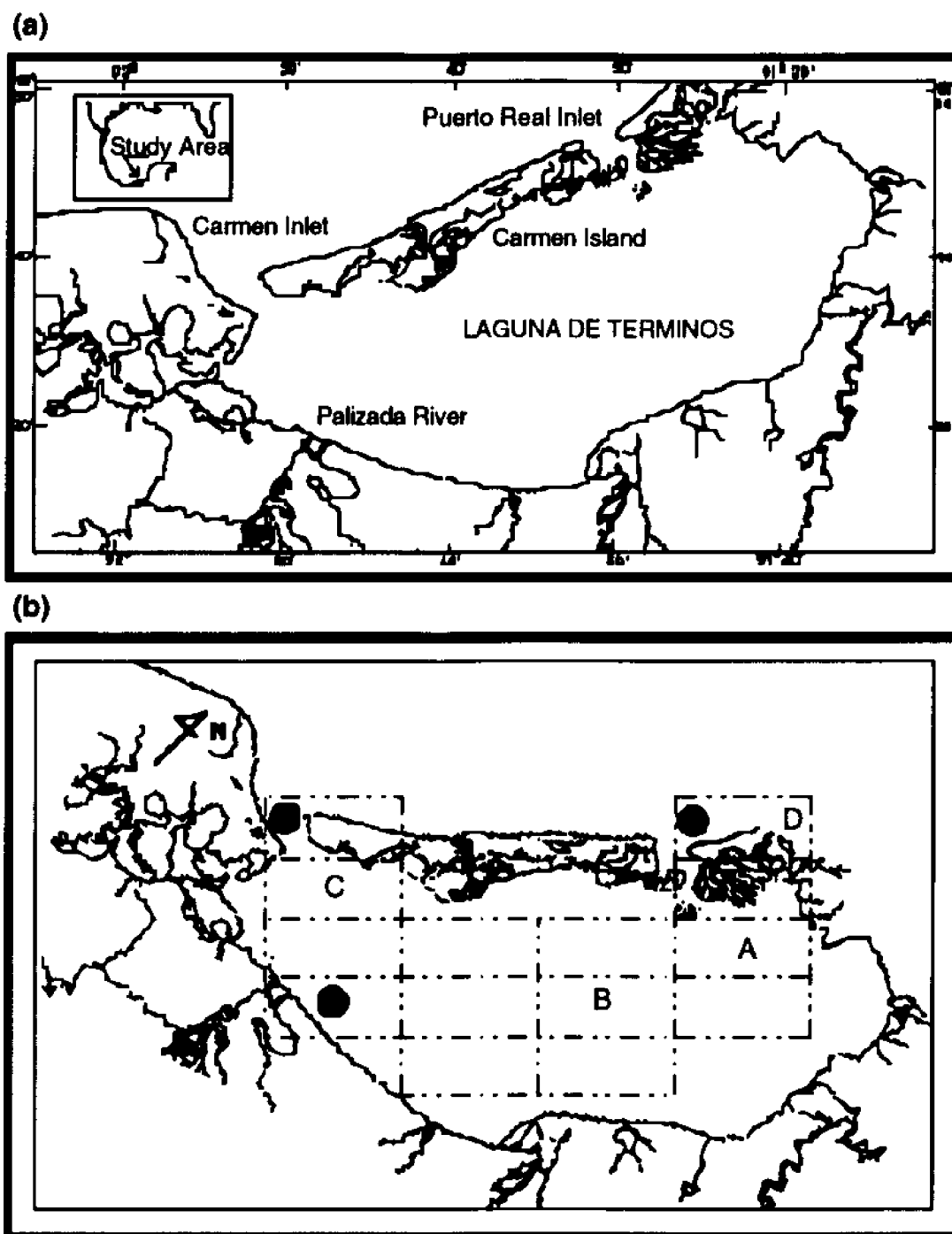


Figure 2.1 - (a) Map for Laguna de Terminos, Mexico. Scale 0.3 km = 1 min. (b) Spatial grid for simulation model. Cell size is 10 km². Dots indicate field stations used for environmental forcing functions. Letters show cells used in table 2.1 and figure 2.7.

lagoon's various habitats as nursery grounds (Yáñez-Arancibia and Day 1982, 1988). Laguna de Terminos has a strong net east to west water flow, caused by prevailing south-eastern trade winds (Gierloff-Emden 1977). This circulation pattern maintains semi-permanent gradients in salinity, turbidity, nutrient levels and sediment types, and promotes spatial/temporal assemblages of foraminifera, benthic macrofauna, fish and shrimp (Day *et al.* 1982).

Statistical analyses of the biology of Laguna de Terminos in relation to aquatic environmental parameters such as salinity, turbidity, and temperature identified common fish life history strategies and ecological tolerance ranges (Yáñez-Arancibia *et al.* 1980, 1985a, b, 1986, 1988a). Using environmental factors, seasonality and these life history strategies as criteria for the dominant species (in number and biomass), Yáñez-Arancibia *et al.* (1986) identified four particular fish assemblages as "functional groups". This functional groups have distinctive migration patterns, including marine stenohaline and euryhaline seasonal visitors, permanent residents and occasional visitors. An example of the marine stenohaline group is the pigfish, Orthopristis chrysoptera, whose habitat utilization patterns are discussed by Díaz-Ruiz *et al.* (1982). O. chrysoptera lives on the seagrass beds around Carmen Island and Puerto Real Inlet (Figure 2.1) as a fingerling, then migrates through the lagoon to the freshwater areas (salinity < 10 ppt) near the Palizada River as a juvenile. During peak river discharge, the adult pigfish moves to saltier parts of the lagoon at Puerto Real Inlet or to shallow waters offshore (salinity > 33 ppt) to reproduce. Such knowledge of life history patterns in relation to environmental factors form the rules for a ROE model, as described below.

METHODS

Numerical Techniques

There are two major categories of mathematical models applicable to animal movements. Those that use differential calculus to solve diffusion equations and those that use probability functions to create diffusion. Both can be modified to incorporate environmental forcing functions. The difference is that differential models add parameters to the equations, making them larger and more complex, while probability models modify the existing probabilities as a function of multiple interactions. We will briefly describe both because we use the former approach to structure equations, while using the latter to change parameter coefficients as a function of habitat suitability.

General advection-diffusion (differential) models view entire populations with little detail of individual movement. In these types of models, inert particles (e.g., environmental insensitive fish or element concentrations such as chlorine) are spatially distributed, according to Fick's three-dimensional diffusion equation (Okubo 1980):

$$\frac{dA(x,y,z)}{dt} = \frac{\partial^2}{\partial x^2} \left(\frac{k_x^2}{4} A(x,y,z) \right) + \frac{\partial^2}{\partial y^2} \left(\frac{k_y^2}{4} A(x,y,z) \right) + \frac{\partial^2}{\partial z^2} \left(\frac{k_z^2}{4} A(x,y,z) \right) \quad (2.1)$$

where A is the concentration of a variable (e.g., fish eggs) at any particular point in a 3-D space (x,y,z) dt is time-step, and k's are the diffusion coefficients. Each variable may use different diffusion coefficients. Fisheries management has used these models (Jones 1959, 1976, cited in Mullen 1989), to describe fish dispersion and local population dynamics (Okubo 1980). In the ROE model we use the physiological tolerance ranges as a surrogate for the diffusion coefficients (discussed below).

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$$\frac{d A(x,y,z)}{d t} = \frac{\partial^2}{\partial x^2} \left(\frac{k_x^2}{4} A(x,y,z) \right) + \frac{\partial^2}{\partial y^2} \left(\frac{k_y^2}{4} A(x,y,z) \right) + \frac{\partial^2}{\partial z^2} \left(\frac{k_z^2}{4} A(x,y,z) \right) \quad (2.1)$$

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Probability models, also known as random-walk models, simulate individual migration tracks and are based on the assumption that the probability of discrete movements for a single animal, during each time step, is the same in every direction (DeAngelis and Yeh 1984). For example, if an animal is initially situated at a point (i,j) in a two-dimensional grid of uniformly spaced points, the organism can potentially move with equal probability (maximum $p = 0.25$) in any of four directions to the points $(i, j-1)$, $(i, j+1)$, $(i-1,j)$ or $(i+1,j)$. It is possible to modify these models so that a particular direction is preferred (e.g., $p_{i,j-1} = 0.7$) as long as the total p doesn't exceed 1.0. The probability distribution for a random-walk model is the probability for arrival at a given radial distance from the starting point as long as radial symmetry is assumed (DeAngelis and Yeh 1984). Thus, a population of fish starting from a common initial point and moving according to pure random walk shows no average spatial displacement in any direction. The net result is a population that behaves similarly to one modeled with simple advection-diffusion equations (Saila and Shappy 1963).

Probability models may incorporate environmental controlling functions in the form of probability distributions as a function of space and time (DeAngelis and Yeh 1984). Introduction of these biased rules to modify movement implies complex decision-making on the part of the organism. The more sophisticated models can accurately simulate responses to heterogeneous environmental conditions (Saila and Shappy 1963, Kareiva and Shigesada 1983, Marsh and Jones 1988). Simulation experiments using modified random-walk models are not based on a general mathematical solution but rather on specific case scenarios. Thus, generalizations and

extrapolations from these models to other sites tend to be extremely difficult (Rohlf and Davenport 1969, Smith 1974).

In relation to fish dynamics, the diffusion and probability approaches differ because the former models fish population as a function of all spatial interactions; while the latter models organism movement as a function of its previous location in space, keeping a record of individual tracks. The advantage of the diffusion approach is that it calculates distribution densities across an entire landscape. The advantage of the probability approach is that it offers more spatial control of point-to-point migration probabilities. Mullen (1989) suggested combining both models with the use of a "variable diffusivity" model, in which the local environment affects local population dynamics by creating unique diffusion coefficients for each spatial coordinate across a heterogeneous landscape. The construction and implementation of such a hybrid model was the major objective of this research.

Landscape Techniques

Digital versions of the Laguna de Terminos landscape boundaries were created by overlaying a grid of 14 rectangular (10 km^2) cells over the lagoon (Figure 2.1 b). The total number of fish in a cell was treated as a state variable(i.e., a population in a fixed region of space changing only due to births, deaths, immigration and emigration). This allowed the population to remain static or flow into adjacent cells as a function of environmental forcing functions (Figure 2.2). These forcing functions (i.e., water column salinity, temperature, and chlorophyll concentrations - a proxy for food) were incorporated into population equations as response coefficients for fish.

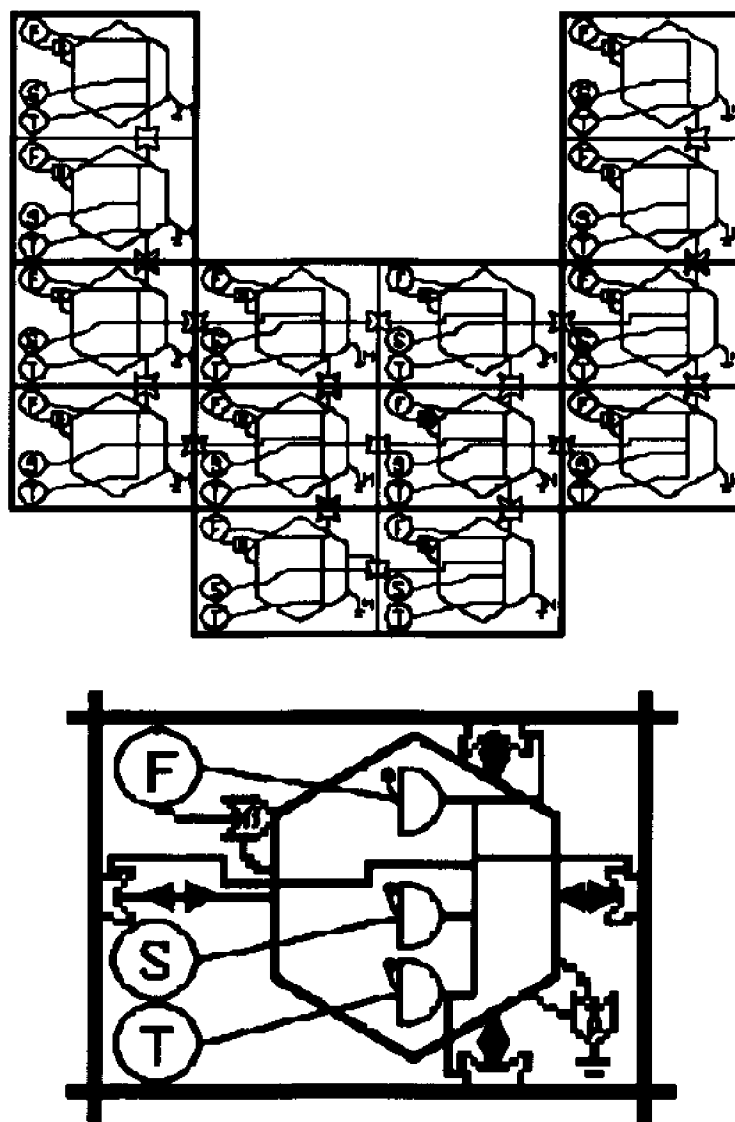


Figure 2.2 - (a) Spatial grid with cell model for fish population. (b) Detail of population model computed in each cell using Odum's symbols (1972). F = food (chlor. a in mg m^{-3}), S = salinity (S), T = temperature ($^{\circ}\text{C}$), b = births and m = deaths.

A difference equation was used to describe fish population density changes in a cell (Equation 2.2). The model was initialized with a population confined to a single two-dimensional cell. The number of fish crossing from one cell to another depended on population size (P) and a migration parameter (K), such that unidirectional flow across a single boundary (KP) could be summed for all sides of each cell and expressed as:

$$dP_{i,j} = ((K_{i-1,j,i,j})(P_{i-1,j}) + (K_{i+1,j,i,j})(P_{i+1,j}) + (K_{i,j-1,i,j})(P_{i,j-1}) + (K_{i,j+1,i,j})(P_{i,j+1})) \\ + (- (K_{i,j,i-1,j})(P_{i,j}) - (K_{i,j,i+1,j})(P_{i,j}) - (K_{i,j,i,j-1})(P_{i,j}) - (K_{i,j,i,j+1})(P_{i,j}))$$

(2.2)

where $K_{i,j+1,i,j}$ is the fish flow parameter from cell $_{i,j+1}$ to cell $_{i,j}$ and $P_{i,j}$ is the population density for cell $_{i,j}$ and dt is the unit time step (Sklar *et al.* 1985).

The fish migration parameter (K) varied between 0 and 1 as a function of cell-specific physiological tolerance ranges of the fish population (Lara-Dominguez and Yáñez-Arancibia, Programa EPOMEX, Unpubl. data) and potential pathways between adjacent grid cells. An index was implemented to normalize physiological tolerance ranges for habitat evaluation, following a calculation developed by the U.S. Fish and Wildlife Service (1981). This environmental suitability index to modify migration (K) coefficients was based on the idea of variable diffusivity, as mentioned above (Mullen 1989) and is similar to the equations of Ollason (1987) and Nisbet and Gurney (1982) for spatial interactions in patchy environments. The variable diffusivity concept allowed us to set simple behavioral rules in our model. That is, the decisions for fish migration (and its rate) depended on the multiplicative interaction of fish density with their environmental (e.g., salinity) and physiological (e.g., birth rate) requirements. Each environmental and physiological factor was transformed into a coefficient, weighted according to specific ecological

tolerances for stenohaline fishes (Díaz-Ruiz *et al.* 1982; Lara-Dominguez and Yáñez-Arancibia, Programa EPOMEX, Unpubl. data), and expressed as a combined suitability index (CSI). This CSI was then used to determine K of the source cell such that:

$$K = 1 - \text{CSI} \quad (2.3)$$

The CSI was based on the food supply (F, chlorophyll $\mu\text{g m}^{-3}$), salinity (S) and temperature (T, °C) according to the equation:

$$\text{CSI} = (S \cdot T \cdot F^2)^{1/4} \quad (2.4)$$

(U.S. Fish & Wildlife Service, 1981). The exponent of 1/4 normalizes the equation between 0 and 1 and F is squared as a weighting factor that stresses the relative importance of food. In this model, we introduce the concept of a spatial CSI. Using CSI to determine fish diffusion coefficients was conceptualized as a population's "need" to leave a cell because environmental conditions no longer corresponded with that population's optimum physiological requirements and tolerance ranges. It is also plausible, however, to add temporal variation to the habitat CSI, thereby increasing its effectiveness in capturing seasonal or age-specific environmental requirements.

The population density (P) in equation 2.2 was combined with more "classical" parameters of population change (Gause 1934, Hardin 1960). Birth (β ; individuals recruited per individual per day) and death (μ ; individuals per day) rates were based on a simplified Nisbet and Gurney (1982) equation for population flux in a patchy environment:

$$\frac{\partial P_{i,j}}{\partial t} = (\beta - \mu)P - \left[\frac{\partial M_i}{\partial i} + \frac{\partial M_j}{\partial j} \right] \quad (2.5)$$

where the net population flux, $\partial P/\partial t$, for each cell_{i,j} is a function of spatially articulate migration function for each axis (M_i and M_j).

To simplify the calculations in this conceptual model, mortality rates were kept constant, and birth rates were partitioned into two components (for sensitivity analysis), an intrinsic birth rate and a birth rate effected by the food supply (i.e., fecundity:food ratio). The birth rate was modified by the fecundity:food ratio to normalize the fish population response to available food and allow reproduction capacity to increase as a function of chlorophyll in a cell. The intrinsic birth rate was also controlled by the recruitment period. In this model, reproduction was set to occur between June and December. However, any period can be set to match population life-cycles.

Finally, cybernetic feedbacks (Margalef 1968, 1982) and ecological processes (Odum 1983) were added. We allowed the fish population to affect food content in two ways: (1) by eating, thereby diminishing the food supply, and (2) by excreting nutrients to the water column, thereby enhancing the food supply, according to the equation:

$$F_{i,j} = \rho Ch_{i,j} - \alpha P_{i,j} + \gamma P_{i,j} \quad (2.6)$$

where $F_{i,j}$ is food stock at a given cell, Ch is the chlorophyll a calculated for that day in that cell, and $P_{i,j}$ is the fish population, the coefficient ρ is a conversion constant for chlorophyll to carbon, α is a constant converting population density into food stock deletion due to feeding, and γ is a proportionality constant for fish excretions to food stock (Table 2.1).

Table 2.1

Fish migration equations and coefficients.

$$P(t) = P(t - dt) + ((K_{i-1,j,i,j}) (P_{i-1,j}) + (K_{i+1,j,i,j}) (P_{i+1,j}) + (K_{i,j-1,i,j}) (P_{i,j-1}) + (K_{i,j,i+1,j}) (P_{i,j+1}) - (K_{i,j,i-1,j}) (P_{i,j}) - (K_{i,j,i+1,j}) (P_{i,j}) - (K_{i,j-1,i,j}) (P_{i,j}) - (K_{i,j,i+1,j}) (P_{i,j}) + \beta(P) - \mu(P)) \cdot dt$$

Initial value for $P(t)$ = 500,000 individuals in Puerto Real cell (Cell D).

$P(t)$ = Fish population in cell at time t

$P(t-dt)$ = population at time $t-dt$

$(K_{i-1,j,i,j}) (P_{i-1,j})$ = Fish population from adjacent cell

$$(K_{i-1,j,i,j}) = 1 - CSI_{i-1,j}$$

$(K_{i,j,i-1,j}) (P_{i,j})$ = Fish population to adjacent cell

$$(K_{i,j,i-1,j}) = 1 - CSI_{i,j}$$

$$\beta(P) = \beta \cdot P$$

$$\beta = (0.0071 \cdot (F_{i,j} \cdot 2))$$

$$\mu(P) = \mu \cdot P$$

$$\mu = 0.0051$$

$$CSI_{i,j} = (S_{i,j} \cdot T_{i,j} \cdot F_{i,j}^2)^{1/4}$$

Combined suitability index for cell_{i,j}

$$CSI_{i,j} = (S_{i,j} \cdot T_{i,j} \cdot F_{i,j}^2)^{1/4}$$

$S_{i,j}$ = salinity index for cell_{i,j}. Salinity value is geometrically determined.

$T_{i,j}$ = temperature index in cell_{i,j}. Temperature value is geometrically determined.

$F_{i,j}$ = food index in cell_{i,j}. Food value in cell_{i,j} is:

$$F_{i,j} = \rho Chl - \alpha P_{i,j} + \gamma P_{i,j}$$

$$\rho = 40$$

$$\alpha = 1$$

$$\gamma = 0.001$$

Chl is chlorophyll value determined geometrically.

Geometric algorithm

$$Z = -((a \cdot i + b \cdot j - d) / c)$$

Z = parameter value.

i = coordinate value on x-axis

j = coordinate value on y-axis

From 3 pre-defined stations:

$$a = j_1 \cdot (Z_2 - Z_3) + j_2 \cdot (Z_3 - Z_1) + j_3 \cdot (Z_1 - Z_2)$$

$$b = Z_1 \cdot (i_2 - i_3) + Z_2 \cdot (i_3 - i_1) + Z_3 \cdot (i_1 - i_2)$$

$$c = i_1 \cdot (j_2 - j_3) + i_2 \cdot (j_3 - j_1) + i_3 \cdot (j_1 - j_2)$$

$$d = i_1 \cdot (j_2 \cdot Z_3 - j_3 \cdot Z_2) + i_2 \cdot (j_3 \cdot Z_1 - j_1 \cdot Z_3) + i_3 \cdot (j_1 \cdot Z_2 - j_2 \cdot Z_1)$$

The migration model incorporated this dynamic as a pseudo-feedback loop to food availability (i.e., chlorophyll). While decreasing the plankton biomass in a cell, fish populations also increased the food availability by making nutrients for primary production. Nutrients were not modeled per se. Rather, a nutrient-to-chlorophyll conversion constant was estimated (γ in Equation 2.6, Table 2.1), multiplied by the stock of fish, and added back to the chlorophyll state variable with each iteration of the model.

Forcing Functions

Environmental (salinity and temperature) and primary productivity variables were used to control fish behavior within and across cells. Geometrically obtained parameter distributions were constructed from patchy field data (Yáñez-Arancibia *et al.* 1988a). Due to the shallowness of the lagoon, we assumed a homogeneous water column. Field data for salinity, temperature, and chlorophyll concentrations from three locations (the two inlets and river-mouth stations) were used to calculate temporal forcing functions for the entire lagoon. In other words, the distance between each location was used to geometrically extrapolate a forcing function input for each cell within the landscape grid. Given spatial coordinates for any empirical parameter, its value (z) is solved by linear relationships according to:

$$Ai + Bj + Cz + D = 0 \quad (2.7)$$

In which any three noncolinear points with Cartesian coordinates (i_1, j_1, z_1) , (i_2, j_2, z_2) and (i_3, j_3, z_3) can be solved using determinants and expanding by

minors for every row, then evaluating each determinant. The general form of such an equation is:

$$\begin{aligned}
 & [j_1(z_2-z_3) + j_2(z_3-z_1) + j_3(z_1-z_2)] i + [z_1(i_2-i_3) + z_2(i_3-i_1) + z_3(i_1-i_2)] j \\
 & + [i_1(j_2-j_3) + i_2(j_3-j_1) + i_3(j_1-j_2)] z + [i_1(j_2z_3-j_3z_2) + i_2(j_3z_1-j_1z_3) + i_3(j_1z_2-j_2z_1)] \\
 & = 0
 \end{aligned}
 \tag{2.8}$$

The results were "contour" maps of the environmental forcing functions based on the three field stations indicated in Figure 2.1.

Migratory fish in Laguna de Terminos have shown preferences for food supply and salinity (as an indicator of different water masses; Yáñez-Arancibia et al. 1988b). From the four migratory patterns for dominant species in Laguna de Terminos (Yáñez-Arancibia et al. 1988b), we selected one of these functional groups to test the ROE model. The environmental preferences from the marine stenohaline seasonal visitors were entered into the tolerance range algorithm.

To develop and test these migration modeling concepts, we used the simulation language "STELLA®" (Richmond *et al.* 1987) on an Apple Macintosh IIx computer. STELLA's object-oriented construction of model interactions and processes and its graphical interface simplified the creation and solution of spatially complex differential equations (Costanza 1986).

RESULTS

The ROE model was run for five years using Eulers' integration method with a dt of 1 day and forcing functions repeated annually. The output of the geometric algorithm for calculating the spatial distribution of the

environmental forcing functions (Equation 2.8) was validated with field data from a different set of cells (Yáñez-Arancibia and Day 1982) than the ones (Yáñez-Arancibia *et al.* 1988a) used to compute the isolines. Values of four cells from the geometric interpolation output were compared with field data from the same location. In general, the results complied with the empirical data distribution and correlation coefficients showed significant correspondence between both empirical and simulated data (Table 2.2). Monthly forcing functions shown as landscape maps (Figure 2.3) indicated that spatial gradients for salinity and chlorophyll varied more often than temperature. The annual temperature ranged only from 23° to 32°C while salinity ranged from 0 to 40, and chlorophyll ranged from 0.9 to 5.8 mg • m⁻³. The spatial and temporal patterns indicated that salinity decreased during the later part of the year in the southern sections due to a combination of high river discharge and northern frontal passages (Yáñez-Arancibia *et al.* 1988a), while chlorophyll *a* decreased during the dry season (i.e., late spring-early summer) in the northern sections. Generally, spatial patterns appeared to be controlled by river discharge and tidal exchange. High salinity, low chlorophyll waters were prevalent for the northern region while low salinity, high chlorophyll waters were found mostly in the south.

An arbitrary number of 500,000 fish was set as the initial population into the Puerto Real cell (cell D) for the simulation run. The total population stabilized at a yearly average of 413,740 and ranged from a monthly minimum of 229,386 to a maximum of 589,748 by the end of the spawning season. The spatial distribution of the population throughout the cells varied from a minimum of 28 individuals (0.005 % of total population at that time)

Table 2.2

Correlation coefficients for environmental parameters at different sampling stations (predicted values vs. field data)

	cell A	cell B	cell C	cell D
Salinity	0.956 (11) ^a	0.894 (12)	0.853 (12)	0.809 (12)
Temperature	0.943 (9)	0.947 (9)	0.963 (10)	0.937 (12)
Food (Chlor. <i>a</i>)	0.749 (16)	0.703 (19)	0.738 (22)	0.787 (18)

Location of calibration cells indicated on figure 2.1

a- parentheses indicate number of samples

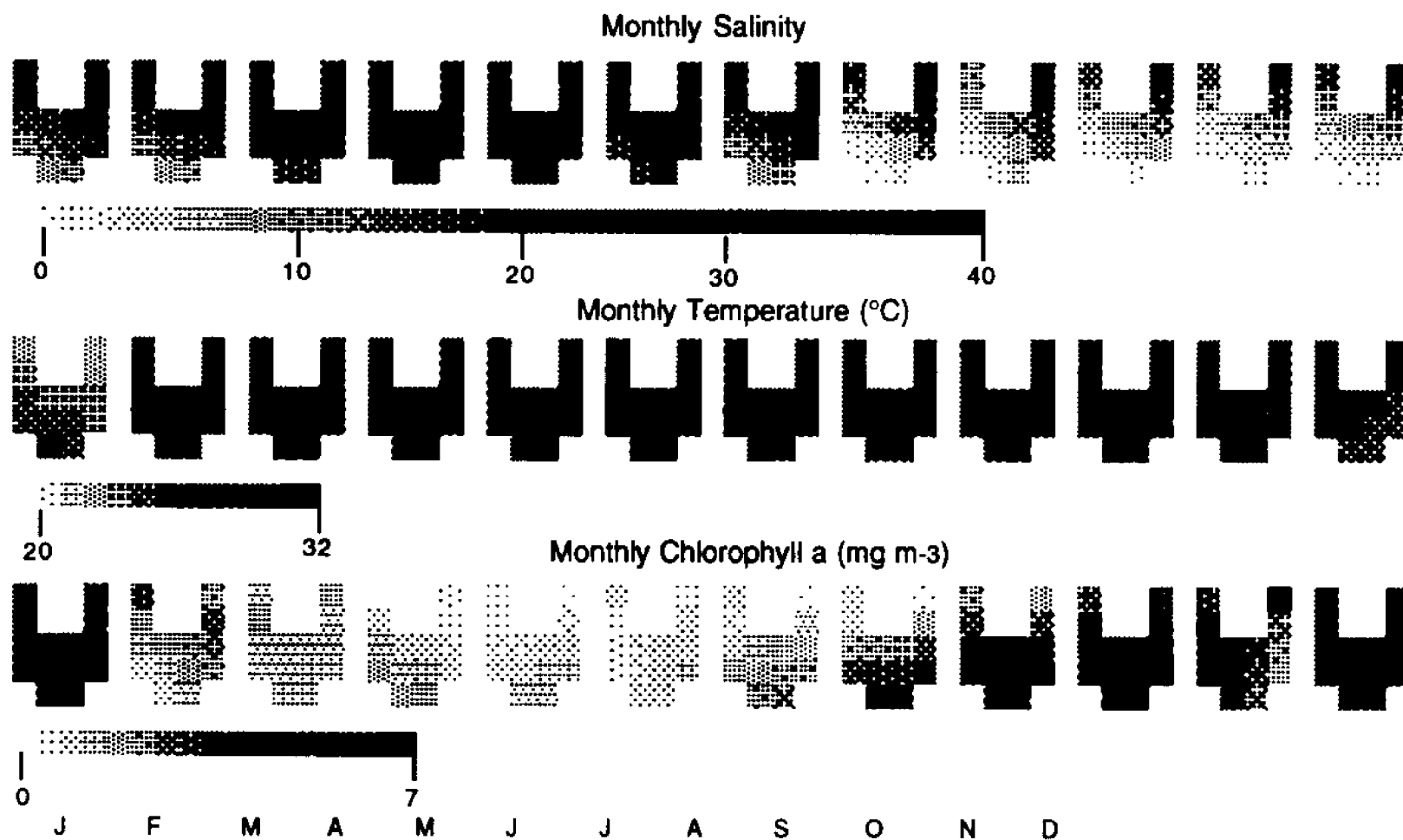


Figure 2.3 - Monthly distribution of environmental parameters on ROE Model grid. Output of geometric interpolation.

obtained in the West Inlet cell, to a maximum (3,451,410 - 58% of total population) in a cell near the area of river discharge.

