A Conceptual Model of the Galveston Bay Ecosystem

Galveston Bay
National Estuary Program
GBNEP-42
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The Galveston Bay National Estuary Program

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The Galveston Bay National Estuary Program

Texans increasingly express their expectations for a clean environment in terms of entire ecosystems. Until recently, our tendency was to view environmental problems in isolated pieces we could understand—indeed this view was institutionalized (and seemingly immortalized) in an elaborate mosaic of fragmented jurisdictions. The Galveston Bay National Estuary Program (GBNEP) is a forerunner in elevating hands-on management of coastal environments to the level of the ecosystem; and in doing so, is encouraging an integration of traditionally disparate institutions.

The GBNEP was established under the authority of the Water Quality Act of 1987 to develop a Comprehensive Conservation and Management Plan (CCMP) for Galveston Bay. The purpose of the CCMP is to address threats to the Bay resulting from pollution, development, and overuse. To address these threats, five years of work commenced in 1990, consisting of three phases: (1) Identification of the specific problems facing the Bay; (2) A Bay-wide effort to compile data and information to describe status, trends, and probable causes related to the identified problems; and (3) Creation of the CCMP itself to enhance governance of the Bay at the ecosystem level. The GBNEP is accomplishing this work through a cooperative agreement between the U.S. EPA (Region 6) and the State of Texas (administered by the Texas Natural Resource Conservation Commission.)

The structure of the GBNEP reflects a strong commitment to consensus-building among all Galveston Bay user groups, government agencies, and the public. The GBNEP "Management Conference" consists of six Governor-appointed committees with broad representation, totaling about one hundred individuals. Meetings of these committees are also open to the public, and public participation in policy-setting and in Bay management are considered strengths of the program. When submitted to the Governor of Texas in late 1994, the CCMP will reflect thousands of hours of involvement (much in the form of volunteer time) by individuals who in various ways use, enjoy, or help govern this vital coastal resource.

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PREFACE

The goal of this project was to achieve scientific consensus on some conceptual models of the Galveston Bay ecosystem. To achieve this end, the habitat models were developed and circulated to a large group of experts. The author then met with these scientists, singly and in groups, for lengthy discussions and critique of the models.

The following scientists provided invaluable comments on the habitat models during these discussions. Neal Armstrong and George Ward of the University of Texas Center for Research on Water Resources in Austin; Terry Whitledge and Edward Buskey of the University of Texas Marine Science Institutute in Port Aransas; Eric Powell of Texas A&M University at College Station; Cynthia Howard of the University of Houston - Clear Lake; Roger Zimmerman, Tom Minello and Peter Sheridan of the National Marine Fisheries Service Southeast Fisheries Center in Galveston; Bob Bass of the U.S. Army Corps of Engineers in Galveston; and Albert Green, Lynn Benefield and Larry McEachron of the Texas Parks and Wildlife Department in Austin, Seabrook and Rockport, respectively. Additional written or telephoned comments were provided by Sammy Ray, Andre Landry and Don Harper of Texas A&M University at Galveston; Frank Fisher of Rice University; James Lawrence of the University of Houston - University Park; David Flemer of the Environmental Protection Agency Gulf Breeze Laboratory; and Will Roach, Tom Czapla and Fred Werner of the U.S. Fish and Wildlife Service - Houston.

The detailed habitat models were revised to accommodate the review comments and scientific consensus regarding the habitat-based conceptual models was thus achieved. The simple, non-technical overview models were then constructed, focusing on the theme that distant events anywhere in the watershed could potentially affect the bay ecosystem. The issue of perturbations and their management was taken to the GBNEP Scientific/Technical Advisory Committee (S/TAC) which achieved consensus regarding the sources of perturbation and the physical, chemical and biological perturbations expected to occur. The following members of the S/TAC provided evaluations regarding the influence, scientific credibility, and manageability of these perturbations. Jerry Wermund of the University of Texas Bureau of Economic Geology; Ernst Davis of the University of Texas School of Public Health - Houston; James Lawrence of the University of Houston - University Park Department of Geosciences; Bruce Smith of the Texas General Land Office; Gary Powell of the Texas Water Development Board; Albert Green of the Texas Parks and Wildlife Department Resource Protection Division; Will Roach of the U.S. Fish and Wildlife Service; Rick Medina of the U.S. Army Corps of Engineers - Galveston; Dick Brown of the Gulf Coast Waste Disposal Authority; and Joe Kolb of the Enron Corporation.

The complete draft of the models was then distributed to the scientific advisors, the GBNEP review panel, and additional reviewers. Written comments were submitted by Neal Armstrong of the University of Texas; Terry Whitledge of the University of Texas Marine Science Institute; Eric Powell and an anonymous reviewer at Texas A&M University - College Station; James Lawrence of the University of Houston - University Park (GBNEP Designated Reviewer); Roger Zimmerman and an anonymous reviewer of the National Marine Fisheries Service; David Flemer and Ken Teague of the Environmental Protection Agency; Gary Powell of the Texas Water Development Board; Tom Calnan of the Texas General Land Office; Tracey Koenig and Keith Kindle of Turner, Collie and Braden, Inc.; Glenda Calloway of Ekistics Corporation; and Sandra Hoover of the GBNEP Citizens Advisory Steering Committee.

The success of these models is due to the unstinting willingness of these reviewers to devote large chunks of their busy lives to my estuarine education. They called my attention to many obscure and unpublished reports, as well as commissions of error or misunderstanding. Although I have not always followed all of their advice and counsel, I am especially grateful for their unselfish sharing of their vast knowledge of the inner workings of estuaries. I alone am responsible for errors of fact or misunderstanding which remain in the models. Although I suspect that many of these scientists may still disagree on minor interpretations, particularly omissions, I am confident that the goal of scientific consensus has been achieved.

Robert W. McFarlane

A CONCEPTUAL MODEL OF THE GALVESTON BAY ECOSYSTEM

Robert W. McFarlane, Ph.D.
Principal Investigator

EXECUTIVE SUMMARY

The goal of this project was development of a set of habitat-based, problem-oriented, nested, hierarchical, box-and-arrow conceptual models tiered to three levels of complexity. (1) Simple, nontechnical models that facilitate understanding of important issues by the public focus on the landscape approach and provide an overview of the ecosystem. (2) Complex detailed models that reflect scientific consensus describe the structure, function and connectivity of the habitat components of the ecosystem and it s connections to adjacent habitats. (3) Simple technical models useful to decision-makers, resource managers and bay users describe the interconnectedness of the ecosystem.

The bay ecosystem can be greatly influenced by actions occurring far from the bay. It is dependent upon some distant actions, such as spawning of shrimp and finfish in the Gulf of Mexico or precipitation runoff in a remote portion of its watershed. It can be impaired by other actions, such as wastewater discharge and oil or chemical spills. Seven distinct habitats comprise the bay ecosystem: open-bay water, open-bay bottom, oyster reefs, seagrass meadows, peripheral mudflats, peripheral marshes, and peripheral marsh embayments. The physico-chemical conditions within these habitats vary spatially and temporally. The habitats are connected to adjacent riverine-floodplain and nearshore gulf ecosystems and distant portions of the continent. The dominant characteristic of the ecosystem is continual physical, chemical and biological change.

Each habitat component involves dozens of species linked together in complex food webs. Many organisms utilize more than one habitat, particularly those highest in the food chain. Both grazing and detrital food webs are prominent in the ecosystem. Nutrients enter from the riverine connections, are regenerated by the benthic microbial community, and are extracted from the atmosphere. The plankton-grazing food web supports the oyster harvest and contributes, via intermediaries, to the fish harvest. Detritus comes from the rivers and all component habitats. The detritivore food web supports the shrimp and blue crab harvest and contributes to the fish harvest.

Perturbations which affect the ecosystem have been identified but consensus regarding the influence of these perturbations on component habitats, the scientific reliability of opinions regarding these influences, and manageability of the perturbations was not achieved. The habitat approach may not be an effective way to evaluate perturbations.

I. INTRODUCTION

Estuaries such as Galveston Bay are complex and constantly changing ecosystems. To optimize management of the anthropogenic factors which affect the ecosystem, and to be able to predict the potential impact of a proposed action, it is necessary to understand how the system is structured and interacts with its environs. Knowledge of the structure of the ecosystem, and the diverse plants and animals which build and inhabit its distinct habitats, does not automatically lead to understanding of its functions. It is also important to understand how it acquires its materials and energy, processes its waste products, and interacts with adjacent waters and the surrounding landscape.

Conceptual models of complex systems can be useful management tools if they identify the critical components of the ecosystem and demonstrate the important, and often hidden, linkages between these components. Over the past decade scientists have come to appreciate that ecosystems seem to be organized in a hierarchical fashion. Each successively higher level of organization appears to operate at rates which cycle on longer time periods. Some systems appear to be able to constrain the activity of lower levels. Some systems are nested within other systems (Allen and Starr, 1982; O'Neill et al., 1986). Identification of these constraint mechanisms is very important because any action or event which can disrupt a constraint may result in instability of the system. Environmental managers must take care to avoid or minimize any perturbation that will disturb the natural constraints of the estuarine ecosystem. These constraints have proven difficult to establish and identify. Taylor and Blum (1991) caution that the use of graphics facilitates the ability to act as if ecological relations are decomposable into systems and manageable by analysts external to the system but this may be an illusion.

The goal of this project was development of a set of habitat-based, problem-oriented, nested, hierarchical, box-and-arrow conceptual models sensitive to spatial and temporal scales and tiered to three levels of complexity:

1) simple, non-technical models that will facilitate understanding of important issues by the public (see II. Overview of the Ecosystem);

2) complex, detailed models that reflect scientific consensus regarding ecosystem structure and function (see III. Components of the Estuarine Ecosystem); and

3) simple, technical models that will be useful to decision-makers, resource managers, and bay users (see IV. Interconnectedness of the Ecosystem).

The number of living species which inhabit Galveston Bay and its surrounding wetlands is known only to an order of magnitude; certainly more than 500 species (199 species of fishes alone), perhaps less than 1000 species. The conspicuous species - large plants, vertebrates, large invertebrates - are easily identified. As one descends the size scale into the microscopic range, less and less is known about relationships between successively smaller organisms in their natural environment. Phytoplankton are poorly understood, while bacteria, fungi, and viruses are hardly known at all. In theory, each species occupies a unique ecological niche. Any attempt to understand the interconnections between all of these species quickly boggles the mind and overwhelms our mental capacity. We need to simplify the ecosystem even to begin to study it.

Ecologists have traditionally envisioned the system from two viewpoints. Those scientists most interested in species have emphasized populations, guilds, and communities. By dealing with tangible entities and their aggregates, these ecologists have learned much about the structure of ecosystems. Other scientists have been fascinated by processes and functional phenomena, such as energy transfer, nutrient cycling and productivity. While the concept of trophic levels facilitates understanding of energy transfer and nutrient cycling, it often proves very difficult to assign a given species to a single trophic level. Many, perhaps most, species range broadly across trophic levels at different ages and developmental stages of their life cycle. Trophic level may be a non-entity (Scheiner et al., 1993). Descriptions of structure and function may not meld together neatly, even though they represent different observations of the same underlying ecosystem.

To complicate the issue, functional redundancy has been commonly observed. Many species can perform essentially the same ecosystem task. This implies that an ecosystem does not require a unique set of species at a particular point in space and time. The ecosystem persists while its components may vary, as long as appropriate functional interactions persist. Thus desirable species, from the human point of view, can be replaced by less desirable or undesirable species as environmental conditions change. If the conditions persist, a slightly different ecosystem may prevail. This ability to fluctuate confounds our attempts to understand ecosystems.

The multitude of available species and their functional redundancy and variability result in a paradox. A common suite of species appears to be widely available for the length of the Gulf coast. Indeed, many of these species, or closely related and functionally equivalent congeners, are distributed south to Yucatan or beyond, and north along the Atlantic coast. Yet each estuary appears to be a unique ecosystem. Matagorda Bay or the Sabine estuary are quite distinct from Galveston Bay, and these three are quite different from the estuaries of Louisiana, Mississippi, Alabama, or Florida. The same suite of species respond to unique environmental conditions to produce a different ecosystem in each estuary. It cannot be assumed that a structural or functional phenomenon studied in one estuary will be exactly replicated in another estuary, even when the species involved are the same.

To understand the complex interactions between structural and functional ecosystem components a conceptual model should be constructed. This model will be an abstraction of reality, but it should preserve important aspects of the real system. Ideally, the coupled model described will consist of several sub-components, each representing a small facet of the ecosystem. The coupled model may then be used to understand how the sub-components interface with one another, and the response of the entire system to large scale disturbances.

The GBNEP Scientific/Technical Advisory Committee conceptual model subcommittee hoped that these conceptual models would be useful for the following management tasks:

1. Demonstrate the diverse habitat types, their susceptibility to climatically-based physical forcing, and the complex history of anthropogenic perturbations to the estuary.

2. Provide an "ecological manual" for the estuary that will simplify the real ecosystem while preserving essential features, and improve communication between decision-makers, advisors, and the public.

3. Summarize the different management objectives of various agencies, and guide management and regulatory decisions to assure they are not at cross-purposes.

4. Assist in the development of appropriate segmentation schemes; monitoring programs; assessment of cumulative impacts; qualitative and semi-quantitative models; and predictive, quantitative, computer-based models which may be needed to meet program goals.

5. Aid in matching the scale of a problem (perturbation) to the scale of processes that result in altered ecological structure and rate of outputs, and determining the appropriate level of biological and ecological aggregation in addressing a specific environmental problem.

6. Codify scientific knowledge and theoretical constructs regarding the estuary to achieve scientific consensus, improve communication, and transfer this knowledge to other users of the bay.

The extent which the models developed herein will contribute to these ambitious goals will be determined in the future. It is difficult to describe the structure and function of a complex ecosystem without resorting to technical terminology. A glossary has been provided to facilitate understanding.

II. OVERVIEW OF THE ECOSYSTEM

An estuary is a semi-enclosed body of water with salinity intermediate between salt and fresh water. The Galveston Bay system is set apart from the Gulf of Mexico by a barrier island and two peninsulas. Freshwater flowing from the landmass is detained by these barriers, which are pierced by three inlets: the large, man-modified Bolivar Roads; the small, natural San Luis Pass; and the smallest, man-made Rollover Pass (see Figure 1). The brackish water ecosystem within the bay is maintained by the solar-powered hydrologic cycle. Sunlight, warming the surface of the Gulf of Mexico, evaporates gaseous water vapor which rises into the atmosphere and is carried over the landmass by prevailing southerly winds. This represents the uphill portion of the hydrologic cycle. Cooling over the continent, the moisture condenses and falls to earth as precipitation, initiating the downhill component of the cycle. A portion of the rainfall evaporates or moves upward through green plants as evapotranspiration, returning to the atmosphere. Another portion sinks into the soil, eventually to emerge as groundwater, slowly advancing toward the gulf. The remainder flows across the surface of the earth coalescing into rivulets, brooks, streams and rivers. Enroute, both surface runoff and groundwater acquire a number of chemicals in solution. This freshwater inflow transports dissolved and suspended materials to the estuary.

Texas history has been shaped by rivers that provided water, transportation, and a means of waste disposal. Although the total surface of the rivers and streams is small compared to the land mass and the Gulf of Mexico, rivers are among the natural ecosystems most intensely used by man. The role of rivers and streams has changed drastically over the last century. When Europeans first colonized the North American continent, rivers were the arteries of the emerging nation, used for exploration and commercial transport, and they dictated settlement patterns. Today rivers and their riparian wetlands function as kidneys, processing and purifying the wastes of an industrialized nation (Meyer, 1990). A river is sometimes likened to the veins of a leaf, branching out from its stem and midrib to smaller and smaller tributaries. But rivers flow in the reverse direction and, more appropriately, should be considered as the entire leaf, bounded by the dimensions of the watershed, exporting a portion of the organic production of the watershed via tributaries of ever-increasing dimension to downstream habitats.

The character of streams and rivers changes from source to mouth in a predictable fashion, in what is termed the river continuum (Vannote et al., 1980). Stream size and water volume increase, and both the kind of plants and animals and the overall number of species change as well. **Upland ecosystems** contribute surface runoff and groundwater inflow (springs and seeps) to **stream-riparian ecosystems**, often filtered by greenbelts of riparian corridor vegetation. The upper tributaries may be shaded, with very few, if any, rooted plants and algae growing in the waters. The organisms using these streams depend on decomposing organic matter and terrestrial animals imported from adjacent terrestrial habitats for their sustenance. As the streams increase in width they are less shaded and sufficient sunlight penetrates the water to support aquatic plants. In the middle reaches the organic matter produced within the stream may exceed that which is imported, the stream is self-sustaining (autotrophic) in that the organic matter produced by photosynthesis exceeds that consumed by respiration, and species diversity peaks. In the downstream reaches the current is reduced and accumulated suspended sediment decreases light penetration and aquatic photosynthesis. The stream once again becomes dependent on imported organic materials (heterotrophic).

River-floodplain ecosystems contribute water, nutrients and sediments to floodplain forests, which return organic material of terrestrial origin to the river system (Figure 2). The **estuary ecosystem** is closely coupled, with two-way interchange, to the river-floodplain and nearshore gulf ecosystems. The **nearshore gulf ecosystem** is a primary contributor of organisms, as larvae and juveniles of many marine species enter the estuary seeking food and sheltering habitat. A few of the marine species feed in the lower reaches of the river-floodplain ecosystem.

The aquatic ecosystems of the watershed (Figure 2) provide both "goods" and "services" to society. Ecosystem "goods" include food, such as freshwater finfish and estuarine finfish and shellfish. Ecosystem "services" include maintaining the hydrologic cycle, regulating climate, cleansing water and air, maintaining the gaseous composition of the atmosphere, storing and cycling essential nutrients, absorbing and detoxifying pollutants, and providing sites for recreation, tourism, research and inspiration. When societal activities disrupt the essential functions of ecosystems, the assimilative capacity of natural systems is exceeded, and the normal flow of "goods" and "services" provided by healthy ecosystems is impaired. Highly managed ecosystems, such as agroecosystems and urban-industrial ecosystems, are embedded within, and highly dependent upon, unmanaged natural ecosystems which provide our life-support (Odum 1989).

There are no major natural lakes in the watershed but 37 major reservoirs have been constructed, 25 in the upper Trinity River basin alone (Stanley, 1989). Ecologically, this presents a major change when a fast-moving water (lotic) ecosystem encounters a slow-moving water (lentic) ecosystem. As the narrowly channeled river flow enters the broad reservoir, water velocity is greatly reduced and suspended sediments (with attached pollutants) sink to the bottom. With greater water clarity and less downstream transport, plankton shifts from being a minor river component to a major lake component and the food web becomes autotrophic. Species diversity of both plants and animals increases and exotic species, introduced to enhance recreational fishing, become important. The natural flooding regime is altered below the dam and upstream migration is blocked.

Estuaries are among the most naturally fertile waters in the world. This results from their unique juxtaposition at the edge of the continent. Estuaries play a special ecological role because they receive nutrients from four sources: (1) freshwater flowing off the land, (2) tidal exchange with the ocean (Gulf of Mexico in this instance), (3) the atmosphere, and (4) the recycling of material from the estuarine bottom sediments.

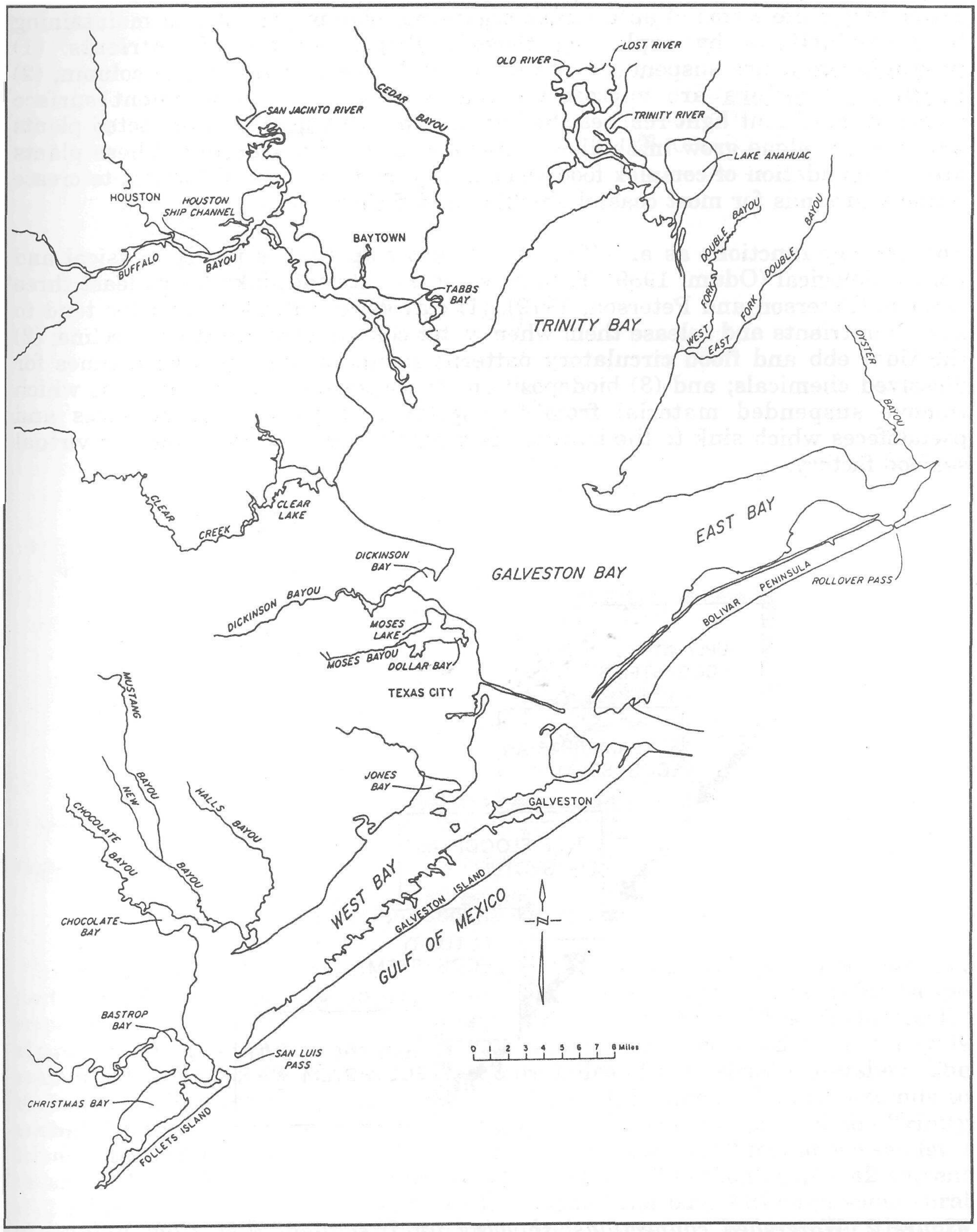


Figure 1. Map of Galveston Bay

Three major life forms of autotrophic organisms play major roles in maintaining high productivity by exploiting these multiple sources of nutrients: (1) phytoplankton are suspended within the sunlit zone of the water column, (2) benthic microflora are microscopic plants living on the sediment surface wherever sufficient light reaches the bottom, and (3) macroflora or rooted plants and rootless algae grow in shallow water and along the shoreline. These plants are the foundation of complex food webs and provide structural habitat to create nursery grounds for most coastal shellfish and finfish.

The estuary functions as an efficient nutrient trap that is partly physical and partly biological (Odum, 1989). Estuaries act as nutrient sinks for at least three reasons (Peterson and Peterson, 1979): (1) clay-sized sediment particles tend to adsorb nutrients and release them when water column concentrations decline; (2) the tidal ebb and flood circulatory patterns result in long residence times for dissolved chemicals; and (3) biodeposition by suspension-feeding animals which remove suspended material from the water and package it as feces and pseudofeces which sink to the bottom. As a result, the estuary becomes a virtual seafood factory.

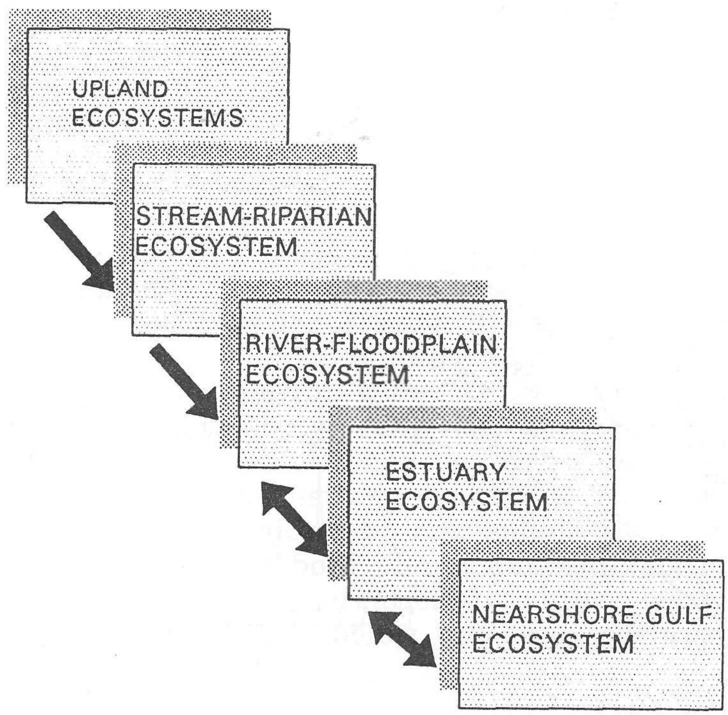


Figure 2. Watershed connections, showing unidirectional flow from upland to stream-riparian to river-floodplain ecosystems and bidirectional interchange between the river-floodplain, estuary, and nearshore Gulf ecosystems.