Two approaches were used to evaluate the ROE model sensitivity and stability. First, we plotted the total population size during the 5-year simulation (Figure 2.4) and found that the population behaved in a sinusoidal manner, declining rapidly during the first part of the year, when there are no births, and increasing steadily in the latter part of the year as new organisms were recruited. These results indicated long-term replicability for the whole population and realistic temporal cycles.

Second, we evaluated population response characteristics in relation to changing birth rates and fecundity:food ratios. This sensitivity analysis showed that the most sensitive factor was birth rate. The sensitivity test showed a stability zone, where the birth rate and fecundity:food ratio interact to maintain the population around the initial number (Figure 2.5). The slope of this zone showed a 10% increase in food:fecundity ratio was needed to compensate for a 7.9% decrease in birth rate.

We used the ROE model to output monthly population maps. These maps not only show the population's spatial distribution among cells, they also provide a daily validation of ROE principles. These landscape maps indicate the spatial dynamics, seasonalities, and annual replicability of the population's migration patterns (Figure 2.6). We plotted the first three years of the simulation to examine similar spatial distributions occurring seasonally and annually. There were some differences during the first two months but we attributed this to the initial lumping of all 500,000 individuals into the Puerto Real cell (cell D). We quantified how much the population was aggregating

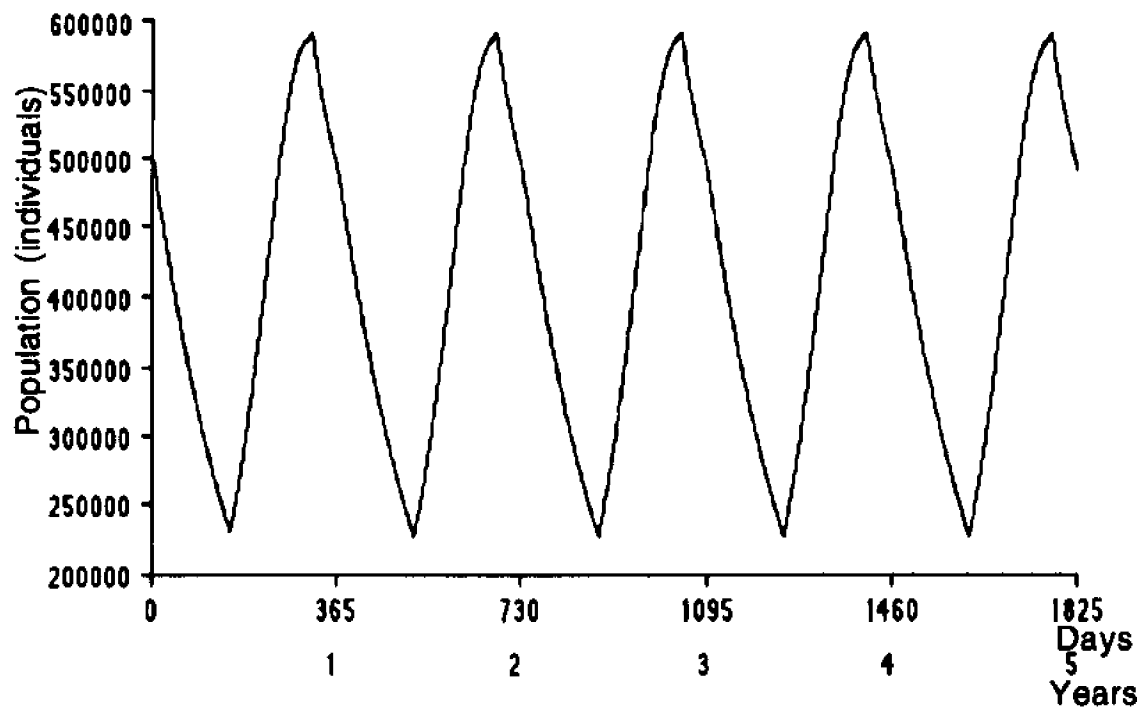


Figure 2.4 - Total simulated population for 5 years.

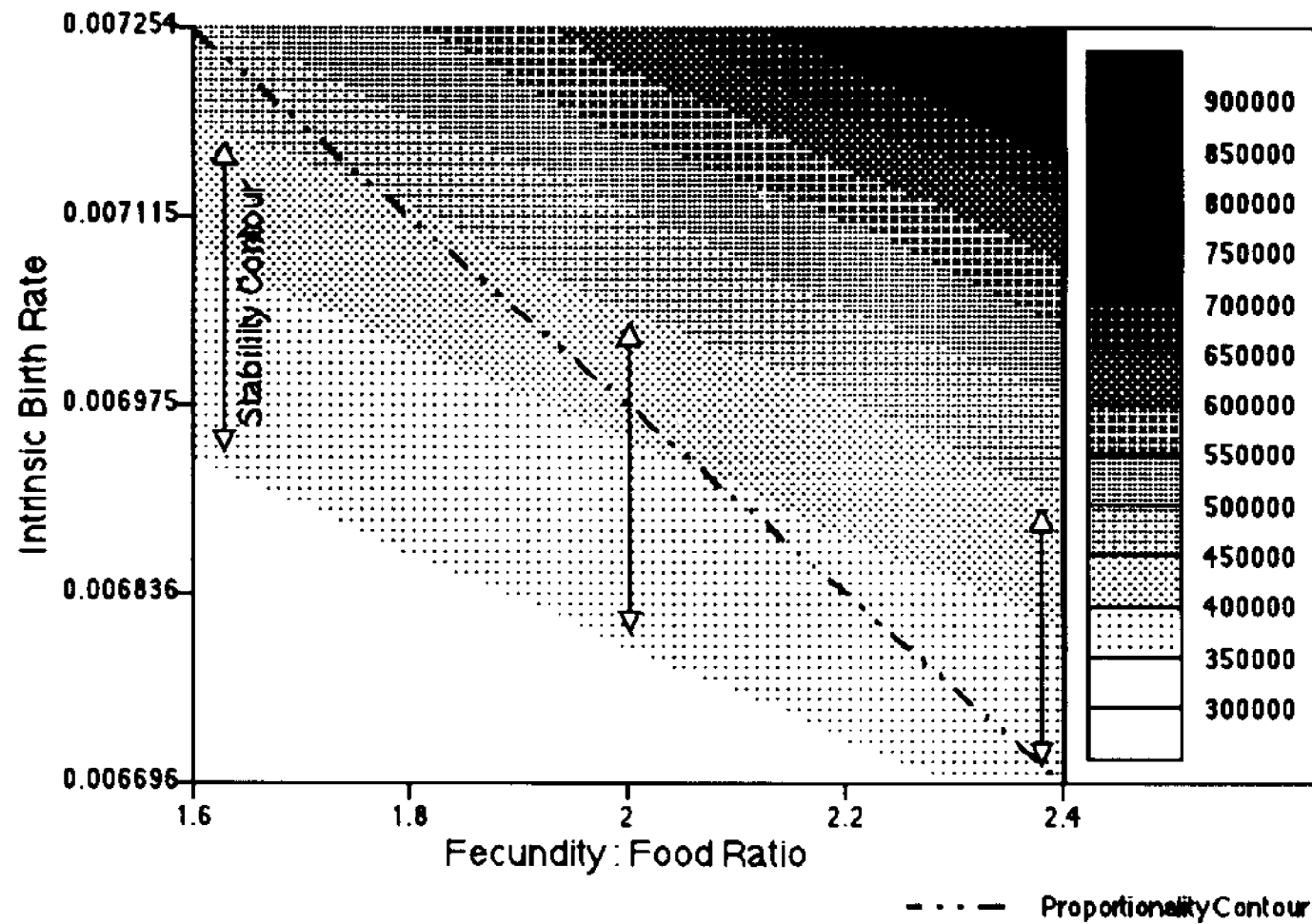


Figure 2.5 - Contour graph for intrinsic birth rate and fecundity:food ratio. Shades depict total population numbers. Arrows depict interacting areas where the original population remains constant. Dashed line show proportionality contour.

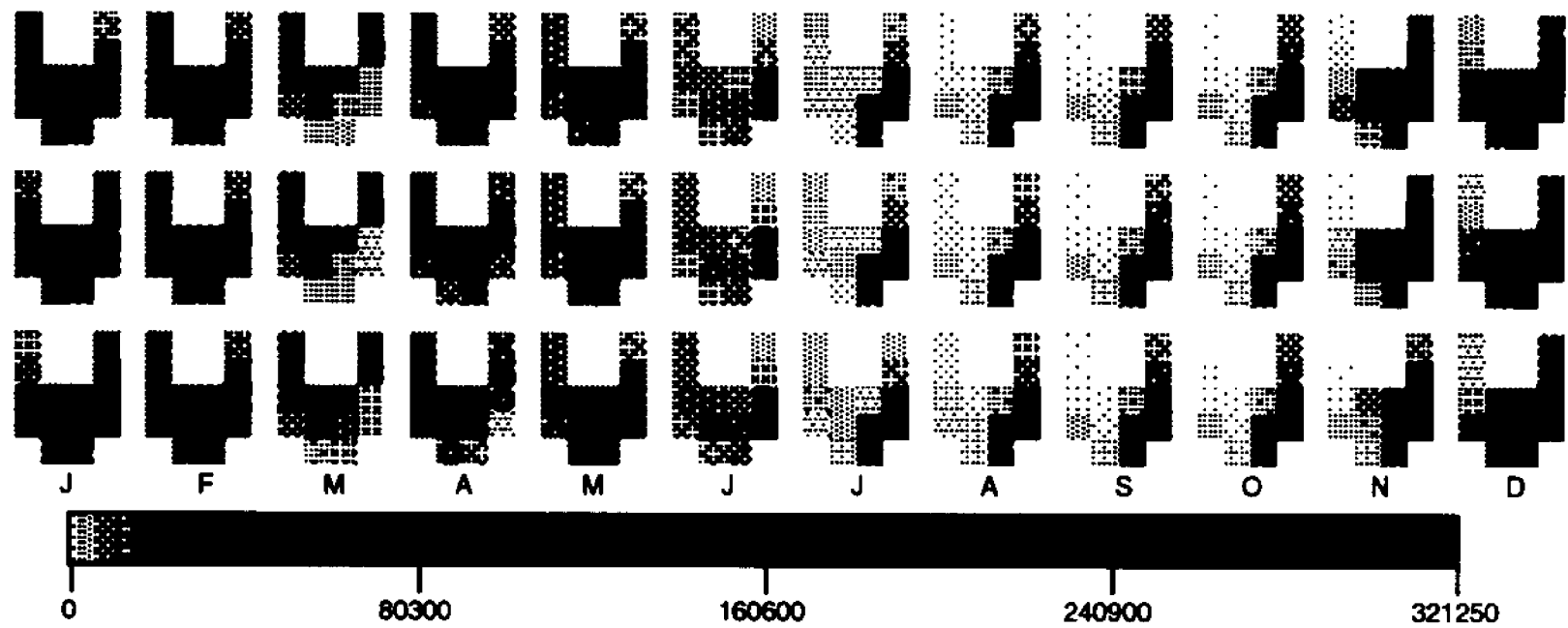


Figure 2.6 - Monthly fish population maps for initial 3 annual cycles.

by examining the percentage of the total population in each cell. Figure 2.7 shows population change in the same cells used for the environmental correlations (Table 2.2). Cell 'A' showed the greatest population change and ranged from a high of almost 60% of the total population to a low of 2%. The lowest density (0.005%) was predicted for cell 'D'.

The results of the ROE model (summarized in Figures 2.6 and 2.7) showed a clear migration pattern. The fish population was evenly dispersed during the first part of the year, aggregated in the central part of the lagoon for a couple of months, and then concentrate on the eastern side of the lagoon during the latter half of the year. This migratory pattern matched the one described by Díaz-Ruiz *et al.* (1982) for the pigfish, *Orthopristis chrysoptera*.

DISCUSSION

The ability to model fish movements is particularly important in coastal areas where land-water interactions are changing rapidly (Copeland *et al.* 1983). As the human population of the world increases, the economic pressures increase to harvest coastal forests, impound wetlands, and pollute estuaries (Odum *et al.* 1988). We recognize that some "balance" between ecology and economy is necessary (Costanza *et al.* 1991). We invoked a landscape modeling approach, since it can be used to identify cumulative impacts (Turner and Gardner 1990), identify spatial and temporal controls (Hyman *et al.* 1990), and predict ecological change (Costanza *et al.* 1990). Numerical simulation techniques applied across a network of interactive cells are superior to a regionally averaged analytical solution, that may be descriptively accurate but tends to have lower effectiveness (i.e., explanatory power) resulting from low spatial articulation (Costanza and Sklar 1985).

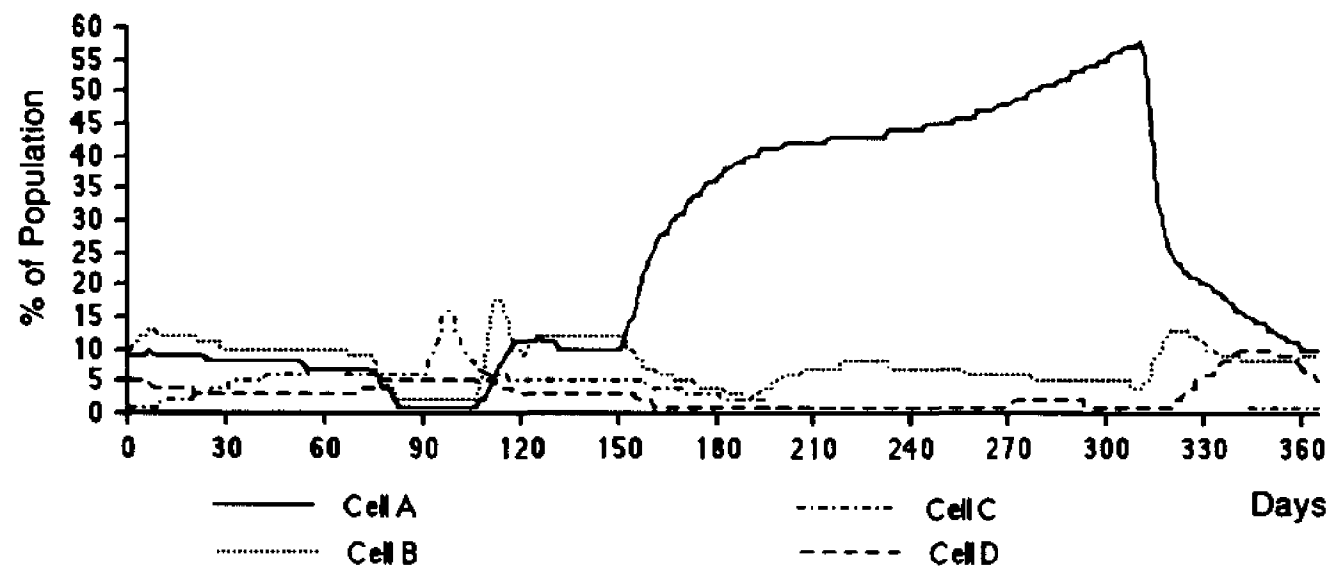


Figure 2.7 - Percentage of Fish Population at calibration cells

We succeeded in designing and testing a regional organism exchange (ROE) model across a network of interacting cells, and in producing a landscape description of organism movement in relation to ecological processes. The simulated migratory patterns (Figure 2.6) resembled those described by Díaz-Ruiz *et al.* (1982) for stenohaline fishes. We showed that simulated population migration data can be easily validated against empirical data, by examining output from each cell on individual basis (Figure 2.7). We also demonstrated how ecological forcing functions at a few points can be spatially interpolated for input into a grid-like landscape model. As a demonstration of a conceptual design for a spatial simulation model, the variable-diffusivity concept (Mullen 1989) appeared to be an effective way to combine probability and mechanistic models.

An important new topic in landscape ecology is the idea of scale (Turner and Gardner 1990, Rastetter *et al.* 1992). Changing the cell size and making the ROE model more spatially articulate will increase a ROE model's computational complexity by increasing the number of equations needed to spatially represent an area. Decreasing the current cell size by half will quadruple the number of differential equations and increase cell-to-cell border exchanges by 16 fold. Nevertheless, if one wants to validate migration patterns against actual fisheries data or evaluate impacts of point sources, it is important that the measurement and simulation scales match as closely as possible (Sklar *et al.* 1990). Using very large cells can create instabilities in a ROE model because populations may aggregate in a single cell in a few time steps. Decreasing the cell size increases stability by reducing the migration parameter (K) and creating more realistic swimming or exchange distances during a model iteration. Similarly, a rescaling of food consumption, mortality

and recruitment rates should increase validation and model effectiveness (i.e., explanatory power), at least to some upper boundary (Costanza and Sklar 1985).

We assumed that our three environmental parameters (salinity, temperature, and chlorophyll) were representative of the overall ecological conditions in Laguna de Terminos and were good regulators of population movements. Salinity and temperature were chosen because of their physiological significance (Lagler *et al.* 1977), their ease of measurement, and their conservative behavior (i.e., there were no significant feedbacks from the fish population). Only one non-conservative forcing function was used (chlorophyll), because we wanted to design a simple ROE model to evaluate its conceptual framework, and because chlorophyll represented food availability and could be considered as a proxy for other food sources (i.e., zooplankton and secondary consumers). The high correlation between the environmental ROE output and field data (Table 2.2) showed the presence of environmental gradients and their persistence over the seasonal cycle. These correlations also indicated the importance of the marine and freshwater inputs as the overall indicator of habitat type. Salinity and temperature, as forcing functions, provided a good environmental framework for fish cues, and chlorophyll, as the biotic driving force, emphasized the degree to which organisms were tied to their food supply.

Spatial simulations of population dynamics should include ecological, as well as, biological forcing functions. Life cycles studies on fishes have shown that there are deterministic physiological triggers and environmental cues that drive migratory habits (McCleave *et al.* 1984). Other studies have shown that age and size influence feeding, migration, and reproductive

capacity (Lagler *et al.* 1977). The results from the sensitivity analysis on birth rate and food:fecundity ratio corroborate these ideas (Figure 2.5). The success of a population to persist throughout time depended heavily on the number of individuals recruited into the population and the environmental carrying capacity implied by the food:fecundity ratio. This modeling approach, however, was substantially simplified by focusing on adult fish only and thereby keeping mortality constant throughout the simulations. We fully recognize the subtleties and significance that variations in predation mortality can exert on recruitment success (Houde 1989a, b). The increased layers of complexity involved in varying mortality and partitioning its impact into starvation and predation components that vary independently and in unison through ontogenetic and season time scales will have to be left for future research.

Given that the ROE model results were realistic and sensitive to environmental conditions, our assumptions appear appropriate. Although three ecological parameters proved sufficient as part of this spatially simplistic modeling exercise, our recommendations for more complex ROE simulations would include: (1) additional environmental parameters, (e.g., type of sediments in the case of benthic organisms and depth) for better control of organism flow from cell-to-cell; (2) cell-specific biological parameters (representing nursery areas or protection from predators) for better control of organism processes within a cell; (3) life stage changes (growth and sexual maturity); and, (4) trophic interactions for more realistic ecological structure.

A ROE model can be used for testing landscape hypotheses and asking questions which explore how biological, physiological, and

environmental cues and controls interact to influence population dynamics. As a demonstration of a management tool for evaluating the impacts of ecological and land-use change on migrating organisms, a number of structural elements (e.g., cell size) and mechanisms (e.g., primary production) need to be enhanced. There are many ways to implement such tests. For example, the design of a "suitability index" can be switched from static (one tolerance range throughout the year) to dynamic (temporal variation of the tolerance range), parameters, such as, mortality could be made more realistic, scale independent variables (e.g., fractals) could be used to adjust parameters, and food supplies (e.g., phytoplankton) could be made temporally more dependent upon organism interactions with biogeochemical processes or expanded to include zooplakton and other secondary and tertiary consumers such as, ichthyoplankton and juvenile fish.

CONCLUSIONS

- The output of the geometric algorithm for calculating the spatial distribution of forcing functions closely followed the distribution of the empirical data. Correlation coefficients from randomly selected cells indicated significant correspondence between both empirical and calculated data.

- Sensitivity analysis showed that there is a stability zone, where the birth rate and fecundity:food ratio interact to maintain the population around the initial value.

- The simulated migratory pattern matches that described by Díaz-Ruiz et al. (1982) for stenohaline fishes. The results of the migration model displayed annual stability on temporal and spatial cycles. The monthly maps

showed that populations tend to concentrate during the rainy season far from the inlets, distribute themselves across the lagoon during the winter, and to aggregate on the eastern side during the dry season.

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**CHAPTER 3. LANDSCAPE ECOSYSTEM MODEL FOR AQUATIC PRIMARY
PRODUCTION AND FISH MIGRATION IN LAGUNA DE TERMINOS,
MEXICO.**

INTRODUCTION

Laguna de Terminos is Mexico's largest coastal lagoon and is one of the few areas on the Gulf of Mexico where there has been minimal human impact. The natural resources of the Laguna de Terminos region are considered of ecological importance (Yáñez-Arancibia and Day 1988a, Lot and Novelo 1988), but also play a substantial part in the economic future of the region. The different plant communities in the lagoon are a source of food and habitat for ecologically and commercially important species (Day and Yáñez-Arancibia 1985, Rojas-Galaviz *et al.* 1992). Laguna de Terminos supports the largest and most economically important shrimp fishery in Mexico (*Peneaus setiferus*) and important finfisheries as well (Soberón *et al.* 1986, Yáñez-Arancibia and Aguirre-León 1988).

Recently the degree of human impact has increased. Activities include highways and canals constructed in wetlands, agricultural activities in seasonally flooded freshwater wetlands south of the lagoon, and shrimp pond construction (Gobierno del Edo. de Campeche 1988). Such developmental activities are a potential threat to the continuation of the high natural resource productivity of the region (Centro de Ecodesarrollo 1982). Therefore, these activities are management issues, that must be addressed, if the natural resource productivity of Laguna de Terminos is to be preserved.

This situation also presents the opportunity to develop a sustainable economy integrated into the natural ecosystem. The juxtaposition of important regional fisheries and the development pressure presents an opportunity to implement innovative management plans for sustainable development. These management plans would synthesize the environmental

and ecological forcing functions of Laguna de Terminos in relation to the overall consequences of projected development. Destruction of habitat, and changes in primary production may lead to changes in secondary production and in patterns of fish migration (Day and Yáñez-Arancibia 1985). In this study, we use ecological modeling to further our understanding of these interactions between habitat primary production and nekton dynamics, and to predict the impacts of environmental and anthropomorphic change.

One of the factors which makes Laguna de Terminos amenable to modeling is the amount of information available about the system (see reviews in Yáñez-Arancibia and Day 1988a and Lara-Dominguez *et al.* 1990). Research in Laguna de Terminos has been carried out for over two decades and ranges from single taxonomic studies on flora or fauna (Carvajal 1975, Caso 1979, Román 1986, Lot and Novelo 1988) to ecosystem level studies (Yáñez-Arancibia *et al.* 1980, Day *et al.* 1987, Rojas-Galaviz *et al.* 1992). These studies have created a large database capable of serving as baseline for monitoring the consequences of modifications and projected development, and for the development of sound resource management. The need to consolidate such environmental information into a form accessible to both scientists and resource managers has become a pressing issue (Sklar and Costanza 1990, Turner and Gardner 1990, Ryan 1992) where modeling can play a valuable role.

Several hydrologic and biological models have been developed for Laguna de Terminos. Dressler (1981) and Graham *et al.* (1981) implemented vertically-integrated, finite-difference hydrodynamic models which simulated flow patterns and residual circulation. Kjerfve *et al.* (1988) developed a model simulating the dispersion of dissolved and particulate conservative

constituents based on the assumption of vertical homogeneity. The results from this model were tested by Jensen *et al.* (1989) using satellite images of sediment circulation. Soberón (1987) constructed an ecosystem level biological model that subdivided Laguna de Terminos in four characteristic habitats and analyzed phytoplankton productivity and nekton interactions with Campeche Sound. Reyes *et al.* (1992, Chapter 2) developed a Regional Organism Exchange (ROE) model for fish migration. Although the approach of the ROE model was generic, it was calibrated for Laguna de Terminos with empirical data. Building on these efforts, we developed a landscape model for Laguna de Terminos. This spatial ecosystem model was used to predict hydrodynamics, nutrient dynamics, primary productivity and fish population distribution within the lagoon. We use the model to test how interactions among habitats affect primary production and consequently fish migratory patterns.

We hypothesized that physical, chemical and ecological dynamics at the landscape level interact to create the high aquatic primary production (APP) in Laguna de Terminos and that the landscape distribution of APP is a consequence of the environmental functions. In testing these hypotheses, we addressed the following questions: (1) Which functions are the most significant to determine the APP level? (2) How sensitive is the landscape APP to climatic variability? (3) How sensitive is this APP to manipulation of adjacent areas (i.e., changes in hydrology and transformation of vegetated areas)?

With respect to the fish population, a third hypothesis was tested: Migratory movements of some fish populations inside Laguna de Terminos are a function of spatial and temporal distribution of "optimal" physiological

and ecological conditions. These conditions are related not only to abiotic parameters but also to biological ones, such as food availability. Using the output of a spatial aquatic primary production model, several questions can be addressed. They include: (1) What external environmental and biological functions effect migratory behavior? (2) What is the relative importance of physiological (e.g., salt and temperature tolerances) and ecological (e.g., food) factors? (3) Does migratory behavior reflect only environmental conditions or are there other interacting factors (e.g., spawning, breeding season)?

To answer these questions, we designed a landscape ecosystem model capable of simulating and predicting spatial and temporal fluctuations of APP and fish distribution in Laguna de Terminos. The specific objectives of this model were to: (1) develop a grid model based on spatial units (10 km²) for Laguna de Terminos that would represent spatial habitat heterogeneity; (2) compute the spatial and temporal distribution of annual environmental parameters, nutrients and APP gradients for Laguna de Terminos; (3) account for variability in each spatial unit as habitat changes occur (i.e., addition of mangrove and seagrass bed production, and deltas); and (4) simulate annual migration patterns for fish population growth (recruitment), mortality, and grazing coupled to the output from the APP model.

STUDY SITE

Laguna de Terminos is a large (2500 km²), shallow (mean depth 3.5 m) coastal lagoon bordering the southern Gulf of Mexico in Campeche, Mexico (Figure 3.1). The lagoon communicates with the Gulf of Mexico through two deep inlets at each end of Carmen Island.

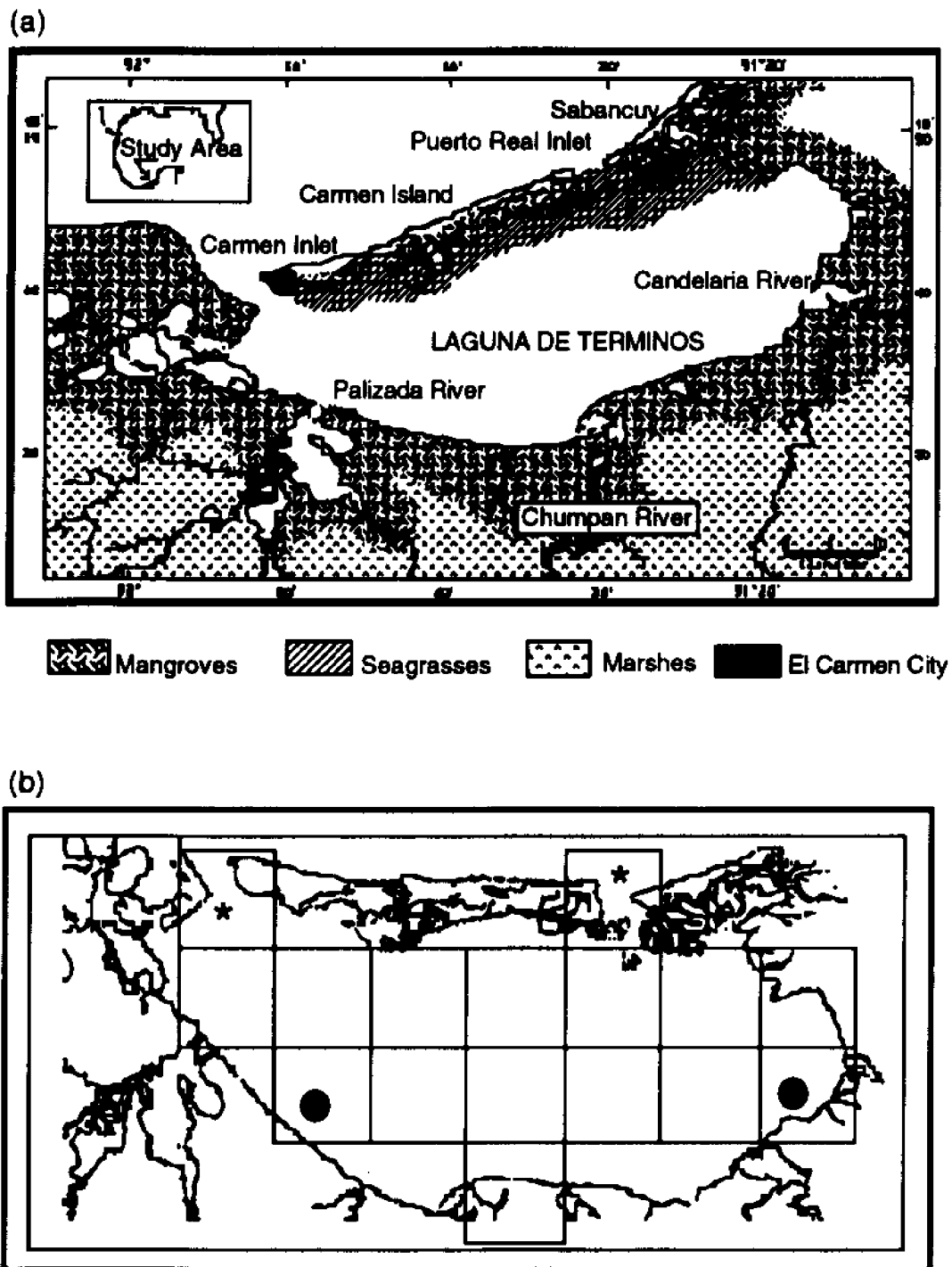


Figure 3.1 - Localization map for Laguna de Terminos, Mexico. (a) Inlets, major rivers, intertidal communities, Carmen Island and El Carmen city. (b) Spatial grid for simulation model. Each square is 10 km². Dots indicate cells with river inputs and asterisks show cells with tidal pumping.