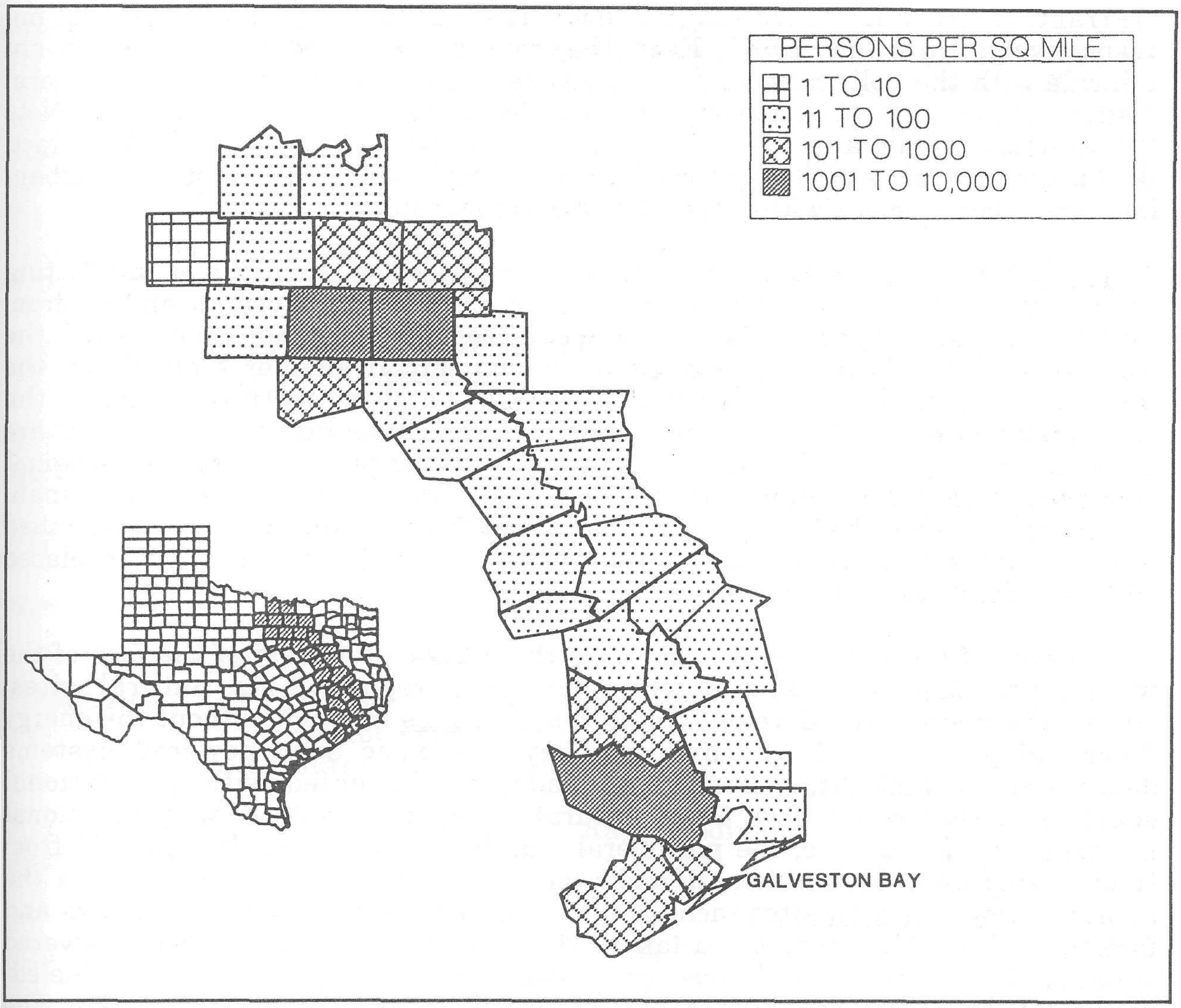


Figure 3. Population density of the Galveston Bay watershed.

A Landscape Approach

The realization that an estuary is affected by and reflects ecological processes and perturbations that occur far upstream in its watershed suggests that a landscape approach would be useful to understanding the system. This dramatically changes the scope of the issue. The 600 square miles covered by the bay is equivalent to only 2.4% of the 25,256 square miles of terrestrial watershed. The drainage basin stretches northward 400 miles and, in Cooke County, extends to within 6 miles of the Red River and Oklahoma. The sinuous path of the Trinity River extends for 715 miles from Trinity Bay to its source 1250 feet above sea level (Stanley, 1989). This large watershed is inhabited by 7.7 million people; 42 percent (3.2 million) live in the four counties which bound the bay. Although some rural counties (Jack, Leon, Trinity, Freestone, and Montague) have fewer than 20 persons per square mile, the urban centers can reach 2000 persons/sq. mi

(Tarrant, Harris and Dallas counties have 1348, 1625, and 2105 persons/sq. mi, respectively; Kingston, 1991). Even though the watershed boundaries do not coincide with the political boundaries used to aggregate census data, the general distribution of population density for the watershed is indicated in Figure 3. Note that Galveston Bay, at the lower extremity, is dwarfed by its watershed. In fact, the 600 square miles of Galveston Bay are matched by 580 square miles of urban-industrial development within the city limits of Houston.

A landscape is a heterogeneous land area composed of a cluster of interacting ecosystems that are repeated in similar form throughout (Forman and Godron, 1986). For our purposes, the landscape is considered synonymous with the watershed. Viewed from the window of a commercial airliner high above, the landscape resembles a mosaic of differing patches scattered across the countryside. All landscapes share a common fundamental structure; they are composed entirely of patches, corridors, and a background matrix. The original matrix for the upper watershed was blackland prairie and post oak savannah. The middle reaches drained pine and hardwood forest, while the lower watershed was comprised of coastal prairies. Today much of the matrix has been replaced with crop lands and exotic grasses.

The impact of development by humans is the drastic alteration of the face of the watershed. The landscape patches can be categorized as natural sites, domesticated sites, and developed sites. Natural sites function without the energy flows being controlled by humans. They are basic solar-powered systems dependent on sunlight, rainfall and winds, supplemented with gravitational energy to power water flow. Some natural sites are subsidized with additional insetenergy; for example, the peripheral marshes of Galveston Bay benefit from tidal energy delivering nutrients and removing waste products to and from the habitats. Domesticated sites include agricultural lands, managed woodlands and forests, and artificial ponds and lakes. These sites are subsidized solar-powered systems that benefit from human-controlled work energy, such as fossil-fueled-powered farm machinery, human and animal labor, imported fertilizers, etc. The amount of energy consumed per unit area per year (energy density) may reach twice that of natural sites (Odum, 1989). The amount of air, water and soil pollutants released at these sites is also increased. Developed sites are the urban and industrial sites fabricated by humans. These are fuel-powered systems and the amount of energy consumed per unit area each year may be 10 times that typical of natural sites. Concomitantly, the volume of pollutants produced is similarly increased. Developed sites are also parasitic in that they are maintained only by importing large quantities of fuel and materials from outside of their boundaries. Odum (1989) has used the term "ghost acreage" to describe the unbounded area beyond the site which is required to sustain the population within the site. A hypothetical comparison of the characteristics for three potentially contiguous landscape patches is presented in Table 1.

Landscapes exhibit three characteristics - structure, function, and change (Forman and Godron, 1986). Structure results from the spatial relationships among the distinctive ecosystems present. Function arises from interactions among the spatial elements; for example, the flow of energy, materials, and species among the component ecosystems. Change results from alteration in the structure and function of components of the ecological mosaic over time. Human activity has greatly accelerated the rate of change. It is useful to consider the landscape as a hierarchy, a graded series of compartments. Each level in a hierarchy influences what goes on in adjacent levels. Processes found at lower levels are frequently constrained in some way by other processes at higher levels. The different levels of organization have different, and often unique, features. Since they are all linked together, events that happen at one level may affect subsequent events at another level (Odum, 1989).

Table 1. A comparison of ecosystem components typical of native, cultivated and developed landscape patches.

ECOSYSTEM COMPONENT	NATIVE SITE	CULTIVATED SITE	DEVELOPED SITE
Site	Prairie	Corn Field	Shopping Center
Surface	Native Grasses	Row Crop	Building, Parking Lot
Fertilizer	Nitrogen-fixing Microbes, Recycled Manure	Imported Nitrogen, Phosphorus	Processed Sewage
Soil Erosion	Slow Percolation, Water Storage	Rapid Sediment Transport	Rapid Runoff, Pollutants (motor oil,)
Flora	Native High Diversity	Exotic Low Diversity	None
Fauna	Native Resident (meadowlark)	Native Transitory (blackbirds)	Exotic (house sparrow, house mouse, cockroaches)
Corridor	Hedgerow, Riparian Vegetation	Fenceline	Highway

An important consequence of hierarchical organization is that as components, or subsets of components, are combined to produce larger functional wholes, new properties emerge that were not present or not evident at the level below. The emergent property principle defines an emergent property as one that results from the functional interaction of the component parts. Therefore an emergent property cannot be predicted by studying components that are isolated or decoupled from the whole unit.

The scale and pace of events also changes in traversing the landscape. For example, the flow of extreme headwaters is likely to be intermittent, following precipitation events. Further downstream, at lower elevation, sufficient groundwater may enter the brook to provide permanent flow. Thus surface water flow is rapid and pulsed, while groundwater flow is delayed (by days, weeks or months) but prolonged. A single tree can shade the brook from bank to bank and aquatic vegetation may be absent or very limited. As numerous brooks coalesce to create a stream, the width, depth and volume of water increase. Fallen trees provide obstacles, and sediments and leaf detritus gather where currents diminish. Decomposition of organic matter accelerates where microbes and invertebrates find sheltered water. Where adequate light exists, plants take root in softer sediments and dissolved oxygen levels increase. When stream width increases and the overhead tree canopy diminishes, beds of aquatic plants develop. These provide food and shelter for additional fishes and invertebrates, thus biotic diversity increases. As sediment loads accumulate, clear brooks become murky streams and muddy rivers. Plants disappear and photosynthesis declines. Chemical and biological oxygen demand increase and oxygen levels decline. Visual-feeding fishes and invertebrates give way to olfactory-feeders (catfishes) and detritivores (suckers).

A human observer standing on the shore of Galveston Bay typically recognizes entities at two ends of a spectrum - individuals and landscapes. The **individuals** are the actual species seen -the fish reeled in from the waters below, the crab scurrying across the beach, the bird flying overhead. The **landscape** is the surrounding environs - the water, the beach, the nearby marsh and surrounding uplands. Unseen are the intervening hierarchical entities (Figure 4). Individuals have life histories in that they are born in particular places, grow up in certain (perhaps other) habitats, and reproduce to ensure continuity of the species. The aggregate of individuals form a **population** which may migrate to and from the bay. Populations can go extinct. Usually it is difficult to envision a population because there are many individuals, frequently too many to count, spread over a large area, often out of sight. Populations of individuals exhibit birth rates, death rates, and changes in gene frequency, resulting in evolutionary trends.

When populations of different plants and animals intermingle they create a **community**, may compete for scarce resources, establish a food web as they eat and are eaten, and thus exhibit diversity, competition, and predation as community characteristics. Subaerial and intertidal communities, like marshes, are visible and commonly recognized. Submerged communities, like muddy or sandy bottoms and deep oyster reefs, are out of sight and less well known. Communities of plants or shell add structural complexity to the environment while moderating the effect of external forces, such as waves, currents, and predation, on community inhabitants.

Both physical (abiotic) and biological components demonstrate emerging properties in ascending the hierarchy. When the non-living components of the environment are added to communities to create **ecosystems**, new functions like energy flow and the cycling of nutrients arise and can be measured. But ecosystems are difficult to see clearly because they have fuzzy edges and come in

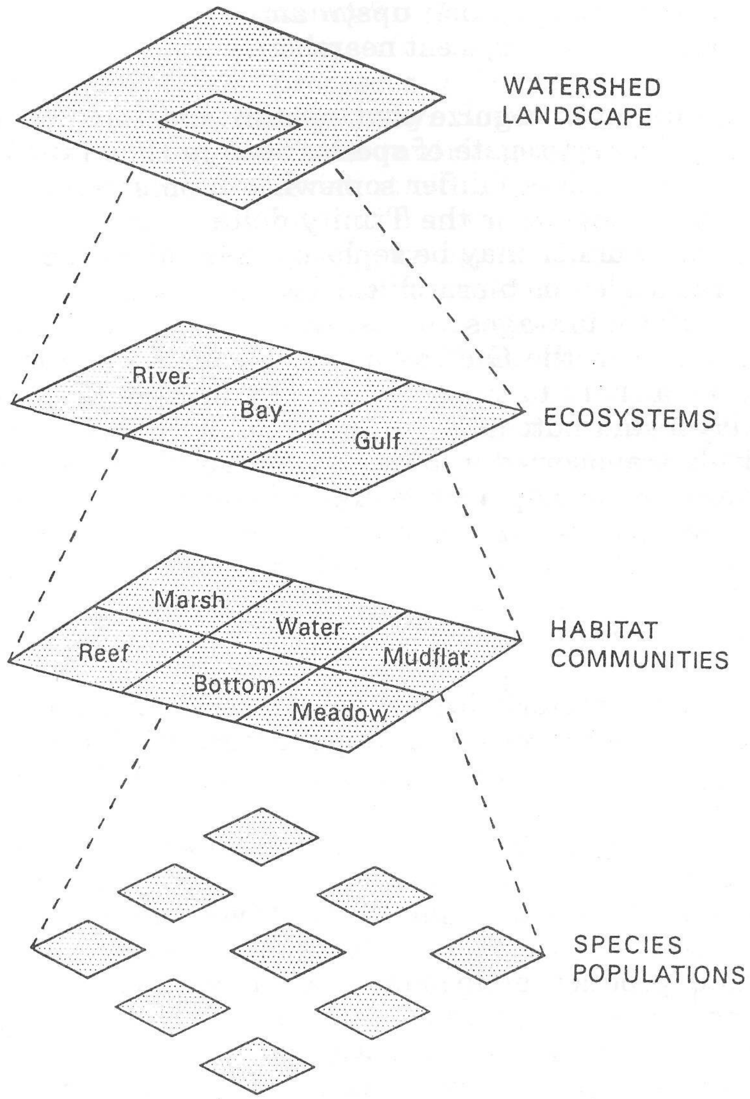


Figure 4. The hierarchical organization of natural systems. The watershed, surrounded by other contiguous watersheds, near the bay is comprised of river, bay and gulf ecosystems. The bay ecosystem is occupied by various types of matrix and patch habitat communities. Each community is created and occupied by populations of various commingling species. Ecosystem characteristics will limit the types of habitats which may occur, while the physical characteristics of each habitat will influence the type of species that occupy the habitat.

all sizes. From the perspective of bacteria and parasites, individual fishes, oysters or humans are wonderful ecosystems. On a larger scale, Galveston Bay can be conveniently considered as a single ecosystem. But the bay is influenced significantly by other ecosystems, upstream and downstream, within the **watershed landscape** and the adjacent nearshore gulf.

Some observers intuitively recognize that spatial and temporal variation affect their view of the bay. The aggregate of species seen in the lower bay (for example, the bay side of Galveston Island) differ somewhat from species frequenting upper bay shorelines (such as Kemah or the Trinity delta). Species commonly observed at one site during the summer may be replaced with other species in winter. The spatial and temporal scales of hierarchical levels are also flexible, even for the same species at different stages of its life cycle. For example, adult gulf menhaden range widely in the Gulf as members of the nekton (free-swimming) community but move inshore to spawn. Their eggs have a brief (48 hr) sojourn in the surface microlayer and hatching larvae continue as members of the plankton community, passively transported into the bay nursery. Larval menhaden prey on zooplankton. Juveniles develop basket-like gillrakers to capture the smaller phytoplankton and prosper as nekton, but lower on the food chain. Before they are one year old, juveniles migrate back to the Gulf to mature and reproduce. This is an example of a single species spending different life stages in different localities as a member of quite distinct communities.

Two other ecosystem characteristics are of interest. Frequently one ecosystem component affects a second component, that in turn affects the first component. Such feedback loops underlie many ecological processes. If the first component stimulates the second component, but the second component then inhibits the first, it is termed negative feedback. If the first component stimulates the second component, which in turn stimulates the first component even further, it is termed positive feedback. For example, under favorable conditions oysters grow rapidly and create more reef surface (oyster shell) which permits more oyster larvae to settle and produce additional reef, a positive feedback mechanism. However, an abundance of oysters may encourage more oystermen to invest in additional boats, which remove more oysters and their shells, reducing the available substrate for oyster larvae, and eventually shrinking the oyster population to a point where it is uneconomical to harvest them; this is negative feedback.

Next, wherever two different components of the landscape come in contact an edge is created. The edge may exist between a patch and the matrix or between two patches. The edge may be sharp and distinct, as where land meets the water, or diffuse, as found at a tidal marsh, where the water's edge advances and retreats with each tide, creating a gradient known as an ecotone. Certain species which require two distinct habitats to meet their life requirements may exist only along edges; others specialize in ecotones. Both are known as edge species. Biologically, edges are where the action is. The nearshore gulf is more productive than the offshore gulf because the edge of the continent provides nutrients and habitat unavailable offshore. Embayments are indentations in the continent, increasing the length of shoreline. Marshes with a reticulated pattern of tidal creeks and blind bayous have more shoreline for a given area and are more beneficial to the estuary than marshes with a straight margin along the bayshore.

Journey To The Sea

It is apparent the effect of the processes occurring within the watershed may extend hundreds of miles to the estuary. Some of these processes are vital. Without freshwater inflow, and the nutrients and sediments transported therewith, the estuary would not exist; it would be a lagoon, a salty extension of the gulf. Rivers do not discriminate. If a material reaches the river, it will be transported, perhaps undergoing transformation enroute. Figure 5 portrays the determinants of water quality in sequential order. Precipitation results in surface runoff and groundwater inflow to initiate the stream. Dissolved and suspended materials are incorporated into the flow from the moment, or even before, raindrops contact the earth. Point and nonpoint source discharges add various contaminants to the flow, particularly from urban-industrial and intensely cultivated sub-watersheds. Stream microorganisms are able to consume or reduce contaminant levels within the waterway. Further processing and settling out occur in each reservoir along the waterway. Flooding of the lower river

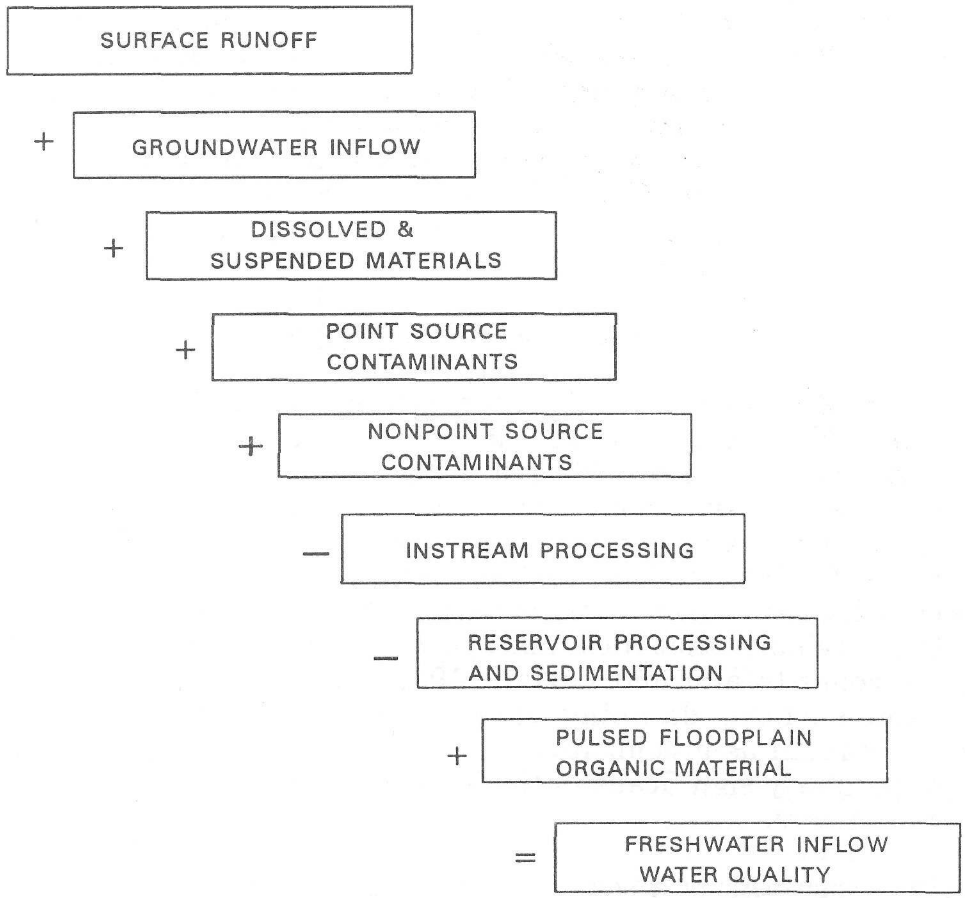


Figure 5. The determinants of water quality. Contaminants are added or removed from stream flow as it moves to the bay.

floodplain periodically introduces pulses of organic material from the forest floor into the river. Water quality may both degenerate and regenerate during passage through various river segments before entering the bay.

The Texas Water Commission establishes water quality criteria and inventories waters of the state biennially (TWC, 1990). When dissolved oxygen levels are below 3 mg/L, a stream segment or other water body is deemed not fishable (that is, unable to support fishes due to lack of oxygen). When fecal coliform bacteria exceed 200 per 100 ml the stream is not swimmable (due to bacterial contamination). A number of Trinity and San Jacinto river segments and coastal streams have been designated as not swimmable; some San Jacinto river segments are not fishable. Numerous headwater tributaries continue to maintain high water quality, but large stretches of the Trinity River and its tributaries exhibit poor water quality, particularly in the vicinity of the Dallas-Ft. Worth metropolitan area. Low dissolved oxygen, bacterial contamination, and nutrient enrichment are persistent problems. Several reservoirs act as waste treatment components, with downstream water of higher quality than incoming flow. Similar circumstances can be found in the San Jacinto basin and several coastal basins associated with the bay. Some stream segments are among the worst in the state. Dissolved oxygen levels frequently decline when passing through urban areas. Stanley (1989) noted that the oxygen sag for the Trinity River extended 300 miles, from Ft. Worth to Lake Livingston. It appears that Lake Livingston, constructed primarily as a source of drinking water for Houston, currently functions as a large, and effective, sewage treatment plant and nutrient sink. Contaminants from the Dallas-Ft. Worth metropolitan area are reduced during the long journey to the bay. Contaminants from the Houston metropolitan area, and the industrial corridor along the Houston Ship Channel, enter the bay without significant reduction.

The Estuarine Landscape

The landcape concepts remain valid in the estuary. Most of the watershed is subaerial. The majority of the estuary is submerged (sub-aqueous). Patches of differing habitat are prominent along the shoreline and across the bottom of the estuary; they are present, but quite subtle, in the water itself. Recreational fishermen search for patches of clear "green water" where artificial lures can be seen by visual-feeding fishes. Other patches are "slicks" that exude a "watermelon" odor attractive to predaceous fish, a phenomenon undescribed by scientists. The possibility that these slicks may be produced by tidally-mixed fronts or convergent zones (Mann and Lazier, 1991) that concentrate floating organic matter on the surface, damping small waves, has not been investigated. Corridors now stretch as greenbelts along the shoreline and small tidal streams. Edges are particularly significant in the estuary, sought by planktonic larvae and patrolled by predators.

The estuarine ecosystem is a composite of strikingly different types of habitats. The largest of these habitats is the 3-dimensional (length, breadth, and depth) open-bay water component to which all other habitats are linked. Equally large in areal extent but virtually 2-dimensional (length and breadth), is the underlying open-bay bottom component. The bottom functions as a matrix in which two distinct types of habitat patches can be found. On hard bottoms with strong currents, patches of oyster reef rise up to provide the only hard substrate and elevated surface above the bay bottom. On softer sediments in shallow water, patches of submerged aquatic vegetation, the subtidal seagrass meadows, can be found near the periphery of the bay. As the bay bottom slopes upward at the edge of the bay, meadows of intertidal vegetation, the peripheral marshes, punctuate the shoreline. Some low-sloping shore zones do not support emergent vegetation but form the intertidal peripheral mud flats. Patches of very soft, unconsolidated subtidal bottom are scattered within various shoreline wetlands to create the peripheral marsh embayments. This conglomerate of habitats is connected upstream to the freshwater riverine/floodplain habitat and downstream to the marine waters of the nearshore gulf, and via migratory birds, to the interior of the continent.

A simplified web of connections between these estuarine habitats is shown in Figure 6. Four habitats are essentially self-sustaining producer or autotrophic habitats - the open-bay water, marsh, seagrass, and mud flats. The dominant producer organisms are indicated - phytoplankton, benthic algae, marsh grasses

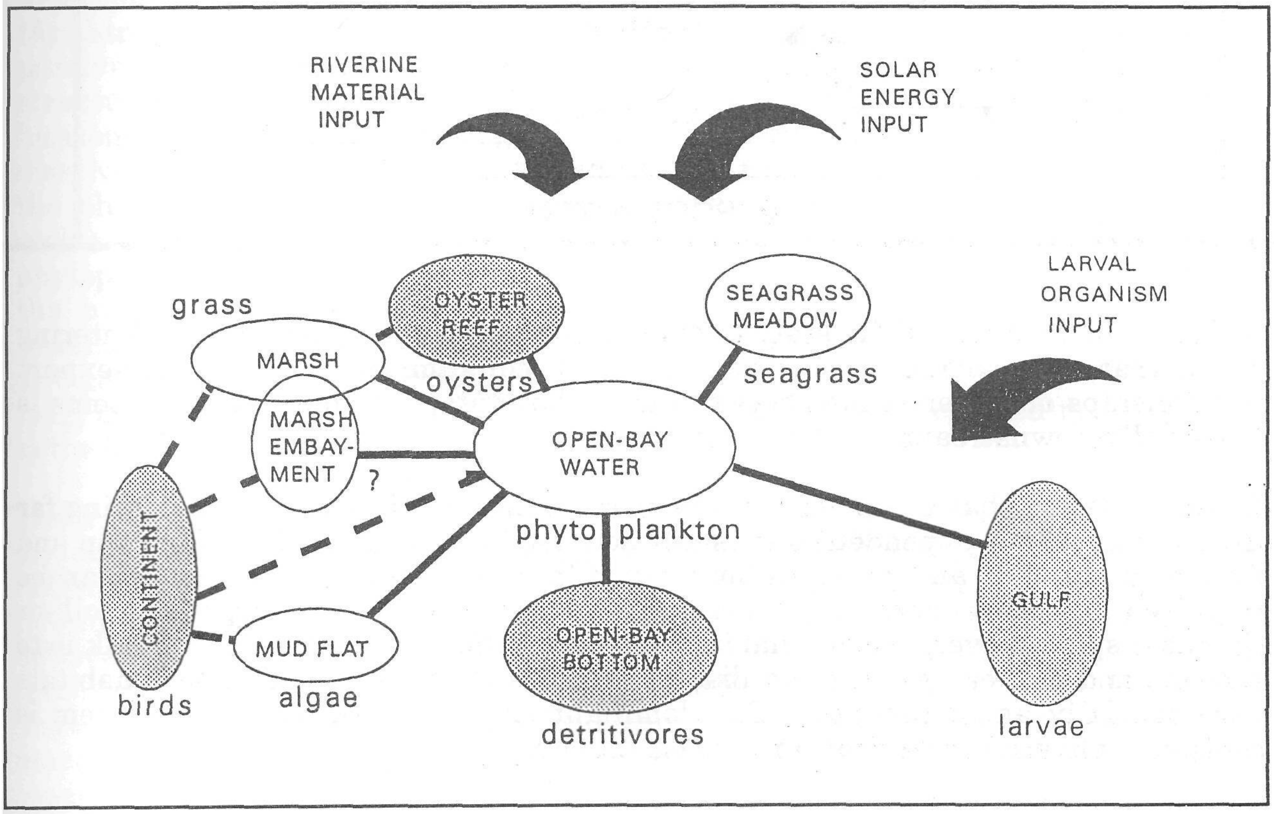
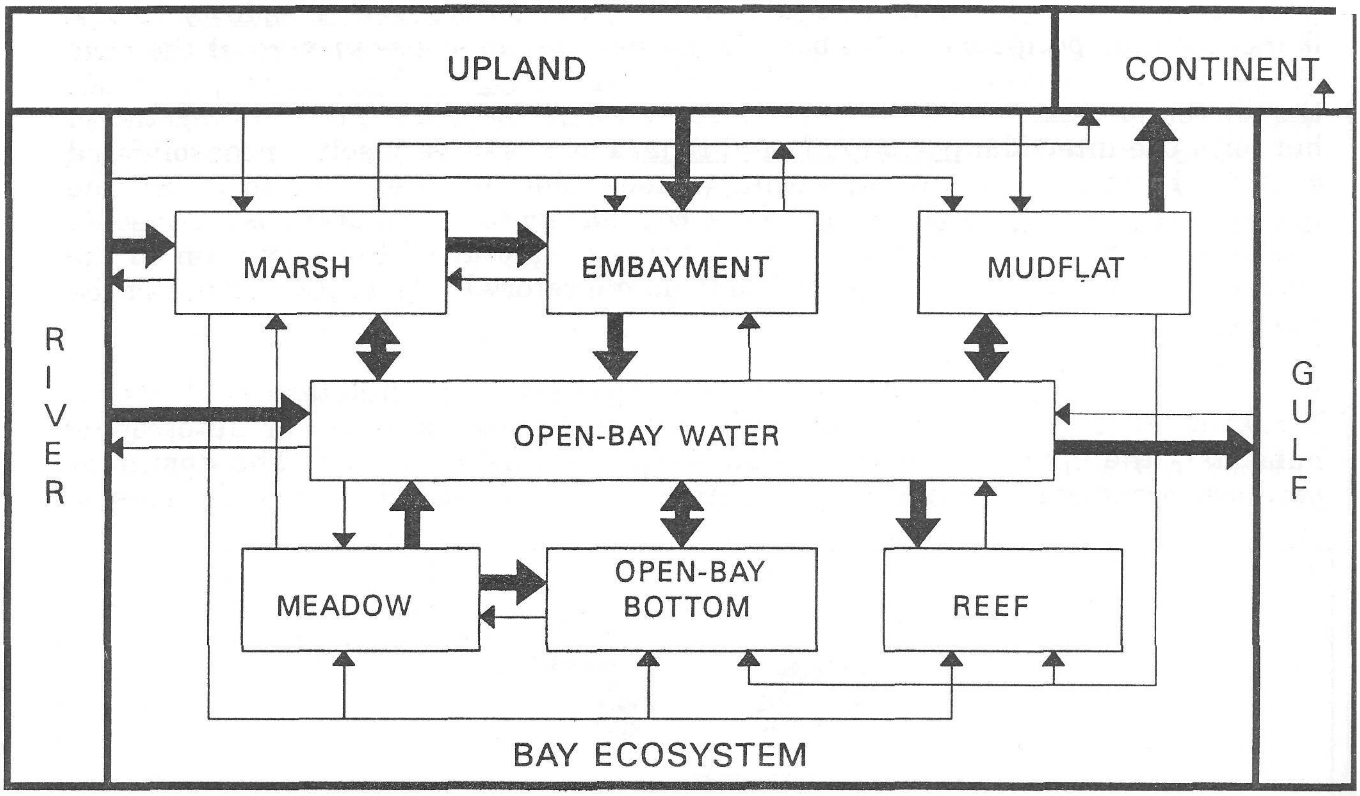


Figure 6. The web of estuarine habitats, indicating the dominant producer organisms of autotrophic habitats (open ellipses) or consumers in heterotrophic habitats (shaded ellipses). The principal external inputs are also indicated (arrows).

Figure 7. The import-export relationships between habitat components of the bay ecosystem and adjacent ecosystems. Major material flow is shown by a heavy line, moderate flow by a thin line; minor flows have been omitted.



rather than producers. The status of marsh embayments is uncertain. Wintering or migrating continental birds are also consumers. The import-export relationships of material flow between these habitats and adjacent ecosystems is essentially downstream, as shown in Figure 7.

In summary, the bay ecosystem can be greatly influenced by activity occurring far from the bay. It is dependent on distant actions, like the spawning of shrimp and finfish in the gulf and precipitation runoff from a remote watershed. It can be impaired by other actions, for instance, waste water discharge and oil or chemical spills. Seven distinct habitats comprise the bay ecosystem and link it to riverine and gulf ecosystems and distant portions of the continent. These habitats vary spatially and temporally. The dominant characteristic of the ecosystem is continual physical, chemical and biological change.

III. COMPONENTS OF THE ESTUARINE ECOSYSTEM

The living components of these habitats have been aggregated into functional groups based upon their distribution within the habitat and their primary feeding technique. These components have been arranged so that the model reflects the general flow of nutrients and energy through the food web of the habitat. The models are not schematics of energy flow or nutrient cycling in the strictest sense. In some instances unique subsystems of the habitat have been identified. The spatial and temporal variations exhibited by each habitat, and limiting factors have been identified where possible. True productivity values (expressed as dry weight of carbon produced per unit area per unit time) are very rare for these habitats. Surrogate measurements (e.g. standing crop) have been provided, and readers are directed to the source literature. Definitions of technical terms may be found in the glossary.

Open-bay Water

This is the largest and most conspicuous habitat of the ecosystem. It has the greatest areal extent, 143,153 hectares , and is 3-dimensional, with an average depth of 2.1 meters, encompassing a total volume of 2.9 cubic kilometers (Armstrong, 1987). Its pelagic inhabitants include all of the active swimmers and passive drifters found in the water column. This habitat has the simplest structure of all (Figure 8) and is essentially featureless except for invisible horizontal and vertical salinity gradients, and at times, gradients of temperature, dissolved oxygen, nutrients and turbidity. The primary producers, which capture the physical energy of sunlight and package and store this energy in organic molecules constructed from carbon dioxide gas, are various groups of phytoplankton. The primary consumers which feed upon these phytoplankton are the numerous and diverse zooplankton and phytoplanktivorous fishes. The secondary consumers principally are nekton, larger organisms capable of self-directed swimming and feeding activity. Food chains in this habitat can be quite long, extending to six or seven levels. Dead organisms and egested material sink to the bottom to be recycled by decomposers.

The autotrophic phytoplankton of Trinity Bay are composed of three major groups: diatoms (42%), green algae (24%), and blue-green algae (cyanobacteria) (23%) (TDWR, 1981). The nannoplankton, composed of the smallest phytoplankton, heterotrophic bacteria and protozoans smaller than 20 µm, are poorly known but believed to be the principal prey of microzooplankton (20-200 µm), such as protozoans, rotifers, and copepod nauplii (Buskey and Schmidt, 1992). The larger phytoplankton (20-200 µm microphytoplankton) are grazed principally by macrozooplankton (200-2000 µm; mesoplankton of some authors) such as copepods (Parsons and Takahashi, 1984). The largest megazooplankton (larger than 2 mm; macroplankton of some authors) are gelatinous invertebrates, such as comb jellies, sea walnuts and other jellyfish, voracious planktivores which, in turn, are eaten by marine turtles (now extremely rare in the ecosystem). Zooplankton exhibit two major life strategies. Those organisms which spend their entire life cycle as plankton are termed holoplankton, and copepods, cladocerans, and chaetognaths are major representatives. Other prominent planktonic organisms actually spend only a brief part of their life cycle as zooplankton. These meroplankton include the larval stages of fishes, crabs, shrimp, oysters and barnacles, many of which retreat to other habitats as juveniles or adults.

Most of the nekton are fishes which consume phytoplankton, zooplankton, or other fishes. Birds prey on the nektonic organisms, especially aerial foragers (e.g. terns), surface gleaners (e.g. gulls and white pelicans), and divers (e.g. waterfowl, grebes, and cormorants). Birds are also an important link in nutrient cycling, transporting nutrients to terrestrial habitats. Humans are very important predators in this habitat; harvesting and harvest management can alter the composition and size of fish populations.

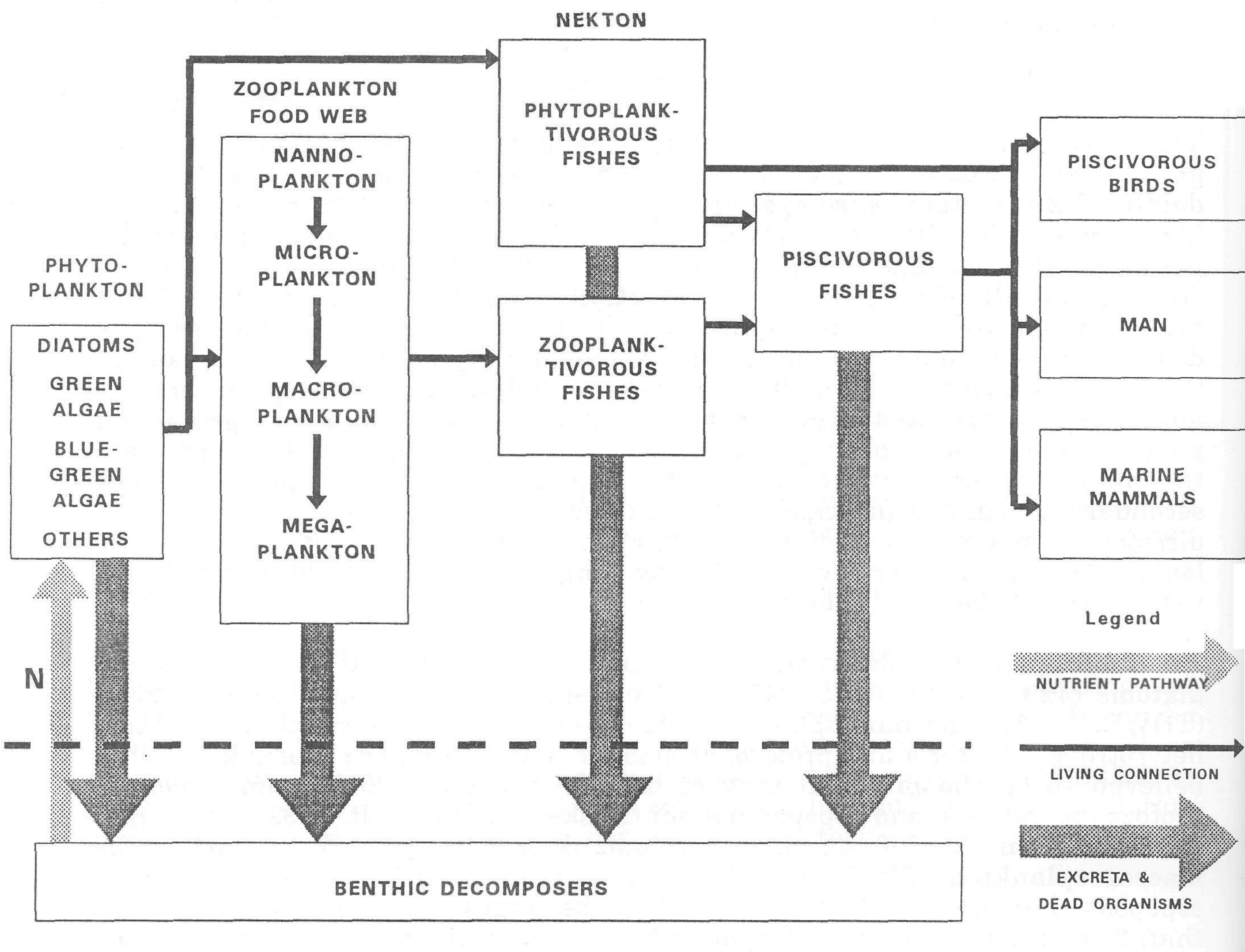


Figure 8. Connectivity of the open-bay water habitat.

Spatial Variation: The most conspicuous physical variable of this habitat is the salinity gradient, which can range from 0 ppt (parts per thousand) near the mouths of the major rivers to 30 ppt or more at the outlet to the Gulf of Mexico. The density gradient can provide vertical salinity stratification although wind-driven waves in this shallow ecosystem produce substantial mixing.

Phytoplankton- Although phytoplankton are the base of the open-bay water food chain, the phytoplankton of Galveston Bay have received very little attention from the scientific community (Sheridan et al., 1989; Buskey and Schmidt, 1992). The phytoplankton of Trinity Bay and upper Galveston Bay have shown distinct spatial differences (TDWR, 1981). Diatoms became increasingly abundant with increasing salinity along the gradient from the upper to lower reaches of Trinity Bay. Green algae and blue-green algae were more abundant in the upper bay and declined as salinity increased. The phytoplankton in lower Galveston, East or West Bays are poorly known. Diatoms dominate year-round in lower Galveston Bay and West Bay. Freshwater forms become prominent in Trinity Bay during periods of high freshwater inflow from the Trinity River. Species diversity was lower, but cell numbers higher, in low salinity waters (<15ppt) compared to higher salinities (>16ppt).

Zooplankton- The most abundant holoplankton in Trinity Bay and upper Galveston Bay are copepods, primarily *Acartia tonsa*; the meroplankton are dominated by barnacle nauplii. Freshwater inflows influence the zooplankton community by (1) importation of freshwater forms, (2) importation of food resources in the form of nutrients, phytoplankton and detritus, and (3) flushing of resident populations (TDWR, 1981). On the other hand, when freshwater inflows decline, saltwater intrusion may (1) import marine plankters, (2) import marine phytoplankton as a food source, and (3) increase salinity. Thus freshwater inflow and salinity changes can affect species composition, seasonal occurrence, and species distributions in Trinity Bay.

At the other end of the salinity spectrum, in the saline waters of Christmas Bay, lies a similar zooplankton community. The same calanoid copepod, *Acartia tonsa*, was the dominant species, accompanied by another copepod found in Trinity Bay, *Oithoina colcarva*. These copepods and a planktivorous ctenophore, *Mnemiopsis mccradyi*, formed a stable community throughout the year. Although many other holoplankters and meroplankters appeared seasonally, these three may have been the only self-sustaining species in Christmas Bay (Bagnall, 1976). This food chain spanned several trophic levels, as *Acartia* were eaten by *Mnemiopsis*, which in turn were consumed by *Beröe*. Zooplankton have not been studied in East Bay.

Nekton- An ecological classification of the fishes of Barataria Basin, Louisiana, based on their life cycle patterns (Conner and Day, 1987), has been modified for application to Galveston Bay. Freshwater fishes reproduce in freshwaters but may enter the estuary as subadults or adults, particularly during periods of high freshwater inflow when estuary salinities are depressed and marine fishes are absent (Table 2); examples are gar, shad, catfish, and sunfishes. Estuarine fishes spend their entire life cycle within the estuary; e.g. killifish, silversides, pinfish, gobies, bay anchovy and hogchokers. Estuarine/marine fishes exhibit two strategies. Some spawn in offshore waters but certain life stages are spent in nearshore waters and within the estuary; e.g. gulf menhaden, mackerel. Others spawn in nearshore waters and use the estuary extensively as a nursery; e.g. croaker, spot, striped mullet, red drum. Marine species enter the estuary only as subadults or adults and may be restricted to higher salinity waters; e.g. star and banded drum.

Table 2 demonstrates that different fishes enter the estuary for different purposes, which influences their spatial distribution within the estuary. The 186 fish species of Barataria Basin were classified as 31 freshwater, 23 estuarine, 26 estuarine-marine, and 106 marine species, based on combined studies and sampling techniques (Conner and Day, 1987). The 162 fish species listed by Parker (1965) for Galveston Bay can be similarly classified as 29 freshwater, 23 estuarine, 24 estuarine-marine, and 86 marine species. Nine percent were judged abundant, 28% common, 23% uncommon, and 41% rare. Among 22 euryhaline species found at all salinities, 27% were abundant, 59% were common, 14% were uncommon, and none were rare; 14% were classified as freshwater species, 41% were estuarine, 32% were estuarine-marine, and 14% were marine. Thus euryhaline fishes appear be very successful in terms of relative abundance and exhibit all types of life cycles.

Table 2. Aquatic zone distribution of fish life cycle events.

	FISH LIFE STAGE				
FISH CLASS	EGGS	LARVAE	JUVENILES	SUBADULTS	ADULTS
Freshwater	Freshwater	Freshwater	Freshwater	Freshwater/ Estuary	Freshwater/ Estuary
Estuarine	Estuary	Estuary	Estuary	Estuary	Estuary
Estuarine/ Marine 1	Neashore	Nearshore/ Estuary	Estuary/ Freshwater	Estuary/ Freshwater	Nearshore
2	Offshore	Nearshore	Estuary	Nearshore	Offshore
Marine	Offshore	Offshore	Offshore	Nearshore/ Estuary	Nearshore/ Estuary

Source: Conner and Day (1987), modified.

Sheridan (1983) reviewed two years of Galveston Bay trawling data which encompassed 364,815 fishes of 96 species. He categorized the catch by four ecological zones (channel, open water, shore, and the peripheral lakes, lagoons and bayous) and seven geographic subareas (Gulf of Mexico, Bolivar Roads tidal pass, lower, and upper Galveston Bay, mouth of the San Jacinto River, Trinity Bay, and East Bay). These data exhibited distinct spatial differences in catch rate (fish per trawl) for ecologic zones and geographic subareas, even for abundant ubiquitous species.

Monaco et al. (1989) provided information on spatial distribution (based on salinity - tidal fresh <0.5 ppt, mixing 0.5-25 ppt, seawater >25 ppt), relative abundance, and life stage for 9 macroinvertebrate and 22 fish species of Galveston Bay. Parker (1965) described the status of 162 fish species of Galveston Bay, including salinity preference (0-5, 5-10, 10-20, 20-35 ppt) for most of them. Loeffler (Append.III.2, Loeffler and Walton, 1992) listed 138 fish species captured in the TPWD Coastal Fisheries monitoring program, categorized by gear type (gillnet, trawl, and bagseine reflect water depth and distance from the shoreline) which brings the total list of fishes known from Galveston Bay to 199 species.

Temporal Variation: Most of the groups of organisms in Galveston Bay display distinct seasonality in their occurrence and relative abundance.

Phytoplankton- Phytoplankton abundance and diversity vary significantly with season, apparently associated with maximum nitrate concentrations influenced by freshwater inflow. In Trinity Bay, a blue-green alga, *Oscillatoria*, bloomed in July while a green alga, *Ankistrodesmus*, peaked in September and October. Among the diatoms, *Cyclotella* peaked in January, *Skeletonema* bloomed in February, while *Nitzchis* reached its maximum densities in May and June (TDWR, 1981). Buskey and Schmidt (1992) concluded there was little evidence for a consistent seasonal pattern in phytoplankton production.

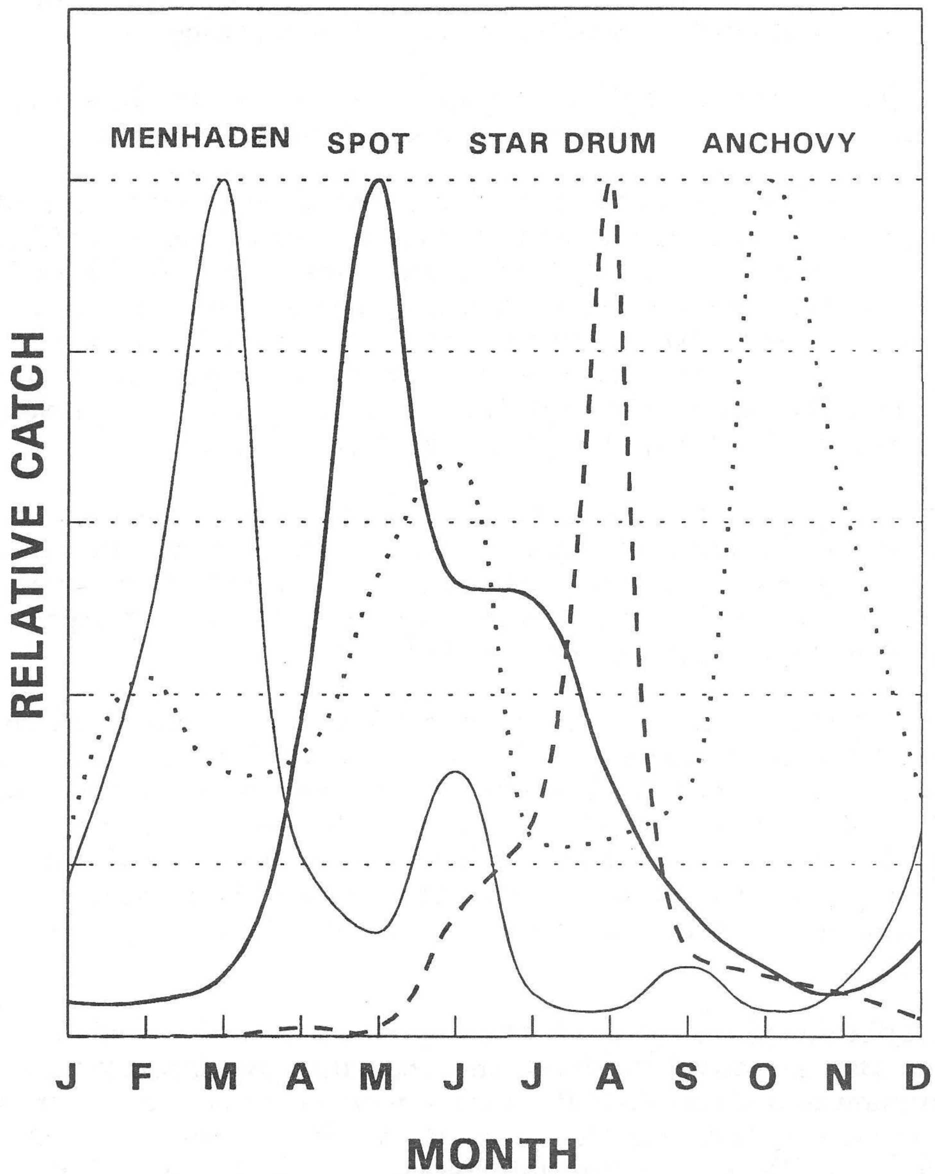
Zooplankton- Optimal conditions for growth and survival occur at different times of the year for different species. In Trinity Bay, immature barnacles were prominent in late winter and early spring, their period of greatest spawning activity. Copepod nauplii and protozoans were dominant in April. The copepod *Acartia* peaked in summer and early fall (TDWR, 1981).

In Christmas Bay, neither salinity nor temperature appeared to explain the variation in density of *Mnemiopsis*, *Oithoina*, or *Acartia* (Bagnall, 1976). The population of *Acartia* was low from December to February and fluctuated throughout the remainder of the year. *Oithoina* and other copepods were abundant throughout the year but peaked in September. Neritic zooplankters from the nearshore gulf entered the bay during periods of high salinity in late summer and fall and constituted an important perturbation to the bay zooplankton assemblage.

The meroplanktonic larvae of four sympatric species of hermit crabs in Christmas Bay effectively divided the year into overlapping breeding seasons (Fotheringham and Bagnall, 1976). *Clibanarius vittatus* larvae were present from April through October, *Pagurus longicarpus* from September through May, *P. pollicarus* from December through February, and *P. annulipes* while present throughout the year, was most abundant through spring and summer.

Minello and Matthews (1981) have demonstrated that changes in the vertical distribution were a major factor influencing the variability found in zooplankton density estimates. Nocturnal densities were far greater than diurnal densities at the same site.

Figure 9. Seasonality of fishes in trawl catches. These four species, which are not equally abundant, respectively reach their peak abundance at different seasons of the year.



Source: Sheridan 1983

Holt and Strawn (1983) have shown that macrozooplankton in Trinity Bay exhibited two distinct seasonal assemblages. Larval and juvenile crustaceans dominated the warm (>22°C) season assemblage of spring and summer. Fish larvae and juveniles dominated the cool season assemblage when lower salinities prevail. The fishes spawned in the fall and winter and young fish were abundant during winter and spring. Major changes in macrozooplankton populations were due to temporal rather than spatial factors.