Meteorology

There are three climatic seasons in the region: the dry season from February to May; the rainy season from June to September; and the season of winter storms or "nortes" from October through January (Yáñez-Arancibia and Day 1982). The rainy season has almost daily afternoon and evening showers. Winter storms are generally strongest and associated with rains during northwestern frontal passages (Carvajal 1973, Day *et al.* 1982). For most of the rest of the year, there is a sea breeze system with winds predominantly from the north-northeast and east-southeast. The easterly orientation of the sea breezes reflects the regional influence of the trade winds (Cruz-Orozco *et al.* 1979, Mancilla and Vargas 1980). Annual precipitation averages 168 cm and daily mean air temperature ranges from 15 to 39 °C (Cruz-Orozco *et al.* 1979a, b, c, d).

Circulation Pattern

The water circulation in the lagoon is a westerly net flow reflecting the prevailing easterly winds (Gierloff-Emden 1977, Mancilla and Vargas 1980). The shallow water column tends to be vertically homogeneous due to wind mixing (Kjerfve *et al.* 1988). Mancilla and Vargas (1980) measured a net westerly water flux of $1.17 \cdot 10^8 \text{ m}^3 \text{ d}^{-1}$ at Carmen Inlet. Graham *et al.* (1981) developed a hydrodynamic model of the lagoon and computed a maximum flux through the two passes of about $5.18 \cdot 10^8 \text{ m}^3 \text{ d}^{-1}$. This simulation predicts that about one-fourth to one-third of the water that enters Puerto Real Inlet moves westward through the lagoon and leaves through Carmen Inlet within a typical tidal cycle. There is a mixed diurnal tide with a range of about 0.5 m which is in phase at the two inlets (Instituto de Geofísica 1990). Water

entering through Carmen Inlet affects, at most, the western third of the lagoon (Yáñez-Arancibia and Day 1988b). Freshwater from the rivers generally prevents saline waters entering Carmen Inlet from flowing directly along the southwestern shore (Graham *et al.* 1981). Water flows in for longer periods (~ 15 h) than out during a typical tidal cycle at Puerto Real Inlet, while the reverse is true at Carmen Inlet.

The lagoon receives discharge from the Palizada River (a distributary of the Grijalva-Usumacinta River system, the largest in Mexico and second largest in the Gulf of Mexico) and two smaller rivers: the Candelaria and the Chumpan. The southwestern part of the lagoon receives more than 70% of the freshwater input (Phleger and Ayala-Castañares 1971). Annual average discharge of the Palizada and Candelaria rivers is $11.35 \cdot 10^8 \text{ m}^3$ and $1.45 \cdot 10^8 \text{ m}^3$, respectively (Figure 3.3 a; Sec. de Recursos Hidráulicos 1980). Maximum discharge coincides with the rainy season (Yáñez-Arancibia and Day 1988a).

Water Chemistry

The temporal distribution of inorganic nutrients is correlated with salinity and riverine input, especially during the wet season. Salinity ranges from 25 to 36.5 in the northeastern part of the lagoon near Puerto Real Inlet, and from 0 to 28 in the southern and western zones (Phleger and Ayala-Castañares 1971). Inorganic nutrient levels reflect local conditions such as turbulence, sediment type, and biological activity (Day *et al.* 1982). Spatially, there is a decrease in NO_3 and PO_4 along the increasing salinity gradient (South to North), but it is especially pronounced for NO_3 (Day *et al.* 1982).

This spatial depletion may reflect nitrogen as normally being limited in estuaries (Kemp 1989).

Botello and Mandelli (1978) measured oxygen and nutrient concentrations during the wet (Nov.) and dry (May) seasons. In November at peak river discharge, PO_4 and NO_3 were 2.6X and 2.2X higher, respectively, than during the dry season, while dissolved oxygen reached 147% saturation. During May, the middle of the dry season, the concentration of NH_4^+ was 3.8X higher, and dissolved oxygen saturation was 99%. The high river discharge (and consequently high nutrients) leads to higher gross and net aquatic primary productivity, reflected in higher oxygen levels. Oxygen supersaturation during the wet season indicated high net primary production (Day *et al.* 1982).

Primary Producers

There are a number of plant communities in Laguna de Terminos including, mangrove forests, submerged aquatic plants, and phytoplankton. Patterns of aquatic primary production and intertidal community distribution reflect conditions of water circulation, water clarity, salinity and nutrient concentrations (Figure 3.1 a; Day and Yáñez-Arancibia 1985, Rojas-Galaviz *et al.* 1992).

Dissolved oxygen, productivity and phytoplankton chlorophyll concentration values, measured for a number of sites throughout the lagoon (Day *et al.* 1982), were higher in turbid, low-salinity, river-influenced areas. Chlorophyll *a* concentrations ranged from 0.3 to 8.2 mg m^{-3} . There was a seasonal pattern in chlorophyll *a* concentration, with the lowest mean value (0.3 mg m^{-3}) during the dry season (Feb. - Jun.) and the highest mean value

(8.2 mg m⁻³) during and following the rainy season. Phytoplankton productivity ranged from 0.87 (dry season) to 15.5 g O₂ m⁻³ d⁻¹ during the wet season (Day *et al.* 1982, 1987, 1988).

There are distinct spatial and temporal patterns of APP regulated by sunlight, river discharge and mangrove drainage (Day *et al.* 1988). River discharge leads to a seasonal pattern in transparency due to suspended material inputs. The fluvial discharge also adds nutrients to the system in pulses. These factors create a spatial gradient of higher APP nearshore than towards the center of the lagoon (Day *et al.* 1988). Nutrient inputs coming from the fringe mangroves increase APP. All these effects contribute to a peak in APP that occurs during the rainy season, even though solar irradiance is low due to heavy cloud cover (Day *et al.* 1988) and sediment load is high.

Almost all of the lagoon is bordered by mangrove swamps, which extend up the rivers and associated embayments to the limit of the marine influence. Three species, Rizophora mangle (red mangrove), Avicennia germanis (black mangrove), and Laguncularia racemosa (white mangrove) dominate species composition of these swamps (Day *et al.* 1988). Day *et al.* (1987) measured the composition and productivity of the mangrove swamps on transects at the mouth of the Palizada River and at a high salinity site on the lagoon side of Carmen Island. Trees at the river site were on the average taller (15-25 m as compared to 5-10 m at the island site) and more robust (Day *et al.* 1987).

Riverine input affects mangrove productivity. The highest total litterfall at both sites occurred during the rainy season with high river flow. Total

litterfall was 1265 g dry weight $\text{m}^{-2} \text{y}^{-1}$ at the riverine site and 986 g dry weight $\text{m}^{-2} \text{y}^{-1}$ at the high salinity (fringe) site (Day *et al.* 1987). Litter decomposition was more rapid at the riverine site. Measurements of mangrove leaf decomposition showed that 24% of the original weight remained at the riverine site after 6 months as compared to 50% at the fringe site.

Extensive seagrass beds occur along the lagoon side of Carmen Island and especially in the inshore delta of Puerto Real Inlet. Less vigorous stands grow along the eastern and southeastern shore. The most abundant species is Thalassia testudinum. Hornelas (1975) measured 382 g dry weight m^{-2} of total biomass for Thalassia along the inner side of Carmen Island, while Day *et al.* (1982) reported 468 g dry weight m^{-2} during the dry season and 408 g dry weight m^{-2} during the wet season for several sites along the eastern shore. Diplantera wrightii is the colonizing species, especially in the Candelaria delta region (Moore and Wetzel, 1988; Rojas-Galaviz *et al.* 1990).

Nekton

Nekton are a conspicuous and important ecological component of Laguna de Terminos and support economically important fisheries, and thus, have been treated in detail (Yáñez-Arancibia *et al.* 1980). These authors discussed the ecology for 121 fish species: 15 species had a ample distribution inside the lagoon and composed 78% of the total number; 55 species (45%) used the lagoon as a nursery moving either from offshore or the riverine systems into the lagoon (Groups 1 and 3, Table 3.1); 12 species (10%) were identified as permanent residents (Group 2, Table 3.1); and 55

Table 3.1

Fish functional groups in Laguna de Terminos.

Group overall statistics, species examples and migratory pattern description are presented.

Temperature in °C.

F. Group / Pattern	Species	Life stage / Season	Tolerance ranges	Description
1 Seasonal visitor, stenohaline	<u>Archosargus rhomboidalis</u>	Fingerlings / Dry season	Salt: 15 - 35	Moves through Puerto Real Inlet, staying near the eastern shore and up to the Candelaria River, then crosses lagoon towards the island; afterwards moves out through Puerto Real to offshore
	<u>Orthopristis chrysoptera</u>	Juveniles / Rainy season	Temp: 22 - 32	
	<u>Haemulon aurolineatum</u>	Adults / Nortes season (offshore)		
2 Estuarine residents	<u>Bairdiella chrysoura</u>	Whole life cycle / All year round.	Salt: 0 - 36	Spawned near the Palizada delta, drifts towards the island and uses either western shore or island, and then moves towards south shore (deltas) to breed and spawn
	<u>Bairdiella ronchus</u>		Temp: 20 - 32	
	<u>Arius melanopus</u>			
3 Seasonal visitor, euryhaline	<u>Bagre marinus</u>	Fingerlings / Winter storms	Salt: 0 - 36	Spawned offshore, moves through Carmen Inlet, staying close to the western shore, towards the Palizada delta and then flowing out with peak river discharge again through Carmen Inlet
	<u>Cynoscion arenarius</u>	Juveniles / Dry season	Temp: 21 - 31	
	<u>Stellifer lanceolatus</u>	Adults / Rainy season (offshore)		
	<u>Centengraulis edentulous</u>			
4 Temporary visitors	<u>Eucinostomus gula</u>	All year round	Salt: 0 - 38	Occasional visits lagoon, through both inlets.
	<u>Arius felis</u>		Temp: 20 - 33	

Sources:

Díaz-Ruiz *et al.* (1982), Yáñez-Arancibia *et al.* (1988b), Lara-Dominguez (In prep).

species (45%) were occasional visitors (Group 4, Table 3.1), being captured with no discernible frequency (Yáñez-Arancibia *et al.* 1982). These life history patterns were attributed to either trophic dynamics or reproductive cycles. Twenty two per cent of the fish species were herbivores, detritivores, or omnivores, that is, first order consumers (Riley 1963); 51% were primarily carnivores with organic detritus as a major dietary component (second order consumers); and 26% were higher carnivores, feeding on some small first-order and second-order consumer fishes and macrobenthic organisms. These second-order consumers showed the greatest affinity for a particular habitat, since many have fairly specific feeding habits (Yáñez-Arancibia *et al.* 1986). Also because of their numerical abundance and habitat specificity, second-order consumers were used to characterize a particular fish community (Yáñez-Arancibia *et al.* 1985b, 1986).

Statistical analyses of environmental factors such as salinity and turbidity, in relation to fish assemblages, identified common feeding strategies and similar tolerance ranges to environmental factors (Yáñez-Arancibia *et al.* 1980, 1985a, 1985b, 1986 and 1988b). Using these criteria for dominant species (in number and biomass), particular fish assemblages were categorized into four functional groups (Table 3.1) and each group had distinctive migration patterns (Yáñez-Arancibia *et al.* 1986, 1988b). These functional groups are: seasonal visitors with stenohaline and euryhaline preferences (groups 1 and 3), permanent residents (group 2) and temporary visitors (group 4). Food supply and salinity (as an indicator of different overlapping water masses) are among the main driving forces for these movements (Yáñez-Arancibia *et al.* 1980, 1986).

METHODS

We developed a 2-dimensional, vertically-integrated, temporally and spatially articulated, simulation model (after Sklar *et al.* 1985) for Landscape Aquatic Primary Production in TERminos lagoon (LAPPTER). The Regional Organism Exchange (ROE) model (Reyes *et al.* 1992) was transformed into a subcomponent of LAPPTER and will be referred as the Regional Organism Exchange for TERminos lagoon (ROETER) model from here on. The LAPPTER model contains global (i.e., uniform distribution) environmental forcing functions for seasonal light, precipitation, temperature and turbidity (Secchi disk), and point-source forcing functions such as, river discharge and tidal inputs, and mangrove litterfall. LAPPTER was designed to simulate vertically averaged distribution and fluxes for two abiotic state variables (i.e., salinity and total inorganic nitrogen) and five biotic state variables (i.e., seagrasses, phytoplankton, benthos, zooplankton and detritus). The ROETER model uses the same global and local forcing functions and simulates fish population distribution based on population threshold responses to their environment (a more detailed description of assumptions, mechanisms and algorithms is presented in Reyes *et al.* 1992. Chapter 2).

Because Laguna de Terminos is well mixed, we divided it into a two-dimensional grid. The model is an array of interacting cells that represent fixed areas in Laguna de Terminos (Figure 3.1 b). A square, fixed grid of equally sized cells was chosen to represent space, because this method does not impose any a priori structure on the system (Sklar *et al.* 1985). The square grids have exchanges across the four sides and were classified into habitats units according to the particular plant communities and water inputs.

Each habitat or model unit represented the main processes and dynamics among the state variables. Boundary conditions were mostly mangrove.

The landscape model was simulated on an Apple Macintosh desktop computer. The model used the simulation language "STELLA™" (Structural Thinking Experimental Learning Laboratory with Animation; Richmond *et al.* 1987). Using this simulation language allowed the graphical construction of interactions and processes occurring on each state variable; the software kept track of the graphic connections and establishes the differential equations to be solved by numerical methods (Costanza 1986). The exchange rates and initialization parameters were presented either as linear equations or field data.

Conceptual Diagram

The lagoon area was divided into 16 cells of 10 km² representing the open water habitat of Laguna de Terminos (Figure 3.1 b). A conceptual unit model for the water column habitat was developed using the symbolic language of Odum (1972). The open-water habitat was divided into water column and benthic interactions. Figure 3.2 a, depicts this conceptual diagram with global and local forcing functions. These forcing functions were modified according to the particular spatial location of each cell. Each open-water cell was connected to adjacent cells by the exchange of water and materials. Mangrove litterfall data and the seagrass production submodel were added according to vegetation maps (Figure 3.1 a).

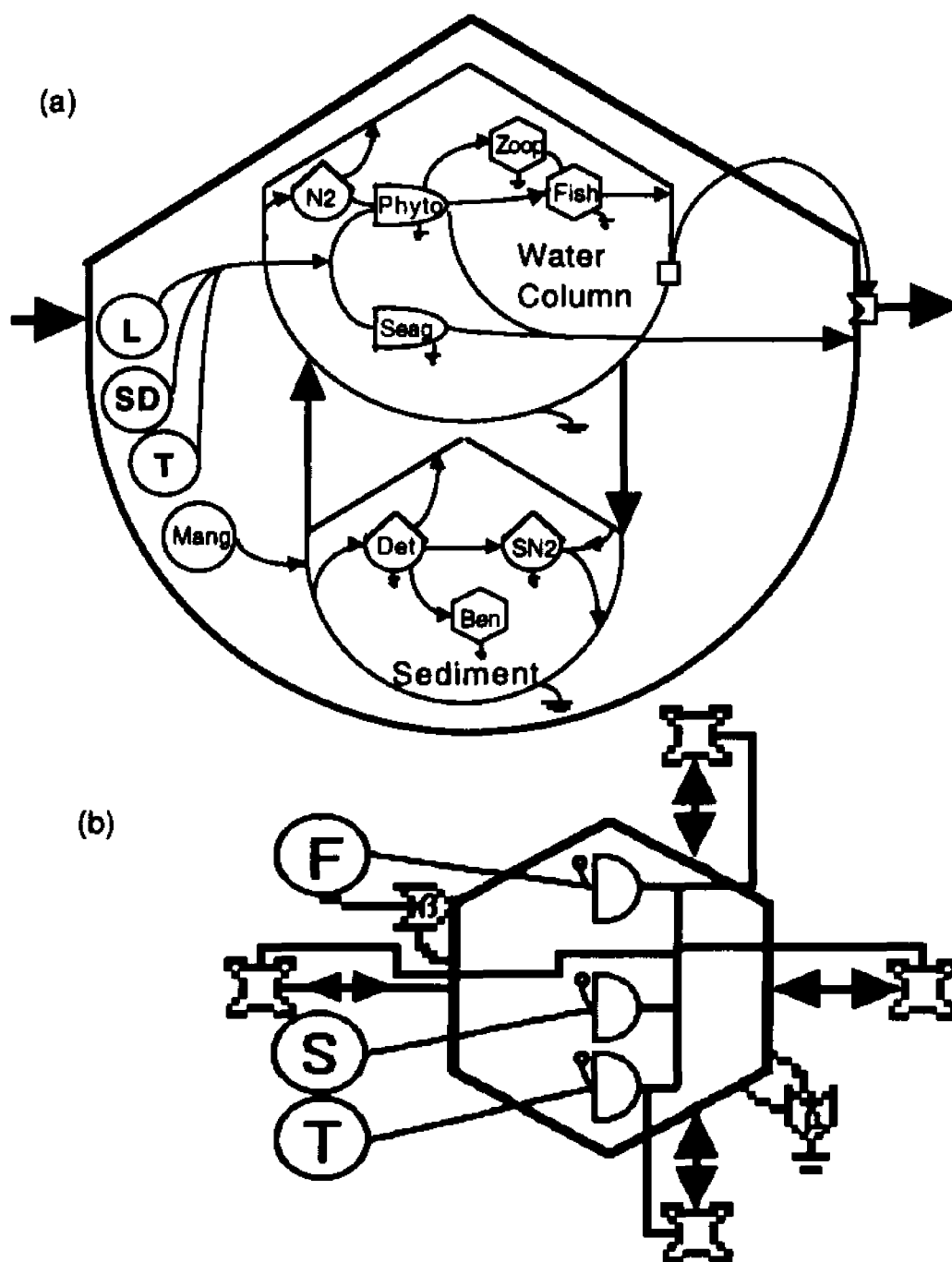


Figure 3.2 - Conceptual diagrams for spatial units of LAPPTER and ROETER using Odum's (1972) symbols. (a) Open water model. L is light, SD is Secchi disk, T is temperature, N2 and SN2 are TIN in water and soil, respectively. (b) Fish population unit model. F is food supply.

Figure 3.2 b, depicts a detailed conceptual diagram for the fish population unit model incorporating the global and local forcing functions. These forcing functions were incorporated as coefficients for fish response to changes from the open water unit model in salinity, temperature, and phytoplankton standing stock, a surrogate for fish food for the non-herbivores.

Forcing Functions

Water temperature and Secchi depth values were obtained from a monthly survey of 16 stations in Laguna de Terminos over a 3 year period (Day *et al.* 1982). Monthly means per station were computed using these data. Each field station was located in the lagoon and referenced spatially into the model grid, so monthly isoline maps could be plotted.

Monthly isoline maps for each parameter were computed by dividing the lagoon into 18 triangles, where each of the three vertices is one of the field stations (Day *et al.* 1982), and the values inside these triangular planes are solved using a geometrical algorithm. For months with missing station values a new triangle was computed using the three nearest stations.

Solar irradiance has been recorded by Madden (Coastal Ecology Institute, LSU. Pers. comm., 1991) and Rivera-Monroy (Dept. Oceanography and Coastal Sciences, LSU. Pers. comm., 1992). Light records included 1989 to 1992. We constructed a theoretical irradiance model using this data base and the algorithm recommended by Kirk (1983) to calculate the daily insolation (Q_s) as:

$$Q_s = \int_0^N E(t) dt \quad (3.1)$$

where N is daylength, $E(t)$ is hourly total irradiance, and t is time between sunrise and sunset in hours. $E(t)$ was calculated as the daily irradiance in Laguna de Terminos, correcting for latitude and seasonal solar declination, following the set of equations suggested by Kirk (1983). This Q_s was used as a global forcing function for the model (Figure 3.3 b).

Mean underwater light (I) in the mixed layers was calculated from the incident light values using the Secchi disk readings and computed using:

$$\langle I \rangle = \frac{I_0 (1 - e^{-kz})}{kz} \quad (3.2)$$

where I_0 is mean daily solar radiation in $E \text{ m}^{-2} \text{ d}^{-1}$, k is an extinction coefficient equal to $1.44/\text{Secchi depth}$, and Z is depth of mixed layer (Holmes 1970). Solar radiation in MJ (megajoules) was converted to Einsteins of photosynthetically available radiation using a conversion factor of $8 \text{ E} = 1.92 \text{ MJ}$ (Kirk 1983).

Data of maximum daily rain for a station on the western side of the island at Carmen City and another at Sabancuy near Puerto Real Inlet has been reported by Cruz-Orozco *et al.* (1979) and Soberón *et al.* (1988). Based on these records, two significant polynomials ($p < 0.05$) were used to interpolate between months (Figure 3.3 c).

River discharge data for the Palizada and Candelaria was available for 1970 to 1979 (Sec. de Recursos Hidráulicos 1980). Figure 3.3 a, shows mean monthly river discharge, maxima and minima. Daily interpolations were used and added into the two cells that represent river deltas (Figure 3.1).

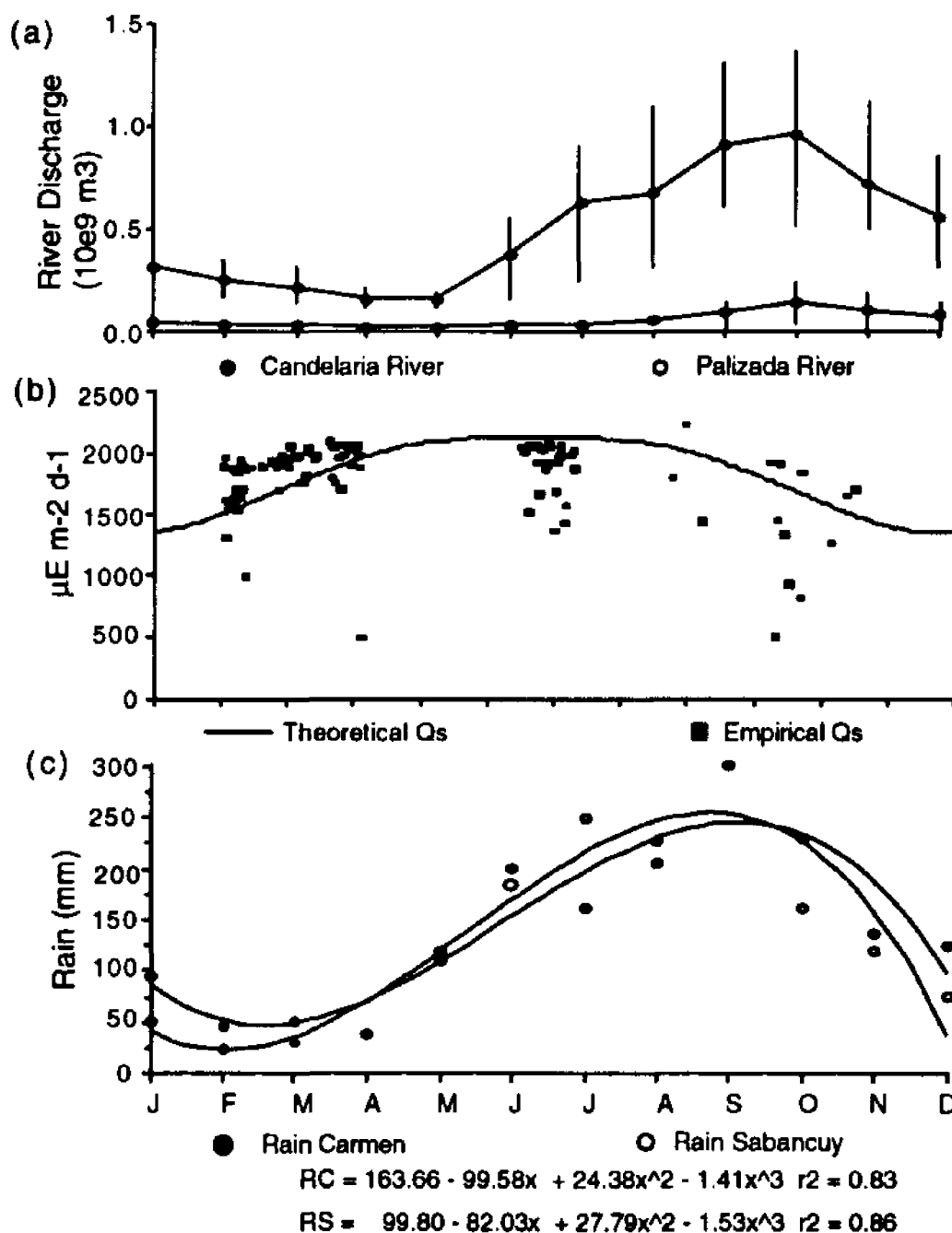


Figure 3.3 - Environmental parameters for Laguna de Terminos. (a) Monthly river discharge. Vertical bars indicate discharge range from 1970 to 1979. (b) Annual solar irradiance. Theoretical and field values. (c) Daily maximum rainfall on El Carmen City and Sabancuy. Polynomials used for the simulation are also presented.

Tidal pumping was computed for the cells which represented the inlets (Figure 3.1) by using the harmonic constituents of the tide (Donkers 1964). The vertical tide at a given place can be expressed in terms of a sum of harmonic terms (Donkers 1964):

$$H = S_o + \sum_{n=1}^{\infty} h_n \cos (\omega_n t + \alpha_n) \quad (3.3)$$

where H is height of the tide (m) at any time (t). S_o is the height of the mean water level above the datum used and each cosine term is a tidal constituent. The amplitudes h_n , of the constituents were derived from observed tidal data at both inlets (Instituto de Geofísica 1990). The frequency, ω_n is given in degrees per mean solar hour. The initial phase α_n of the constituent was determined from the observed tidal data (Instituto de Geofísica 1990). The principal harmonic components for each inlet are given in Table 3.2.

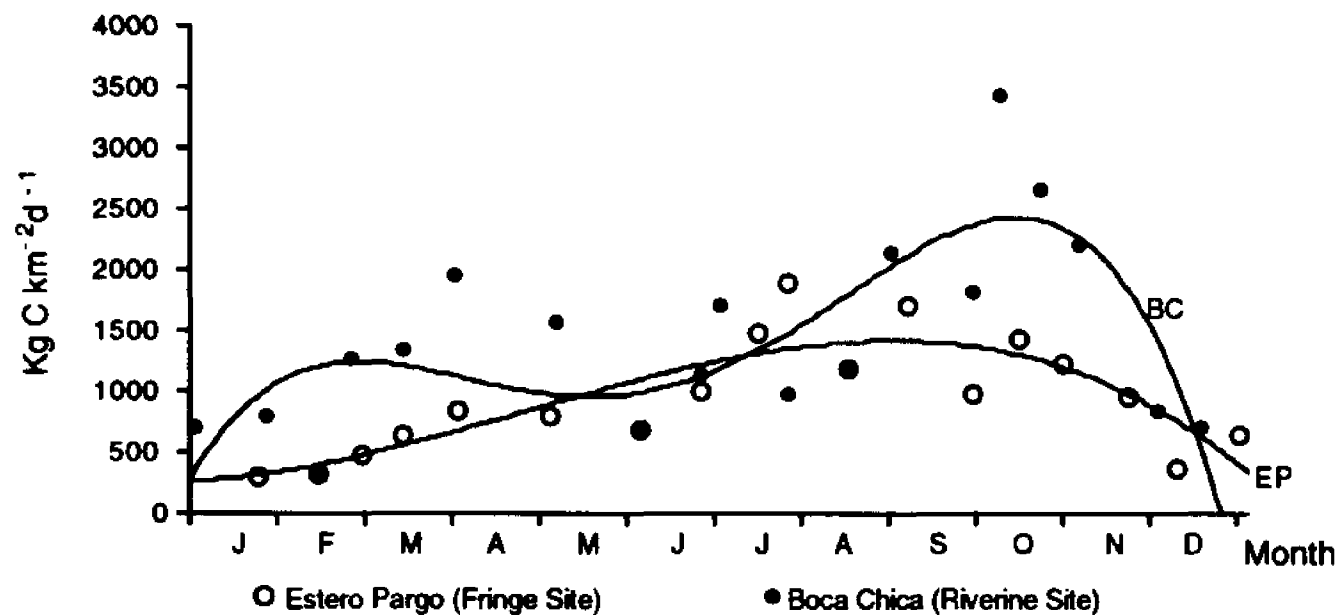
The only biotic forcing function utilized in the model was mangrove litterfall production. Mangroves surrounding the lagoon play a key part in controlling APP (Day *et al.* 1987, 1988). Therefore, the exportation component of mangrove litter was input into the model after data from Day *et al.* (1982, 1987). Two different kinds of mangrove communities have been studied in Laguna de Terminos; riverine and fringe forests. Daily litterfall in the model was computed by a significant ($p < 0.05$) polynomial regression of litterfall measured by Day *et al.* (1982; Figure 3.4). Predicted litter production per km^2 was used as Kg C input to each appropriate border cell. The mangrove area bordering each cell was known from recent maps (INEGI 1987).

Table 3.2.

Principal harmonic components for tidal computations¹.

Principal Harmonic Components at Puerto Real, Campeche.			
Component	h (m)	Phase α_n (°)	Frequency ω_n (hr)
M2	0.111	037.2	12.42
S2	0.018	011.3	12.00
K1	0.120	288.4	23.93
O1	0.138	289.7	25.82
Principal Harmonic Components at Carmen Inlet, Campeche.			
Component	h (m)	Phase α_n (°)	Frequency ω_n (hr)
M2	0.076	091.1	12.42
S2	0.020	87.8	12.00
K1	0.119	310.5	23.93
O1	0.115	298.0	25.82

¹ Source: Instituto de Geofísica 1990.



$$EP = 245.34 + 1.22x + 4.90e-2x^2 - 1.42e-4x^3 \quad R^2 = 0.71$$

$$BC = 237.00 + 42.20x - 0.591x^2 + 2.94e-3x^3 - 4.58e-6x^4 \quad R^2 = 0.60$$

Figure 3.4 - Litterfall production at two mangrove communities in Laguna de Terminos. Fringe and riverine data (after Day *et al.* 1987) and polynomial regression.