Nekton-Holt (1976) analyzed biweekly trawling and seining data from Trinity and Tabbs Bays and discerned two temporal species-groups. A warm season group extended from April though November and a cool season group from November through April. The seasonality of fish populations was primarily due to the migration of juveniles and the young of euryhaline marine species. The changes were correlated with temperature.

Figure 9 illustrates the seasonality of four estuarine-marine fishes collected by trawling. Gulf menhaden peaked in March, spot in May, star drum in August, and bay anchovy in October. The seasonal sharing of bay resources by brown shrimp (fall-spring) and white shrimp (summer-fall) is a similar example.

Productivity: The average standing crop of phytoplankton was 171,400 cells/liter for a one year study of Trinity Bay (TDWR, 1981). The overall mean density of zooplankton for the same stations was 21,971 organisms/m^3.

For one station in West Bay, gross productivity was 1.17 mg carbon/liter/day; net productivity was 0.84 mg C/l/da (Corliss and Trent, 1971). Several estimates of overall mean primary production rate of 35 mg C/m^3/hr exist (Buskey and Schmidt 1992).

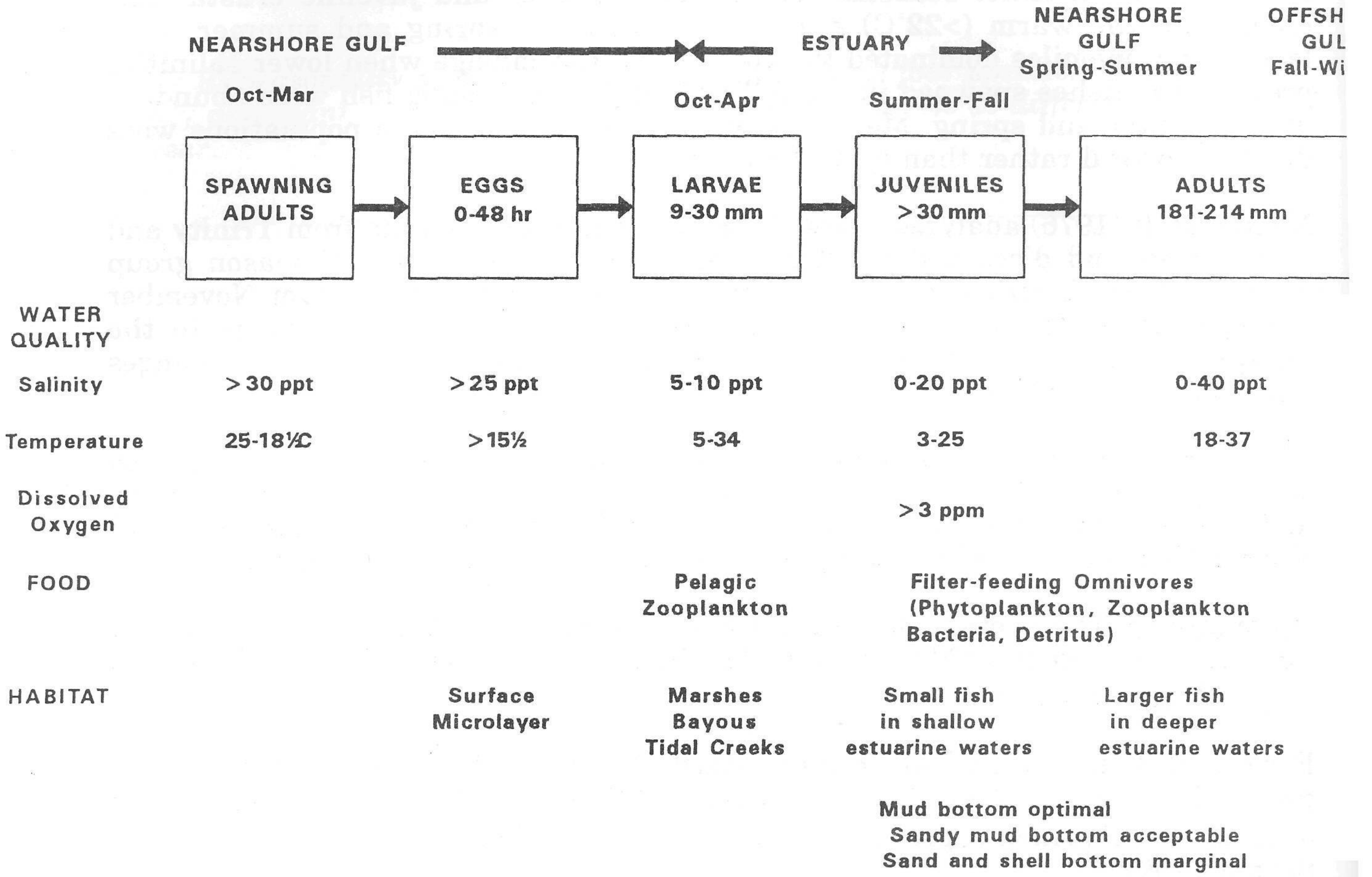
Habitat Subsystems: The surface microlayer of open-bay water habitat frequently supports a distinct community at the air-water interface, a region of high light intensity and oxygen concentration. This aggregate of minute organisms - phytoplankters, zooplankters, and the eggs and larvae of fishes - is sometimes termed the neuston. Special collecting techniques are required to sample this subsystem and this has not been done for Galveston Bay.

The navigation channels, which typically exhibit higher salinities along the bottom, serve as conduits for polyhaline and euhaline fishes (Sheridan, 1983; Parker, 1965). Nearshore species frequently penetrate farther into the bay in the channels than in the open bay.

Limiting Factors: Light
Inorganic Nutrients
Temperature

Key Species- The **Gulf menhaden** is an ecologically important pelagic fish (Figure 10). Adults spawn in both nearshore and offshore Gulf waters. The buoyant eggs apparently require high-salinity marine waters for proper egg development (Christmas et al., 1982) and hatch within 48 hours. The larvae are passively

Figure 10. The life cycle of Gulf menhaden.



transported by currents into estuarine waters within 3 to 5 weeks. The food resources and protective habitats of the estuary seem necessary for successful transformation the larvae into juvenile fishes (Lassuy, 1983a). Postlarvae seek shallow, quiet, low salinity areas near shore and marsh shoreline appears optimal. Larvae are selective particulate feeders and nauplii and adult copepods are favored prey. During transformation into juveniles their gill rakers develop into a basket-like sieve enabling them to become omnivorous planktivores, consuming phytoplankton, zooplankton, and organic detritus. Thus they function as primary, as well as secondary, consumers, shortening the food chain and hastening the conversion of phytoplankton into consumer biomass. In turn, menhaden are important forage fishes for larger piscivorous fishes and birds, and are harvested commercially by man.

As they grow, menhaden move from marshes to peripheral embayments and tidal creeks, foraging far upstream even into freshwater cypress embayments, thence to deeper and deeper water. Most juveniles return to Gulf waters in the fall and return to the estuaries in spring. Few reproduce before their second year. Fully grown adults are seldom encountered in the estuary. Critical habitats are the low salinity marshes for larvae and shallow low salinity embayments and bayous for juveniles. These shallow habitats exclude the larger predatory fish but the resultant larger juveniles later provide greater biomass to these same predators.

The **bay anchovy** is an equally, or perhaps more, important forage fish with a very different life history in the bay. It is a permanent resident which spawns in the bay (Monaco et al., 1989). Although small (less than 4 inches long when mature), they are the second-most abundant fish (Atlantic croakers being most abundant) in the bay (Sheridan, 1983; Reid, 1957). They are most abundant in open-bay waters, nearshore and mid-bay, where they feed nocturnally on a large variety of zooplankton, changing diet as they grow. During the winter, they feed extensively on benthic organisms and detritus. They, in turn, are prey for red drum, sand and spotted seatrout, silver perch, Atlantic needlefish, ladyfish, lizardfish, Atlantic croaker, and southern flounder. These predator-prey relationships indicate their **key role** in the estuarine food web, directly linking the open-bay water to the bottom habitat, and small pelagic zooplankters and benthic worms to larger fishes of commercial and recreational importance and to numerous birds. They are abundant at all times of the year. Additionally, the bay anchovy may indicate poor water quality (Bechtel and Copeland, 1970). With its small size and short food chain, it can become the dominant species in polluted waters (Monaco et al., 1989).

Open-bay Bottom

This is the second largest habitat of the ecosystem, being equivalent to the open-bay water habitat less those areas of the bay bottom covered with oyster reef or seagrass meadow. Armstrong (1987) included the open-bay water habitat as part of the open-bay bottom. This habitat is essentially two-dimensional; while its length and breadth are measured in kilometers, its depth is measured in centimeters. For the most part, the surface is featureless except for sculpted waveforms, trawl marks, and evidence of bioturbation.

The food web of the bottom habitat is based on detritus (Figure 11). Except for shallow shoreline areas where light penetrates the turbid water to reach the bottom, photosynthetic algae and primary productivity are very limited or nonexistent. Some organic matter reaches the bay bottom in the form of "planktonic rain" as dead organisms or egested material sink to the bottom. Other organic matter is imported as dissolved organic matter (DOM) and fine or coarse particulate organic matter (FPOM, CPOM) transported from the riverine and peripheral wetlands or submerged aquatic vegetation (SAV).

The most striking feature of this food web is the key role of the fungi and bacteria which comprise the benthic decomposer organisms at both the beginning and the end of the food chains. Plant material has limited usefulness in its raw state. It must undergo "conditioning" or partial digestion by microorganisms. Few animals manufacture the digestive enzymes necessary to break down cellulose products. Bacteria are capable of this but apparently their activity is limited to the surface of the plant material. More important are various fungi which are able to extend hyphae deep into cracks and crevices of plant material to extract nutrients. In doing so, the microbes release various nitrogen compounds to the water column. Various protozoans and other organisms which comprise the microfauna (small enough to pass through a 0.062 mm mesh screen; 2/1000ths of an inch) consume bacteria directly, egesting fine particles of organic material in doing so. In this manner organic molecules become bundled into bite-sized packages; first as fungi and bacteria, then as larger protozoans. The protein content of the food "packages" also increases, creating higher quality food.

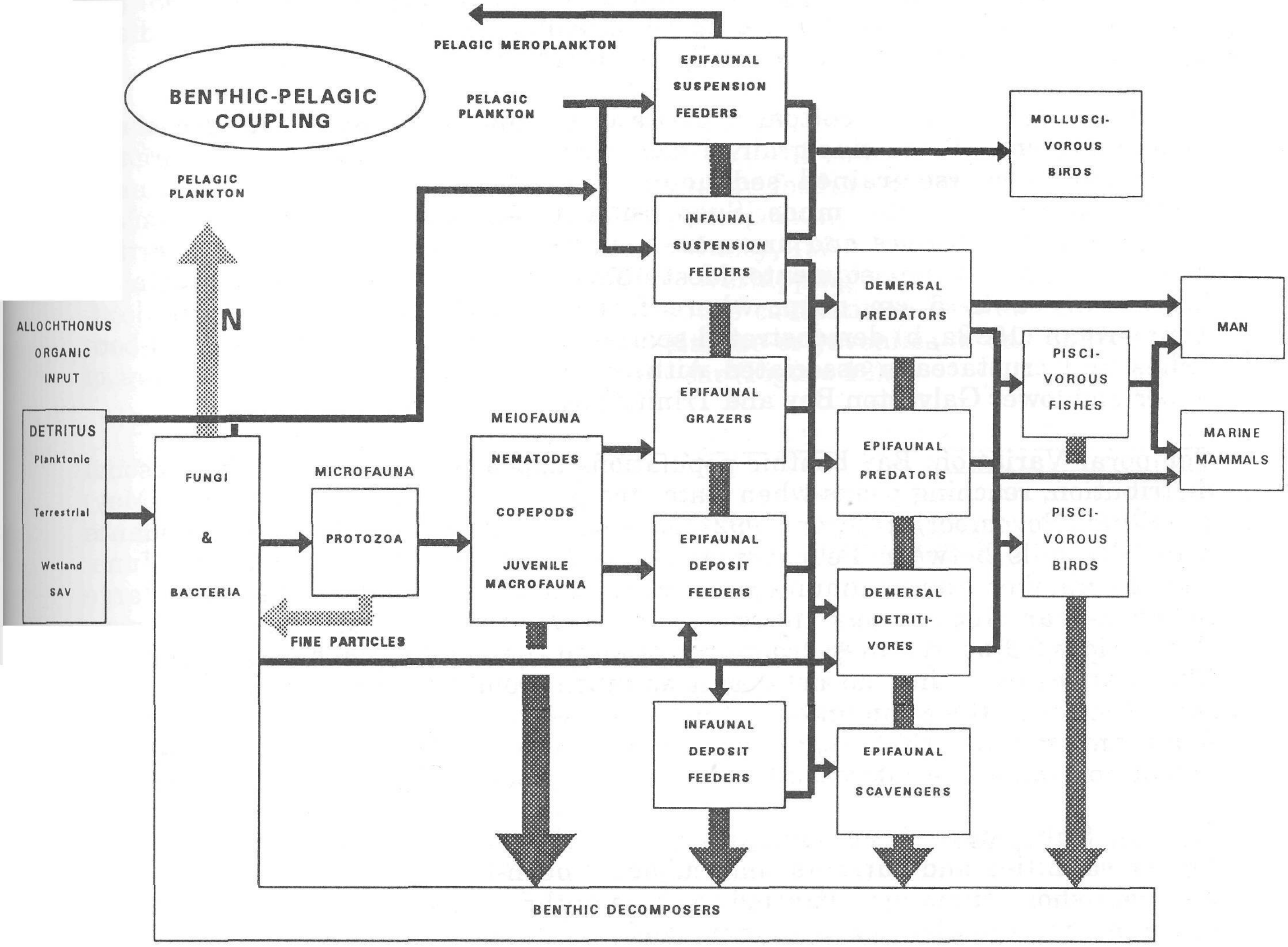
The next component is the diverse meiofauna comprised of organisms between 2/1000ths and 2/100ths of an inch (0.062-0.5 mm) in size. Nematodes are most numerous but copepods and juvenile stages of the larger macrofauna are also abundant. These organisms find protozoans and bacteria to be conveniently-sized prey. The meiofauna are most abundant in sediment with high silt fractions.

As the food web organisms increase in size they also begin to subdivide the habitat into two components. One diverse assemblage of organisms, the <u>epifauna</u>, lives on the surface of the bottom sediment. Another assemblage burrows into the bottom sediment, either superficially under a dusting of flocculant sediment, or deeper in vertical tubes; these organisms form the <u>infauna</u>. Epifaunal and infaunal organisms share feeding habits. Some feed by straining suspended particles from the water column, the <u>suspension feeders</u> (e.g. bivalve mollusks). Others feed by ingesting the sediments and extracting nutrients as it passes through the digestive tract; these are known as <u>deposit feeders</u> and include many worms. Gastropod mollusks graze along the sediment surface. Both mobile and sessile animals exist here. Many crabs forage on the surface but burrow beneath it to escape detection by larger predators between foraging excursions. Scavengers and several trophic links of predators are found on the bottom. Numerous fishes (e.g. croakers, spot, mullet and drum) and shrimp forage on benthic organisms. These are considered as <u>demersal predators</u> or detritivores in this model to indicate their ability to move freely within the water column. Diving birds (particularly ducks) reach the benthos to consume small mollusks and other organisms.

The benthos is closely coupled with the open-bay water habitat. Pelagic plankton, which frequently undergo diurnal vertical migrations, are consumed by epifaunal and infaunal suspension feeders. At the same time many mollusks and other benthic organisms contribute planktonic larvae to the meroplankton assemblage. Mysids and ostracods spend time on the bottom and in the water column. Denitrifying bacteria release nitrogen compounds to the sediment and thence to the overlying water column.

<u>Spatial Variation</u>: The distribution of benthic invertebrates in the ecosystem is influenced by sediment type, salinity, and temperature (White et al., 1985). Six different assemblages have been identified. The <u>open bay center</u> assemblage is found in predominantly mud bottoms of lower Galveston Bay and East Bay, with a somewhat different assemblage in West Bay; polychaetes are the predominant group of organisms. The <u>open bay margin</u> assemblage is found in shallow water with predominantly sand bottoms on the bay side of the Bolivar Peninsula and Galveston Island plus the landmass margin of West Bay and Christmas-Bastrop Bays. Crustaceans are the most abundant organisms, and the West-Christmas-Bastrop Bay area differs from East Bay. The <u>river-influenced</u> assemblage

Figure 11. The connectivity of open-bay bottom habitat. The fungi and bacteria which comprise the benthic decomposers are vital at both ends of the food web. The benthic-pelagic coupling provides a vital link to the open-bay water habitat.



dominates all of Trinity Bay and Upper Galveston Bay, eastern East Bay, and Chocolate Bay. It is a high-stress mud environment influenced by substantial freshwater inflow and highly variable salinities. Mollusks and polychaetes are prominent. The inlet-influenced assemblage is limited to the sand and shell bottoms in the vicinity of Bolivar Pass and San Luis Pass. Salinity is high and relatively stable and mollusks are the dominant organisms. Two additional distinct benthic communities, the oyster reef assemblage and the grassflat assemblage, will be considered with their respective distinct habitats.

Harper (1992) has included an additional assemblage, the enclosed bay or interreef assemblage, as a subset of the open-bay center assemblage. Harper cautions "that these assemblages are not static and that there are no 'boundary lines' separating one assemblage from another" as they intergrade from one to another along salinity and sediment gradients. Harper also notes that "any given portion of the bay may have an open-bay assemblage one year and a river-influenced assemblage the next year, depending on salinity conditions." LaSalle et al. (1991) reported differences in species richness, dominant species and total organism density between upper and lower Galveston Bay. Ray et al.(1993) and Clark et al. (1993) distinguished three assemblages along a salinity gradient: upper bay, lower bay, and numerically dominant ubiquitous species.

Deposit feeders feed on bottom deposits of organic detritus and its associated microorganisms. Since fine-grained sediments generally contain more organic matter than coarse-grained sediments, deposit feeders are generally more prominent on bay-center muds. Suspension feeders feed on microorganisms in the surrounding waters and are more abundant in bay-margin sands. Vertical variation exists in the sediments. Most infauna are found in the upper sediment layer, only 2 to 5 cm deep, where food and oxygen are most abundant. Zimmerman (1992a, b) demonstrated spatial differences in standing crops of both fishes and crustaceans associated with open-bay bottom in shallow waters of upper and lower Galveston Bay and Trinity Bay.

Temporal Variation: Bay benthic populations appear to have a bimodal seasonal distribution, reaching peaks when water temperature is rising (February to May) or falling (November). Harper (1992) notes that while the spring peak abundance generally falls between February and May, it can occur in January or June. Species number and community structure change seasonally. There are large between-year fluctuations influenced by rainfall patterns, and within-year fluctuations influenced by seasonal variation in the benthic community structure. The changes over time do not result as much from the presence or absence of rarer species in the community as from changes in the abundance patterns of the dominant species that regularly occur. There is evidence that top-down population control results from heavy grazing by seasonal demersal predators.

Habitat Subsystems: The navigation channels provide a benthic habitat with higher salinities and currents than adjacent open-bay bottom. Shrimp, oysters, and near-shore fauna are attracted to these anthropogenic habitats. The adjacent open-bay repositories for both new and maintenance dredged material also provide a different but temporary bottom habitat.

Productivity: Zimmerman (1992b) sampled 16 nearshore open-bay bottom sites in upper and lower Galveston Bay and Trinity Bay in October and estimated standing crops for fishes (0.0474 g dry wt/m^2) and crustaceans (0.0513 g dry wt/m^2). LaSalle et al. (1991) reported total organism densities of 40-133/600cm^2 in the lower bay and 50-120/600cm^2 in the upper bay. Ray et al. (1993) and Clark et al. (1993) reported total mean biomass (wet wt) of 10-45 g/m^2 and mean total abundances of 500-1200 individuals/m^2. Comparisons with other studies (summarized by Harper, 1992) are tenuous due to different quantities of sediment sampled and different sieve mesh sizes.

Limiting Factors: Turbidity
Sediment resuspension
Detritus input
Salinity
Temperature
Predation

Key Species: Two species of penaeid shrimp, the brown shrimp *Penaeus aztecus* and white shrimp *P. setiferus* have key ecological roles in the food chains of estuaries. They both recycle basic nutrients by feeding on organic matter and microorganisms in sediments and they are important prey for many estuarine and marine fishes, invertebrates and birds (Muncy, 1984; Lassuy, 1983b). Both are important commercial species. They have overlapping but distinct spatial and temporal distributions which appear to reduce competition between the species (Turner and Brody, 1983). As a result postlarvae or juveniles of one or the other species can be found in the bay most of the year (Figure 12).

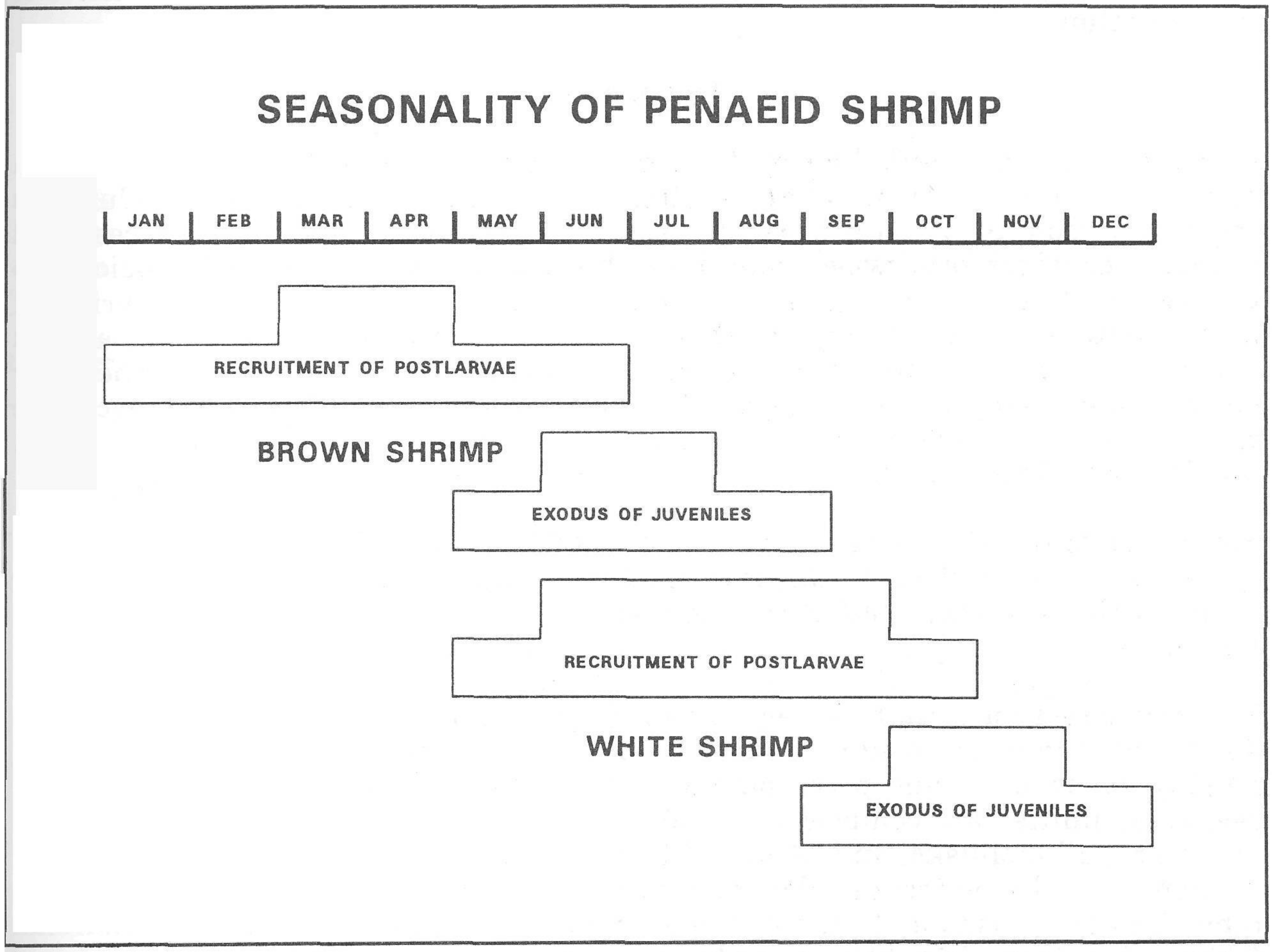


Figure 12. Seasonality of penaeid shrimp, which share bay-bottom habitat by temporal displacement.

Spawning occurs in offshore Gulf waters. Planktonic postlarvae are transported into the estuary by shoreward currents. Four to six weeks later postlarvae transform into juveniles and move to the marsh-open water interface or into seagrass beds. After reaching a length of 60-70 mm, the juveniles move into deeper open water. Brown shrimp begin to migrate toward the Gulf as they reach 90-110 mm in length. White shrimp utilize lower salinity waters as nursery grounds. Autumnal cold fronts trigger mass emigrations of white shrimp 80-110 mm in length (L. Benefield, pers. comm.).

All stages of both species are omnivorous. Larvae consume both phytoplankton and zooplankton. Postlarvae become demersal and indiscriminately ingest surface sediment containing plant detritus, algae, and microorganisms. Juveniles select the organic fraction of sediment and prey on polychaetes, amphipods, nematodes, chironomid larvae, and ostracods. Neither species survive or grow on vegetal-only diets (McTigue and Zimmerman, 1991). Brown shrimp respond more favorably to animal food, while white shrimp are best able to exploit vegetal matter. The differences in the ability of the two species to utilize plant and animal material can be related to resources available at their times of immigration.