Mathematical Description

In each cell, the value of any state variable crossing from one to another depends on its value (A) and connectivity constant (K) such that unidirectional flow across a single boundary is KA . Therefore, the value of A is equal to the sum of inflows minus outflows, and may be expressed as:

$$dA_{i,j} = ((K_{i-1,j,i,j})(A_{i-1,j}) + (K_{i+1,j,i,j})(A_{i+1,j}) + (K_{i,j-1,i,j})(A_{i,j-1}) + (K_{i,j+1,i,j})(A_{i,j+1})) \\ + (- (K_{i,j,i-1,j})(A_{i,j}) - (K_{i,j,i+1,j})(A_{i,j}) - (K_{i,j,i,j-1})(A_{i,j}) - (K_{i,j,i,j+1})(A_{i,j})) \quad (3.4)$$

where $K_{i,j+1,i,j}$ is the water flow parameter from cell $_{i,j+1}$ to cell $_{i,j}$ and $A_{i,j}$ the state variable value in cell $_{i,j}$. Model spatial dynamics are based on this equation, however, there is a difference in how water volume on each cell and the rest of the state variables are handled.

In this model, the water volume varies according to fluvial and tidal inputs. The flows among cells are driven by head differentials. No wind driven circulation was accounted for. Rewriting equation 3.4, the change in the volume of a cell (cV) occurs as a result of inflows (I) and outflows (O) from the water level differentials (W) of adjacent cells (a), and the proportion of water flow (K) as:

$$cV_t = cV_{t-dt} + ((IKIW) - (OKOW)) \quad (3.5).$$

Rewriting for each unidirectional flow:

$$IW = aV - cV \quad \text{and} \quad IK = \begin{cases} \frac{IW}{\sum_{i=1}^4 IW} \\ 0 \text{ if } IW < 0 \end{cases} \quad (3.6)$$

and

$$oW = cV - aV \quad \text{and} \quad oK = \begin{cases} \frac{oW}{\sum_{i=1}^4 oW} \\ 0 \text{ if } oW < 0 \end{cases} \quad (3.7).$$

Note that the maximum number of unidirectional flows is four for every cell (c). Once these equations are calculated, a flux coefficient (k) for the rest of the state variables (Equation 3.4) was calculated as:

$$o_k = \frac{oK}{cV} \quad (3.8)$$

Numerical Techniques for the ROETER submodel.

The ROETER submodel is a mathematical combination of a general diffusion model (Okubo 1980) and a probability model (DeAngelis and Yeh 1984). In diffusion models, inert particles (e.g., environmental insensitive fish components, such as fish eggs, or element concentrations such as salinity or suspended sediments) are spatially distributed according to Fick's three-dimensional diffusion equation (Okubo 1980, Mullen 1989). The ROETER submodel uses physiological tolerance ranges of fish functional groups as diffusion coefficients (Reyes *et al.* 1992). Probability models simulate migration tracks, according to a probability of discrete movements by a single animal during each time step (Rohlf and Davenport 1969). Probability models incorporate environmental controlling functions in the form of biased probability distributions as a function of space and time. Introduction of these biased rules to modify movement implies complex decision-making on the part of the organism and within the model (DeAngelis and Yeh 1984).

The ROETER submodel used a probability function to control the movement of fish within any given cell according to the number of unidirectional flows and a set of behavioral rules that respond to environmental preferences. The ROETER submodel combines the diffusion and probability approaches by using a "variable diffusivity" (Mullen 1989) coefficient (fK). This diffusivity reflects the manner in which the local environment affects the local population dynamics, and creates unique daily diffusion coefficients for each spatial coordinate across the heterogeneous landscape of Laguna de Terminos (Reyes *et al.* 1992). Salinity, temperature, and chlorophyll *a* forcing functions were incorporated into the equations as coefficients for fish threshold responses (i.e., combined habitat suitability indices). The decision to migrate and the rate of migration depends on the multiplicative interaction of fish density with their environmental requirements (e.g., salinity) and physiological (e.g., birth rate) parameters. This variation of the diffusion coefficient allows the local population to remain in place under optimal conditions or flow into adjacent cells as environmental forcing functions vary (Figure 3.2 b).

A difference equation similar to the one used to describe water and the other state variables was used for fish population density changes in a cell (Equation 3.4). The number of fish crossing from one cell to another depends on the population density for any given cell (P replaces A in equation 3.4) and the fish migration parameter (fK).

This fish migration parameter (fK) also varied as a function of fish functional groups (Table 3.1; Díaz-Ruiz *et al.* 1982; Lara-Dominguez In prep.). The environmental and physiological tolerance ranges for each fish group was transformed into a normalizing habitat suitability index (U.S. Fish

and Widl. Ser. 1981). This numerical abstraction for fK is similar to the equations for spatial interactions in patchy environments (Nisbet and Gurney 1982, Ollason 1987). The combined suitability index (CSI) included salinity (S) and temperature ($^{\circ}\text{C}$), and food supply (F; phytoplankton standing stock in g C m^{-2}) according to the equation:

$$\text{CSI} = (S \cdot T \cdot F^2)^{1/4} \quad (3.9)$$

This CSI multiplied by the proportion of unidirectional flow (λ) at a any given cell was used to determine fK :

$$fK_{i,j} = 1 - \lambda \text{CSI} \quad (3.10)$$

The use of a CSI to determine fish diffusion coefficients is the population's "need" to leave a cell because environmental conditions no longer corresponded with that population's optimum physiological requirements and tolerance ranges.

The fish population density equation (Equation 3.4) included "classical" parameters of population dynamics such as birth (β ; i.e., recruitment or individuals successfully added to the population) and death (μ) rates (Gause 1934, Hardin 1968). According to Nisbet and Gurney (1982), an equation for population flux in a patchy environment ($p_{i,j,t}$) incorporates birth and mortality rates such that:

$$\frac{\partial p_{i,j}}{\partial t} = (\beta - \mu) p - \left[\frac{\partial M_i}{\partial i} + \frac{\partial M_j}{\partial j} \right] \quad (3.11)$$

where the net population flux for each cell $\partial p_{i,j}/\partial t$ is a function of spatially articulate immigration and emigration functions ($M_{i,j}$).

In this version of the ROETER model, we simulated only adult organisms. This simplifies the biological functions by keeping mortality rates constant. Birth rates (i.e., the incorporation of new adults into the population) were temporally unique to each of the fish functional groups recruitment season (Díaz-Ruiz *et al.* 1982, Lara-Dominguez In prep.). Cybernetic feedbacks and ecological processes (Margalef 1982, Odum 1983) were added to the population density equation to enhance its realism. This was done in two ways: (1) by ingesting and diminishing the phytoplankton biomass, and (2) by excreting nutrients into the water column and indirectly increasing the phytoplankton standing stock, according to the equation:

$$F_{i,j} = \text{Phyto}_{i,j} - \alpha P_{i,j} + \gamma P_{i,j} \quad (3.12)$$

$F_{i,j}$ is food stock at a given cell, $\text{Phyto}_{i,j}$ is the daily phytoplankton stock, and $P_{i,j}$ is the fish population; α is a constant converting population density into food stock depletion due to feeding, and γ is a proportionality constant for fish excretions to food stock (Reyes *et al.* 1992).

The LAPPTER model simulated ecological parameters and changes in state variables using a 1/4 day time step. The model was run for 5 years and the differential equations were solved by the finite difference using the Euler integration technique. The state variable equations and initial values for a unit model are presented in Table 3.3. The detritus flows from one cell to another as a proxy for suspended material. The zooplankton and benthos variables do not flow from adjacent cells, and they only act as sinks for phytoplankton and detritus, respectively (Table 3.3). Table 3.4 shows auxiliary variables and forcing functions used within the model.

Table 3.3

Difference equations and coefficients, Initial values and sources for

LAPPTER model.

Difference equations	Initial value	Description, source:
Water Volume in cell = V		
$dV_t = V_{t-dt} + (I_k I_W - O_k O_W)$ $I_k I_W$ = equation 3.6 $O_k O_W$ = equation 3.7 $k = C_W / C_V$	365 e6 m ³	Cell water volume using 3.65 m as mean depth k is the portion of waterflow in a cell divided by total cell volume.
Salinity in cell = S		
$dS_t = S_{t-dt} + (I_k I_S - O_k O_S)$ $I_S = 0$ unless $I_k > 0$ $O_S = 0$ unless $O_k > 0$	Salt in Cell	Salinity (S) in cell. Initial value spatially determined by isoline map.
Phytoplankton in cell = Phyto		
$dPhyto_t = Phyto_{t-dt} + (I(PP) + I_k I_{Phyto} - O_k O_{Phyto} - (PhytoZoo) - (PhytoFish) - (PhytoResp) - (PhytoDet))$ PP = Primary Production = 82192 kg C / km ² d * $I(Phyto) * LightCoef * TempCoef * UptakeCoef$ PhytoZoo = Zoo * (1 - $I(Zoo)$) PhytoFish = Phyto * $kPhytoFish$ PhyResp = Phyto * $TempCoef * kPhyResp$ PhyDet = Phyto * $kPhytoDet * InvTCoef$ LightCoef = 0.0 to 1.0 TempCoef = 0.0 to 1.0 UptakeCoef = Phyto * 0.19 $kPhytoFish = 1.6$ $kPhyResp = 0.8$ $kPhytoDet = 2.0$ $InvTCoef = 1 - TCoef$	467 kg C / km ² * Cell Size	Mean Biomass (Day et al. 1988). Production equation. = Max. production (Day et al. 1988) * Standing stock in Michaelis-Mental form. Grazing equations for zooplankton and fish in g / g C d. Phytoplankton Respiration. Phytoplankton transfer to detritus. Light Coefficient is spatially determined by light and Secchi disk data using equation 3.2 TempCoef is spatially determined by water temperature data UptakeCoef = Amount of N ₂ used by phytoplankton. Conversion factor for N:C (Klader and Hammer 1988). $kPhytoFish$ is stochastic coefficient for phyto to fish
Seagrass in cell = Seag		
$dSeag_t = Seag_{t-dt} + (I(PPSeag) - (SeagDet) - (SeagResp))$ PPSeag = Primary Production for Seagrass. = (14.5 DW / m ² d * Veg.Cover) * $I(Seag) * LightCoef * (1 - RainCoef) * TideCoef$ SeagResp = Seag * 0.4 SeagDet = Seag * 0.8 * TideCoef LightCoef = 0.0 to 1.0 TideCoef = 0.0 to 1.0	153 e ³ kg C / km ² * Vegetation cover	Mean Biomass (Homelas 1975). Production equation. = Max. production (Day et al. 1982) * Standing stock in Michaelis-Mental form. Seagrass Respiration. Seagrass transfer to detritus. Light Coefficient is spatially determined by light and Secchi disk data using equation 3.2 TideCoef is tidal coefficient. Amount of seawater present in the area.

Table 3.3 (continued)

Difference equations	Initial value	Description, source:
Mangrove litterfall in cell = Mang		
$dMang_t = Mang_{t-dt} + (f(ML) - ManDet)$ $ML = (MarLFall * FA)$ $= (FluvLFall * FA)$ $ManDet = Mang * kMM * TideCoef$ $= Mang * kFM * RiverCoef$ $kMM = 36$ $kFM = 36$	21200 kg C / km ² * forest size	Mean litterfall biomass * portion of cell size in km ² with mangrove (Day <i>et al.</i> 1987). Litterfall exportation coefficient in g / g C d * inundation coefficient. Marine mangrove production polynomial (Day <i>et al.</i> 1987) * Standing stock area Fluvial mangrove production polynomial (Day <i>et al.</i> 1987) * Standing stock area.
Dissolved Inorganic nitrogen in cell = N2		
$dN2_t = N2_{t-dt} + (R + Upt - (Depo) -$ $(Upt) - kN2)$ $R = SN2 * kR$ $Upt = Phyto * 0.19$ $kR = 0.8$ $kD = 0.26$	5000.40 kg N2	Mean of total inorganic nitrogen for dry and rainy season (Botello and Mandelli 1975). R = Resuspension of nitrogen from sediments (Klader and Hammer 1988). Depo = Deposition. Upt = Amount of nitrogen uptaken by phytoplankton. Conversion factor for N:C (Klader and Hammer 1988).
Inorganic nitrogen in cell's sediments = SN2		
$dSN2_t = SN2_{t-dt} + ((Depo) + (Fixa) +$ $(DetN2) - (R) - (Denitr) - (Burial))$ $Depo = N2 * kD$ $Fixa = 2954.84$ $DetN2 = Detritus * kDetN2 * kSN2$ $R = SN2 * kR$ $Denitr = SN2 * TempCoef * kSN2D$ $Burial = SN2 * kSN2Bur$ $kDetN2 = TempCoef * kDet$ $kDet = 0.25$ $kSN2 = 0.19$ $kSN2D = 6.0$ $kSN2Bur = 0.25$	21430.25 kg N2	Mean of interstitial Inorg N2 in soil (Hopkinson <i>et al.</i> 1988). Fixa = Mean fixation rate for entire lagoon (Stevenson <i>et al.</i> 1988). DetN2 = Remineralization equation. Transfer coefficient for detritus to inorganic nitrogen in sediments. Stechiometric coeff. for organic matter N to C R = Resuspension of nitrogen from sediments (Klader and Hammer 1988). Denitrification equation. Burial equation.
Benthos in cell = Bent		
$dBent_t = Bent_{t-dt} + (Deco - BMort -$ $BResp)$ $Deco = Bent * (1 - f(Ben))$ $BMort = Bent * kBDet$ $BResp = Bent * kBResp$ $kBDet = 0.5$ $kBResp = 0.2$	4300 kg C	Mean Biomass (Soberón 1988). Benthos stock * efficiency rate. Deco = detritus consumption. BMort = benthos mortality. BResp = benthos respiration.

Table 3.3 (continued)

Difference equations	Initial value	Description, source:
Detritus in cell = Det		
$dDet_t = Det_t - dt + ((BMort) + (PhyDet) + (ManDet) + (SeagDet) + k^l Det - (Deco) - (BR) - k^O Det - (Rem))$ $PhyDet =$ $ManDet =$ $SeagDet =$ $Deco =$ $BR = Det * (Burial\ Rate * TempCoef) + (Det * kDResp)$ $Rem = Det * TempCoef * kSN2D$ $BurialRate = 0.25$ $kDResp = 0.04$	3.39e6 kg C	Mean Biomass (Soberón 1988). BMort = Equation from benthos. PhyDet = Equation from phytoplankton. ManDet = Equation from mangrove. SeagDet = Equation from seagrasses. Deco = benthic consumption. BR = Burial and respiration losses. Rem = remineralization equation (Klédéc and Hammer 1988).
Zooplankton in cell = Zoo		
$dZoo_t = Zoo_t - dt + (Phy_to_Zoo - ZooRes - ZooFish)$ $Phy_to_Zoo =$ $ZooRes = Zoo * kZooResp + Zoo * kZooMort$ $ZooFish = Zoo * kZooFish$	12400 kg C / km ² * cell size	Mean Biomass (Soberón 1988).

Table 3.4

Auxiliary variables and forcing functions for LAPPTER model.

Auxiliary Variables		
Name	Description	Value
Irradiance	Correction factor that combines light with Secchi depth and extinction coefficient.	265 to 2112 $\mu\text{E}/\text{m}^2 \text{ d}$
Fixation		2954 kg N / d
Salinity	Spatially determined. Used only as initial value for State Variable	5.4 to 37.7
Forcing Functions		
Name	Description	Value
Rain Carmen	Monthly polynomial regression (Cruz-Orozco 1979 a-d)	41 to 246 mm
Rain Sabancuy	Monthly polynomial regression (Cruz-Orozco 1979 a-d)	18 to 252 mm
Candelaria River	Monthly mean discharge data (Sec. Rec. Hidraulicos 1980)	0.04 to 0.27 $\text{e}^6 \text{ m}^3$
Palizada River	Monthly mean discharge data (Sec. Rec. Hidraulicos 1980)	0.32 to 1.92 $\text{e}^6 \text{ m}^3$
Light	Theoretical model	1340 to 2130 $\mu\text{E} / \text{m}^2 \text{ d}$
Tide Carmen In.	Tidal model	-0.15 to 0.36 m
Tide P Real In.	Tidal model	-0.13 to 0.45 m
Water Temp.	Spatially determined by isotherm map.	21.9 to 38.3 $^{\circ}\text{C}$
Secchi Depth	Spatially determined by isoline map.	1 to 3.7 m
Marine Litterfall	Fringe mangrove daily litterfall production. Polynomial regression (Day <i>et al.</i> 1987)	296 to 1880 kg $\text{C}/\text{km}^2 \text{ d}$
Fluvial Litterfall	Riverine mangrove daily litterfall production. Polynomial regression (Day <i>et al.</i> 1987)	315 to 3440 kg $\text{C}/\text{km}^2 \text{ d}$

RESULTS

Hydrodynamics

The model was run for 10 years to test for stability in the hydrodynamics components. For the first calibration run the reported mean depth of 3.5 m was used for all 16 cells (Day and Yáñez-Arancibia 1982). The total volume increased during the first year by 4.0%. From year 2 on, the total water volume fluctuated regularly in response to tidal pumping and river discharge. A backcalculation of the surplus water was made to obtain a new mean depth of 3.65 m. Using this new mean depth as initial value and running the model for 10 years provided a variation of 0.9 to 1.1 % of the mean. Figure 3.5 shows the total water volume varied from year to year. Most of the seasonal signal was due to river discharge. After the first 3 months the model is stable and presented the same annual cycle.

Annual water volume data for years 2 to 5 follow each other closely (Figure 3.5 b). Although this annual water volume varied little from year to year, there was a strong season signal. During the dry season (Feb. - May), when there was only tidal pumping introducing water, the lagoon's total volume dipped below the annual mean. The peak in water volume corresponds with maximum river discharge and rainy season (Jun. - Sep.). Then as freshwater inputs diminished during the norte season, the total volume reverted towards the mean.

A comparison of flows through the two inlets showed that Carmen Inlet had larger magnitudes and variation in water flux than Puerto Real Inlet (Figure 3.6 a, positive figures are water going out, and negative values are

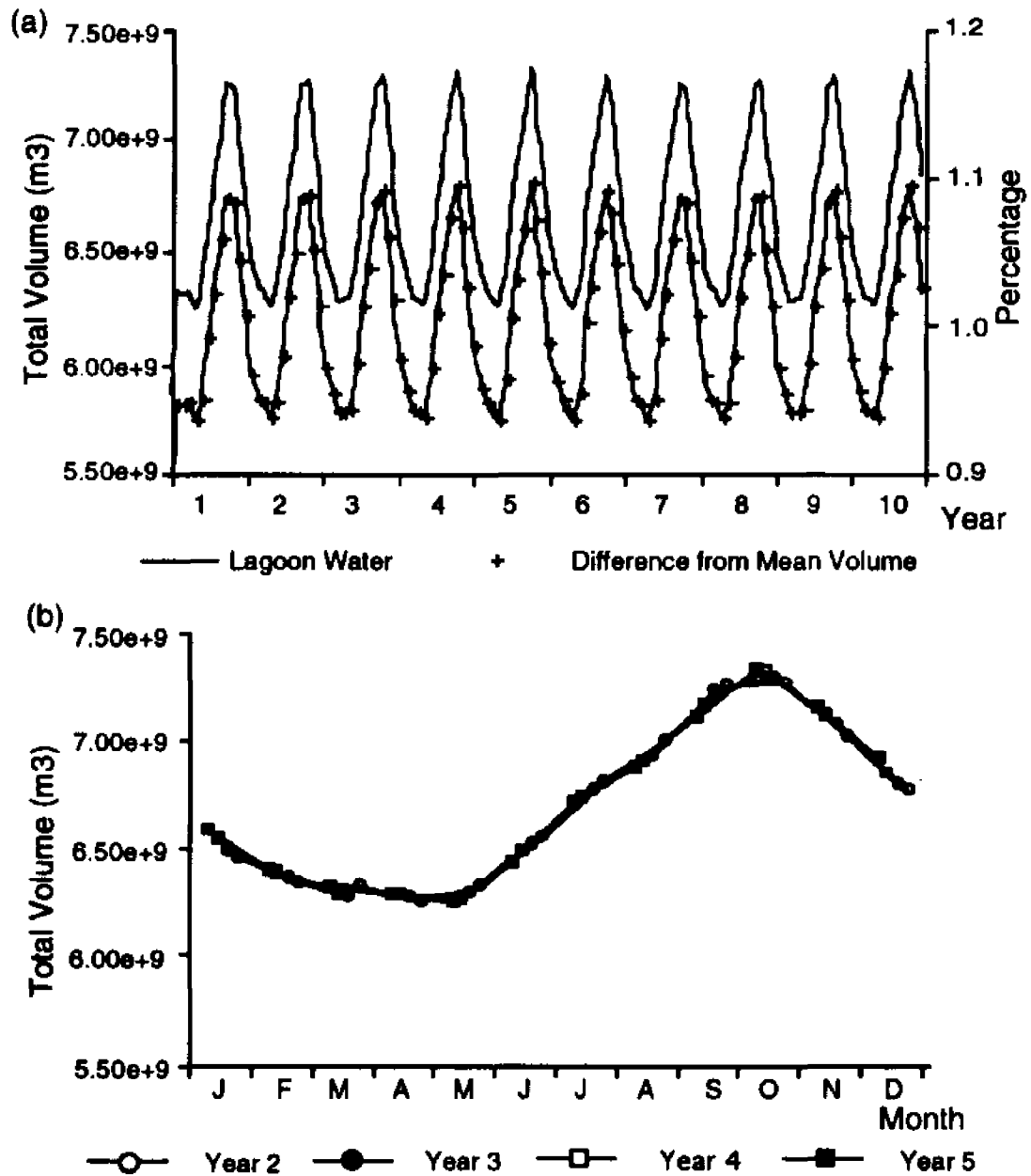


Figure 3.5 - Total lagoon volume for 10 simulated years. (a) Total volume and percentage of difference from mean volume. (b) Annual pattern for years 2 to 5.

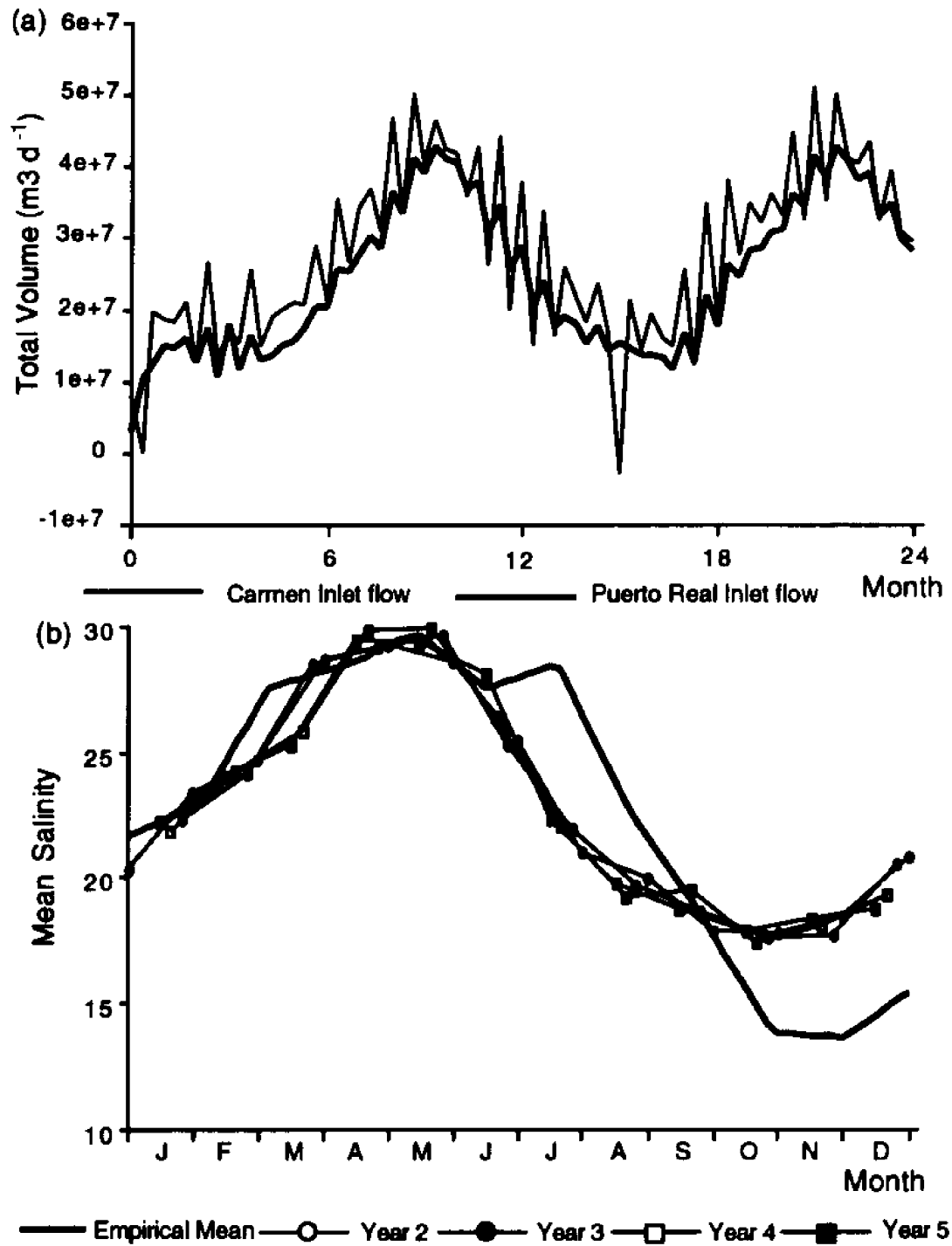


Figure 3.6 - (a) Water flux for Carmen and Puerto Real Inlets. Annual cycle for years 2 to 5 of the simulation. (b) Annual simulated salinity and field data (after Yáñez-Arancibia *et al.* 1988a).

water coming in) and agreed with the reported westerly flow of Laguna de Terminos (Day *et al.* 1982). The maximum net outflow was $5.49 \times 10^7 \text{ m}^3 \text{ d}^{-1}$, which is 47% of that observed by Mancilla and Vargas (1980). The river discharge signal still can be seen in the annual pattern, but during the dry season tidal pumping is amplified due the lack of freshwater inputs.

The salt variable was used as a conservative parameter to observe inert particle fluxes among cells and to evaluate the hydrology, since it was only influenced by amount of water added to the model. Simulated salinity has a distinct seasonal pattern with highs during the early part of the year (dry season) and lows during rainy and nortes seasons (Figure 3.6 b). Mean annual salinity was 22.89. A least-squares regression analysis of the 61 monthly salinity values collected by Day *et al.* (1982) against the simulated means resulted in a highly significant linear regression with a r^2 of 0.75 ($p < 0.001$).

Primary Producers

The LAPPTER model was run for 5 years only and analyzed for the years 2 - 5. The values of mangrove litterfall were inputted into each unit model; daily storage, respiration and decomposition rates were subtracted, and the remainder was a source for the detritus state variable. Respiration and decomposition rates were calculated from Day *et al.* (1987). Decomposition rate was then multiplied by a habitat inundation coefficient, which varied depending on the proximity to either river or tidal sources and mangrove community type (riverine or fringe; Figure 3.7). There were two peaks of litterfall, during the dry season and during maximum river discharge (Figure 3.7 b). The first peak was a result of the low inundation coefficient.

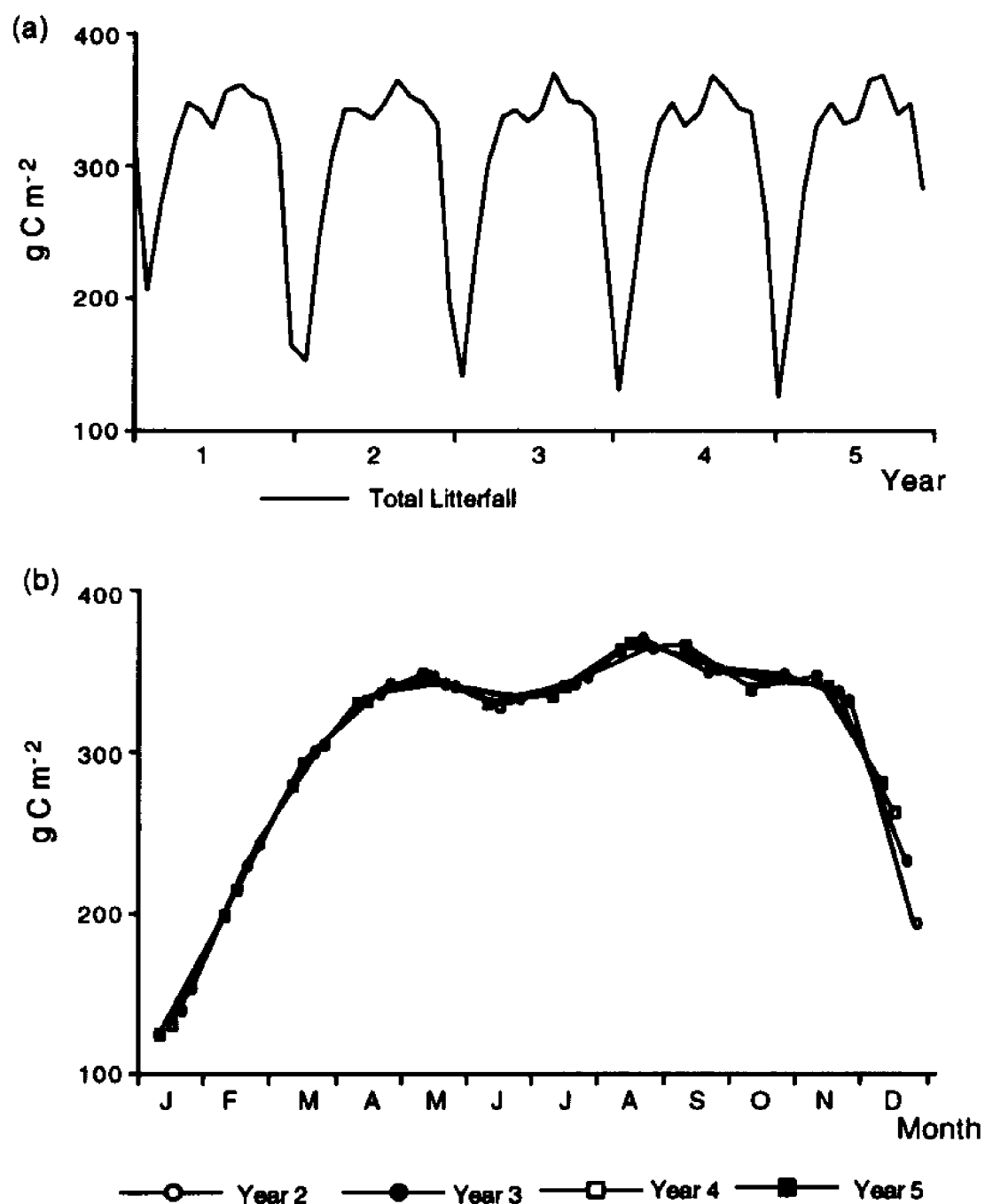


Figure 3.7 - Mangrove litter in Laguna de Terminos. (a) Total litterfall biomass for the 5 simulation years. (b) Annual pattern of mangrove litter.

This allowed litter to accumulate on the ground. The second peak was a combination of high litterfall and the high inundation coefficient for this period. Mean daily litterfall contribution from riverine and fringe communities was 233 and 166 g C m⁻², respectively.

There were higher levels of mangrove litter in the southern part of the lagoon as a consequence of the higher litterfall in that area (Figure 3.8). High values in the eastern part of the lagoon were probably due to a combination of high litterfall in adjacent riverine forests and lower river flushing than along the southwestern shore.

In contrast to mangroves, seagrass production was generally higher in the northern part of the lagoon (Figure 3.9 and 3.10). There was a slight increase in biomass over the 5 years simulated. This may be growth of the seagrass beds, since there are no episodic losses (as occurs from time to time due to fish grazing or storms; Rojas-Galaviz 1992). The calculation of seagrass production also used a uniform depth, but macrophyte production diminishes with depth and this usually happens in Laguna de Terminos between 2 and 4 m (Day *et al.* 1982). We are probably overestimating macrophyte production because we did not include this depth gradient in the seagrass primary production equation. There was a strong seasonal seagrass signal with a peak in May during the dry season (Figure 3.9 b). The seagrass standing stock declined thereafter as freshwater input and turbidity increased. The simulated values were slightly below the field data for the dry season, but agreed with the values for the rainy season (Figure 3.9 b). The annual mean for the simulated production was 167.1 g C m⁻², which was higher than the 158.2 g C m⁻² value reported by Homelas (1975). Spatially,

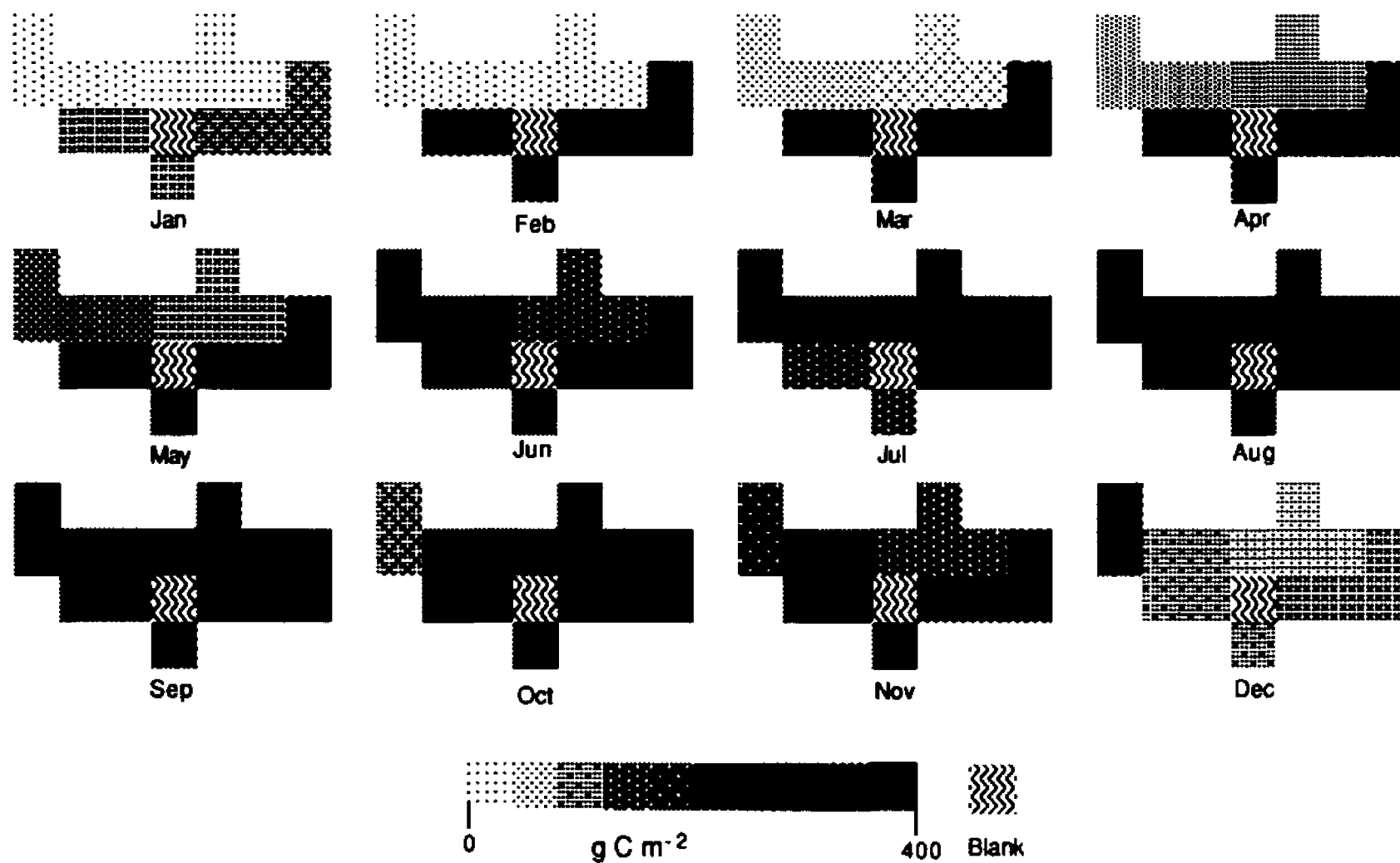


Figure 3.8 - Spatial distribution of exported mangrove litter for simulated year 3.

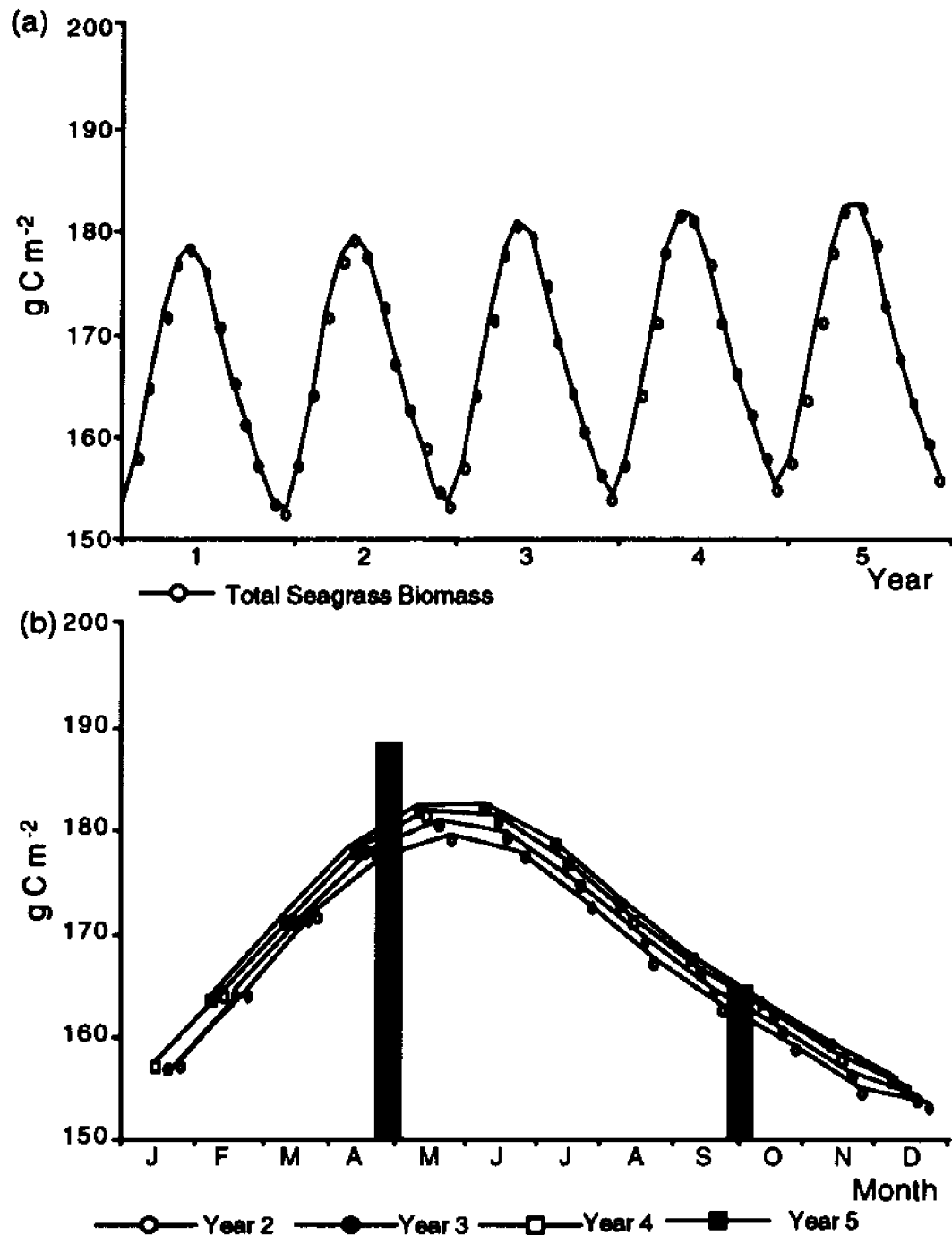


Figure 3.9 - Seagrass standing stock in Laguna de Terminos. (a) Total seagrass biomass for years 1 to 5. (b) Annual pattern of seagrass standing stock. The vertical bars are mean seagrass biomass estimates from Day *et al.* (1987).

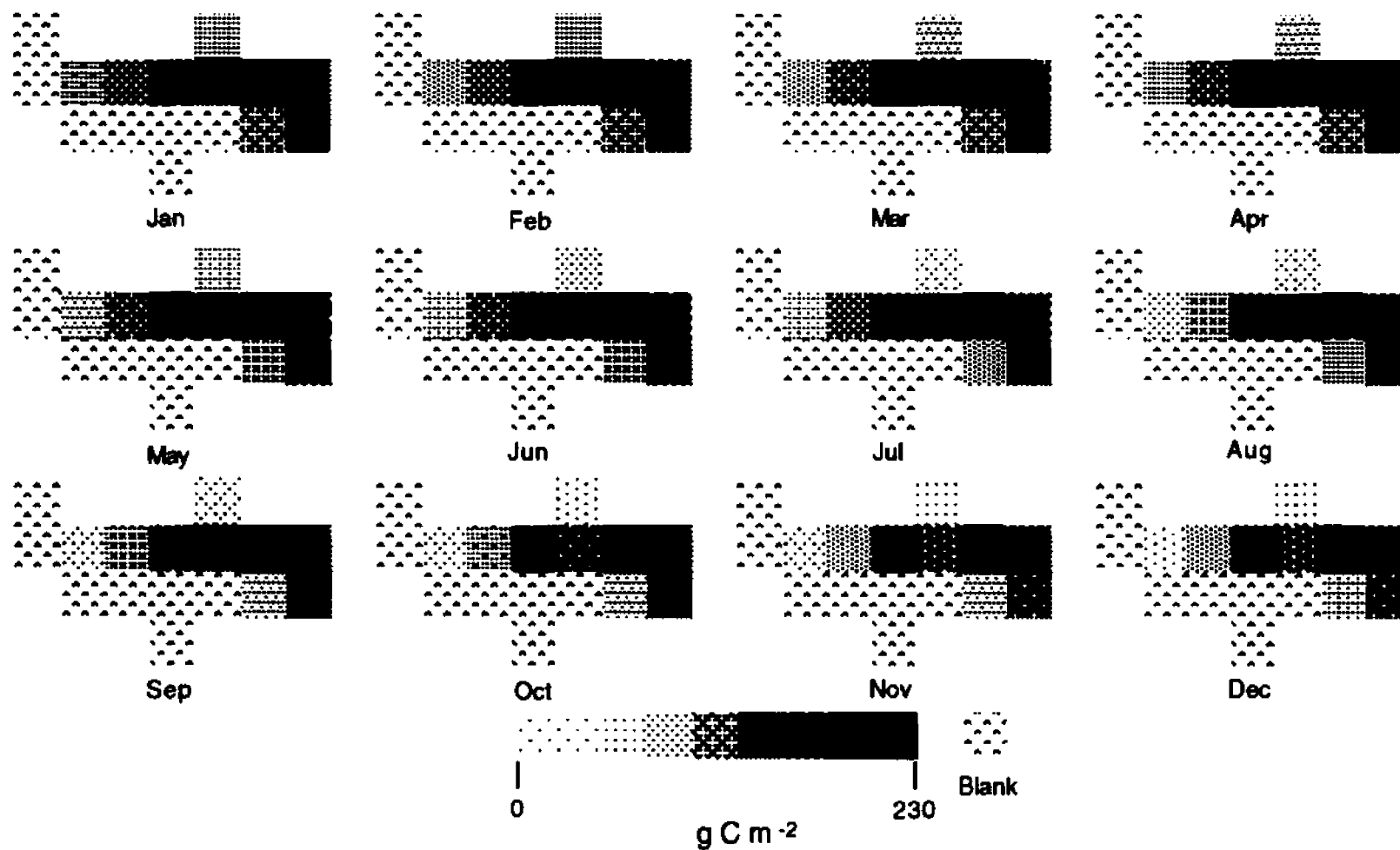


Figure 3.10 - Spatial distribution of seagrass standing stock for simulated year 3.

higher biomass values occurred in areas of strong marine influence (low turbidity; Figure 3.10) and low values in areas with strong riverine influence (high turbidity and high freshwater input tend to have a negative effect on seagrasses productivity; Wetzel and Moore 1984, Moore and Wetzel 1988).

The simulation of phytoplankton biomass was stable and the annual pattern was repeated (Figure 3.11). The simulation results were higher than the field data during the rainy season, probably as a result of an overestimation of incident light in equation 3.1. It is during this season that both turbidity and cloud cover increase, thus reducing both incident radiation and water transparency. A linear regression of the modeled and empirical values resulted in a r^2 of 0.31 ($p < 0.01$). Figure 3.12 depicts annual primary production, phytoplankton standing stock, and environmental parameters used to compute phytoplankton production. We identified two set of parameters as the main controlling factors: one set included turbidity and incident radiation. The other set was river discharge and associated parameters such as total inorganic nitrogen (TIN) in the water column, showing the link between nutrients and phytoplankton production. Spatially, phytoplankton biomass was higher in the southern and western parts of the lagoon, undoubtedly due to higher nutrient levels associated with river inputs (Day *et al.* 1982, 1988). Production was also generally higher during the wet months from June through December (Figure 3.13).

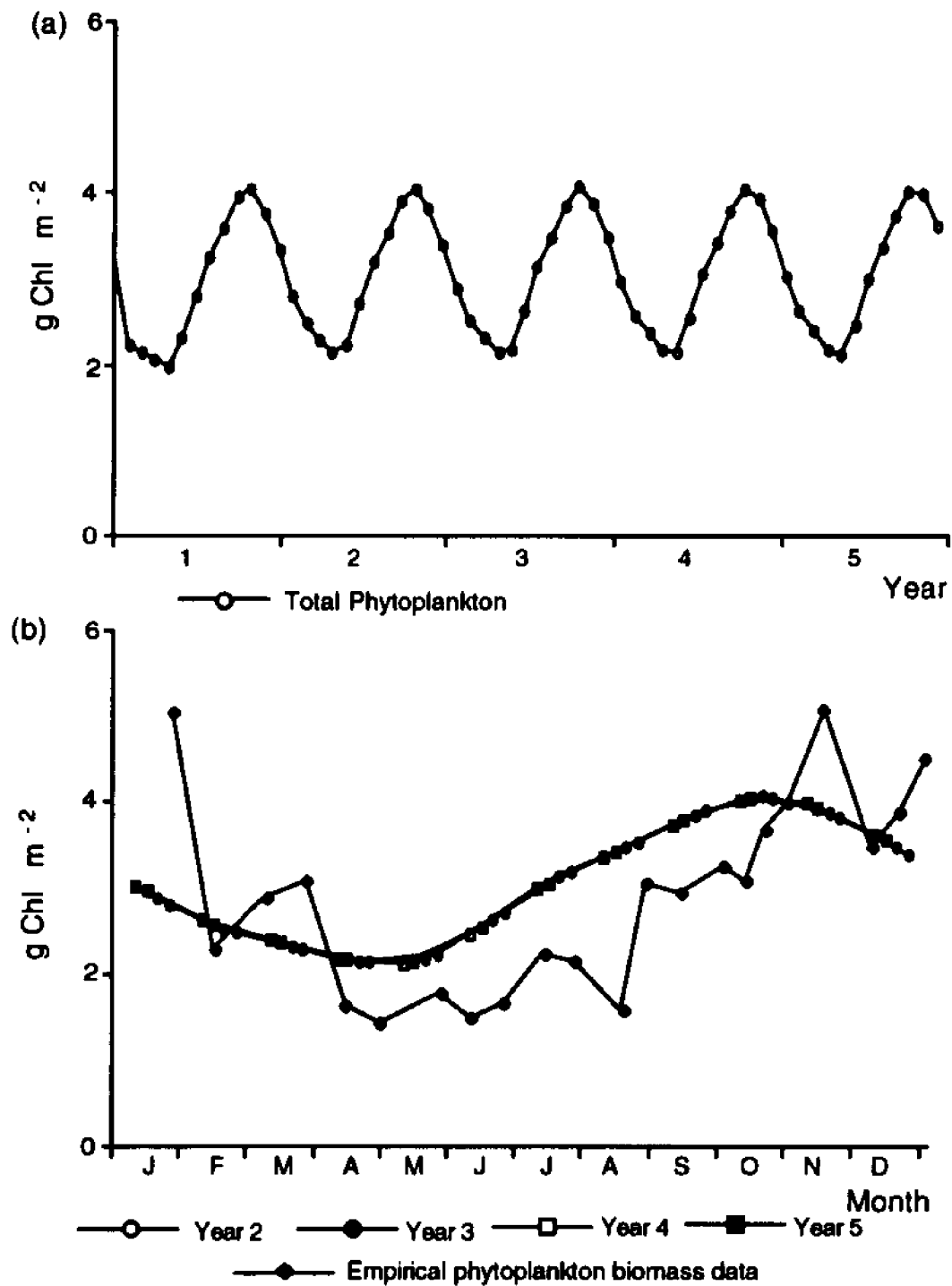


Figure 3.11 - Phytoplankton biomass in Laguna de Terminos. (a) Total Chlorophyll *a* concentration for years 1 to 5. (b) Annual pattern for simulated and field chlorophyll concentrations.

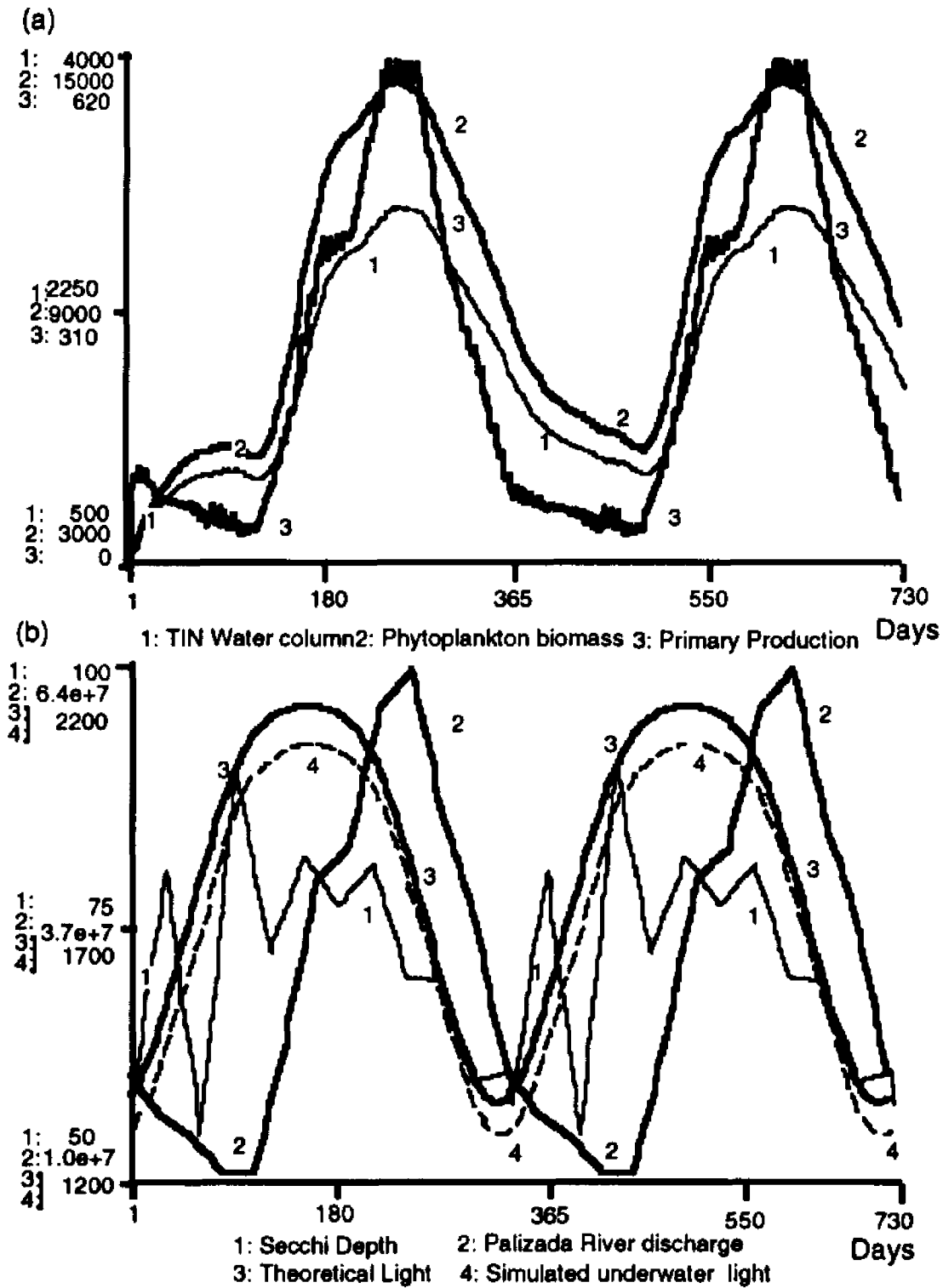


Figure 3.12 - Simulated phytoplankton biomass (kg C) and primary production (kg C km⁻² d⁻¹), and environmental parameters. Total inorganic nitrogen in kg N₂. Secchi depth in cm, river discharge in m³ d⁻¹, and light in $\mu\text{E m}^{-2} \text{ d}^{-1}$. Scales vary according to each parameter.

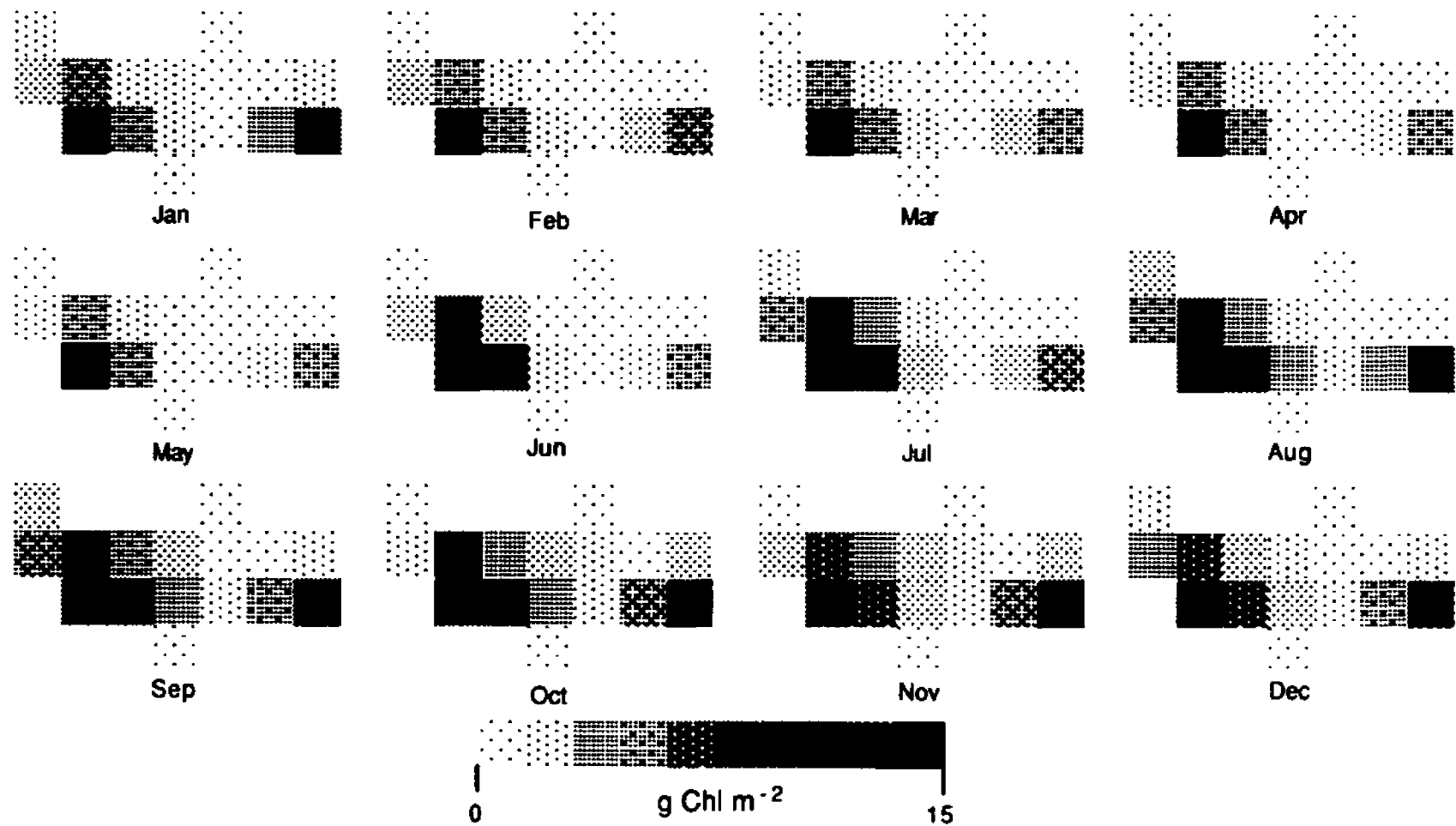


Figure 3.13 - Spatial distribution of phytoplankton biomass for simulated year 3.

Detritus, benthos and zooplankton.

The detritus component was modeled along with benthos and zooplankton. The latter two were modeled as sinks for detritus and phytoplankton, respectively (Figure 3.14 a). The modeled values followed what flowed from the producer-consumer pathways and accumulated in each state variable. The simulated values were inputted with the mean annual concentrations for these components measured by Soberón (1987). Detritus biomass was modeled spatially so that the effects of gradients in river input, mangrove export and phytoplankton production could be evaluated. Detritus peaked during the end of the rainy season due to inputs from the mangroves, phytoplankton and river (Figure 3.14 b). The seagrass inputs to detritus that occurred during the dry season were not discernible on this annual pattern (Figure 3.14 b).

Total Inorganic Nitrogen

The annual pattern for total inorganic nitrogen (TIN) both in water and sediments was a combination of riverine inputs and phytoplankton consumption (Figure 3.15 a). Total inorganic nitrogen in the water column peaked before that in sediments and phytoplankton (Figure 3.12 a), as a direct consequence of riverine input. The lag was probably due to a delay in deposition and uptake by autotrophs in the lagoon. Spatially, highest concentrations of TIN were in areas of highest freshwater input during the end of the rainy season (Figure 3.16). The importance of the different rivers was evident. The Palizada River, on the western side, not only contributed the largest amount of nutrients, but also affected a larger area of the lagoon.