Oyster Reef

Patches of oyster shell, live oysters, and other commensal organisms form a distinct habitat wherever a hard bottom and sufficient current exists. Currents transport food to the reef organisms and carry away sediment, feces, and pseudofeces which otherwise would bury the reef. The habitat is 3-dimensional to the extent that the irregular shells cemented together create a myriad of microhabitats for small species. Oyster reefs are created in the open bay and along the periphery of marshes, and can be either subtidal or intertidal. They may be abundant along the side slopes of navigation channels where tidal exchange currents are dependable, and ancient reefs, exposed by channel construction, provide suitable substrate.

Powell (1993b) estimates a minimum of 10,800 hectares (nearly 27,000 acres) of oyster reef in the Galveston Bay system. This is equivalent to 41.6 square miles, or 10.4% of the bay area. Half of the reefs are concentrated in the central Galveston Bay area.

The oyster reef community is very diverse (Figure 13). While oysters contribute the dominant biomass, other bivalve mollusks, gastropods, barnacles, crabs, amphipods, isopods, and polychaete worms can be abundant. In West Bay, oyster reef communities are comprised of many species, including 18 fishes, 22 shrimps and crabs, 17 mollusks, and 34 annelid worms (Zimmerman et al., 1989). The reef community is heterotrophic, dependent on the importation of food resources from other habitats, principally the open-bay water and peripheral emergent marshes (Figure 13). Nannoplankton and phytoplankton are filtered by oysters and other epifaunal suspension feeders. Dissolved and particulate organic matter, particularly the feces and pseudofeces emanating from the suspension feeders, support various deposit feeders sequestered in the interstices of the aggregated shell. Oyster reefs are most successful where bottom currents sweep sediments away from the reef; otherwise, the oysters can be inundated with their own feces and pseudofeces to the point where filter-feeding is inhibited. Crustal algae attach to shell substrate in some instances, particularly in shallow shoreline areas. This algae supports a small grazing food chain.

Secondary consumers on the oyster reef are predators in the broadest sense, for they include parasites and pathogens which are important oyster population control agents. Demersal fishes with crushing teeth (e.g. black drum) and epifaunal crustaceans (e.g. stone and blue crabs) prey on small oysters with thin and weaker shells. Oyster drills capable of drilling through the shells of larger, but immobile, prey reverse the usual large predator/small prey size ratio. A separate food web encompasses small fishes (e.g. gobies) and crustaceans (numerous crabs) which do not consume oysters but exploit the 3-dimensional microhabitat provided by the aggregated oyster shells.

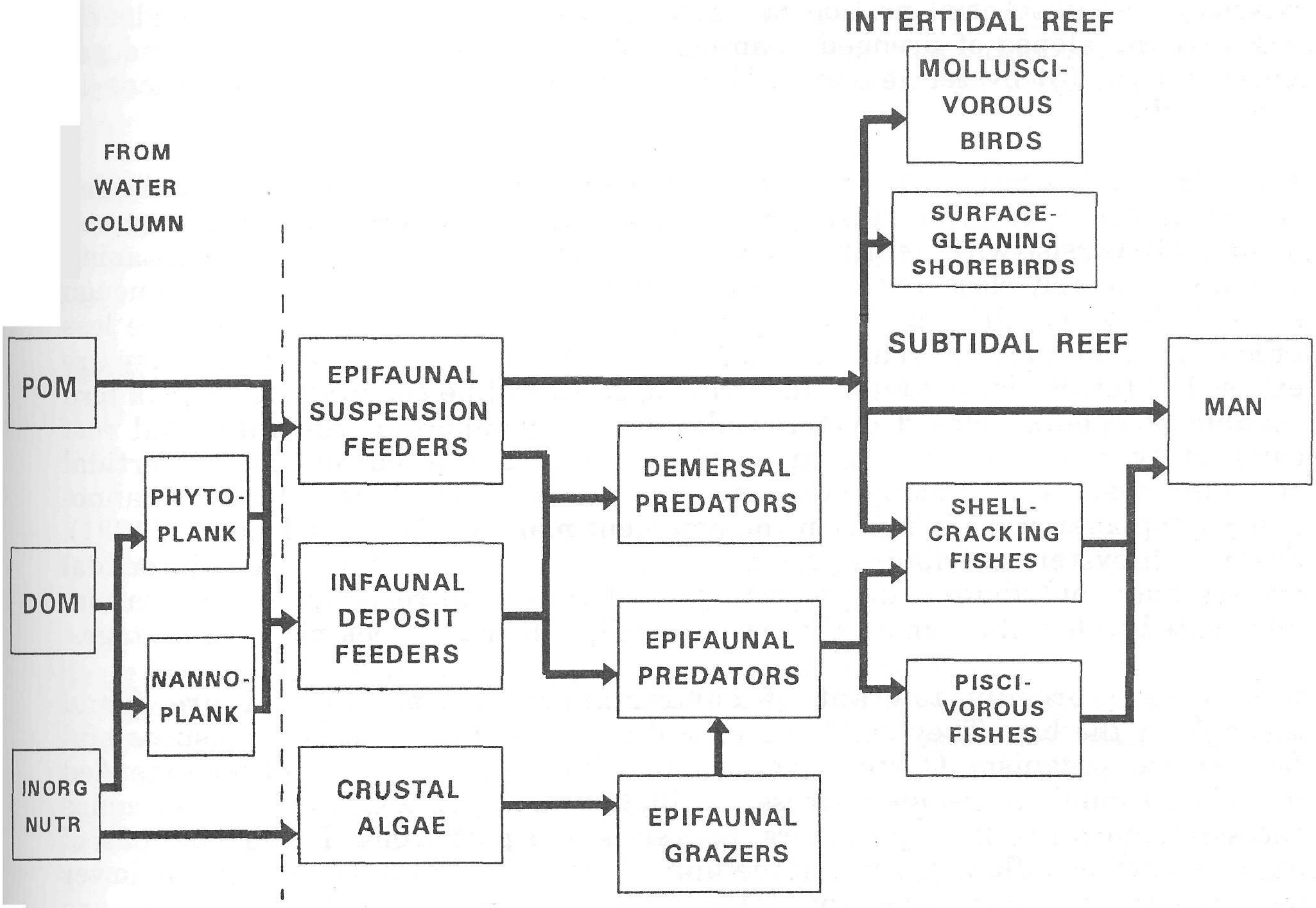


Figure 13. Connectivity of oyster reef habitat. Nutrients, organic material and plankton are imported from the open-bay water habitat.

Oysters perform a valuable ecological service as filter-feeders in the estuary. If an average oyster filtered one liter of water per hour (a conservative estimate, Powell et al., in press) and an average oyster reef contained 38.2 oysters per square meter (Zimmerman et al., 1989), oysters would completely filter the water overlying the reef every 2 to 3 days. Thus a large, healthy oyster population is able to filter large volumes of water and represents a significant ecological benefit to the estuary. At the same time, their propensity to bioaccumulate and biomagnify pollutants makes them important indicator organisms for determining the health of the estuary.

Spatial Variation: Powell (1993a) distinguishes four types of natural reefs that have existed over historic time, and four types of reefs that have originated through man's influence. Natural reefs include (1) alongshore reefs oriented parallel to shore and located near or attached to the shoreline; (2) reefs extending perpendicular from the shoreline or a point nearshore out into the bay; (3) patch reefs composed of one or more small, more-or-less circular bodies; and (4) barrier reefs extending across or nearly across the bay. Anthropogenic reefs, which constitute a substantial portion of existing reefs in Galveston Bay, include: (1) reefs on the slopes of dredged channels; (2) those associated with oil and gas development; (3) oyster leases; and (4) those resulting from modifications in current flow.

While the most prominent, and commercially exploited, oyster reefs are subtidal, the importance of intertidal oysters should not be overlooked. Oysters can apparently persist with as little as 8 hours of immersion daily (Bahr and Lanier, 1981); they simply close and shut out the aerial environment at low tide. Although susceptible to freezing and high temperatures, intertidal oysters experience less predation from aquatic predators, such as oyster drills and stone crabs. They are exposed to terrestrial predators including specialists like the oystercatcher, a bird capable of opening closed oyster shells. Other members of the intertidal reef community are exposed to turnstones and similar shorebirds. But intertidal shoreline oysters are ideally positioned to exploit the rich community of nanno- and phytoplankton draining from the emergent marshes (Bahr and Lanier, 1981). Since each oyster contributes prodigious numbers of propagules, these intertidal oysters may contribute a disproportionate share of the recruitment population, distributed widely throughout the estuary during their 2-4 week planktonic stage.

Oysters are broadly tolerant of environmental variations and are found throughout the bay. They employ a reproductive strategy that is very successful for a sessile organism. Oysters exposed to salinities less than 5 ppt for extended periods succumb to osmotic stress. In high salinity zones, oysters experience excessive mortality from predators, parasites and pathogens. During periods of high freshwater inflow, oysters in the upper bay succumb but oysters in the lower bay experience relief from predators, parasites and pathogens which are intolerant of lowered salinities. During drought periods, lower and middle bay reefs experience increased predation while upper bay populations benefit from increased salinities in the absence of predators. The net result is that, despite unpredictable environmental variation, oysters somewhere in the bay will experience suitable conditions for growth and reproduction. Their planktonic larvae will be broadly distributed throughout the bay and spat will survive wherever compatible conditions can be found.

Temporal variation: Oysters are permanent residents of the estuary and not subject to migratory movements for recruitment or spawning. Oysters may spawn during all but the coldest months (Dec-Feb) but spawning is most prevalent during late May and June, as water temperatures increase, and again in September, as temperatures decrease, thus the abundance of meroplanktonic larvae is seasonal (Cake, 1983).

Habitat Subsystems: The subtidal and intertidal subsystems (discussed under Spatial Variation above) are the important habitat subsystems.

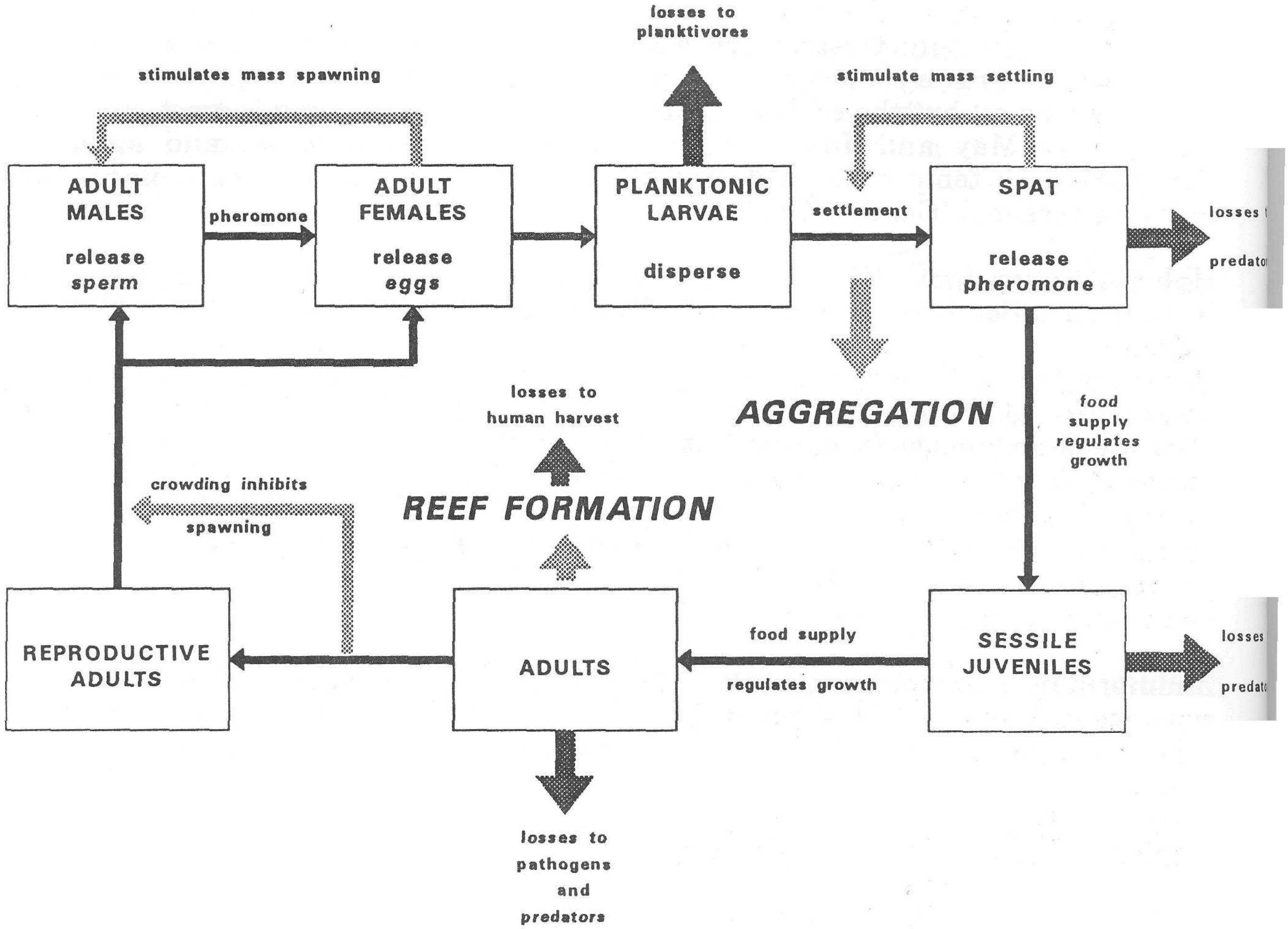
Productivity: Although the commercial harvest of oysters is reasonably well documented, it is difficult to extend this data to a per unit area productivity value. Reef areas are inexactly known but a minimum of 9883 acres (1613 ac closed to harvest; Quast et al., 1988) are regulated by the TPWD, with shallow and intertidal reefs unmapped. Private oyster leases in Texas averaged 333 lb/acre of oyster meat from 1977-90 (= 37.3 g wet wt/m^2/yr) but this value includes oysters produced on closed reefs elsewhere and transported to private leases for depuration (Campbell et al., 1992).

Zimmerman and others (1989) reported summer densities of 34 fish, 105 crustaceans, and 18,981 annelids per square meter of oyster reef in West Bay. Winter densities declined to 4 fish, 36 crustaceans, and 122 annelids per square meter.

Limiting Factors: Extremes in salinity
High turbidity
Weak current
Substrate availability
Phytoplankton
Predators, parasites, pathogens
Extremes in temperature
Suspended particulates

Keystone Species: The American oyster, *Crassostrea virginica*, as creator of this habitat, is the keystone species. Its life cycle is affected by several positive feedback mechanisms, as shown in Figure 14. A pheromone in semen stimulates females to release eggs, culminating in mass spawning to maximize fertilization. As larvae settle to the bottom and attach themselves to a suitable hard substrate, they release a pheromone which stimulates other larvae to settle nearby. This leads to aggregation of the spat, the precursor of reef formation. As aggregates of juvenile oysters grow into adults and enlarge their shells, the mass of shells creates new suitable substrate for the attachment of new spat, which grow larger, creating new substrate, etc. The end result of this positive feedback mechanism is formation of a reef which, in time, rises above the bottom surface into stronger currents, and may culminate by rising above the low tide water surface to create an intertidal reef. As the reefs enlarge they tend to become oriented perpendicular

Figure 14. The life cycle of American oysters, a keystone species.

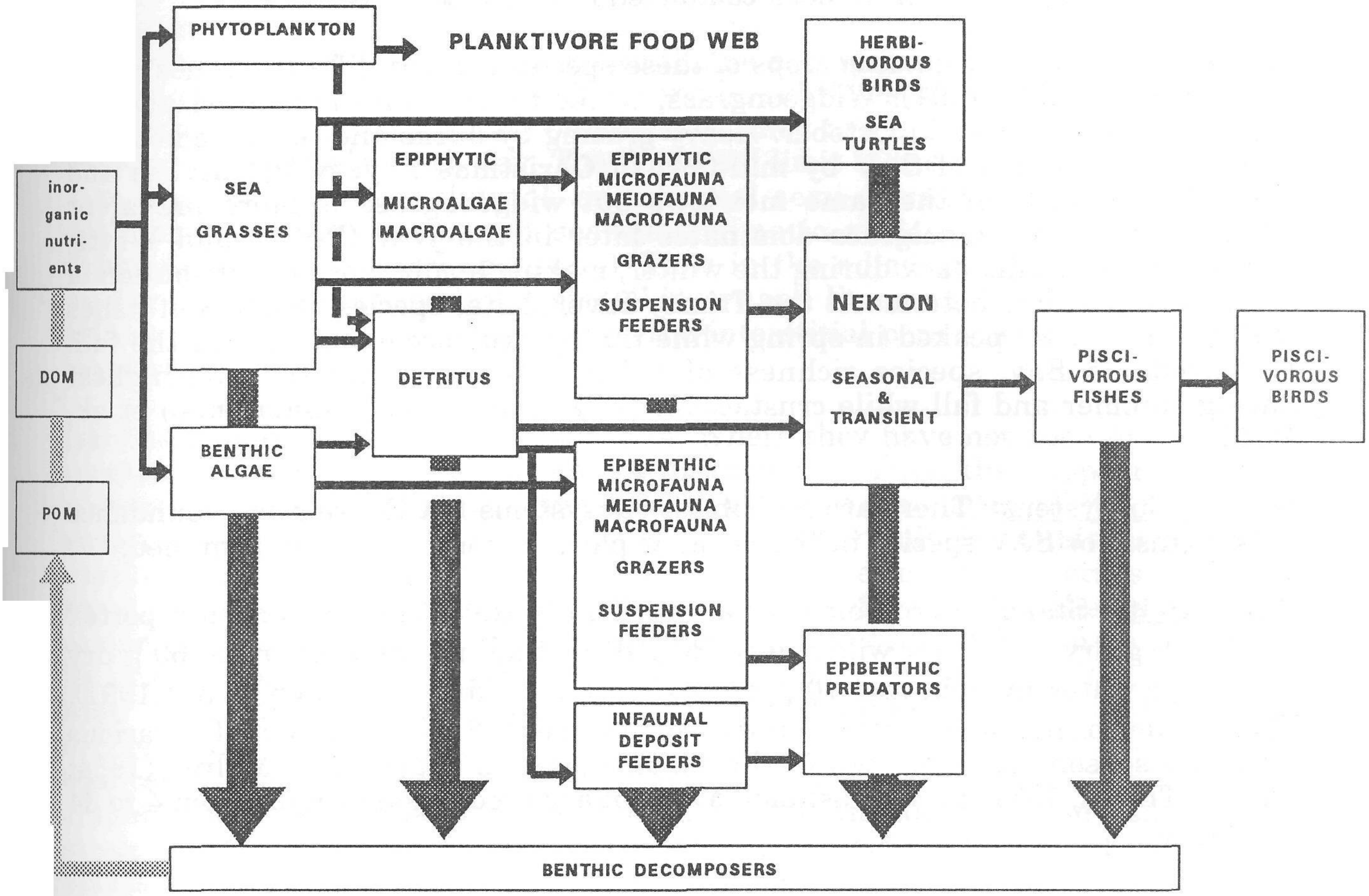


to the prevailing currents, resulting in the maximum number of individuals gaining access to planktonic food particles. As they rise above the bottom, the reefs alter bottom current patterns, leading to silt deposition on the reef flanks and smothering of oysters at those points. If too many adults result in crowding and competition for reef space or food supplies, a negative feedback mechanism reduces spawning behavior. This may act through reduced food supply leading to a decrease in available energy for reproduction.

Seagrass Meadow (Submerged Aquatic Vegetation - SAV)

Patches of submerged aquatic vegetation, composed of freshwater or marine plants and their attached epiphytic algae, form 3-dimensional habitat in soft sediments along some shorelines. This habitat provides food resources and protective cover for a number of associated species and contributes substantial quantities of detritus to the food web (Figure 15). The fauna associated with these patches of SAV is quite diverse and includes 20 fish and 15 crustacean species (Zimmerman et al., 1990; Czapla, 1991). Seagrass beds may be particularly important when they are positioned adjacent to a marsh that is well-drained at

Figure 15. The connectivity of seagrass meadow habitat.



low tide. Small organisms are able to forage and seek shelter in both habitats alternately, foraging in the intertidal marsh meadow at high tide and retreating to the seagrass meadow at low tide. This is especially apparent in Christmas Bay.

Spatial Variation: Freshwater and oligohaline species are limited to the Trinity River delta. Water nymph (*Najas guadalupensis*) pondweed (*Potamogeton pusillus*), and dwarf spikerush (*Eleocharis parvula*) are limited to the intertidal zone (Pulich et al., 1991; White and Paine, 1992). Wild celery (*Vallisneria americana*) is restricted to the subtidal zone, 0.2-0.8 m below mean low water. Widgeongrass (*Ruppia maritima*) is truly euryhaline, occurring at the Trinity River delta, along the mesohaline northern and southeastern shores of Trinity Bay, and in Christmas Bay. The polyhaline marine grasses - shoal grass (*Halodule wrightii*), clovergrass (*Halophila engelmanni*), and turtlegrass (*Thalassia testudinum*) - are currently restricted to Christmas Bay. Species richness of fishes and crustaceans was highest in Christmas Bay (Zimmerman et al., 1990).

Species distribution and relative abundance within seagrass beds are apparently related to water transparency, salinity, temperature, substrate, bottom topography and depth (Schomer et al., 1990; Kantrud, 1991). In Tampa Bay, seagrass species exhibit distinct zonation patterns relative to depth and salinity. No studies of this nature have been conducted in Galveston Bay.

Temporal Variation: Standing crops of these species peak at different times of the year (Pulich et al., 1991). Widgeongrass, water nymph, and pondweed peak in July; wild celery peaks in October. Heavy grazing by ducks and coots leads to the rapid disappearance of SAV by mid-fall. In Christmas Bay, widgeongrass and shoalgrass coexist in the same meadows but widgeongrass is more prevalent during spring and shoalgrass dominates later in the year (Pulich and White, 1989). All species die back during the winter, making a substantial contribution of detritus on the bay bottom. At the Trinity River delta, species richness of fishes within the habitat peaked in spring while that of crustaceans peaked in the fall. In Christmas Bay, species richness of fishes within the habitat was highest during summer and fall while crustaceans peaked in the fall (Zimmerman et al., 1990).

Habitat Subsystems: There are no habitat subsystems but the relative abundance of "seagrass" or SAV species in the meadow patches has not been determined.

Productivity: Standing crop biomass at the Trinity River delta has been reported as 47-205 g dry wt/m^2 for wild celery, 30 g dry wt/m^2 for widgeongrass, 69 g dry wt/m^2 for water nymph, and 70 g dry wt/m^2 for pondweed (Pulich et al., 1991). The number of fish and crustacean macrofauna per 2.8 m^2 of meadow for various sites and seasons are provided in the same reference. Gloyna and Malina (1964; cited in TDWR, 1981) provide estimates of primary production ranging from 4 to 34 g/m^2/day.

Based on 10 cm diameter (78.5 cm^2) core samples, the data of Czapla (1991) extrapolate to standing crop biomass of *Halodule wrightii* as 8-24 g dry wt/m^2, and *Halophila engelmanni* up to 6.4 g dry wt/m^2, in Christmas Bay. Percentages of below ground biomass to total biomass ranged from 65 to 86 percent for *Halodule*. Densities and numbers per core for the major faunal categories are also provided in the same reference.

Limiting Factors: Water transparency
Salinity
Temperature
Substrate
Bottom topography
Depth
Nutrients

Key Species: The various species of submergent vegetation are obviously key to this habitat for in their absence the habitat does not exist, and the habitat is seasonally absent after autumnal harvest by herbivores and winter die-back.

Peripheral Marsh

Approximately 61% (142 miles) of the Galveston Bay shoreline is vegetated by intertidal emergent plant communities (Paine and Morton, 1991). These marshes are uniquely subjected to predictable, periodic subsidies of tidal energy (importing nutrients and exporting waste products) as they are inundated by bidirectional flooding once or twice each day. The landward limit of the high tide line is highly dynamic, influenced by diurnal, or subequal semi-diurnal, tidal exchange, the declination of the moon, and seasonal climatic variation (which alter wind direction and atmospheric pressure). Flow in the adjacent upland watershed is unidirectional, influenced by gravity (Wiegert and Freeman, 1990). Flow onto and off the marsh watershed, and through the interstitial pore space of the sediment, results from both gravity and tides.

Intertidal marshes are highly productive. Where they have not been disturbed by construction, transportation, or energy-extraction activity, they appear to be the ecosystem least affected by human agriculture or industry. With their soft substrates and twice-daily tides, they are not very suitable habitats for large grazing herbivores, such as bison or cattle. Unlike the continental grass, desert or forest ecosystems, the extinction of large herbivores did not alter the vegetational composition and productivity of intertidal marshes. While they can be converted by extensive and expensive modification to create agricultural habitat, there has been no shortage of agricultural land in the Galveston Bay area to drive such conversion. Yet since the 1950s, 25,400 acres of emergent wetlands around Galveston Bay have been converted to upland rangeland, and 3,600 acres to cropland and pastureland (White et al., 1993). In addition, the osmotically-stressed intertidal system is not an easy target for the invasion of extraneous plants and animals (Wiegert and Freeman, 1990). Only in freshwater tidal lands have introduced species, such as water hyacinth and nutria, caused physical obstruction and destruction. Thus the brackish and saltwater marshes represent a remnant "wilderness" surrounded by greatly modified ecosystems.

Emergent marsh plants exist in three worlds - air, water and sediment (Figure 16). Their culms and leaves are continually exposed to direct sunlight, neither filtered nor attenuated, the basal stem is bathed in water, while their roots are anchored in anaerobic sediments. They are able to extract or interchange abiotic carbon from all three environments and their physical presence promotes the production of biotic carbon in four different compartments. As photosynthesizers, the emergent macrophytes produce carbon molecules that support a grazing, herbivorous, terrestrial food chain. Typically, only about 10% of this primary production is incorporated into the grazing food chain. The remainder is diverted to the detrital food web. The enormous productivity and detrital pathways of these marshes have long been recognized. Frequently overlooked is the fact that secondary production by the primary consumers of this green plant material is one of the largest of any terrestrial system studied (Wiegert and Freeman, 1990).