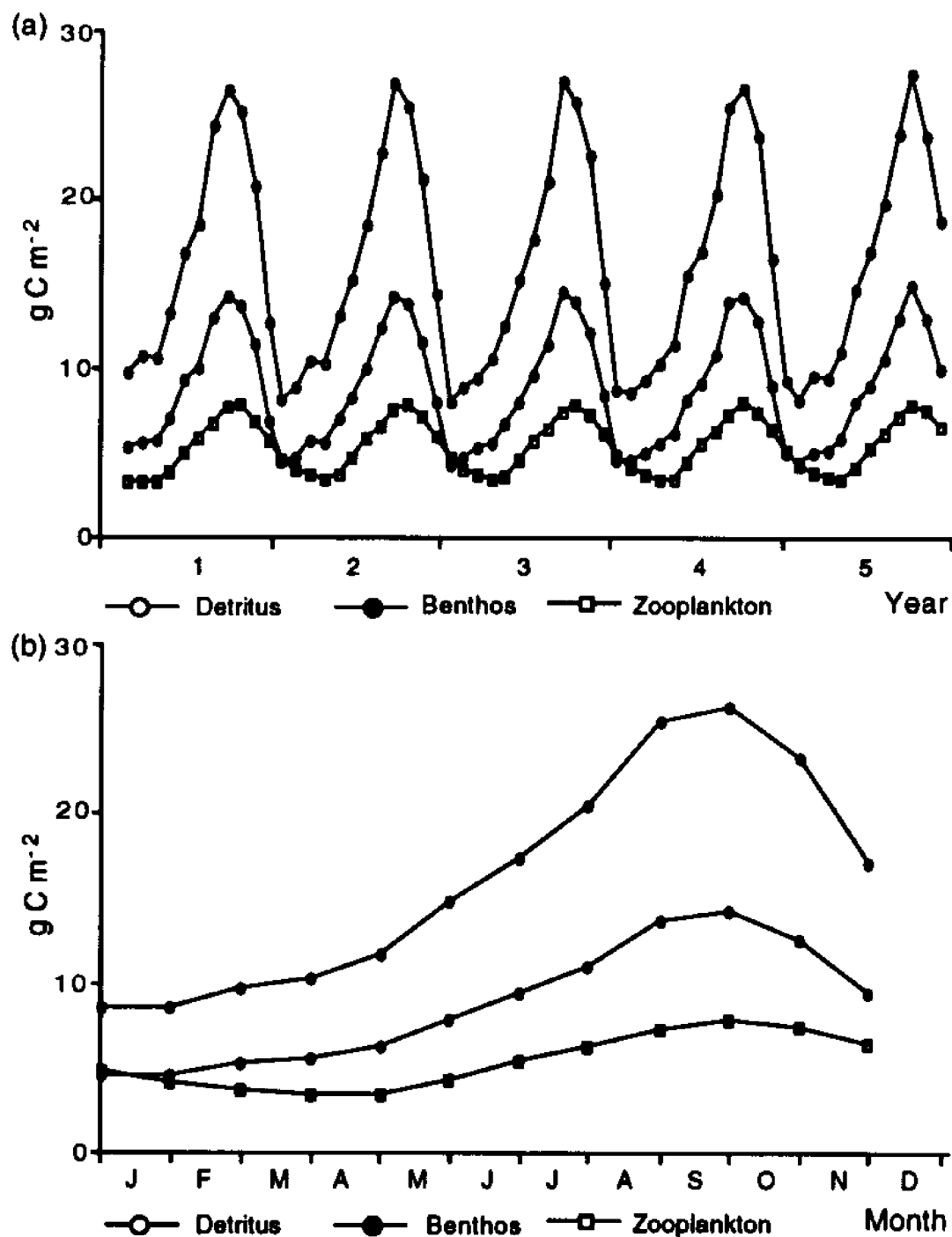


Figure 3.14 - Mean biomass for detritus and first order consumers stocks in Laguna de Terminos. (a) Mean biomass for years 1 to 5. (b) Annual pattern of detritus, benthos and zooplankton biomass.

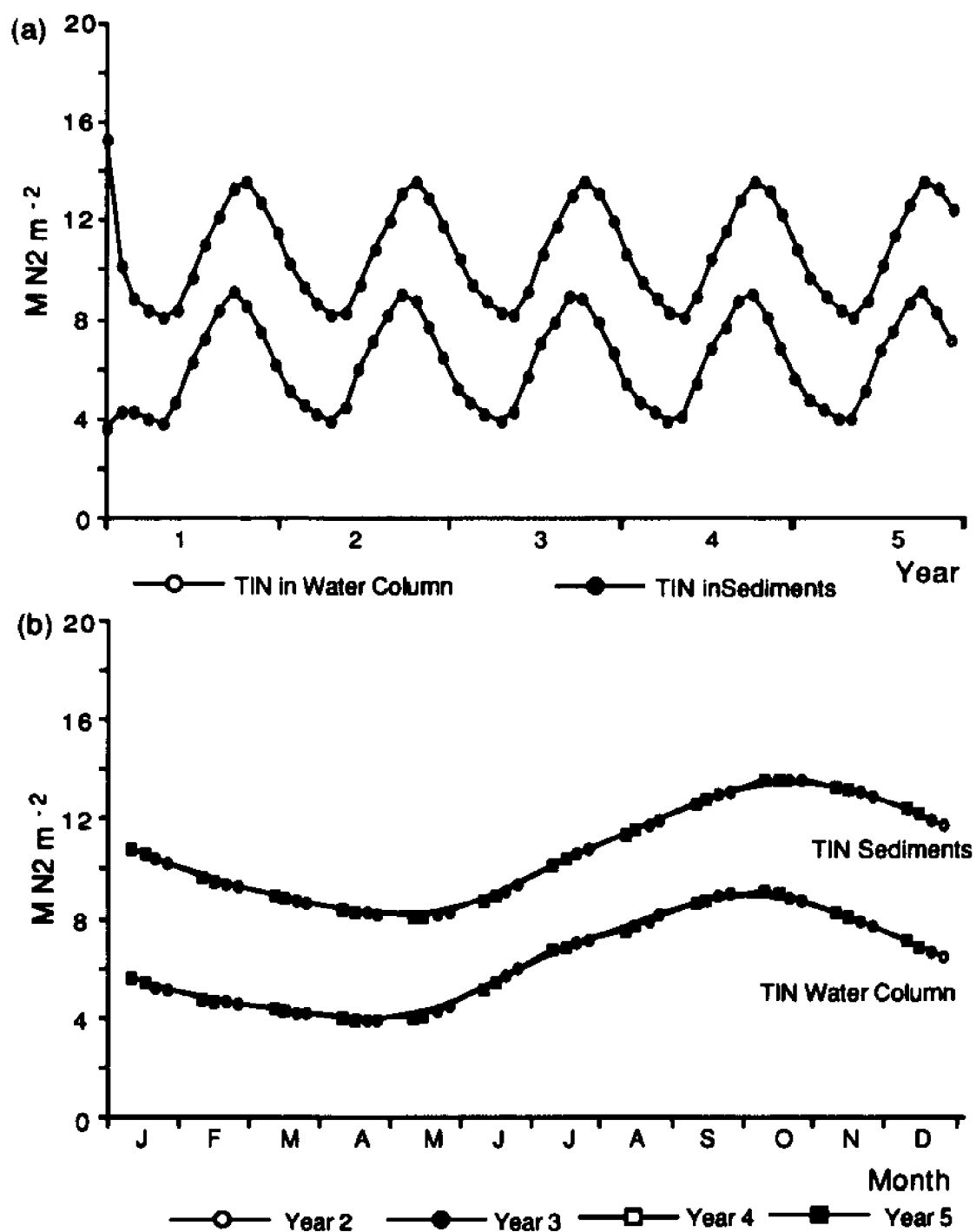


Figure 3.15 - Total inorganic nitrogen (TIN) in the water column and sediments of Laguna de Terminos. (a) Simulated TIN for years 1 to 5. (b) Annual pattern of TIN in water and sediments.

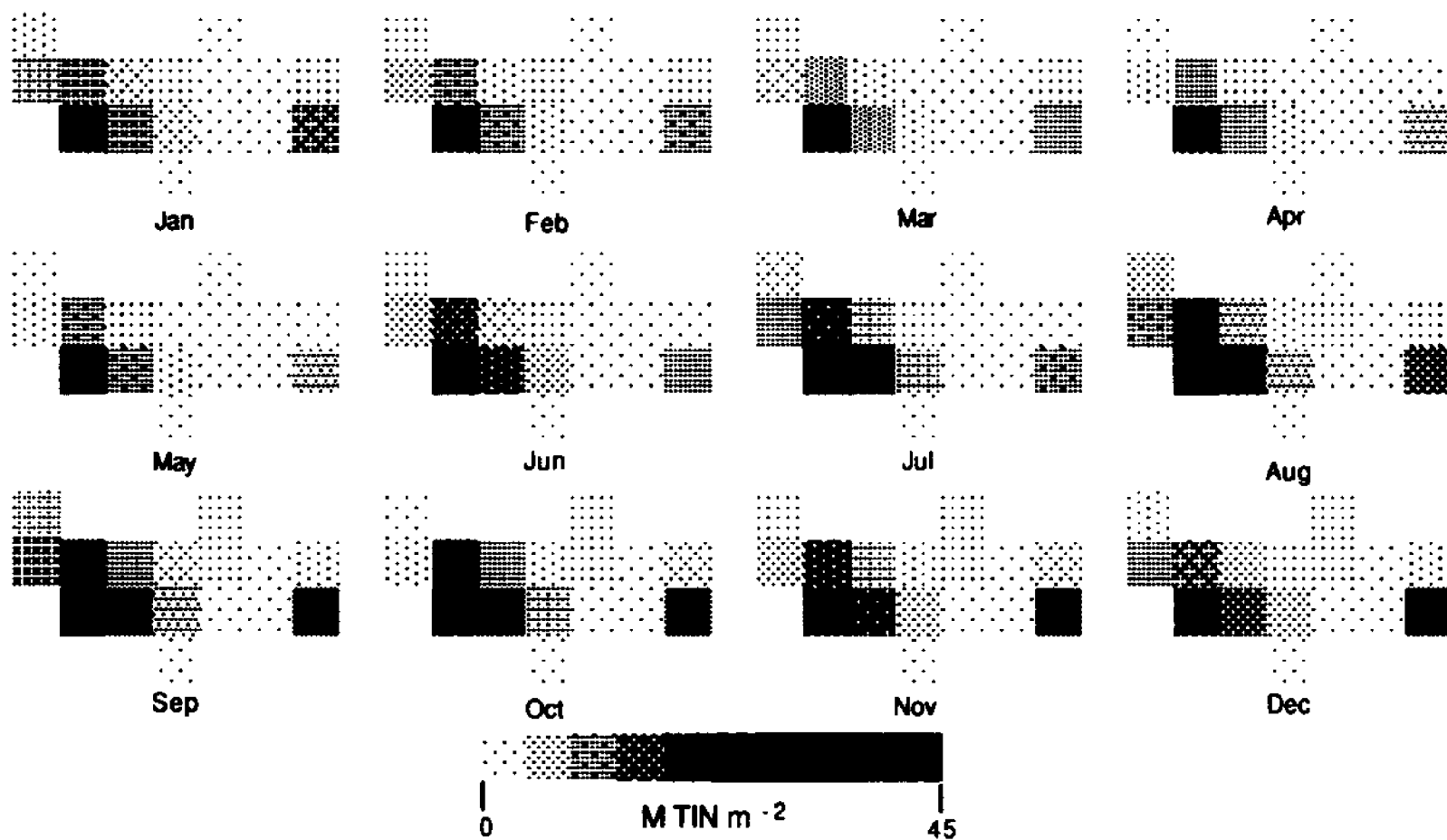


Figure 3.16 - Spatial distribution of TIN on water column for simulated year 3.

The nutrient gradient from the river mouths to the sea, characteristic of Laguna de Terminos, was one of the main reasons that productivity in the lagoon peaked during the rainy season and not during the maximum incident light period of the dry season (Day *et al.* 1987).

Fish Migration

The ROETER model was used to simulate each of the 4 fish functional groups (Table 3.1) for 5 years. The same CSI equation was applied to all the groups. Specific tolerance ranges were used for each functional group, however, as a control for migration behavior. Mean biomass concentration for the total fish population in Laguna de Terminos was 432 kg C km⁻² (Soberón 1987). The means for all four groups were calculated based on this figure and the proportions given by Yáñez-Arancibia *et al.* (1988b). This gave a mean biomass of 23.67 for group 1; 56.85 for group 2; 11.45 for group 3, and 34.13 kg C km⁻² for group 4. At the beginning of each simulation run, using these means, the population biomass was evenly distributed over the grid. The distribution of the population was then allowed to stabilize for an annual cycle.

Functional Group 1.

This group of fishes was comprised of second order consumers (carnivores, and occasionally detritus and filter feeders) with a high salinity preference. Simulated mean annual biomass for years 2 to 5 was 21.95 kg C km⁻² and the recruitment season from Jun. to Oct. The spatial output from the model indicated that this group remained primarily in the eastern and

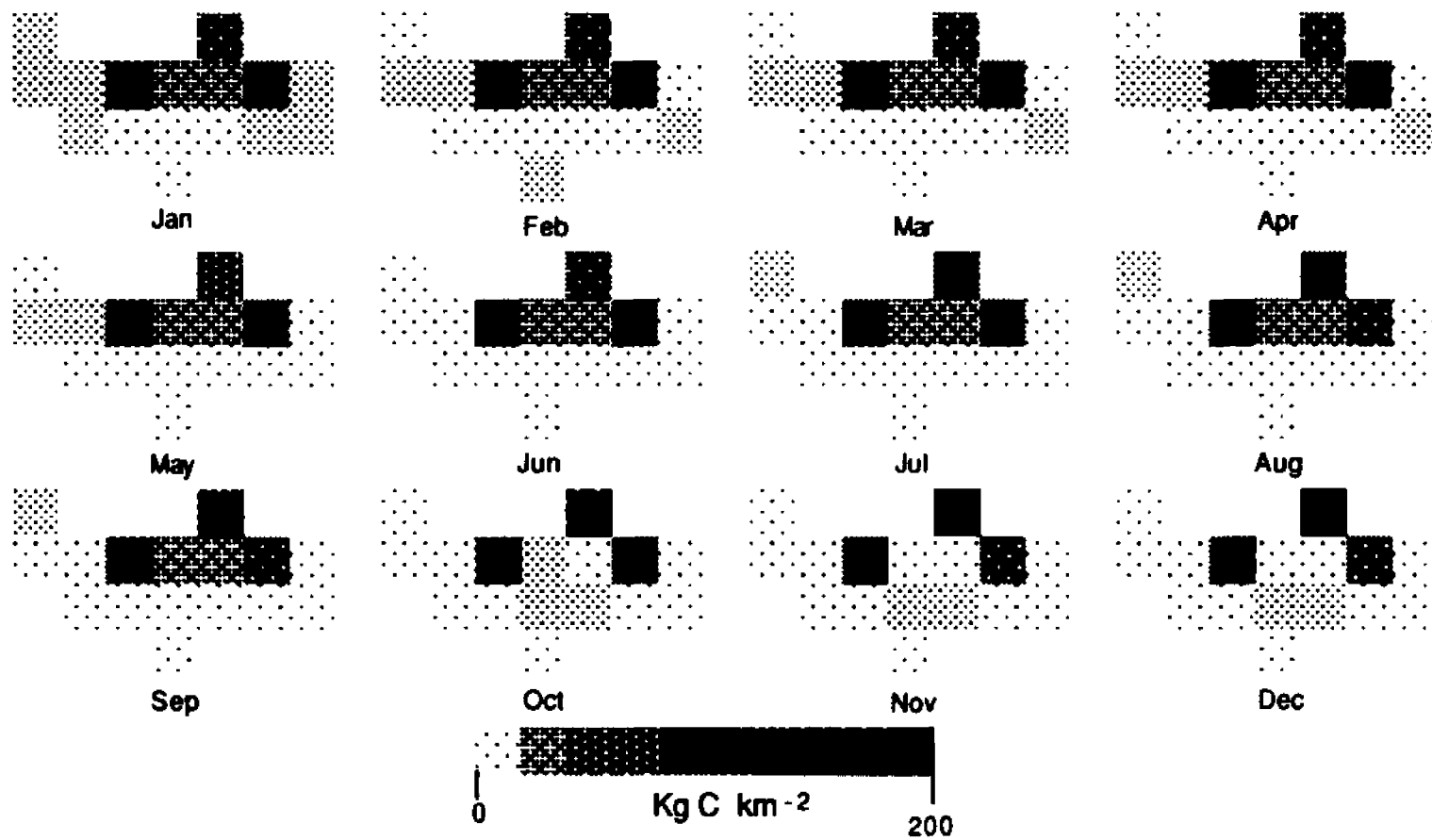


Figure 3.17 - Spatial distribution of fish functional group 1.

northern portions of the lagoon (Figure 3.17). During the dry season this functional group spread over a larger part of the lagoon, in response to higher salinity. They were always absent from the delta areas probably because salinity never got higher than 15. As freshwater input increased, the population was restricted to high salinity areas near Puerto Real Inlet where the seagrass beds were abundant. As the norte season progressed the simulated fish moved toward areas that had higher food concentrations (as indicated in Figure 3.13).

Functional Group 2.

This group was composed by second and third (exclusive carnivores) order consumers with a euryhaline salinity tolerance. These were mostly estuarine fishes that complete their entire life cycle inside Laguna de Terminos. Mean annual biomass was 56.44 kg C km⁻² for years 2 to 5. The main factor responsible for their spatial distribution appeared to be food availability. These fishes dominated the river mouth areas year-round. They concentrated heavily in the Palizada delta during the dry season, and expanded evenly through the lagoon during the rainy and norte seasons (Figure 3.18).

Functional Group 3.

This group was composed of second and third order consumers with a preference for low salinity. These fish immigrated into Laguna de Terminos through Carmen Inlet, and primarily utilized the western shore and Palizada delta during the norte season (Figure 3.19) as is typical for this group

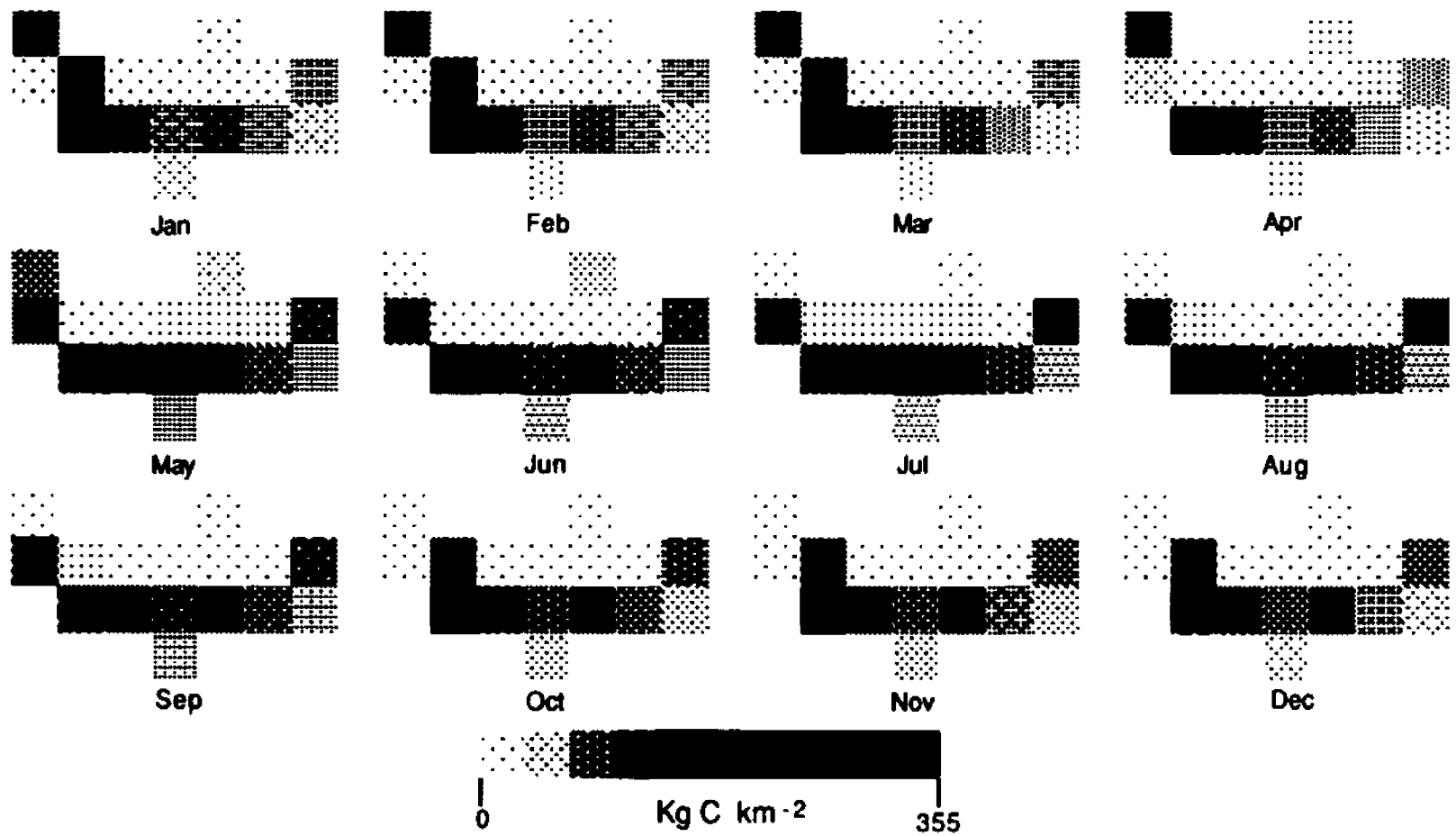


Figure 3.18 - Spatial distribution of fish functional group 2.

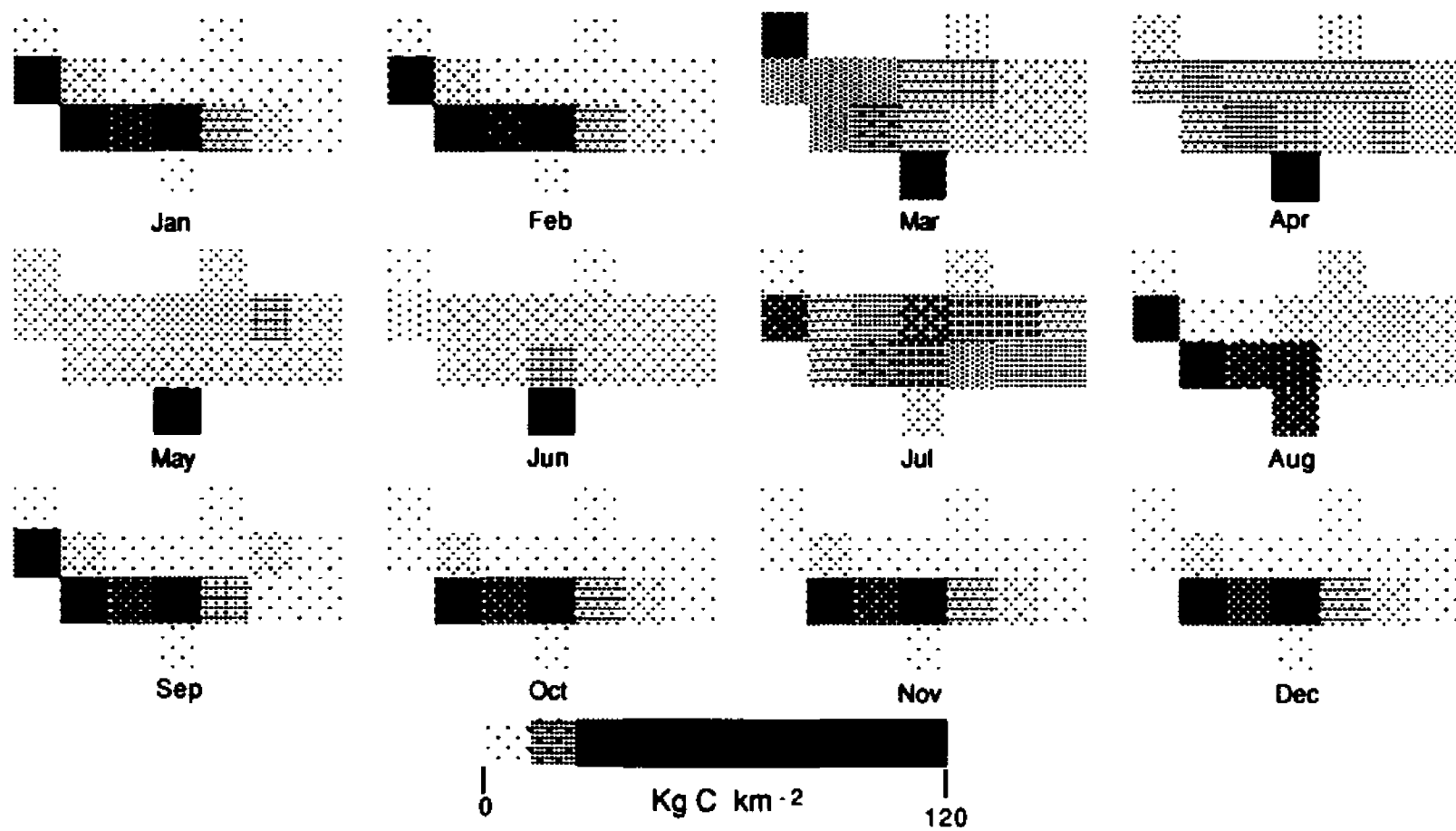


Figure 3.19 - Spatial distribution of fish functional group 3.

(Yáñez-Arancibia et al. 1985a). Recruitment occurred all year, and simulated annual mean biomass was 10.27 kg C km⁻² for years 2 to 5.

Functional Group 4.

This group was composed of temporary visitors which were first and second order consumers. This group was euryhaline and did not have a seasonal preference for any area (Yáñez-Arancibia *et al.* 1980). These fish after entering Laguna de Terminos were encountered in all habitats (Figure 3.20). Mean annual biomass was 27.85 kg C km⁻² for years 2 to 5, without a distinct recruitment season (Yáñez-Arancibia *et al.* 1980).

DISCUSSION

Modeling of primary producers and consumer in Laguna de Terminos has provided a better understanding of lagoon ecological functioning. Dynamic spatial ecosystem modeling can be an important tool for ecological analyses and management of tropical zones in Mexico, as well as in other developing countries that lack the resources to generate broad scale monitoring programs and intensive sustained research. Ecosystem modeling fulfills a need for holistic tools that supply decision makers with environmental information and analysis tools that can be easily implemented. That is one reason that we constrained the development of this model to an off-the-shelf desktop computer and software packages, instead of using more efficient but extremely expensive, high-end technology used in other landscape simulations (Costanza *et al.* 1986, Costanza *et al.* 1990). By this, we sacrificed some degree of size and spatial definition.

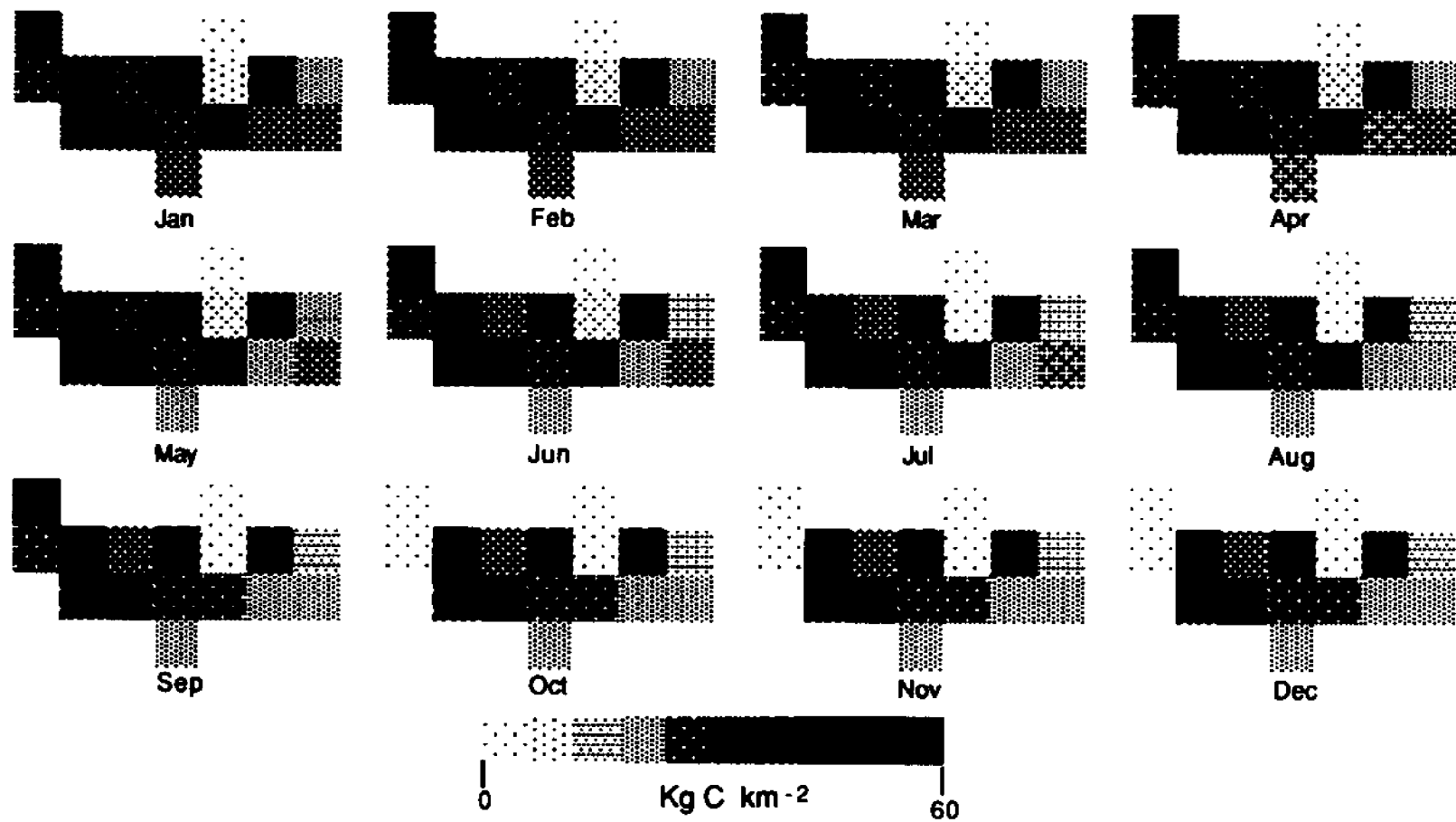


Figure 3.20 - Spatial distribution of fish functional group 4.