The closely ranked stems of the emergent plants create a habitat that supports epiphytic algae and shelters phytoplankton and epibenthic algal assemblages. These, in turn, support additional grazer and planktivore food webs which incorporate important fishes and crustaceans, including forage fish, juvenile game fish, shrimp and crabs. The outpouring of bacteria and plankton on the falling tide support adjacent oyster beds and reefs, while seagrass meadows shelter small fishes returning from intertidal zone foraging. Irregularly flooded brackish marshes depend on rainfall and slow drainage to transport carbon compounds to bay waters (Borey et al., 1983; Hall and Fisher, 1985).

Spatial Variation: On a macro-scale (bay-wide) emergent marshes are most influenced by the estuary salinity gradient. The most widely accepted subdivision of the salinity gradient is that of Cowardin et al., (1979): fresh <0.5 ppt salinity, oligohaline 0.5-5 ppt, mesohaline 5-18 ppt, polyhaline 18-30 ppt, euhaline 30-40 ppt, hyperhaline >40 ppt. While this classification defined brackish as mixohaline (0.5-30 ppt), other authors treat brackish as synonymous with polyhaline when describing marsh vegetation. Although the salinity gradient is virtually continuous, the boundaries of the various communities can be sharp (Wiegert and Freeman, 1990). On a micro-scale (an individual marsh) the type of marsh community which develops is largely determined by the depth and duration of inundation, which depends on the slope and elevation of the land surface. Recent calculations suggest that Galveston Bay marsh habitat was flooded about 80% of the time during 1900-1991 (T. Minello, pers. comm.). Wind modification of complex tidal patterns in this estuary render tide predictability haphazard at best.

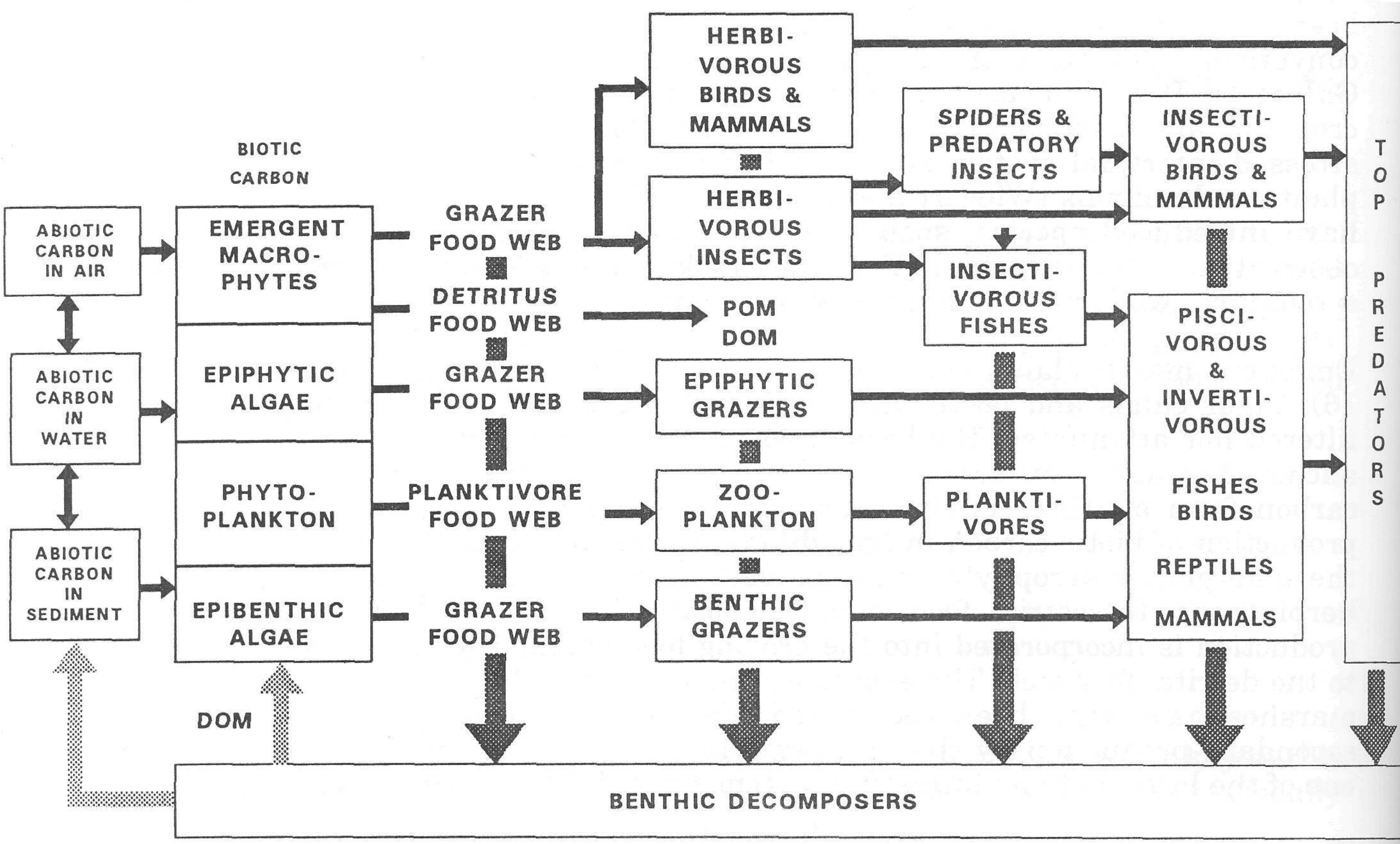


Figure 16. The connectivity of marsh habitat.

The salinity gradient typically runs lengthwise along the estuary, from the point of freshwater inflow to the gulf passes. The gradient also runs laterally, from the bay shoreline to the adjacent uplands. The upslope vegetation is subjected to flooding less frequently and for shorter duration. Combined with precipitation runoff from the adjacent uplands, water salinity may be lower, although soil salinity may be higher, due to greater evaporation from exposed soil at low tide. Where topography results in occasional-to-rare flooding of low-lying areas, hypersaline conditions are created by evaporation and halophytic plants predominate, or unvegetated salt pans may develop.

Plant species richness and diversity are inversely correlated to salinity. Interspecific competition also structures plant communities. For example, smooth cordgrass (*Spartina alterniflora*) seems to grow best at very low salinity but it rarely occurs at these locations. This species appears to be stressed at salinities greater than 25 ppt, but less so than its competitors, and nearly pure stands of smooth cordgrass can be found at high salinities. In addition, smooth cordgrass responds to its position within the marsh. It reaches its greatest aboveground height, biomass and net productivity along levees and creek banks. At higher elevations, where the duration of inundation is lessened, the plant is much shorter and less productive. Multiple edaphic factors seem to be involved (Wiegert and Freeman, 1990) but there are distinct <u>edge effects</u> in both *Spartina* and *Juncus* marshes. White and Paine (1992) provide species lists for dominant plants of various marshes and localities around Galveston Bay.

<u>Temporal Variation</u>: Ecologically, there are distinct differences between various marsh types. Smooth cordgrass (*Spartina alterniflora*), an indicator species for salt marshes, dies each winter but remains standing. The dead culms continue to provide substrate for epiphytic algae and physical cover for small animals before slowly descending into the water where decomposition can accelerate. Thus a slow, nearly continuous source of detritus is provided to decomposer organisms even though production of the grass is seasonal. Black needlerush (*Juncus roemerianus*), which occurs in patches upslope and upstream from the cordgrass, remains standing, green, and photosynthetically active throughout the year; individual shoots may stand for 2 to 4 years before dying (Stout, 1984).

Tidal freshwater marshes are characterized by a large and diverse group of broadleafed plants, grasses, rushes, shrubs, and herbaceous plants (Odum et al., 1984). All of the species die at the end of the growing season and the habitat essentially disappears over the winter, resulting in 100% turnover of plant material annually. Plants of the low marsh decompose very rapidly; those of the high marsh have much slower rates of decomposition. As a result, the low marsh releases a pulse of nutrients to the estuary during the winter, while the high marsh maintains a seasonal litter layer over the winter and releases its nutrients to the estuary in spring. The species composition of high and low freshwater tidal marshes can change during extended periods of drought or flooding.

<u>Habitat Subsystems</u>: All of the emergent marshes have elevational and salinity gradients, frequently with distinct borders marking a transition from one

dominant species to another. These zones exhibit characteristic growth and decomposition patterns.

Productivity: Fisher et al. (1972) reported primary productivity of 820 g dry wt/m^2/yr for freshwater marsh and 1100 g dry wt/m^2/yr for salt-brackish marsh in Galveston Bay. Hall and Fisher (1985) reported net annual aerial productivity of 550-900 g C/m^2 for *Spartina patens* and *Distichlis spicata* in an irregularly flooded brackish marsh on East Bay, and 71 g dry wt C/m^2 for a dense epibenthic blue-green algal mat in the same marsh. Borey et al. (1983) reported 1100-1800 g dry wt/m^2/yr net aerial primary production for a similar nearby marsh. Adams (1977) reported average annual net production of 819.5 g dry wt/m^2 for the Trinity River delta, ranging from 215 g dry wt/m^2 for arrowhead (*Sagittaria graminea*) to 2984 g dry wt/m^2 for common reed (*Phragmites communis*) (reported in TDWR, 1981). The same study reported net periphyton production as 0.155 g dry wt/m^2. Sears (1981) estimated net aerial primary productivity for *Spartina alterniflora* as 1847-2078 g/ m^{2}using several methods.

Limiting Factors: Nutrients
Tidal exchange
Soil and water salinity

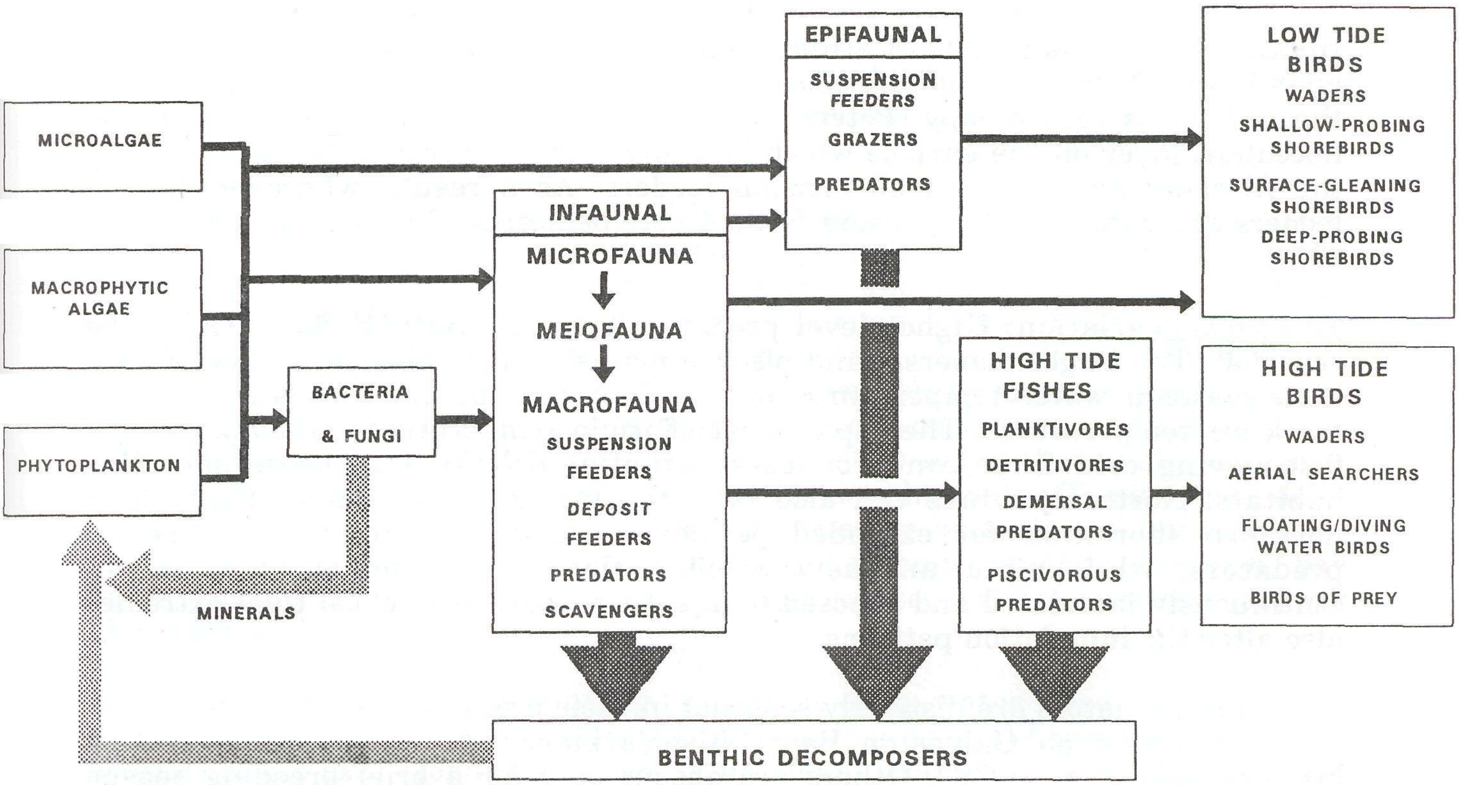
Key Species: There appear to be sufficient salt-tolerant plants so that no one species dominates to the extent that a given category of marsh would be nonexistent in the absence of that species. Smooth cordgrass, at the upper salinity limit and deepest edge of the marsh, is the closest approximation of a keystone species (see glossary).

Intertidal Mud Flat

The intertidal mud flat habitat is an exceptionally open ecosystem (Figure 17) both physically and biologically (Peterson and Peterson, 1979). It lacks the emergent grasses and other plants of the peripheral marshes, or the submerged grasses of the seagrass meadows. The flat is "vegetated" by microalgae, macroalgae and phytoplankton. Inputs of organic and inorganic material and detritus are important to its functioning. The only animals relatively fixed in position and restricted to a single habitat are the components of the benthic infauna and, to a lesser extent, the epifauna. The benthos is supported by primary production from outside of the habitat and imported via water currents and tidal action.

The components of the higher trophic levels appear temporarily. At high tide, planktivorous, detritivorous, and demersal fishes move onto the flats to feed, followed by piscivorous predators, both birds and fishes. At low tide, gleaning and probing shorebirds feed on the exposed surface while waders seek prey stranded in tidal pools. Overall, nutrients and organic particles (passively) and motile organisms endlessly move in and out of the habitat.

Figure 17. Connectivity of intertidal mud flat habitat.



Bacteria and fungi play an important ecological role in mineralization, converting dead organic matter to inorganic nutrients. They also serve as a trophic intermediate between relatively indigestible plants and consumers of plant detritus (Peterson and Peterson, 1979). These microbes consume indigestible cellulose and lignin, add protein, and transmit energy and nutrients to detritivores. Fecal pellets are again colonized by decomposers and cycled through detritivores once more. This process of microbial renewal on detritus may be an important rate-limiting step which determines the abundances of deposit-feeding species, such as snails, in the community.

The sediments of algal flats serve as a nutrient sink. Nutrients and other chemicals adsorb to sediment particles. In this shallow zone, the sediments are subject to resuspension by wave action and bioturbation from the many infaunal animals. Biodeposition by suspension feeders in the form of feces and pseudofeces adds to the nutrient bank. When chemical concentrations in the water column decline, the sediments give up their adsorbed nutrients to establish chemical equilibrium.

<u>Spatial Variation</u>: Position along the sloping, intertidal bottom will affect species distribution. The upper portions of the slope will have longer, potentially detrimental, exposures to the aerial environment at low tide. At high tide, phytoplankton will be "spread out" over a shallow euphotic zone rich in nutrients and minerals. The intertidal zone is a physically rigorous place to live.

Organisms are exposed to air, direct sun, and wind which lead to desiccation, and seasonally to overheating and even freezing, during most tidal cycles.

Infaunal species may interact strongly enough to affect distribution patterns and abundance. Deposit feeders are mobile and tend to increase the water content of the sediments they occupy (Peterson and Peterson, 1979). This creates a loose, flocculant layer on the surface which is easily resuspended and tends to clog up the filtering apparatus of suspension feeders. As a result, wherever deposit feeders are abundant, suspension feeders may be scarce (Peterson and Peterson, 1979).

Temporal Variation: Higher level predators on the intertidal flats tend to be seasonal. The larger demersal and piscivorous fishes may avoid very low or very high seasonal water temperatures, which fluctuate rapidly as shallow waters track air temperatures. The rapid onset of frigid temperatures accompanying a fast-moving cold front can produce substantial fish kills in these shoreline habitats. Northerly winds can also blow the water off of shallow flats along northern shorelines for extended periods, exposing the flats to terrestrial predators, while simultaneously keeping flats along the southern shore continuously inundated and exposed to aquatic predators. Cyclical tidal extremes also alter the inundation patterns.

Shorebird predators are distinctly seasonal in their presence and abundance. Few shorebirds nest on Galveston Bay (Wilson's plover, American oystercatcher, black-necked stilt, willet). Others are absent only for a brief breeding season (piping plover). Most shorebirds migrate through the area during spring or fall, or winter on the bay. Epifaunal and infaunal animals can be subjected to brief but intense predation from flocks of migratory shorebirds.

Habitat Subsystems: Other than the water depth gradient along the bottom slope, there are no subsystems of this habitat.

Productivity: There are no estimates of productivity, nor the areal extent, of this habitat in Galveston Bay.

Limiting Factors: Water transparency
Temperature
Tidal range
Nutrients

Key Species: There are no key species identified for this habitat.

Peripheral Marsh Embayment

Conspicuous features of the bay watershed topography are a number of shallow, soft-bottomed, unvegetated lakes which occur near the terminus of the drainage bayous. Examples are Salt Lake, Nick's Lake, Alligator Lake, Oyster Lake, Hall's Lake, Carancahua Lake, Greens Lake, and Swan Lake which are connected to West Bay and the Christmas Bay complex; Dollar Bay on Galveston Bay; Robinson

Lake on East Bay; and Cotton Lake, Lost Lake, and Old River in the Trinity River delta. Each of these water bodies is directly connected to the bay system, surrounded with distinctly-edged emergent marsh habitat. These bays are subjected to highly variable salinity. Their deep, unconsolidated mud bottoms, which poorly support the weight of humans, have inhibited scientific study of the systems. High turbidity, perhaps wind-generated, hinders the growth of submergent aquatic vegetation.

These embayments appear to be highly productive nursery areas. Conte (1971, 1972a,b) sampled Alligator and Oyster Lakes and reported brown and white penaeid shrimp, grass shrimp, sergistid shrimp, and 5 species of mysid shrimp. Minello and others (1991) collected brown shrimp, grass shrimp, blue crabs, pinfish and bay anchovies in Hall's Lake. Bay anchovies, gulf killifish, diamond killifish, spotted seatrout, spotfin mojarra, brown shrimp, white shrimp, grass shrimp, blue crabs, and mud crabs were collected in Carancahua Lake (McFarlane, unpubl.). Conner and Truesdale (1972) noted that shallow, turbid, soft-bottomed lakes and blind bayous of interior marshes of the Trinity River delta were the target habitats of many migratory marine animals. Atlantic croaker, gulf menhaden, sand seatrout, bay anchovy, hogchoker, pinfish, ladyfish, bay whiff, southern flounder, brown shrimp, and white shrimp were particularly abundant in these habitats.

With a high ratio of surrounding marsh to open water area, these marsh embayments appear ideally positioned to support a detrital-based food web. The benthos of the exceptionally soft, nearly flocculant, bottom sediment is unknown. Microbial decomposers undoubtably fill a critical ecological niche. Phytoplankton and zooplankton are unknown. The abundance and diversity of secondary consumers attests to the efficacy and productivity of the primary consumers. The vertical structure of the surrounding marshes provides protective cover for the smallest species and life stages while shallow open water excludes large predators.

No model has been constructed for this habitat due to insufficient information.

Spatial Variation: Unknown, but differences in salinity regime between upper bay and lower bay localities are anticipated.

Temporal Variation: Unknown, but differences in rainfall patterns and flooding regimes may produce seasonally distinct salinity regimes in Trinity River delta embayments, with seasonal flooding, versus lower bay area embayments, which receive less seasonal precipitation.

Habitat Subsystems: None known.

Productivity: Unknown, but anticipated to be high.

Limiting Factors: Unknown.

Key Species: Unknown.

Riverine/Floodplain Ecosystem Connection

Food webs in Galveston Bay are essentially of two types (Armstrong, 1987). One web is based on grazing carbon produced by photosynthetic plankton, as described for the open-bay water habitat. This web is pelagic, relatively simple, and involves few species. The second web is detrital-based. Some detritus is produced external to the bay ecosystem and transported to the bay with river and stream inflow. Other detritus is produced peripherally in the emergent marshes and seagrass meadows of the bay ecosystem. A third, and internal source, is planktonic "rain"; as outlined in the other habitat descriptions. Detritus-based food chains are more complex than grazing chains, with more links between consumers, and major roles for microbial populations.

Armstrong (1982) has calculated that freshwater inflows transport 96% of the carbon and nitrogen, and 95% of the phosphorus, reaching Galveston Bay, with the remainder contributed by peripheral marshes. This view is supported by another study of a marsh on East Bay which estimated that only 2-6% of net aerial primary production was exported to the bay (Borey et al., 1983). Yet 95% of the annual carbon flux within the bay is believed to come from phytoplankton (Armstrong, 1987). There are two types of carbon flux within the bay ecosystem. The first relates to carbon turnover within the bay water column; it is here that phytoplankton and the grazing food chain are most important. The phytoplankton support the pelagic grazers, the benthic suspension feeders of the oyster reef and open-bay bottom communities, and contribute detritus to the benthos as well. The second carbon flux involves carbon imported from the riverine floodplain and peripheral marshes. This carbon has been likened to the flywheel of a reciprocating engine; it provides sufficient energy and material to keep the engine going (G. Ward, pers. comm.). The relative importance of plankton versus detritus as the base of secondary productivity in the bay deserves further study. While imported detritus is certainly important to the benthos near river termini and adjacent to marshes, the extent of its contribution to community metabolism in the center of the bay is unknown. Certainly detritivores are both prominent and dominant components of the ecosystem.

Nutrients in lentic ecosystems, such as lakes and reservoirs with slow-moving water, tend to cycle, from dissolved forms into vegetative forms, then detritus forms, to sediment forms, and back to dissolved forms, etc. They remain in place for extended periods or very slowly move downstream. Nutrients in lotic ecosystems, such as fast-moving streams and rivers, also cycle in a similar manner but, while doing so, they are displaced downstream more rapidly. Thus nutrient cycles are stretched into "nutrient spirals" in riverine ecosystems (National Research Council, 1992).

Streams and rivers are longitudinally linked systems, and processes which take place upstream have impacts on downstream components. The biological community changes in a predictable manner, responding to changes in channel geomorphology and available resources. Much of the degradation of organic matter occurs in moderate sized channels, and lateral linkages to the riparian zone are as vital as the longitudinal links of the river continuum (Meyer, 1990).

Floodplains play a critical role as sediment and nutrient filters and as habitat for fishes at certain life stages.

Microbial organisms are critical components in the sequential decomposition of leaf litter to coarse, then fine, particulate organic matter (Figure 18). Nutrient export from river floodplains is pulsed. Leaves from terrestrial plants and trees are seasonally dropped to the forest floor where leaching and disintegrative processing begins. Overbank floodwaters and dewatering redistribute this organic material downstream, at times sweeping the forest floor clean of leaf litter. At least two microbial loops are involved in the decomposition process. Microbial loops are fueled by dissolved and particulate detritus that is consumed by bacteria, which then become food for protozoa and other organisms. Shredding insect larvae in the unstable stream and river sediments participate in reducing detrital particle size and harvesting attached microbes. Grazers and filtering or gathering collectors inhabit stable substrates, such as snags and logs. Dissolved (DOM), coarse particulate (CPOM), fine particulate organic matter (FPOM), and invertebrate drift organisms are exported to downstream habitats.

Spatial Variation: The path taken by water as it flows through the terrestrial ecosystem, both as surface water and shallow groundwater seepage, will determine its elemental composition when it reaches the stream. Elemental cycling in lotic ecosystems is continuously displaced downstream by flowing water, interrupted by overbank displacement and temporary storage during flooding events. Floodplains alternately serve as sinks and sources of chemicals.