The hydrodynamics output from the LAPPTER model followed closely what other models have indicated; a water circulation pattern from east to west and a larger outflow through Carmen Inlet than Puerto Real (Dressler 1981, Graham *et al.* 1981, Kjerfve *et al.* 1988, Jensen *et al.* 1989). The simulated water volumes values, however, were up to 50% lower than the values from the hydrodynamic model by Graham *et al.* (1981). This difference in volume storage could be attributed to the LAPPTER model not accounting for winds or rain, especially during the norte season. Both factors affect lagoon circulation (See section on mathematical description) and volume. Wind, in particular, is an important environmental component and should be considered for more detailed hydrological analyses. Wind could also be responsible for the shortage of salt in the lagoon, since it effects the mixing of the riverine and marine waters. The water volume discrepancy could also be partially a result of using different data sets collected over different time periods, hydrodynamic measurements (1980-1981) and available river discharge data (1970's). Inclusion of wind measurements are a priority for further modeling of Laguna de Terminos.

Temperate estuaries are very strongly influenced by the distinct seasonal patterns of light and temperature. Seasonal patterns of production, regeneration, and migration can be largely explained by these forcing functions (Mann 1982, Day *et al.* 1989). In contrast, tropical regions lack a strong seasonality of incident light and temperature thus, it has been postulated that primary production is relatively constant in tropical waters (Cushing 1959, Mann 1982). Nevertheless, research from Laguna de Terminos and other tropical coastal systems show that there is a strong seasonality which in most cases is due to such local forcings as rainfall, river

flow, or upwellings in the coastal ocean (Day *et al.* 1982, 1987, Sandoval-Rojo 1988). Results from the LAPPTER model demonstrated that patterns of biomass and production were associated mainly with patterns of river discharge and nutrient availability during one season and rainfall and cloud coverage during another. Seagrasses and phytoplankton in Laguna de Terminos responded differently to annual environmental cues. Phytoplankton peaked during the rainy season when river influence and water-borne nutrients promoted high productivity. Conversely, seagrass production peaked during the dry season when sea water and sunlight had their highest influence. This implies that phytoplankton must be nutrient limited and benthic macrophytes are light limited (since they rely on nutrients in sediments as the main source; McMillan 1977). The spatial distribution of phytoplankton also indicated nutrient dependency. Highest concentrations were predicted near the deltas, expanding only when river discharge was highest. Seagrass productivity decreased in response to light reduction (i.e., suspended sediments).

LAPPTER slightly overestimated phytoplankton production during the rainy season when light was not only limited by suspended sediments but also by cloud cover. This factor should be addressed in future studies. More accurate incident light during storms and nortes could improve LAPPTER predictions.

The response of the system to mangrove litterfall suggests that mangroves are important sources of organic matter. Mangrove detritus contributed approximately 15% of water column organic matter. The different production levels by the different mangrove communities led to spatial variations in organic matter which were not due to other environmental

parameters such as water clarity and nutrient inputs. Thus, the flushing of the mangrove communities is important in both the total organic matter in the water volume and its spatial distribution (Flores-Verdugo *et al.* 1987).

Seagrass production contributed to the overall production of Laguna de Terminos in two ways. The first contribution was in the temporal domain, the production of these communities peaked late in the dry season, as opposed to during the wet season for other producers. This production helped to maintain higher production values when phytoplankton productivity was at its minimum. This "seasonal programming" in which different producer groups reach a maximum at different times has been pointed out by several authors as among of the factors that contribute to the high year-round total productivity (primary and secondary) in Laguna de Terminos (Day *et al.* 1982, Yáñez-Arancibia and Day 1982, Yáñez-Arancibia 1986, Rojas-Galaviz *et al.* 1992). The second contribution of seagrasses production comes from their spatial distribution on the northeastern side of the lagoon, where water is clearer and salinity higher than the western side, which is dominated by the Palizada discharge. This particular spatial distribution compensated for the lower production by phytoplankton due to the lack of inputs of terrestrial nutrients (Wetzel and Moore 1984, Kemp *et al.* 1988, Moore and Wetzel 1988).

The LAPPTER model indicated that Laguna de Terminos is a very dynamic environment, in which changes in production, salinity and temperature occur rapidly. These fluctuations tax any organism unless it has specific adaptations to these changes. Fish migrate into coastal embayments presumably due to the differential availability of food resources and protection from predators (Mann 1982, Gross *et al.* 1988). Estuarine residents

have developed physiological and ecological adaptations to live in these areas. Ecological preferences by residents and temporary visitors (functional groups 2 and 4, Table 3.1) indicated that these organisms are euryhaline and eurythermic. Thus, under the assumptions of the ROETER model, the mechanisms for spatial distribution for these groups should be food availability. The spatial distribution predicted by ROETER (Figures 3.18 and 3.20) indicated that these species moved around the lagoon regardless of the environmental gradients and concentrated according to the cyclic fluctuations in production. The results from ROETER agreed with the reported spatial distribution for these groups (Yáñez-Arancibia *et al.* 1980, Lara-Dominguez In prep.). However, the predicted spatial distribution of functional group 2 (estuarine residents) did not consider the resources available from the seagrass community next to Carmen island (Figure 3.18). The model assumed that phytoplankton and phytoplankton grazers were simply sources of food and, therefore, ignored the potential of seagrasses not only as a food source but also as habitat.

The simulated spatial distribution of the seasonal visitors, stenohaline (group 1) and euryhaline (group 3), to Laguna de Terminos agreed with the hypothesis that catadromy results when estuarine food productivity exceeds that of the adjacent sea (Gross *et al.* 1988). This behavior also confirms the findings that tropical fishes are more likely to move into coastal areas than temperate ones as postulated by Gross *et al.* (1988). These findings and the results of the modeling show that the benefits from high food sources must exceed the physiological costs due to changes in salinity and temperature (Myers 1949, Day *et al.* 1989). The spatial results for fish groups 1 and 3 indicated that there were areas where salinity, temperature, and food

combined "optimally" for each group according to season. Stenohaline visitors restricted their movements to marine waters inside the lagoon (Puerto Real Inlet and adjacent area), and never utilized the resources available in the river deltas. This behavior by the simulated organisms agreed with the observed life history for the species that comprise this functional group (Yáñez-Arancibia *et al.* 1980, Lara-Dominguez In prep.). The simulated euryhaline visitors tended to use Laguna de Terminos more broadly (Figure 3.19). Nevertheless, this functional group was more concentrated towards the western side of the lagoon in accordance to the distributions reported by Yáñez-Arancibia *et al.* (1980) and this distribution indicated that food was the driving force for fish migration inside the lagoon.

CONCLUSIONS

The development of a landscape ecosystem model for Laguna de Terminos highlighted the importance of each of the several environmental parameters and their spatial influence on aquatic primary production and fish migration patterns. The cyclic pattern of external forcing functions, that progressed from clear skies and water, and low run-off (dry season), to high river discharge and input of terrestrial sediments and nutrients (rainy and norte seasons) into Laguna de Terminos, created distinct temporal signatures and unique spatial distributions for all the ecological processes modeled for this tropical region.

The LAPPTER model accounted for hydrodynamics showing the annual pattern in water volume with westerly flow. The spatial mixing of fresh and salt water favored a gradient for salinity and temperature that helped to determine habitat characteristics important for primary producers and

consumers. The primary producers in Laguna de Terminos reacted in accordance to the annual environmental fluctuation. Phytoplankton and mangrove litterfall peaked during the rainy season when river influence and water-borne nutrients promoted high productivity. Seagrass productivity was highest during the dry season. The difference in both temporal patterns implied that phytoplankton were nutrient limited and benthic macrophytes were light limited. The simulated spatial distribution of phytoplankton biomass also indicated nutrient dependency. Highest concentrations were in the deltas, extending over more of the lagoon when maximum river discharge occurred. Seagrasses responded to this freshwater increase with a lower productivity.

The coupling of APP and fish migration patterns was evident from the output of the model. Simulated fish spatial behavior was highly consistent with field data summarized by Yáñez-Arancibia (1986, 1988b). A better migratory representation was achieved for stenohaline than euryhaline seasonal visitors. The food input was more important when either the food reached the minimum range, or when the salt tolerances remained within acceptable conditions. Further tests of the interactions between APP and nekton dynamics and environmental parameters should focus on predicting impacts of land use change. Modifications to the environment such as habitat destruction or changes in hydrology surely would lead to alterations of the APP and fish migration patterns in Laguna de Terminos. A better understanding at the ecosystem level of the diverse ecological factors and their temporal and spatial dynamics would aid in achieving a sustainable human economy tightly integrated to the natural resources of this ecosystem.

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**CHAPTER 4. ECOLOGICAL AND RESOURCE MANAGEMENT
INFORMATION TRANSFER FOR LAGUNA DE TERMINOS, MEXICO: A
COMPUTERIZED INTERFACE**

INTRODUCTION

One of the most pressing problems facing managers of coastal areas is the management and conservation of coastal resources in the face of multiple human and natural impacts. Management of an environment for multiple uses requires an understanding of the effects of exploitation throughout that ecosystem. Often managers have only limited knowledge about such ecosystems, and that knowledge is inadequate to permit sound decisions (Loewinger 1983). Thus, numerous scientific research projects have been carried out to study fundamental processes important for coastal management (Beyer and Sparre 1983, Cole *et al.* 1990). The transfer of the results of these projects to management solutions has not always been straightforward. Many scientists are not adept at putting their results in a format which is readily usable by managers. Also scientists are often uncertain about the best agency or manager to approach. Moreover, agency personnel are generally overburdened with day-to-day management activities and often see specific scientific results as too esoteric for their needs. Decision makers traditionally have had to rely on "expert judgment" to evaluate possible environmental impacts and the consequences of public and private developments. Finally, there have been no widely acceptable tools to aid in the transfer of science to managers (Westman 1985; McAllister 1988).

Several methodologies have been developed to organize, present, and evaluate impacts and management alternatives including simple extrapolation of existing trends in land use, reaction to crisis, and cost-benefit analysis (Baldwin 1985). The most common technique is the collection of

maps and overlays (McHarg 1969, McAllister 1988), but the lack of flexibility and limited comprehension of landscape dynamics are a serious limitation.

An exciting development in the communication and transfer of scientific results is a body of knowledge whose aim is to facilitate interaction among diverse disciplines. This new discipline, known as "scientific visualization," has as its foundation the adage "a picture is worth a thousand words." Scientists have extensively use graphs, maps and figures to convey information in a more synthesized and appealing way (Tufte 1990). Scientific visualization, however, is not just presenting results in a graphic manner to the general public. It integrates topics as diverse as statistics, mathematical modeling, data base management, and long-term analysis. It allows the scientist to envision the data, simplify the use of different data sets, and enhance analytical potential (Wright et al. 1990).

In the last five years several attempts have been made to create information systems that rely on this relational view and to use more efficiently emerging technologies. The National Center for Supercomputing Applications at the University of Illinois is one of the centers in the forefront of visualization theory. Their emphasis, however, is to use large mainframe computers such as the CRAY (e.g., Dwyer 1990, Robinson 1990). Several agencies have started ambitious projects for information systems using microcomputers and desktop computers, i.e., the National Oceanic and Atmospheric Administration (NOAA) program called COMPAS (NOAA, 1990). This HyperCard™ driven information system compiles information for coastal planning and assessment for the State of Texas. Another example is an analysis system for shrimp harvest data (NOAA, 1989).

Laguna de Terminos is Mexico's largest coastal lagoon and is, thus far, largely unaffected by human activities (Figures 4.1 b and 4.3 a). The status of its relative pristine state, however, is changing because of a number of activities in the area. The city of El Carmen (on the western side of Carmen Island) is growing, leading to mangrove destruction and water quality problems. There is pressure to construct shrimp ponds in mangrove areas and rice agriculture is developing south of the lagoon. Extensive petroleum exploration and drilling in the nearshore Gulf of Mexico poses potential threats from oil spills and pipeline construction. Plans had been laid to increase development in the area, including highways and a bridge connecting Carmen Inlet with the mainland (Villalobos and Yáñez-Arancibia, 1991. EPOMEX Program Pers. comm.). Proper management of this lagoon demands an information system which can be used to understand the biologically dynamic processes in this lagoon and surrounding areas, for both predicting and preventing the potential impacts of development on the ecosystem. The information transfer system described in this paper is designed to address this need.

We developed a bilingual, interactive, and user-friendly information system based on a desktop computer that simplifies the organization and information transfer to environmental managers of research results relating to Laguna de Terminos, Mexico. The system is constructed in a manner that facilitates the addition of modules of information as they are developed. The use of this graphically oriented interface allows the user timely access to a wide range of scientific information. The method applies recent developments in microcomputer technology and makes it possible to deliver to the desk of the researcher or manager a wide range of capabilities and

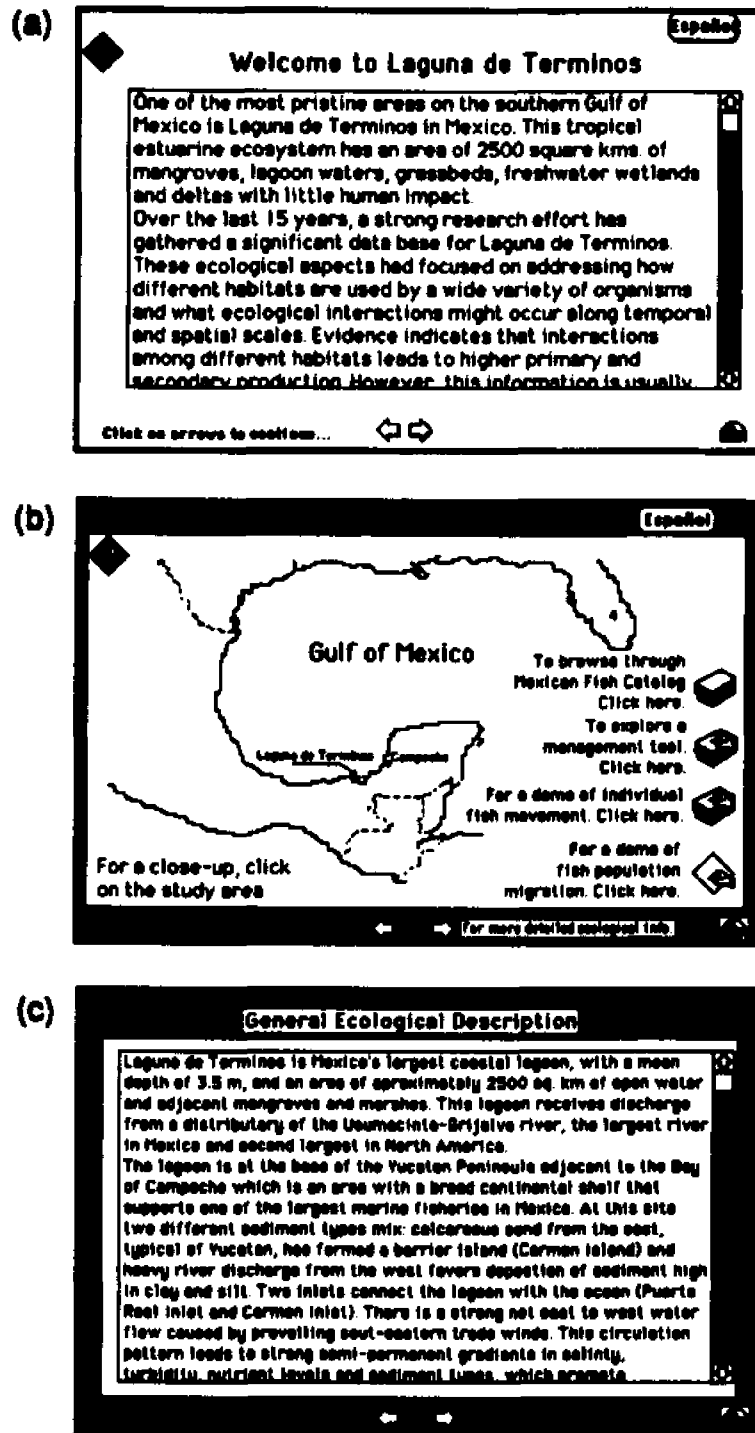


Figure 4.1 - (a) Introductory screen to the presentation. (b) Location Map of Laguna de Terminos, Mexico. (c) General ecological description card.

data that previously could only be accessed on expensive and user-unfriendly mainframe computers.

The program presently includes information on: (1) sediment, vegetation and intertidal community distribution maps; (2) annual climatological graphs for atmospheric and aquatic parameters; (3) a catalog of dominant species of fish with life histories and habitat preferences, scientific names and taxonomic descriptions; (4) a modeling tool for predictions of shrimp aquaculture scenarios; and, (5) computer simulations of individual and population migrations of fish.

STUDY SITE

Laguna de Terminos is located in the southern Gulf of Mexico (Figures 4.1 b and 4.3 a; summarized in Yáñez-Arancibia and Day 1988). This tropical estuarine ecosystem has large areas of mangroves, submerged grassbeds and freshwater wetlands. It is shallow (mean depth 3.5 m) with an area of approximately 2500 km² comprised of open water and adjacent mangroves and marshes. The highly productive waters of Laguna de Terminos support Mexico's largest and most economically important marine fishery (Yáñez-Arancibia and Aguirre-León 1988). Diverse marine organisms use its various habitats extensively as nursery grounds (García-Cubas 1981, Roman-Contreras 1988, Yáñez-Arancibia and Day 1982 and 1988). Laguna de Terminos has a strong net east to west water flow, caused by prevailing easterly trade winds. This circulation pattern maintains semi-permanent gradients in salinity, turbidity, nutrient levels and sediment types, and promotes assemblages of foraminifera, benthic macrofauna, and the migration of fish and shrimp (Day *et al.* 1982).

METHODS

The information system we developed has three components: the computer, the programming language for the interface, and the simulation language used on the modeling tools. Important considerations in its development were (1) user friendliness, (2) a fast learning curve, (3) existing software capable of generating graphically oriented presentations, and (4) low cost, portable and readily available hardware.

The Computer Hardware and Software

The choice of hardware was based on two criteria. First, to create a multimedia database, a computer capable of high definition graphics and sound was required. Second, we wanted to take advantage of a machine already in use in government agencies that had a record of "user-friendliness." The Apple Macintosh desktop computer meets both criteria. A small machine such as the Mac Plus model allows the development of a product that will have visual appeal to a large audience. The special characteristics of a multimedia data base can be fully exploited because, many software products already exist to prepare and enhance databases. Maps, graphics and other visual and sound formats can be used to ease information transfer and enhance tutorial properties of the presentation.

The presentation of scientific data in an easy-to-use, appealing format for the environmental manager can be accomplished using the programming language HyperCard as a presentation tool. HyperCard differs from many other programming languages in that lines or strings of code are integrated into modules. These modules are organized in a hierarchical structure and presented as objects or icons ("buttons"). The program or "stack" is activated

by positioning the pointer or cursor on the icon and clicking the pointer (mouse). Therefore, the information produced by research projects can be organized, prioritized and presented on a group of stacks. Alternatively, specific queries can be made by the user through the mouse and keyboard. HyperCard takes an additional step in the management of relational data compared to traditional systems. It allows the information and results from specific queries to be presented as different screens ("cards") that the user can "browse" at leisure. The user has the flexibility to explore between files and view information in a large variety of contexts. The system requires minimum training and is highly user interactive.

In combination with HyperCard, the simulation language "STELLA®" (High Performance System 1987) was used to develop simulation models. This simulation language facilitated the construction of model interactions and processes using a graphical interface, and simplified the creation and solution of differential equations (Costanza 1986). The results are then used by the interface to create animations or graphs. Therefore, the user has access immediately to data generated by the simulation models. A resource manager, familiar with STELLA, could change the model parameters to test new scenarios.

RESULTS

The multimedia data base has been designed as a system or "shell" and here we only present examples of the modules, because a detailed view of the whole presentation would be voluminous. The presentation can incorporate future modules with different case scenarios or particular training programs allowing the data base to grow and to be customized to cover

specific requests or needs of special user-groups. The shell may continue to be developed as an interactive computer presentation with the assistance of administrative staff and scientists.

A conceptual diagram for the presentation system is presented in Figure 4.2. The shell serves as a general introduction to the use and organization of the database. The information is arranged on different levels, from an introduction to Laguna de Terminos and its ecological importance (Figure 4.1) to results and case scenarios of the various efforts for resource management and scientific research on Mexico's coastal zone.

The presentation begins with a brief introduction to Laguna de Terminos and its environmental and ecological value (Figure 4.1 a). From here, the user can then choose among the several modules (Figure 4.1 b). The options include a detailed view of the study area, a fish catalog, a management tool for shrimp aquaculture, and two different simulation models of fish migration. Once a module is chosen, various data sets are available to the user. Each module is shown as a series of cards in which data are visualized in different formats.

Maps and Environmental Data Module

The introduction to this module presents a map of Laguna de Terminos with site names and the general water circulation pattern (Figure 4.3 a). Each name is "active" and clicking on it will give a brief description of the environmental characteristics of that area (Figure 4.3 b). Subsequent cards present sediment and intertidal community maps with active zones (Figure 4.3 c), where the user can query more specifically for habitat details. A submodule for environmental information is accessible either from the

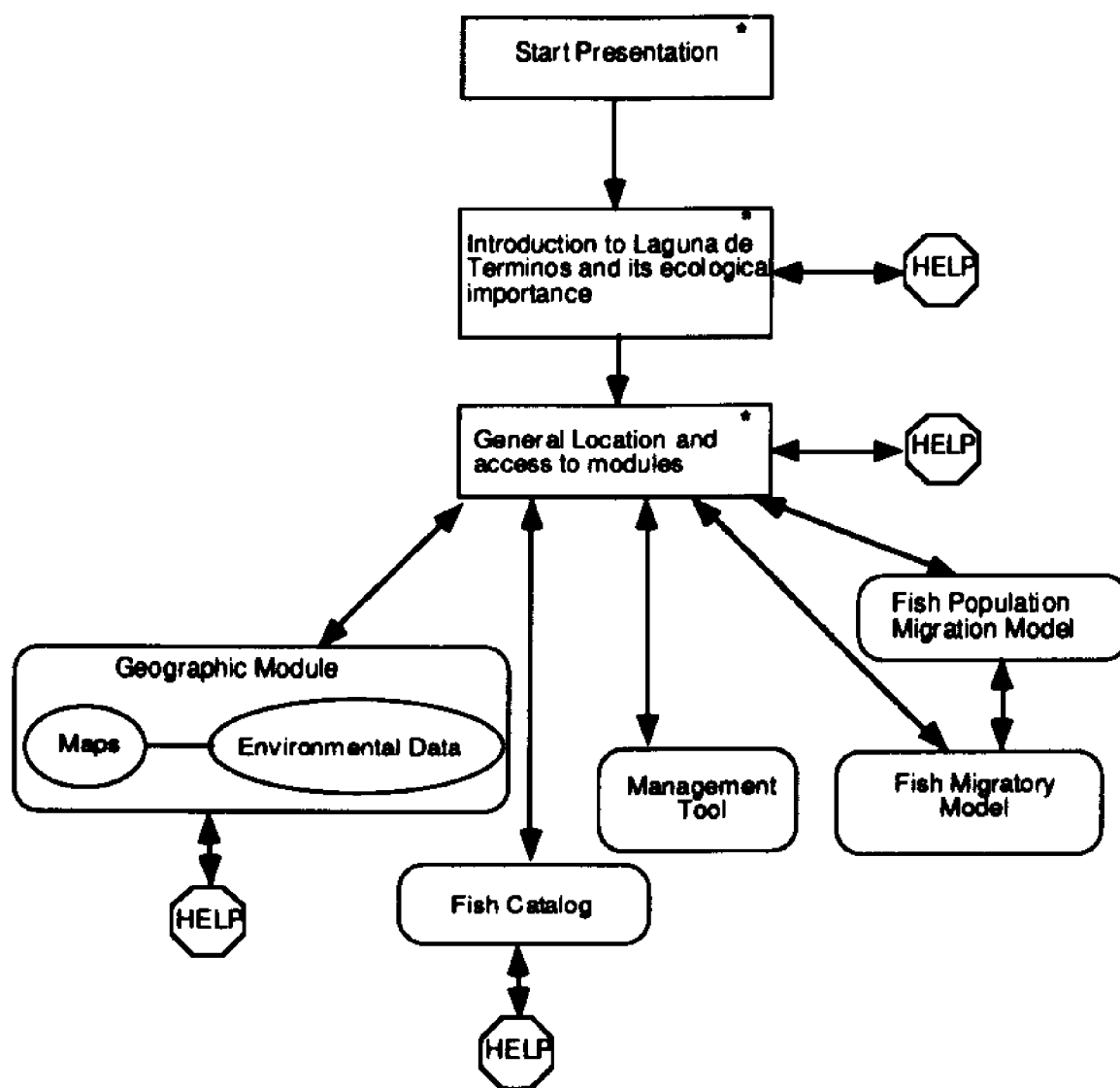


Figure 4.2 - Conceptual design or shell of the presentation. Arrows indicate interaction between modules. Asterisks indicate in which screens the user has access to the Spanish version of the program.

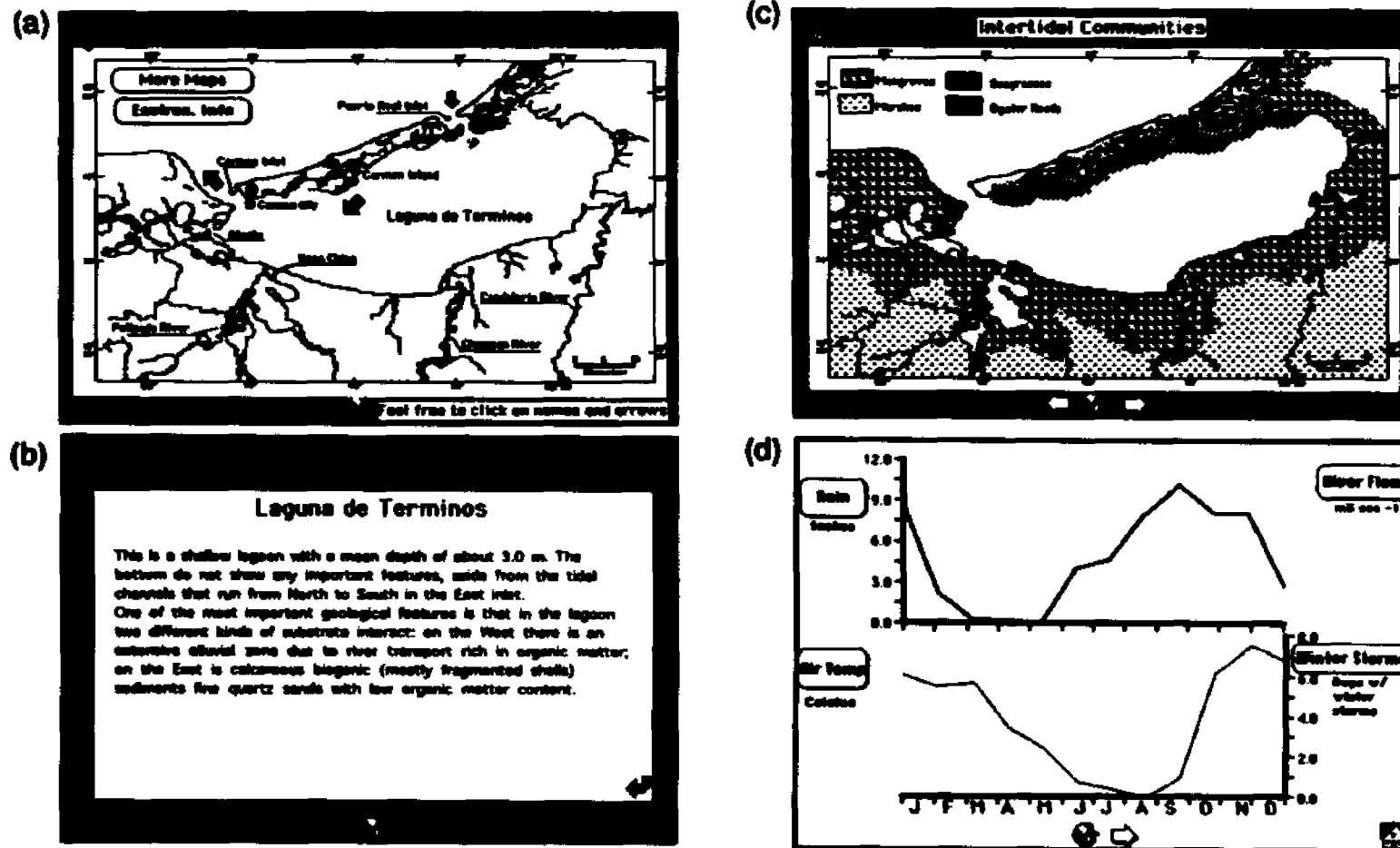


Figure 4.3 - (a) Screen with map of Laguna de Terminos. Each map is "active" and show a brief description of the physical environment. The two large buttons give access to maps for habitats, intertidal communities and sediments, or climatological graphs. (b) Card display when the Laguna de Terminos name button is clicked. (c) Intertidal communities map. (d) Environmental parameters screen.

introductory map (Figure 4.3 a) or at the end of the maps submodule. This submodule comprises annual meteorological and aquatic data. The information is presented in graphic form that can be either overlaid one parameter over the other or examined individually as in figure 4.3 d.

Fish Catalog Module

The dominant ichthyofauna of Laguna de Terminos are presented in this module (Figure 4.4 a). Information on life cycles and habitat preferences of 19 dominant species described by Yáñez-Arancibia *et al.* (1985) is included. The user can access this information by activating the corresponding buttons. Each card depicts a picture of the organism and a brief description of habitat preferences (Figure 4.4 b). A "meristics" button gives access to the description of taxonomic features. The "life cycle" button displays a cross section of Laguna de Terminos with salinity values and vegetation, where the corresponding life history cycle is shown (Figure 4.4 c). The "Simulated distribution" button displays the individual simulation program for that particular species, at the end of the run, the user returns to the fish card.

Management Tool Module

The management tool is a hypothetical model of the local shrimp fishery of Laguna de Terminos (Figure 4.5 a), utilizing the interface between HyperCard and STELLA. This module is an example of how managerial tools can be provided to the user with minimum training or specifications. The simulation model combines the shrimp life cycle and relates it to mangrove area used as nursery ground. The model attempts to answer the questions

(a)

Fish Catalog

The ichthyofauna of Laguna de Términos comprises more than 211 species. From these about 56 dominate the fish assemblages in abundance.