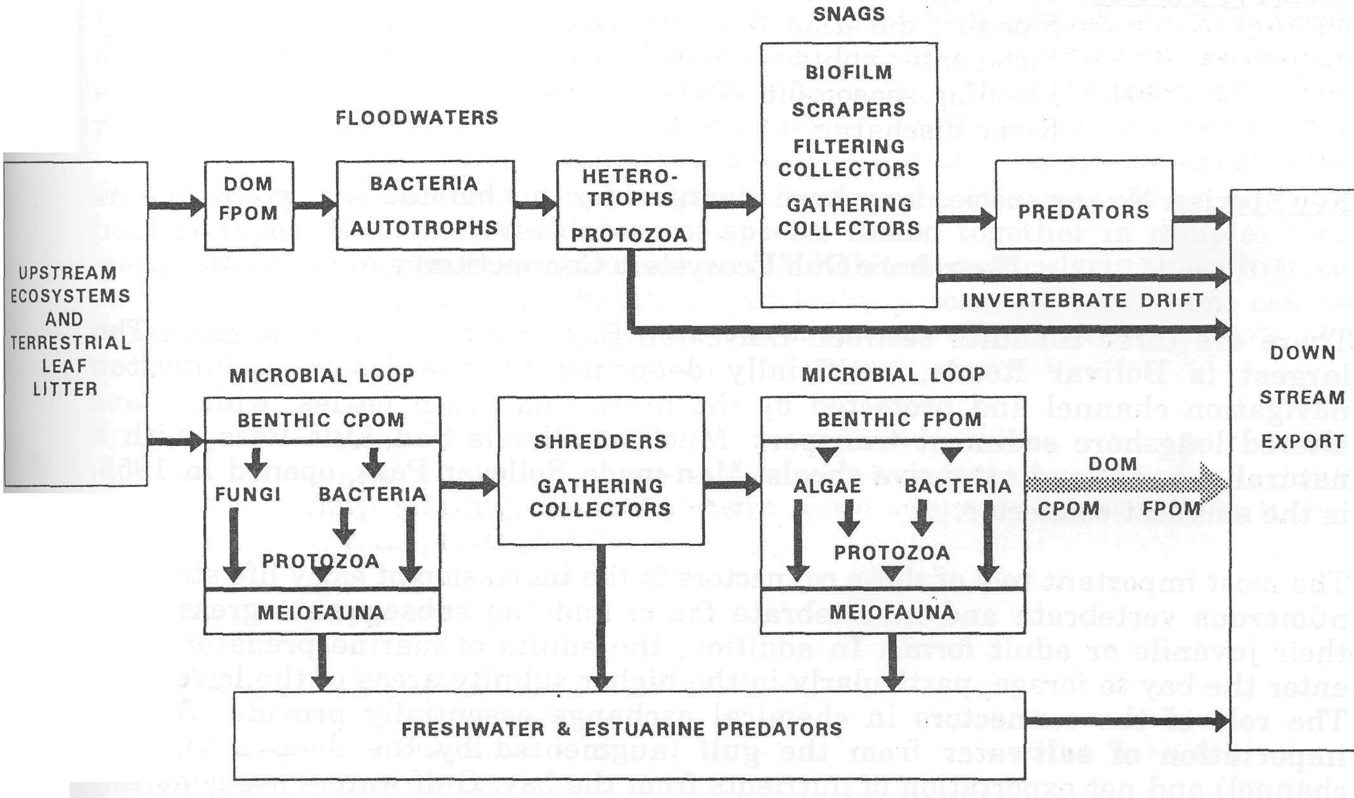


Figure 18. Connectivity of the riverine/floodplain habitat.

Streams are a mosaic of different substrate patches. Substrate is a determinant of species distributions. Stream morphology and discharge volume influence bottom sediment distribution and discharge velocity. Habitats are distinguished by substrates of different stability - shifting sands, muddy sediments, and stable woody debris. For the most part, the food webs are heterotrophic mosaics.

Bottomland forests have characteristic alluvial floodplain microtopography involving channel, bank levee, first and second terrace flats and ridges, etc. (Wharton et al., 1982) which influences plant cover types and biogeochemical cycling.

Temporal Variation: The export of nutrients and drift organisms from rivers and riparian wetlands is influenced by the hydrologic regime and antecedent conditions. Exports will be greater during wet years, but a wet year preceded by one or more dry years, when organic matter was stored, may produce a large export pulse.

Habitat Subsystems: Tributary streams, mainstream channels, bottomland hardwood forests, cypress swamps, and freshwater marshes are all components of the riverine/floodplain habitat mosaic.

Productivity: Sheridan et al. (1989) indicate an estimated average primary productivity of 700 g dry wt/m^2/yr for woodlands/swamps.

Limiting Factors: Flooding frequency
Flooding duration
Floodwater volume
Flooding seasonality
River discharge

Key Species: No key species have been identified for this habitat.

Nearshore Gulf Ecosystem Connection

There are three conduits between Galveston Bay and the Gulf of Mexico. The largest is Bolivar Roads, artificially deepened by the Houston-Galveston navigation channel and protected by the north and south jetties, which have altered longshore sediment transport. Much smaller is San Luis Pass, with a natural channel and extensive shoals. Man-made Rollover Pass, opened in 1955, is the smallest connector.

The most important role of these connectors is the ingression of early life stages of numerous vertebrate and invertebrate fauna and the subsequent egression of their juvenile or adult forms. In addition, the adults of marine predators may enter the bay to forage, particularly in the higher salinity areas of the lower bay. The role of the connectors in chemical exchange essentially provides for the importation of saltwater from the gulf (augmented by the deep navigation channel) and net exportation of nutrients from the bay. Gulf waters are generally considered to be nutrient-poor. A distinctly visible mixing zone of bay water extends into the gulf at Bolivar Roads and San Luis Pass except during periods of exceptionally low freshwater inflow.

Intracontinental Ecosystems Connection

Galveston Bay's aquatic habitats, like the surrounding terrestrial habitats, are inhabited by more avian species in the winter than during the summer. These habitats provide important wintering and migratory foraging sites for many kinds of birds. Many arctic-nesting birds winter here or arrive after long trans-Gulf flights on their way northward. The buildup or restoration of energy reserves is critical to their reproductive success on arctic nesting grounds (Ankney and MacInnes, 1978).

Birds recycle nutrients within habitats (ingesting protein, fat, carbohydrate, etc. and egesting inorganic compounds), transfer nutrients between bay habitats (from foraging sites to roosting and nesting sites) and export nutrients to nesting or wintering areas.

Spatial Variation: The morphology and foraging behavior of the various groups of water birds restricts them to certain habitat types (Table 3), thus influencing their distribution in the Galveston Bay ecosystem. Tidal stage may restrict their use of specific habitats to flooded or exposed-surface time periods.

Temporal Variation: Most of the herons, egrets and ibis nest in the Galveston Bay area and occur year-round. Very few waterfowl and shorebirds nest locally, and most species exhibit distinct seasonality in both presence and abundance (Table 4). Flocks of herbivorous, piscivorous, and invertivorous birds can exert substantial harvesting pressure when they descend on concentrations of marsh plants and prey organisms.

In summary, the Galveston Bay ecosystem is composed of at least seven different habitat types. Each involves dozens of species linked together in complex food webs. Many organisms utilize more than one habitat, particularly those highest on the food chain. Additional habitats, particularly zones of transition, can be described.

Table 3. Bird use of bay habitats (asterisks).

	OPEN BAY WATER	OPEN BAY BOTTOM	S A V	OYST REEF	EMER MARSH SW	EMER MARSH FW	ALGAL FLAT	EMBAY MENT	RIVER FLOOD PLAIN
Aerial Seachers:									
Terns	*				*	*	*	*	
Gulls	*								
Brown Pelicans	*								
Floating Birds:									
Dabbling Ducks					*	*		*	*
Geese					*	*		*	*
White Pelicans	*								
Diving Birds:									
Diving Ducks	*	*	*						*
Grebes	*	*	*					*	
Loons	*	*							
Cormorants	*	*							*
Waders:									
Herons, Egrets					*	*	*	*	*
Ibis					*	*	*	*	*
Shorebirds:									
Surface-gleaning					*	*	*	*	*
Shallow-probing					*	*	*	*	*
Deep-probing					*	*	*	*	*
Oystercatchers				*					
Residents:									
Rails					*	*			
Seaside Sparrows					*	*			
Marsh Wrens					*	*			

Table 4. Seasonality of waterbird occurrence. Presence is indicated by a single line, presence in abundance by a double line.

```
Month                          J  F  M  A  M  J  J  A  S  O  N  D
------------------------------------------------------------------
Common Loon                   ------------                  -----
Pied-billed Grebe             -------------           -----------
Eared Grebe                   =============                ======
White Pelican                 =============          ============
Double-crested Cormorant      =========----                 -====
Olivaceous Cormorant                  --------------------
White Ibis                              --------------------
White-faced Ibis                          -----------------
Fulvous Whistling Duck                   -==--------======--
Black-bellied Whistling Duck                --------------
White-fronted Goose           ======--                    --=====
Snow Goose                    ======--                    --=====
Canada Goose                  --------                    -------
Green-winged Teal             ============                 --====
Mottled Duck                  -----------------------------------
Mallard                       ----------                      ---
Pintail                       ============--          -==========
Blue-winged Teal              ---=========---      -=========----
Shoveler                      =============--         --=========
Gadwall                       ============                 -=====
Widgeon                       ----------                   ------
Canvasback                    ----------                     ----
Ring-necked Duck              ---------                      ----
Lesser Scaup                  ------------                   ----
Bufflehead                    ---------                       ---
Red-breasted Merganser        ------------                    ---
Ruddy Duck                    ------------                   ----
Black-bellied Plover          =============-----------===========
Golden Plover                           ====
Wilson's Plover                     ----------------------
Semi-palmated Plover          --------------         ------------
Piping Plover                       ------             ------
Killdeer                      ===================================
Black-necked Stilt            ---------==================--------
Avocet                        ------------           ------------
Greater Yellowlegs            =========-----       -----=========
Lesser Yellowlegs             ------======         -======-------
Willet                        ===================================
Long-billed Curlew            ------=======        -========-----
Ruddy Turnstone               --------=======       ===========--
Sanderling                    ============------------===========
Semi-palmated Sandpiper                 -===-      -=====---
Western Sandpiper             ===============       =============
Least Sandpiper               ---------------      --------------
Dunlin                        ------------                -------
Short-billed Dowitcher                -----        ----
Long-billed Dowitcher         =============      --==============
Common Snipe                  ==========---              ========
------------------------------------------------------------------
```

=== Abundant   --- Common   Source: Dauphin et al. 1989

IV. INTERCONNECTEDNESS OF THE ECOSYSTEM

Section II described the seven distinct components, or habitats, that comprise the bay ecosystem; how the bay ecosystem is influenced by, and dependent upon, its watershed; and how the bay ecosystem is connected to its adjacent ecosystems, the riverine/floodplain and nearshore gulf, and distant ecosystems on the continent. Section III outlined the elements and connectivity within each of the habitat components. While the biotic elements of each habitat were emphasized, the abiotic constituents are equally important. The populations of organisms are responding to the availability of chemical materials, physical substrates, and other elements.

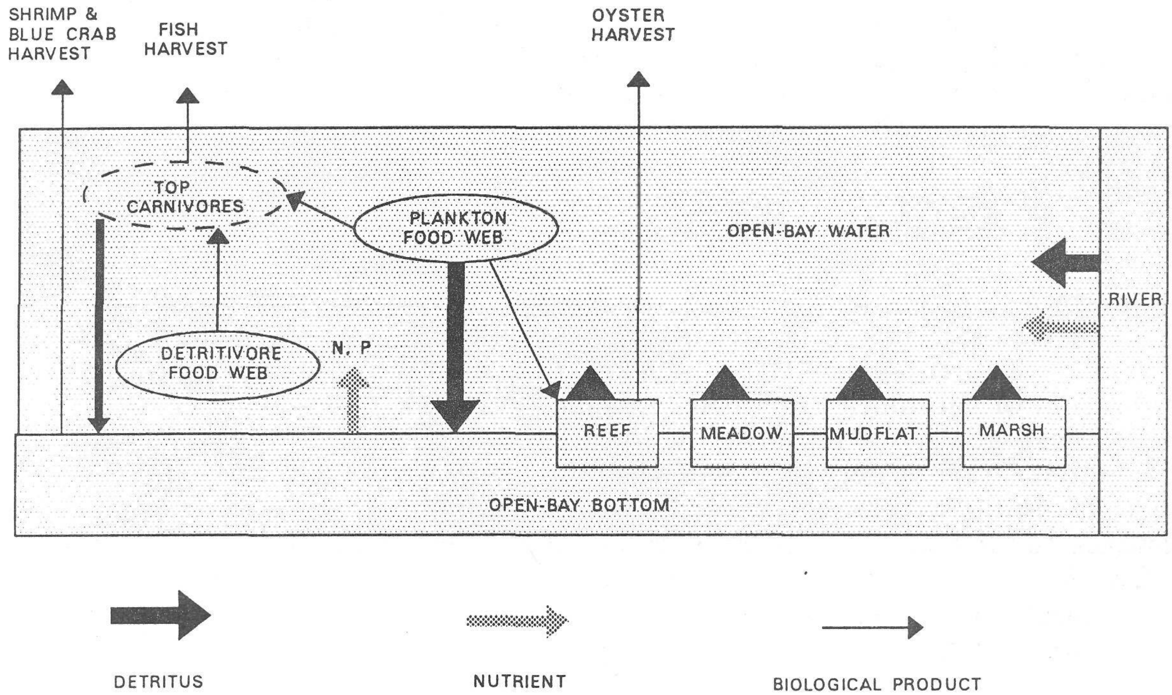
Each system exhibits not only the characteristics of its components, but also characteristics of its own which arise from combinations and interactions of the components (TGLO, 1976). Humans are most concerned with the exploitation and preservation of the biotic constituents for commercial harvest and recreation. To achieve these goals, we must be aware of the interconnectedness of the system. The common link which connects the biological and nonbiological entities is energy. Energy acquisition and use is basic to every organism. There is a network of connections between the populations of the different species which inhabit the bay. The food web is the most conspicuous connection but more complicated and subtle linkages with heat, salinity, nutrients, sediment and other components are equally important.

The bay ecosystem has been defined as an interacting, interdependent group of components, functioning as a whole. Each component has characteristics, but is linked to, may influence the control of, or be controlled by, other components (TGLO, 1976). Recognition of these control mechanisms is vital to our management of the bay.

The basis for organization within any ecosystem is the food web. Physical energy, in the form of sunlight, is captured by **primary producers** or plants that transform the physical energy into chemical energy by the process of photosynthesis. The primary producers vary in each habitat. It is terrestrial vegetation in the watershed, emergent plants and both benthic and epiphytic algae in marshes, phytoplankton in the open-bay and nearshore gulf, submergent plants and epiphytic and benthic algae in seagrass meadows, benthic algae on shallow open-bay bottoms and mudflats, and crustal algae on shallow oyster reefs. The chemical energy is stored as organic compounds in all of these primary producers.

The size range of primary producers is very broad, from microscopic single-cell phytoplankton to large multi-celled macrophytes in seagrass meadows and marshes. Following death, the primary producer plants attract **decomposer** organisms such as microscopic bacteria and fungi. This is a vital stage in the food web for many of the larger consumers cannot digest the energy-containing chemical compounds found in plants until they have been processed by microorganisms that have the requisite digestive enzymes. The mixture of dead

Figure 19. Detrital transport in the Galveston Bay ecosystem. Detritus is generated in the open-bay water habitat and imported from the reef, meadow, marsh, and mudflat habitats and the riverine/floodplain ecosystem.



plant material covered with decomposer organisms is called **detritus** and it is an important energy storage mechanism in the ecosystem.

Both pelagic grazing and detrital food webs are prominent in the ecosystem. The importance of detritus to the ecosystem is shown in Figure 19. Nutrients enter from the riverine connections, are regenerated by the benthic microbial community, and are extracted from the atmosphere (as carbon dioxide). The plankton-grazing food web supports the oyster harvest and contributes, via intermediaries, to the fish harvest. Detritus input comes from the rivers and all other habitats. The detritivore food web supports the shrimp and blue crab harvest and contributes to the fish harvest.

The next level of the food web is composed of **primary consumers**, organisms which eat the primary producers. Since the primary producers are either macrophytes (such as submerged aquatic vegetation) or microphytes (such as phytoplankton), primary consumers are herbivores. In one sense, the decomposers which feed on primary producers are also primary consumers, as are detritivores. Some primary consumers also feed on other primary consumers and thus become omnivores. The third trophic level includes the **secondary consumers**, or carnivores, animals that only eat other animals. Primary and secondary consumers, and their egested material, are linked to the decomposers as well. Often it is difficult to designate a given species to a single consumer level. For the purposes of this discussion, all consumers will be aggregated into a single consumer category.

The inputs for any trophic structure are energy and materials. The dominant source of energy is sunlight, either direct or indirect. Sunlight reaches the terrestrial landscape and the subaerial portion of the marshes unimpeded. It is rapidly attenuated in the subaqueous habitats, and functional only at relatively shallow depths in the estuary. Materials can be generally categorized as freshwater, inorganic nutrients, organic matter, and sediment.

Figure 20 illustrates the flow of energy and materials in the estuary and its adjacent ecosystems, the riverine floodplain and nearshore gulf. Freshwater arrives as precipitation and surface runoff. Its quantity, seasonality, and point of entry establish the salinity gradient in the estuary. In addition to this critical role, it also transports inorganic nutrients, organic matter, and sediment. Thus freshwater inflow directly regulates the transport of the other material to the estuary. If inflow is inadequate, or inappropriately timed, it acts as a **constraint** on other material inflow. These constraining mechanisms have been described as "work gates", for a small amount of expended energy in the water movement controls a great deal of potential energy in the organic chemical bonds (TGLO, 1976). Note that the riverine inflow also regulates the input of inorganic nutrients and organic matter from the delta marsh, via the flooding regime.

Similarly, wind or tidal action can exert widespread effects. Tides carry inorganic nutrients to marshes and remove organic matter and waste products. Winds can resuspend bottom sediments that reduce water transparency and affect photosynthesis in seagrass meadows, by benthic algae, and in open-bay waters (Figure 20). The equilibrium between suspended sediments and bottom sediments is bidirectional. The combination of high tides and winds can push sediment into marsh areas where it is entrapped. Because sediments often have inorganic nutrients (and pollutants) adsorbed to them, this can result in nutrient storage (TGLO, 1976). Suspended sediments can affect the biota as well, clogging the feeding mechanisms of various filter feeders (such as oysters or clams), or burying smaller benthic infauna. In either case, the energy flow from producer to consumer, or primary to secondary consumer, can be interrupted.

Some constraints can be long-lasting. As sediment is trapped in a salt marsh, the level of the marsh gradually rises. The vegetation may shift from smooth cordgrass (*Spartina alterniflora*) at a lower level to gulf cordgrass (*Spartina patens*) on higher ground. Not only is gulf cordgrass less productive (fewer pounds per acre of grass produced) than smooth cordgrass, but it will be flooded less frequently (requiring higher tides) which reduces tidal transport of nutrients and detritus back into the estuary (TGLO, 1976). Some marshes may become totally drained at low tide, causing motile species to seek refuge on featureless bottoms where they are vulnerable to predators. Thus shrimp or small forage fishes may be eaten when they are very small, reducing the transfer of biomass between trophic levels.

The transfer of biomass varies between habitats (Figure 20). In the autotrophic nearshore gulf, seagrass meadow, and peripheral marsh habitats producers (P) are eaten by consumers (C) or contribute to detritus (D) reserves; detritivores (primary consumers) are also eaten by other (secondary) consumers. The

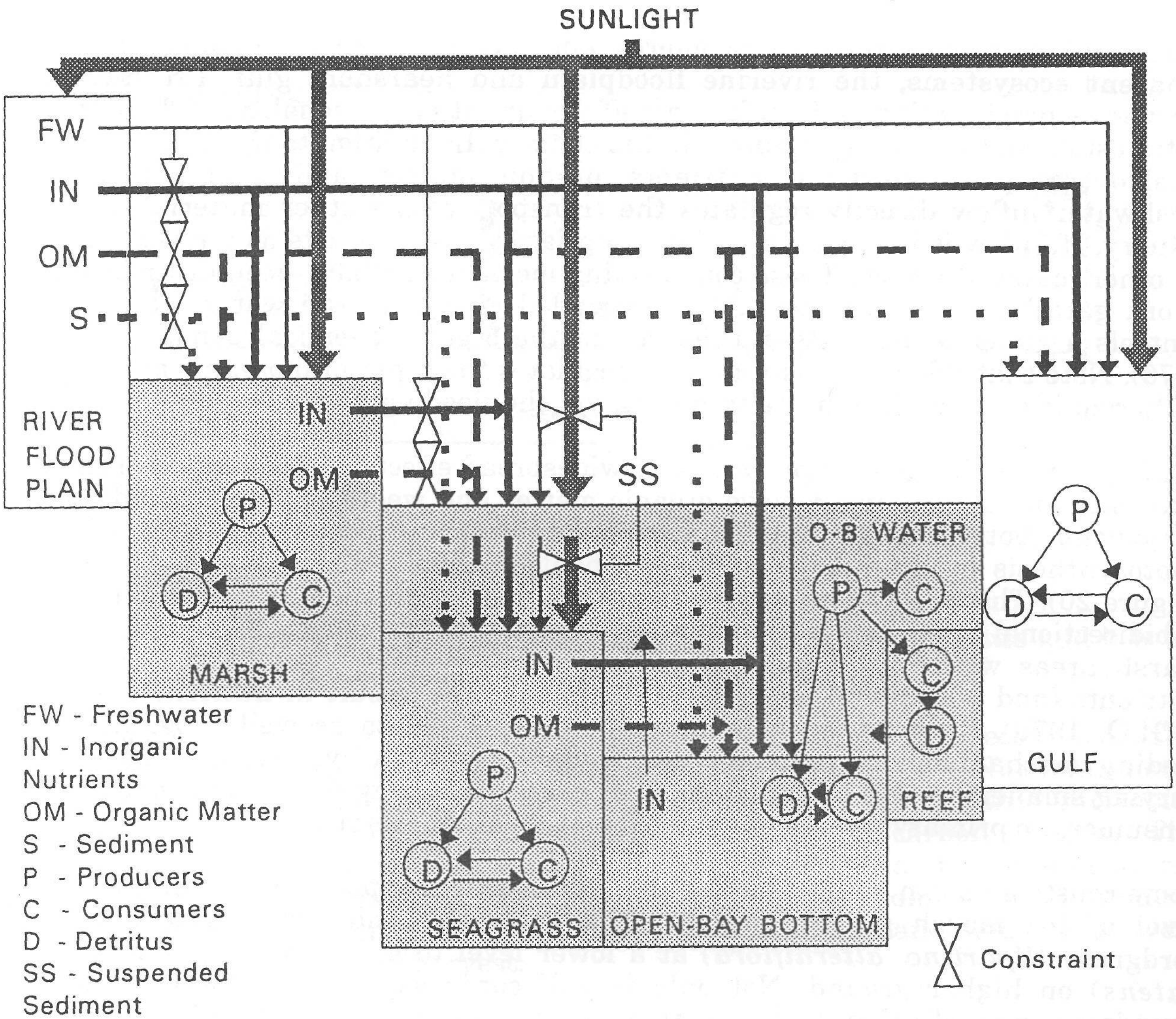


Figure 20. Ecosystem constraints. The movement of freshwater, inorganic nutrients, organic material and sediment to various ecosystem habitats passes through various physical workgates which regulate flow.

autotrophic open-bay water habitat supports pelagic consumers and the heterotrophic open-bay bottom and oyster reefs. On healthy reefs with strong currents, oyster-generated detritus is swept away to bottom habitat. Everywhere one chooses to look, a physical factor can be found that constrains another physical or some biotic factor. Salinity and temperature are universally important in coastal waters.

Individual diagrams showing inputs, outputs, transformations of energy, storage of energy or materials, and controlling factors can be, and should be, constructed for each habitat and ecosystem. Two important observations can be made (TGLO, 1976). First, every ecosystem has a complicated network of pathways and controlling mechanisms which connect organisms and storage compartments. Changing the flow of energy or material in any one pathway will likely result in a change in storage or energy flow through the transforming organisms. Second, there are numerous interdependent connections between ecological systems. Flows of energy and material, as well as controlling factors within each ecosystem, are complex and the result of forces both within and without the system. These ramifications confound human attempts to manage ecosystems.

Spatial Variation of Bay Productivity

Bellis (1974), using data from Galveston Bay and three other estuaries, proposed that the middle reach of an estuary possesses an assemblage of interrelated characteristics such that the concept of a "middle estuary" as a subsystem is useful. He suggested that the middle estuary, with salinities of 5 to 18 ppt, provides the primary support for blue crab, oyster, and shrimp fisheries.

Zimmerman and others (1990) found that the highest numbers of penaeid shrimp, blue crab and commercial fishes were in marshes of the middle and lower bay. Benthic crustaceans which were the prey of these species were also at greatest abundance in these marshes. These authors described the bay interconnectedness as follows:

> "Low salinity (oligohaline) marshes in the upper bay (especially at the Trinity Delta) exported large amounts of organic material to the middle bay. The plants of the river delta defoliate each winter and the entire standing crop is exported downstream. Enriched plant detritus in the middle system increases the productivity of epibenthic detritus feeders (such as peracarid crustaceans) and these were foraged by juveniles of commercially valuable fishes, shrimps and crabs. Because both the marsh and the subtidal bottom in the middle bay had high abundances of forage organisms, the entire area was valuable nursery habitat. The moderate influence of mesohaline to polyhaline salinities in the middle bay also encouraged utilization by consumers. In the lower bay, algal carbon was another base for secondary productivity in marsh and seagrass habitats heavily epiphytized by algae. Finally, the interconnections between the different systems of the bay appeared to be critical to maintaining overall fishery productivity." (Zimmerman et al., 1990).

The mid-bay region was described as the frontal zone where nutrients from the upper bay mixed with immigrating recruits from the lower bay. Organic detritus from the upper bay was an apparent energy source for food chains in the middle bay. The middle bay also supports the greatest concentration of oyster reefs.

In essence, there is no part of the bay which can be "written off" as deserving less protection or vigilance. The upstream riverine ecosystems provide freshwater that maintains the salinity gradient, nutrients that support bay productivity, and sediments which maintain delta marshes. The freshwater marshes are unique habitats which seasonally defoliate completely and provide detritus and nutrients to the middle bay. The saltwater marshes provide detritus, nutrients, and perennial habitat structure which nurture juveniles of important commercial and recreational species. The oyster reefs support a unique community of significant commercial importance. The seagrass meadows, although nearly gone, provide an alternative plant community and sheltering habitat which annually defoliates. The mudflats provide unique access for upper level consumers. The open-bay bottom, although less productive, recycles important nutrients to overlying waters and, by sheer areal extent, supports important detritus-based food webs and commercial harvest, particularly the larger size classes of important organisms. The open-bay water is the only habitat to have significantly increased in size (by 30% in volume, due to subsidence and sea-level rise; Ward, 1993). The open-bay water habitat is the matrix for the grazing food web and connector to all other habitats. Finally, the nearshore gulf is the source of most larval organisms, as well as major predators, and habitat of the ultimate fishery.