There are several strategies utilized by fishes in order to maximize their presence in Laguna de Términos. These utilization patterns include: truly estuarine fishes that spend all of their life cycle inside the lagoon; migratory patterns either from offshore or the riverine systems inwards and sporadic visitors.

In order to present a comprehensive view of these strategies, only some fishes are presented in this catalog. They are assumed to be representative of all the strategies as well as different trophic levels.


➡

(b)

11 / 19
Bairdiella chrysoura

Life cycle
Simulated Distr.

This species occurs in the saltier bays, the young often in grass beds. It rarely reaches a size large enough to warrant its exploitation as either a commercial or sports fish. New York to Mexico.



Silver Perch

Parasite

(c)

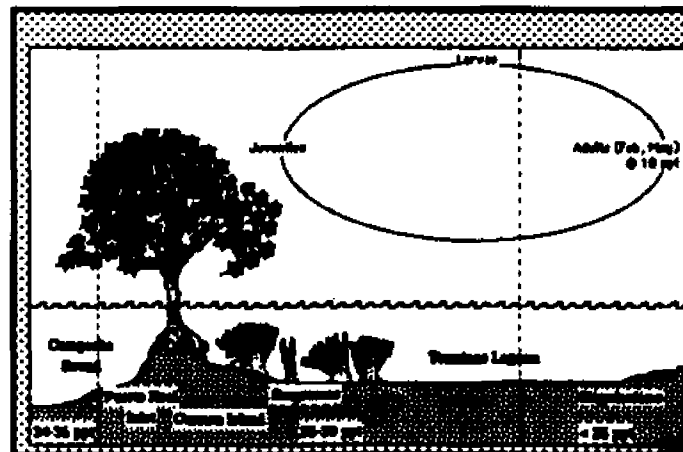


Figure 4.4 - (a) Introductory screen to fish catalog. (b) Fish catalog card with icons for diagram with life cycle and taxonomic key, and an organism distribution model. (c) Life cycle card for *Bairdiella chrysoura*.

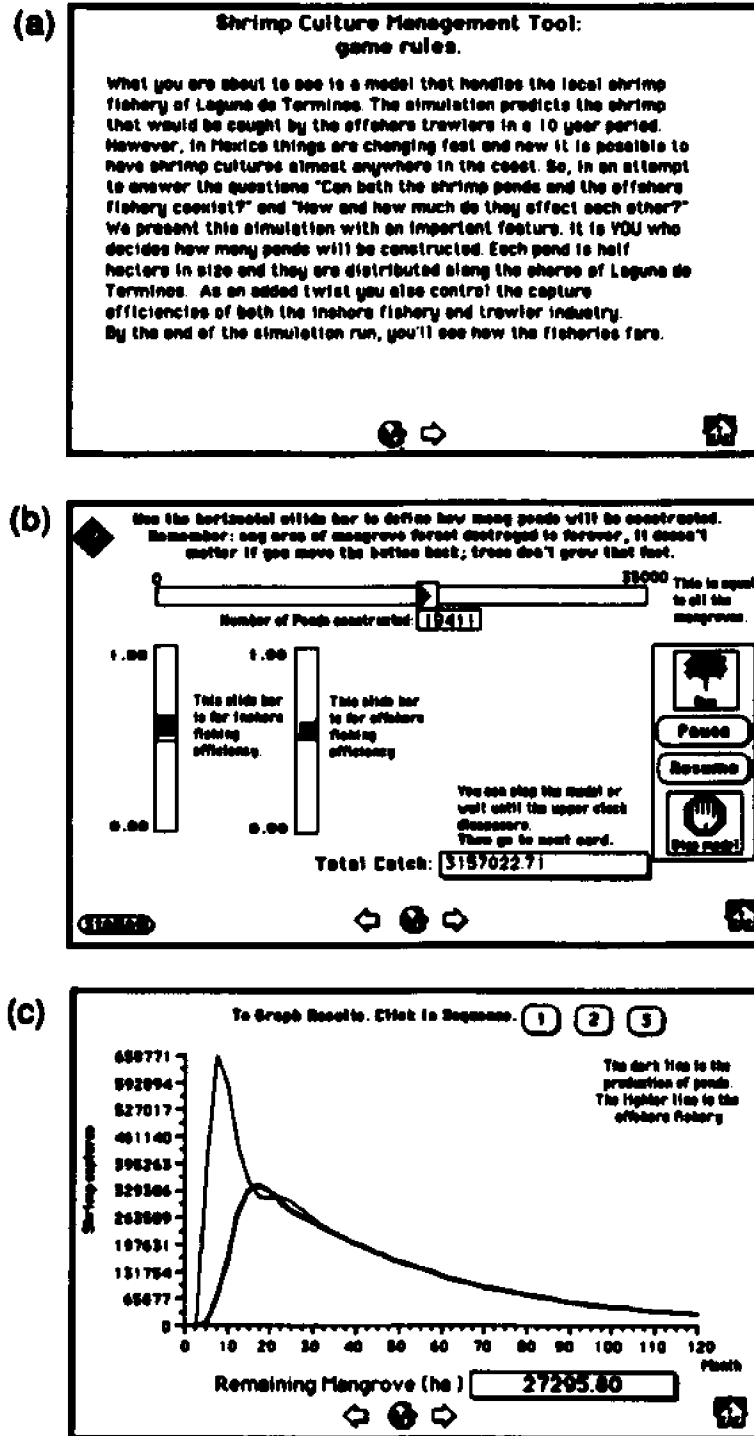


Figure 4.5 - (a) Screen for shrimp culture management tool. (b) Control card for management tool. Total catch is number of juveniles captured for the aquaculture ponds. (c) Card with results of simulation plotted.

"Can both the shrimp ponds and the offshore fishery coexist?" and "How do they affect each other?" The long-term effects of a particular management policy are addressed because the simulation predicts the shrimp that would be caught by both industries over a 10 year period.

The first card states the rules for the managerial tool and the basis of the simulation (Figure 4.5 a). A brief explanation of what questions can be addressed and the extent of the simulation is also provided. On the second card, the user decides how many ponds will be built along the shores of Laguna de Terminos and controls the capture efficiencies of both the mariculture industry and trawler fishery (Figure 4.5 b). This is done by moving the slide bars on the screen. Once the model is running, the number of shrimp juveniles captured by the aquacultural activities is displayed. The model can be stopped at any time, then the user must go to the next card. On the third card, the results are presented in a graph of offshore fishery and aquaculture production (Figure 4.5 c). By activating in sequence the top buttons, the results of the simulation are captured, scaled and graphed. The bottom axis is time and the y-axis, total number of shrimp captured. An estimate of remaining mangrove forest is given.

An important disclaimer should be added to this module. Although conceptually the model is correct and the population dynamics and feedback interaction between mangrove area and recruitment rate are realistic, the data calculated from the model alone are not appropriate for management. The estimated yield captured by both shrimp activities gives the fishery manager only forecasting information. Policy should not be based solely on the results of this model at this time. Better information on the shrimp fishery

is needed and the model is presented as an example of the type of management tools that can be incorporated into this interface. In the future, as more information becomes available, a more accurate model can be included.

Individual Fish Migration Module

A simulation model constitutes the core of this module. The model computes spatial position for an individual fish moving according to daily environmental stimuli. On the first card are given the rules of the simulation model, the rationale that model movement in a heterogeneous environment, and a brief description of the mathematical assumptions driving the fish spatial dynamics (Figure 4.6 a). The second card is the model interface between HyperCard and STELLA (Figure 4.6 b). The user starts the model with the "swim" button and the results of the model are simultaneously translated to spatial coordinates on the screen, causing the fish icon to move, and tracing the movement on the map of Laguna de Terminos. At the end of the run, the results are ready to be interpreted. This model provides a better understanding of environmental processes and illustrates that fish respond to a number of stimuli, and how fish use various habitats.

The purpose of this simulation is to show spatial results for a single generic fish with two different probability distributions driving its searching behavior. It is a generic fish because the behavioral rules are arbitrary. The probabilities are based on a random number generator, where one represents a favorable environment and the other an avoidable environment. For the fish to decide which distribution to follow for its next move, the simulated animal "senses" the environment and compares it to the previous

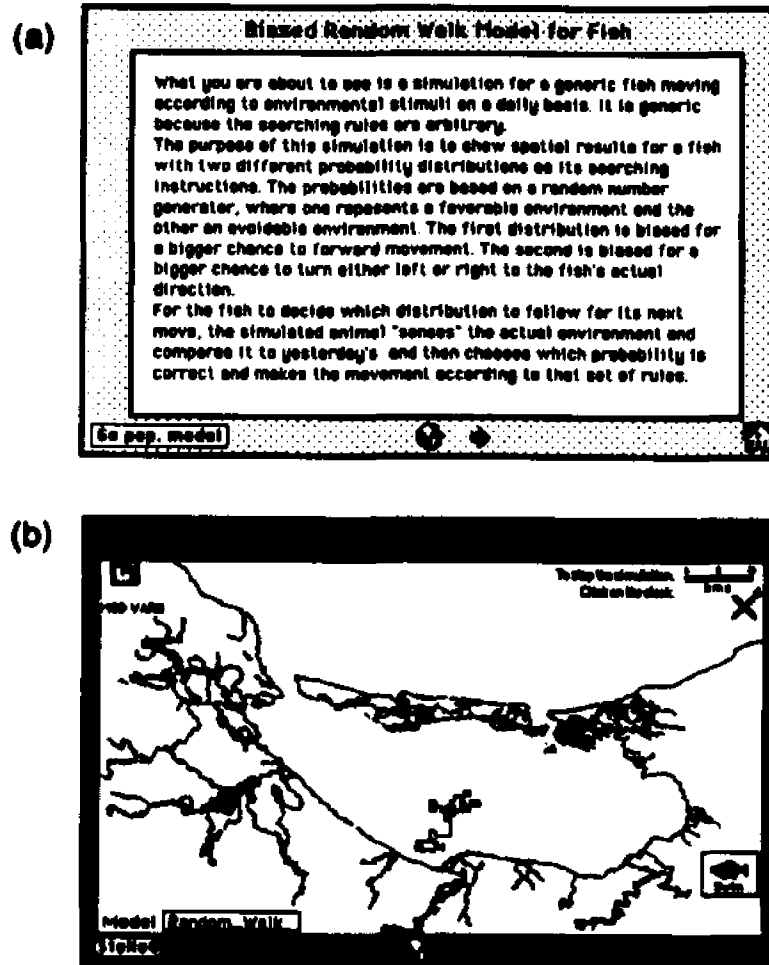


Figure 4.6 - (a) Screen for rules of random-walk fish model. Assumptions are indicated. (b) Card with results of the individual migration model. Individual tracks are drawn in the screen as the model calculates direction of movement. The "swim/fish" button activates the model. The user can modify variables if needed with the left top button.

day and then chooses which probability distribution will enhance its chances of a "better" environment (i.e., higher concentrations of food).

In this model only three environmental parameters define the environment: salinity, temperature and chlorophyll *a*. Thus, the fish is compelled to search for chlorophyll, salinity and temperature (in that order). When the environment has higher concentrations than the day before (the model runs on daily basis), the fish will use a probability distribution in which forward swimming has the highest odds of happening. If the environment has lower concentrations than yesterday's, the fish will draw its next movement from a distribution in which turning left or right have higher odds than moving straight forward.

Population Migration Module

This module presents a simulation model for the migration of a whole fish population (rather than an individual fish as in the previous model). The first card describes how the model runs and what the user has to do to see the animation (Figure 4.7 a). The second card is a description of what the user will see and explains in more detail the instructions to begin the model (Figure 4.7 b). In this model a different approach was taken to the interface. Here, the user has to "step out" of the HyperCard interface and access the program through the normal STELLA interface (Figure 4.7 c). The file and compiler open automatically. The instructions on how to run the program and quit the STELLA application are described on screen. The opening path was intended to be as "transparent" as possible, but also illustrates how other applications can be accessed using HyperCard.

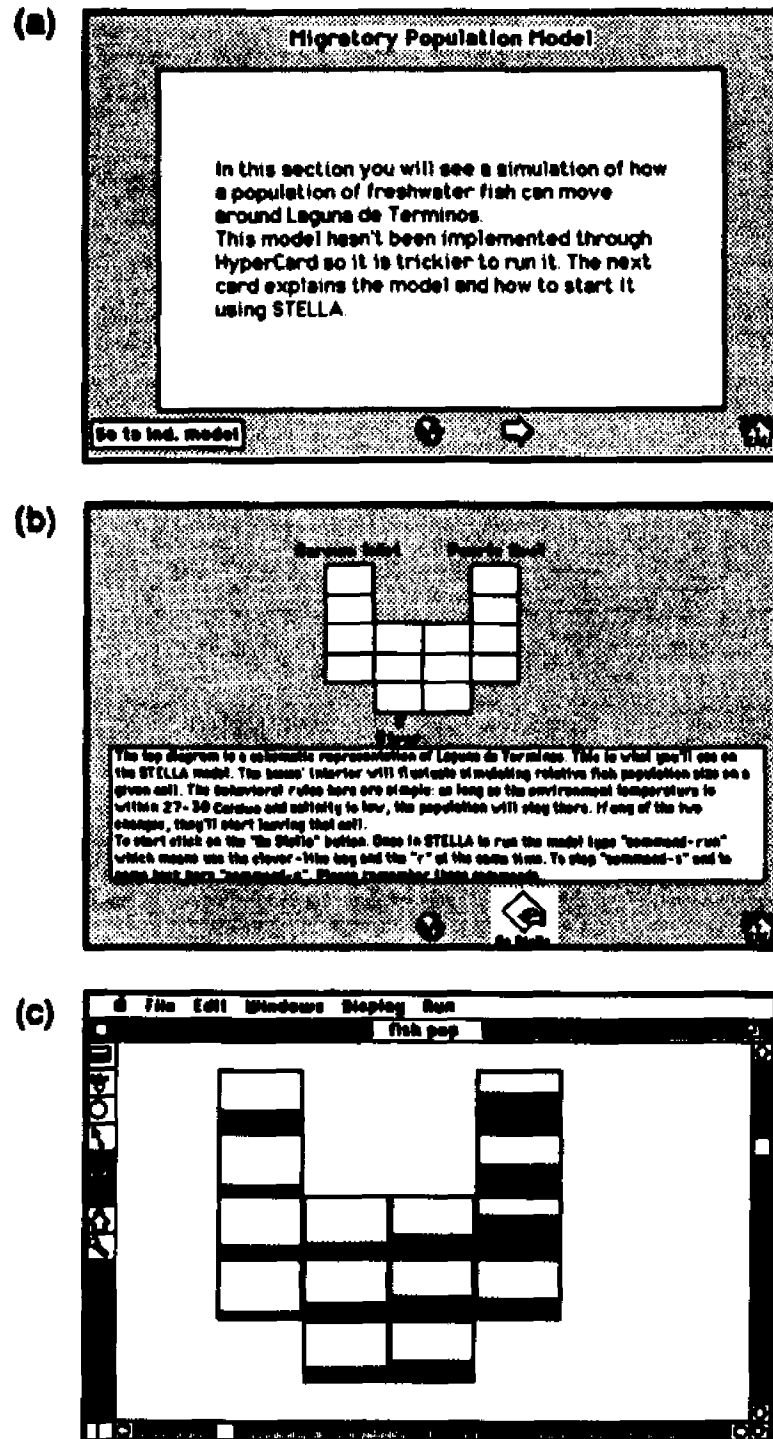


Figure 4.7 - (a) Screen for population migration model. (b) Instructions card for population model. (c) STELLA interface screen. The model shows proportional fish population on each cell.

The model describes a fish population in a heterogeneous landscape. Here the user can observe the predicted distribution of a stenohaline (low salinity tolerance) population moving across a series of cells that represent Laguna de Terminos. The movements are based on specific ranges of habitat preferences for environmental values. The environmental parameters working as forcing functions are: salinity, temperature and chlorophyll *a* (a proxy for food supply). These parameters are computed daily across the landscape and the population distribution from cell to cell reacts to these changes (For a more detailed description of the model the reader is referred to Reyes *et al.* 1992).

DISCUSSION

There is general agreement that the best management plans are those based on a thorough understanding of basic environmental processes. We offer a multidisciplinary approach with the development of this interface. In a short interval, the user can obtain a comprehensive view of the problems and variables that affect the study area. The use of this interface allows a quick "visit" to diverse studies on several disciplines with a multilevel perspective. Technical issues can be discussed and analyzed with sound data.

Although at this moment the interface is ecology-oriented, as more information is gathered it can be added as modules to the shell (Figure 4.2). Note that we are using the term information in its broadest sense. Economic, demographic and social modules can be added, providing a more comprehensive view of the ecosystem to the decision- or policy-makers.

During the last year, we have had the opportunity to demonstrate the interface to various forums, ranging from high-level decision-makers (including the President and Education Minister of Mexico; Reyes *et al.* 1991a), scientists (Reyes *et al.* 1991b), science students, resource managers and laymen (Reyes *et al.* 1990). Suggestions by these groups have been incorporated and new ideas are welcome. The implementation of similar systems is a step toward better utilization of a multidisciplinary approach to scientifically sound management of natural resources.

Lessons learned in both industrialized and developing countries have shown that natural resources and the productivity of natural systems are critically important for sustained economic development (Loewinger 1983, Costanza *et al.* 1991). Economic growth often is accompanied by increasing stress on natural systems and significant adverse effects on environmental quality. Moreover, as Savory (1991) stated, "For future ecologically based economic modeling (resource management) to be sound, it is increasingly apparent that economic ideas will have to be tied to the realities of the process of biological succession . . .". The central issue, then, is to conduct development activities in a fashion that preserves the longevity of our renewable resources for sustained development and that minimizes deterioration in environmental quality.

Unfortunately, on many occasions economic development activities have not shown sufficient concern for preserving ecosystems. Deterioration of environmental quality has been viewed as a necessary cost of rapid economic growth (Hufschmidt *et al.* 1983). The problem of application of sound policy is particularly acute, because many environmental quality effects that are the focus of this approach to economic development are not

easily quantified or valued. It is precisely for these reasons that they frequently have been ignored in traditional project evaluation. The assessment and valuation process can be classified in four steps (Dixon 1986). First, identify the important environmental effects. Second, quantify the effects; in other words, how great are the increases in impact rates and what are the associated reductions in physical outputs, or, what is the decrease in production after the project? Third, place monetary values on these quantified changes. Finally, perform the actual economic analysis. We consider that steps two and three can be simplified greatly by use of the interface we have presented here, facilitating ecological information transfer to decision-makers.

A copy of this program is available at minimal cost, or send three high-density, double-sided floppy disks to E. Reyes. Versions for either black and white for small machines and color for Macintosh II computers are available. Please specify your hardware and STELLA version.

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SUMMARY AND CONCLUSIONS

Ecosystem simulation and analysis provide insights into the mechanics of ecosystem physical and biological interactions. This understanding of the mechanics of the ecosystem allows one to predict biological changes under different physical, chemical, and landscape scenarios. There is general agreement that the best management plans are those based on a thorough understanding of basic environmental processes. Traditional coastal research often focuses on a single taxonomic class or a physical-chemical set of variables. These studies in many instances, have created large data bases, a basic requirement for implementing sound resource management. Lessons from economic development in both industrialized and developing countries have shown that development relies crucially on the productivity of natural resources. It is apparent that future economic plans will have to be tied to the realities of the natural processes of ecosystem.

I developed and tested landscape-level models of aquatic primary production and its interaction with nektonic consumers in Laguna de Terminos, a tropical coastal lagoon in the southern Gulf of Mexico. The main objectives were to: (1) develop an aquatic primary production process-model of the dominant habitat (open water); (2) develop a dynamic spatial population model for migratory species of fish; (3) combine these two models to simulate seasonal variability of nutrients, phytoplankton, organic matter and fish biomass; and, (4) integrate results of this work and past studies in a computer interface to facilitate information transfer to resource managers.

To accomplish these objectives, I designed a spatially explicit model of fish migration (The Regional Organism Exchange model, ROE). Then, I considered ecosystem-scale interactions, such as aquatic primary production (APP) and fish migration, among spatially defined heterogeneous habitats in Laguna de Terminos. Two models, one for Landscape Aquatic Primary Production of TERminos lagoon (LAPPTER model) and the ROE model (Regional Organism Exchange for TERminos lagoon, ROETER), were combined into a dynamic landscape simulation, that includes both primary producers and consumers (nekton). This model combination explored how landscape processes and patterns interact to control the distribution of fish over long time scales and large geographic areas. Finally, a bilingual (Spanish and English), interactive and user-friendly computer interface was developed to enhance information transfer from scientific research, and to provide assessment data for use as a predictive tool for environmental policy makers and resource managers.

The LAPPTER and ROE models are process-based models. A process-based landscape model is a mechanistic simulation of spatial structure. The dynamics for such models are produced by: (1) compartmentalizing the landscape into some geometric design (generally set by local geomorphology or geography); (2) describing interactions within compartments; and (3) describing spatial fluxes among compartments according to location-specific algorithms. The incorporation of feedback loops, neighborhood influences, and spatial exports and imports is made spatially explicit to reflect actual landscape interactions. These models simulate materials flow over large areas and describe the transport of

materials as a function of mass balance in combination with diverse climatic forcing functions.

Laguna de Terminos is Mexico's largest coastal lagoon, with an area of 2500 km² including open water and the adjacent mangroves and marshes. This lagoon receives discharge from a distributary of the Grijalva-Usumacinta River, the largest river system in Mexico and the second largest discharge to the Gulf of Mexico (after the combined Mississippi and Atchafalaya Rivers). Laguna de Terminos is a diverse ecological system. A variety of marine and estuarine organisms use its habitats as nursery grounds. As a result, the highly productive waters of Laguna de Terminos support Mexico's largest and most economically important fishery for the brown shrimp Panaeus aztecus. Controlling influences include ocean-river interactions, mangrove runoff, seagrass/water interactions, and human modifications (both within and among landscape components). This lagoon is well suited for landscape simulation studies and spatially dynamic fish migratory predictions because it is a regional ecosystem with significant physical and biological gradients.

Research in this basin has created a large data base that contains more than 15 years of environmental and biological data. In addition, specific and urgent management issues such as creation of shrimp aquaculture farms out of mangrove swamps, and wetland diversion for agriculture, and urban point source pollution around the lagoon must be addressed in this area. Another management issue in need of resolution is the extensive petroleum explorations and drilling now occurring in the area. The potential impact of these activities and future ones, increases the need for effective management of the lagoon's natural resources. An understanding of ecosystem processes in the lagoon for both predicting and preventing the potential negative

impacts of development on the system can be gained by using dynamic simulation. Ecosystem landscape models are critical tools for ecological and economic analyses in Mexico, as it is in other developing countries that lack the resources to generate broad scale monitoring programs and intensive, sustained, location-specific research.

Two dynamic spatial models were developed at the landscape scale (1000's m²) for Laguna de Terminos using a 1/4 day time-step. Both are 2-dimensional, vertically-integrated, temporally- and spatially-articulated, finite-difference simulation models, one for aquatic primary production and nutrient dynamics (LAPPTER model), and the other for fish migratory patterns (ROE model). Environmental forcing functions such as solar radiation, temperature, river discharge, and tides drive both models. These models were designed to simulate vertically averaged distribution and fluxes for salinity, suspended sediments, total inorganic nitrogen concentration, chlorophyll, organic matter production, and fish standing stocks. The ROE model was first developed and tested against a hypothetical environment and then integrated into the LAPPTER model as a module that uses the output from the primary production model to simulate fish migration behavior. Specific objectives, methods and results from each of the simulation models as well as the information transfer interface are described below.

A spatially-explicit, grid-cell model was developed to understand how landscape processes and patterns control migration of stenohaline fishes in Laguna de Terminos. An interpolation model was used to spatially distribute environmental forcing functions. Behavioral rules for fish movement were based on environmental tolerance ranges and used to create a response matrix. Each cell of the landscape model was 10 km² in size, and included

population parameters (i.e., mortality and birth rates), and plant-animal feedback mechanisms such as fish nutrient excretions. Daily maps of long-term spatial distributions of environmental and population parameters were compared to field data at four locations and were found to be realistic. Results indicate that mechanisms for fish migration are linked to regional physical, chemical, and ecological processes. Sensitivity analyses evaluated the interrelations among food supply, birth rate, and changes in environmental and biological forcing functions. This theoretical approach to fish migration was transformed into a submodel of an aquatic primary production model for the same area.

A landscape model for aquatic primary production in Laguna de Terminos (LAPPTER) described water dynamics on a medium-size scale (10's km²). The model accounted, spatially and temporally, for fluxes and interactions among biotic (i.e., seagrasses and phytoplankton production, and detrital organic matter) and abiotic (i.e., nutrients, salinity) components in the water column. As a submodel of this simulation the ROE model was implemented to investigate trophic pathways. Forcing functions included mean annual solar irradiance, river discharge, tidal pumping, water temperature, and Secchi depth records. The model required these forcing functions to be spatially organized. Therefore, forcing functions with only temporal information were geometrically interpolated across space as a function of grid size and distance between actual data locations. Simulation output was presented either as synoptic tables or as maps. Maps allowed the examination of production figures according to site-specific controls, and the identification of critical habitats along a production gradient.

The landscape aquatic primary production (LAPPTER) model and the Regional Organism Exchange for Terminos lagoon (ROETER) model combination is an attempt to analyze how consumers interact with primary production at the landscape level. This primary producer and consumer coupling tests the interactions and contribution among the various habitats of Laguna de Terminos.

Several migratory patterns have been identified for Laguna de Terminos in which spatial behavior seems to be related to habitat utilization and physiological tolerance ranges by different species. Several fish species utilize the same areas and have similar feeding habits, providing the basis for creating "functional groups". Species that have similar biological and environmental requirements exploit the diverse lagoon habitats similarly. The fish component of this migration model uses, as forcing functions, the output from the LAPPTER model. Several feedback mechanisms are incorporated, such as nutrient supplement as excretion from the fish population, and carrying capacity expressed as food availability. Spatial population dynamics, with the addition of biological dynamics such as birth and mortality rates, combined to produce an analysis of fish behavioral patterns and habitat utilization in a heterogeneous landscape.

Ecosystem simulation and analysis are holistic by nature, potentially underscoring interconnections in space and time, and thus synthesize large data bases, enhance basic ecological understanding, and emphasize future research. Modeling is a tool well suited for the analysis of ecosystems and for answering both basic and applied questions, because models synthesize existing knowledge (both structure and function) into the process of simulating or predicting. The predictive potential of simulation experiments

can aid in resource management decisions. The use of simulation models has led to a growing realization that ecosystem management must be a comprehensive, holistic process.

As an attempt to take these scientific and managerial ideas a step further, an information system was developed for Laguna de Terminos that combined with the output from the LAPPTER and ROETER models. This bilingual (Spanish/English), interactive, and user-friendly information system was aimed to simplify the information transfer of research about Laguna de Terminos to environmental managers.

The multimedia interface was built as a "shell" that can incorporate future information modules with different case scenarios and simplifies the addition of modules specially customized as training programs. The information system was based on an Apple Macintosh computer using the programming language HyperCard®. In addition, the simulation language STELLA® was used to develop several simulation models. The results of this graphically oriented interface allow the user access immediately to a wide range of scientific information presented as maps, graphs, and data generated from computer simulations. The model parameters could be changed to test new scenarios, accordingly to specific requests. The program included animation of fish migrations and predictions for shrimp aquaculture scenarios.

This research also discusses recent developments in microcomputer technology that make it possible to deliver to the desktop computer of the researcher or manager, a wide range of capabilities and data that previously could only be accessed on expensive and user-unfriendly mainframe

computers. The development of this interface offers a truly multidisciplinary approach . In a short interval, the user can obtain a comprehensive view of the problems and variables that affect the study area. Quantifying the effects and impact rates, as well as placing monetary values on these quantified changes, can be simplified greatly by use of this computer interface. Thus, it facilitates ecological information transfer to decision-makers for a better economic analysis of the ecosystem. The implementation of similar systems is a step toward better multidisciplinary approaches to scientifically sound management of natural resources.

VITA

Enrique Reyes was born on December 19, 1960, in Mexico City, Mexico. His undergraduate education was completed at Universidad Autónoma Metropolitana, in Mexico City. At this university, he obtained a Bachelor of Sciences degree in Biology with a minor in Hydrobiology. His undergraduate experience included a year of field and lab research studying the ecology of a population of octocorallia (Plexaura homomalla) in the Mexican Caribbean under the guidance of Professor Oscar Moreno. He graduated in December 1983, and continued his education at the Institute of Marine Sciences and Limnology (ICMyL) of the Universidad Nacional Autónoma de México. While attending graduate school, he participated on six oceanographic campaigns in the Mexican Caribbean and assisted on several projects for environmental impact assessment on the lagoons and surrounding areas of Cancun Island. After completion of his field work at the marine research station "Puerto Morelos" of the ICMyL, he received a Master's of Science degree in Marine Sciences with minor in Fisheries and Biological Oceanography in August, 1988. Under the guidance of Mr. Martin Merino his Master's thesis was entitled "Primary Production Evaluation of Laguna Bojorquez, Cancun, Quintana Roo, Mexico." Since August 1988 he has been at the Coastal Ecology Institute and Department of Oceanography and Coastal Sciences (formerly Marine Sciences) in Louisiana State University's Center for Wetland Resources. His major advisor at Louisiana State University, and for this dissertation, was Dr. John W. Day, Jr.

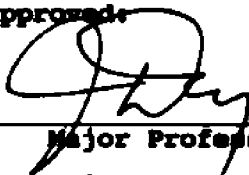
DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Enrique Reyes

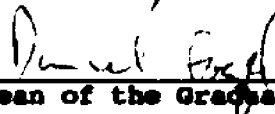
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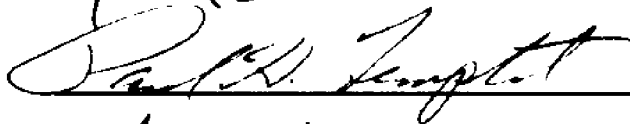


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June 24, 1992