V. PERTURBATIONS AND THEIR MANAGEMENT

Burton (1991) has defined **disturbance** as a discrete event that alters community structure and changes the physical environment and resource availability. A **perturbation** is a disturbance of equilibrium (Webster's Ninth New Collegiate Dictionary). Although equilibrium would appear to be a state which an estuary seldom attains, perturbation is a useful term which implies a greater intensity or effect than a disturbance.

Ward and others (1982) defined perturbation as "any activity that represents a departure from the normal state and can potentially result in effects upon the fish and wildlife resources of [Galveston Bay], either directly upon the organisms involved, or indirectly through alterations in the bay environment." They note that a key element of the definition of "perturbation" is what is regarded as the "normal" state. Dependent upon the temporal scale invoked, climatic extremes, such as floods, hurricanes and droughts, can be regarded as variations in the "normal" state rather than perturbations, although such events are certainly disruptive of the ecosystem.

The Galveston Bay National Estuary Program (GBNEP) has devoted considerable attention to perturbations. Shipley (1991) introduced the Galveston Bay ecosystem impact matrix which related 15 sources of perturbation to 17 valued ecosystem components. The ecosystem impact matrix has been modified to produce a perturbation of estuarine habitats matrix (Figure 21).

Listing the sources of perturbations does not identify the specific perturbations associated with each source. It is easy to confuse cause and effect when dealing with perturbations. For example, shoreline erosion leads to a loss of habitat, and some parts of the Galveston Bay shoreline are experiencing severe erosion. But shoreline erosion itself is an effect, rather than a cause. Wind, wave action, and water level are more likely to be the causes of shoreline erosion. Table 5 lists the physical, chemical and biological perturbations that are likely to disturb ecosystem habitats.

The GBNEP Scientific/Technical Advisory Committee attempted to define interactions between perturbations and ecosystem components. The ecosystem impact matrix was expanded by assigning specific perturbations to each source of perturbation category (Table 6). GBNEP S/TAC members were asked to address each matrix cell about which they were knowledgeable by assigning three scores (ranked 1 to 4) to each cell: (1) the influence of the perturbation on the component (slight, moderate, significant, major); (2) the scientific confidence which could be placed in the influence ranking (low, moderate, high, beyond doubt); and (3) the manageability of the perturbation (none, low, moderate, high). The objectives of the exercise were to identify the significant perturbations, evaluate the reliability of the assessment, and distinguish between perturbations which were manageable and those which were not.

Consensus on the significance of the perturbations was not achieved. There were large differences of opinion on all three rankings for most perturbation

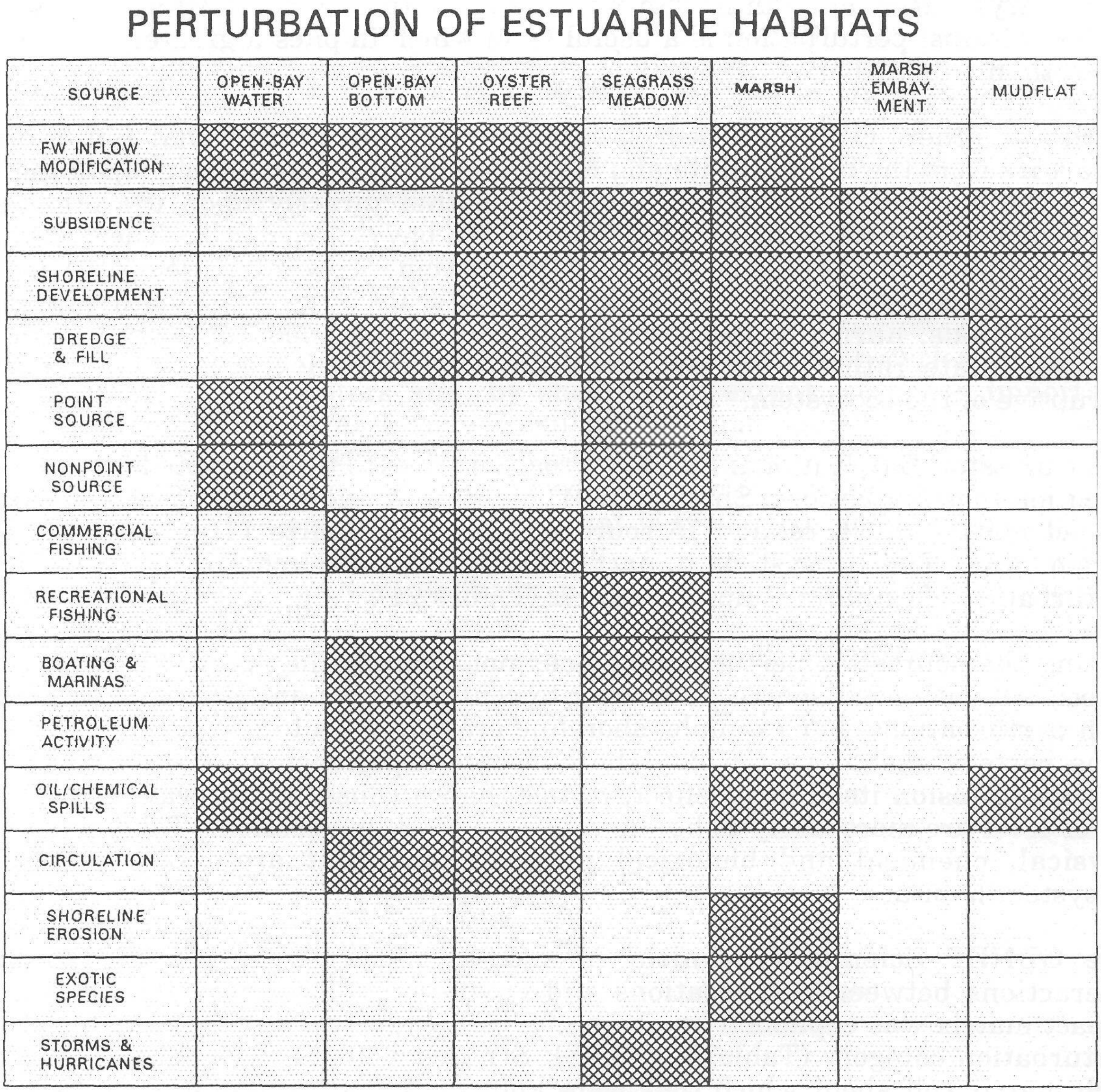


Figure 21. Perturbation of estuarine habitats.

categories. Although information of this nature is potentially the most valuable product of this modeling exercise, it is clear that the scientific and technical community have disparate views regarding the identification and management of perturbations to the ecosystem.

Table 5. Physical, chemical and biological perturbations affecting the estuarine environment.

PHYSICAL PERTURBATIONS	CHEMICAL PERTURBATIONS
Dissolved Oxygen	Contaminants
Dissolved Solids	Nutrients
Drainage Pattern	Organics
Inflow Quantity	Salinity
Marine Debris	Toxicants
Nutrient Transport	
pH	**BIOLOGICAL PERTURBATIONS**
Point of Inflow	Community Structure
Radioactivity	Entrainment
Runoff Speed	Exotic Biota
Runoff Volume	Fouling
Sediment Transport	Habitat Placement
Suspended Sediment	Habitat Structure
Suspended Solids	Impingement
Temperature	Microorganisms
Toxicant Transport	Population Density
Water Depth	Population Structure
Water Clarity	
Water Level	
Wave Action	

Cause and effect can be detailed for each source of perturbation. Figure 22 demonstrates the pathways associated with one source of perturbation - shoreline development. Each type of development produces one or more requirements or actions. For example, an industrial development may require cooling water or a point source discharge of treated or untreated effluent, a navigation channel for ship or barge access, modification of surface water or runoff patterns, the conversion of wetlands, or the construction of bulkheads. These actions result in a number of additional perturbations, or causes, that result in predictable environmental effects. Some of these "effects" in turn become perturbations that ripple through the biotic communities. Techniques such as factor train analysis (Darnell et al., 1976) can be utilized with each source of perturbation. This would produce a minimum of thirteen diagrams for the perturbation sources listed in Table 6.

In summary, designing a simple but technical model that would be useful to bay resource managers and decision-makers has proven to be the most intractable segment of the modeling exercise. A perturbation-based model that would permit bay users to visualize the interconnectedness of specific impacts quickly expands into a myriad of connections that overwhelm, rather than enlighten. Since many perturbations will affect individual species before effects on the habitat can be detected, the habitat approach may not be an effective way to evaluate perturbations.

Table 6. Sources of significant perturbations.

MODIFY FW INFLOW Inflow Quantity Point of Inflow Inflow Seasonality Nutrient Transport Sediment Transport Salinity SUBSIDENCE Water Level DEVELOP SHORELINE Wave Action Nutrient Transport Habitat Placement DREDGE & FILL Suspended Sediment Salinity Water Depth Toxicants Habitat Placement OIL & CHEM. SPILLS Toxicants Fouling STORMS/HURRICANES Wave Action Water Level Salinity Temperature	POINT SOURCES Temperature Water Level Water Clarity Nutrients Toxicants Suspended Solids Dissolved Solids Microorganisms Dissolved Oxygen Salinity pH Radioactivity Impingement Entrainment BOATING & MARINAS Wave Action Nutrients Toxicants Microorganisms Habitat Structure PETROLEUM ACTIVITY Water Depth Salinity Toxicants Habitat Structure	NONPOINT SOURCES Water Level Water Clarity Nutrients Toxicants Suspended Solids Dissolved Solids Organics Dissolved Oxygen pH Salinity Microorganisms COMMERCIAL FISHING Suspended Sediment Toxicants Habitat Structure Population Density Population Structure Community Structure RECREATION FISHING Population Structure Population Density EXOTIC SPECIES Habitat Structure MARINE DEBRIS

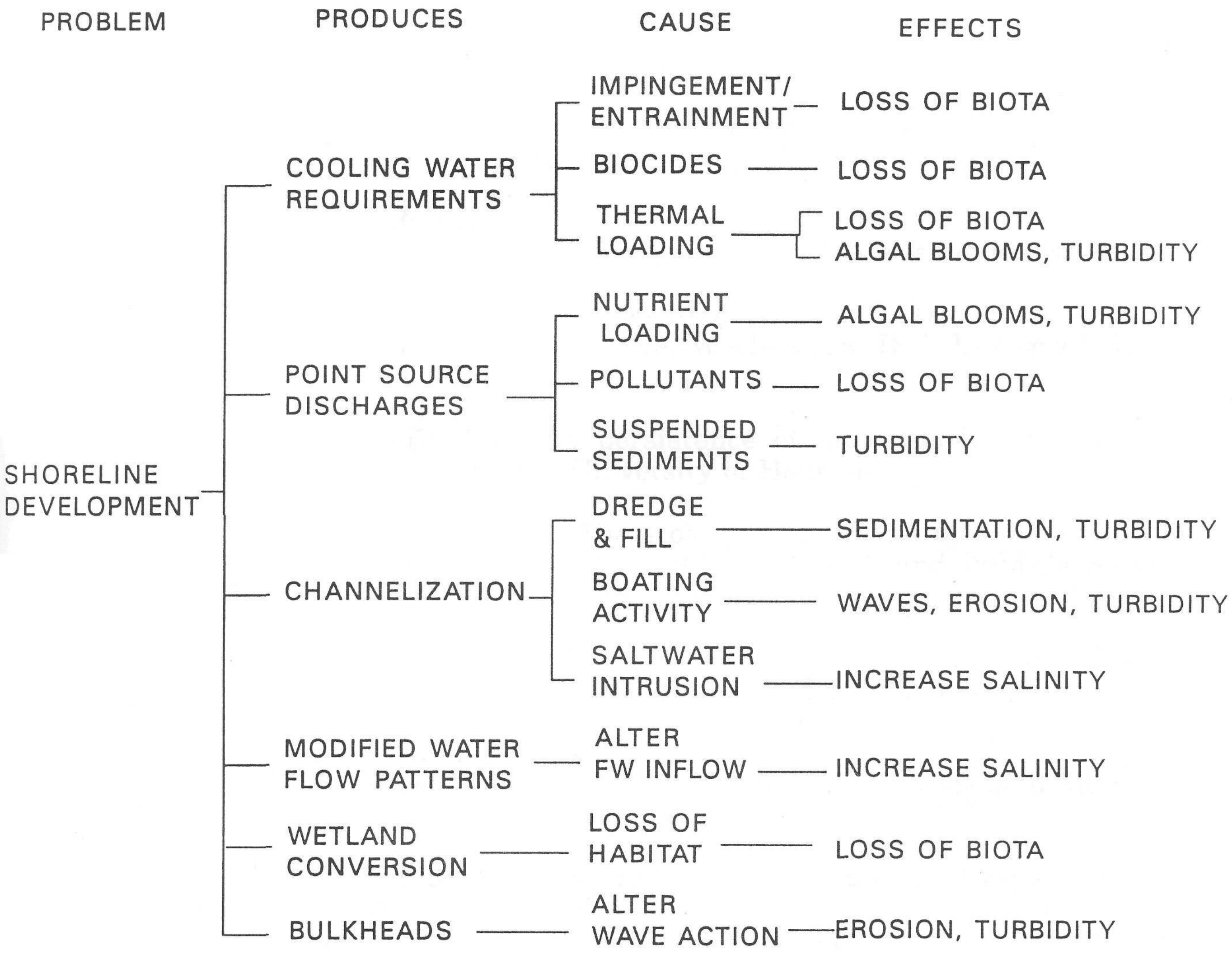


Figure 22. Shoreline development cause and effects. Development results in various actions that produce secondary actions that affect the biota.

REFERENCES

Adams, D.B., 1977. A study of the hydrological and nutrient exchange processes in the Trinity River Delta, Texas. Part II: Marsh habitats and primary production in the Trinity River Delta. Espey, Huston and Assoc. Inc.

Allen, T.F.H., and T.B. Starr, 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, IL. 310 pp.

Ankney, C.D. and C.D. MacInnes. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. Auk 95:459-471.

Armstrong, N.E., 1982. Responses of Texas estuaries to freshwater inflows. p.103-120 *in* Estuarine Comparisons (V.S. Kennedy, ed.), Academic Press, NY.

Armstrong, N.E., 1987. The ecology of open-bay bottoms of Texas: a community profile. U.S. Fish and Wildlife Service, Washington, D.C. Biological Report 85(7.12) 104 pp.

Bagnall, R.A. 1976. Definition and persistence of an estuarine zooplankton assemblage. Ph.D. dissertation, University of Houston.

Bahr, L.M., and W.P. Lanier, 1981. The ecology of intertidal oyster reefs of the South Atlantic coast: a community profile. U.S. Fish and Wildlife Service, Office Biol. Services, Washington, D.C. FWS/OBS-81/15. 105 pp.

Bechtel, T.J. and B.J. Copeland. 1970. Fish species diversity indices as indicators of pollution in Galveston Bay, Texas. Contr. Mar. Sci. 15:103-132.

Bellis, V. 1974. Medium salinity plankton systems. p.358-396 *in* Coastal ecological systems of the United States, Vol. 2 (H.T. Odum, B.J. Copeland, and E.A. McMahan, eds.), Conservation Foundation, Washington, D.C.

Borey, R.B., P.A. Harcombe and F.M. Fisher. 1983. Water and organic carbon fluxes from an irregularly flooded brackish marsh on the upper Texas coast, U.S.A. Estuarine, Coastal and shelf Science 16:379-402.

Burton, G.A., Jr. 1991. Assessing the toxicity of freshwater sediments. Envir. Toxicol. Chem. 10:1593-1627.

Buskey, E., and K. Schmidt. 1992. Characterization of plankton from the Galveston Estuary. p.347-375 *in* Status and Trends of Selected Living Resources in the Galveston Bay system (C. Loeffler and A. Walton, eds.). GBNEP-19.

Cake, E.W. Jr. 1983. Habitat Suitability Index Models: Gulf of Mexico American Oyster. U.S. Dept. Interior Fish and Wildlife Service FWS/OBS-82/10.57. 37pp.

Campbell, P., T. Storck and V. Price. 1992. Trends in Texas commercial fishery landings, 1972-1990. TPWD Management Data Series No. 82.

Christmas, J.Y., J.T. McBee. R.S. Waller, and F.C. Sutter III. 1982. Habitat suitability index models: Gulf menhaden. U.S. Dept. Int. Fish Widl. Serv. FWS/OBS-82/10.23. 23pp.

Clark, D.G., G.L. Ray, and R.J. Bass. 1993. Benthic recovery on experimental dredged material disposal mounds in Galveston Bay, Texas. p.191-197 *in* Proceedings, The Second State of the Bay Symposium, February 4-6, 1993 (R.W. Jensen, R.W. Kiesling and F.S. Shipley, eds.). GBNEP-23.

Conner, J.V. and F.M. Truesdale. 1972. Ecological implications of a freshwater impoundment in a low-salinity marsh. P.259-276 *in* Proceedings, Coastal Marsh and Estuary Management Symposium, La. State Univ. July 17-18, 1972.

Conner, W.H., and J.W. Day, Jr., eds. 1987. The ecology of Barataria Basin, Louisiana: an estuarine profile. U.S. Fish and Wildlife Service, Washington, D.C. Biological Report 85(7.13) 165 pp.

Conte, F.S. 1971. Ecological aspects of selected crustacea of two marsh embayments on the Texas coast. Ph.D. dissertation, 243pp. Texas A&M Univ., College Station.

Conte, F.S. 1972a. The mysidacea of two marsh embayments on the Texas coast. Texas J. Sci. 23(4):597.

Conte, F.S. 1972b. Occurrence of *Taphromysis louisiana* Banner (Crustacea, Mysidacea) in marsh embayments on the Texas coast. Southwestern Naturalist 17(2):203-204.

Corliss, J. and L. Trent. 1971. Comparison of phytoplankton production between natural and altered areas in West Bay, Texas. Fish. Bull. 69(4):829-832.

Cowardin, L.M., V. Carter, F.C. Golet, and E.T. LaRoe, 1979. Classification of wetlands and deepwater habitats of the United States. U.S. Dept. Inter. Fish and Wildl. Serv. FWS/OBS-79/31, 103pp.

Czapla, T.E. 1991. Diets and prey selection of pinfish and southern flounder in a *Halodule wrightii* seagrass meadow. Ph.D. Dissertation, Texas A&M University.

Darnell, R.M., W.E. Pequegnat, B.M. James, F.J. Benson, and R.A. Defenbaugh. 1976. Impacts of construction activities in wetlands of the United States. U.S. Environmental Protection Agency EPA-600/3-76-045.

Dauphin, D.T., A.N. Pettingell, and E.R. Rozenburg. 1989. A birder's checklist of the upper Texas coast. Houston Outdoor Nature Club.

Fisher, W.L., J.H. McGowen, L.F. Brown, Jr., and C.C. Groat, 1972. Environmental geologic atlas of the Texas coastal zone - Galveston-Houston area. Univ. Texas Bur. Econ. Geol. 91pp.

Forman, R.T.T., and M. Godron, 1986. Landscape Ecology. John Wiley and Sons, New York. 619 pp.

Fotheringham, N. and R.A. Bagnall. 1976. Seasonal variation in the occurrence of planktonic larvae of sympatric hermit crabs. J. Exp. Mar. Biol. Ecol. 21:279-287.

Gloyna, E.F., and J.F. Malina, 1964. Galveston Bay water quality study - historical and recent data. Center for Research in Water Resources, Univ. Texas - Austin, 120pp + 9 appendices.

Hall, S.L. and F.M. Fisher, Jr. 1985. Annual productivity and extracellular release of dissolved organic compounds by the epibenthic algal community of a brackish marsh. J. Phycol. 21:277-281.

Harper, D.E., Jr. 1992. Characterization of open bay benthic assemblages of the Galveston estuary and adjacent estuaries from the Sabine River to San Antonio Bay. p.413-450 *in* Status and Trends of Selected Living Resources in the Galveston Bay System (C. Loeffler and A. Walton, eds.). GBNEP-19.

Holt, J. and K. Strawn. 1983. Community structure of macrozooplankton in Trinity and upper Galveston Bays. Estuaries 6(1):66-75.

Holt, S.A. 1976. Temporal and spatial distribution of fishes in the upper Galveston Bay system with particular reference to the cooling waters of Cedar Bayou Generating Station. MS Thesis. Texas and Univ., College Station. 159pp.

Kantrud, H.A. 1991. Widgeongrass (*Ruppia maritima* L.): a literature review. U.S. Fish and Wildl. Serv. Fish and Wildlife Research 10, 58pp.

Kingston, M., ed. 1991. Texas Almanac and State Industrial Guide, 1992-1993. Dallas Morning News. 656pp.

LaSalle, M., R.J. Bass, and G. Ray, 1991. Preliminary character-ization of benthic assemblages of Galveston Bay, Texas: Results from benthic infaunal sampling. p.148-149 *in* Proceedings, Galveston Bay Characterization Workshop (F.S. Shipley and R.W. Kiesling, eds.), GBNEP-6.

Lassuy, D.R. 1983a. Species profiles: life histories and environmental requirements (Gulf of Mexico) -- Gulf menhaden. U.S. Fish and Wildl. Serv. Div. of Biological Sciences, FWS/OBS-82/11.2. 13 pp.

Lassuy, D.R. 1983b. Species profiles: life histories and environmental requirements (Gulf of Mexico) -- brown shrimp. U.S. Fish and Wildl. Serv. Div. Biol. Sci. FWS/OBS-82/11.1 15 pp.

Loeffler, C. 1992. Appendix III.2 Organisms caught by CF monitoring program. p.225-231 *in* Status and trends of selected living resources in the Galveston Bay system (C. Loeffler and A. Walton, eds.), GBNEP-19.

Mann, K.H. and J.R.N. Lazier. 1991. Dynamics of Marine Ecosystems: Biological-Physical Interactions in the Oceans. Blackwell Scientific Publications. 466pp.

McTigue, T.A. and R.J. Zimmerman. 1991. Carnivory vs. herbivory in juvenile *Penaeus setiferus* (Linnaeus) and *Penaeus aztecus* (Ives). J. Exp. Mar. Biol. Ecol. 151:1-16.

Meyer, J.L., 1990. A blackwater perspective on riverine ecosystems. BioScience 40:643-651.

Minello, T.J., and G.A. Matthews. 1981. Variability of zooplankton tows in a shallow ecosystem. Contrib. Mar. Sci. 24:81-92.

Minello, T.J., J.W. Webb, Jr., R.J. Zimmerman, R.B. Wooten, J.L. Martinez, T.J. Baumer, and M.C. Pattilo. 1991. Habitat availability and utilization by benthos and nekton in Hall's Lake and west Galveston Bay. unpublished report, 37pp.

Monaco, M.E., T.E. Czapla, D.M. Nelson, and M.E. Patillo. 1989. Distribution and abundance of fishes and invertebrates in Texas estuaries. ELMR project rpt. NOAA. 107pp.

Muncy, R.J. 1984. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Atlantic) -- white shrimp. U.S. Fish and Wildl. Serv. FWS/OBS-82/11.27 19 pp.

National Research Council (U.S.). 1992. Restoration of aquatic ecosystems - Science, Technology, and Public Policy. 552pp.

Odum, E.P., 1989. Ecology and our endangered life-support systems. Sinauer Associates, 283pp.

Odum, W.E., T.J. Smith III, J.K. Hoover, and C.C. McIvor, 1984. The ecology of tidal freshwater marshes of the United States East Coast: a community profile. U.S. Fish and Wildl. Serv. Wash. D.C. FWS/OBS-83/17. 177 pp.

O'Neill, R.V., D.L. DeAngelis, J.B. Waide, and T.F.H. Allen, 1986. A hierarchical concept of ecosystems. Princeton University Press, Princeton, N.J. 253 pp.

Paine, J.G., and R.A. Morton, 1991. Historical shoreline changes in the Galveston Bay system. p.165-167 *in* Proceedings, Galveston Bay Characterization Workshop (F.S. Shipley and R.W. Kiesling, eds). GBNEP-6.

Parker, J.C. 1965. An annotated checklist of the fishes of the Galveston Bay system, Texas. Publ. Inst. Mar. Sci. Univ. Texas 10:201-220.

Parsons, T.R., M. Takahashi, and B. Hargrave. 1977. Biological Oceanographic Processes. 2nd ed. Pergamon Press.

Peterson, C. H., and N. M. Peterson, 1979. The ecology of intertidal flats of North Carolina: a community profile. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, D.C. FWS/OBS-79/39. 73 pp.

Powell, E.N. 1993a. Status and trends analysis of oyster reef habitat in Galveston Bay. p.207-209 *in* Proceedings, Second State of the Bay Symposium (R.W. Jensen et al., eds.), GBNEP-23.

Powell, E.N. 1993b. Oyster Survey. Report to Galveston Bay National Estuary Program (in press).

Powell, E.N., E.E. Hofmann, J.M. Klinck, and S.M. Ray. *in* press. Modeling oyster populations. I. A commentary on filtration rate. Is faster always better?

Pulich, W.M., and W.A. White. 1989. Decline of submerged vegetation in the Galveston Bay system: chronology and relationships to physical processes. Texas Parks and Wildlife Dept. 27pp.

Pulich, W., Jr., W.A. White, M. Castiglione, and R. J. Zimmerman. 1991. Status of submerged vegetation in the Galveston Bay system. p.127-132 *in* Proc. Galveston Bay Characterization Workshop (F.S. Shipley and R.W. Kiesling, eds.). GBNEP-6.

Quast, W.D., M.A. Johns, D.E. Pitts, Jr., G.C. Matlock, and J.E. Clark. 1988. Texas Oyster Fishery Management Plan, TPWD Fishery Managment Plan Series No. 1.

Ray, G.L., D.G. Clarke and R.J. Bass. 1993. Characterization of benthic assemblages of Galveston Bay: 1990-1992. p.185-190 *in* Proceedings, The Second State of the Bay Symposium, February 4-6, 1993 (R.W. Jensen, R.W. Kiesling and F.S. Shipley, eds.). GBNEP-23.

Reid, G.K., Jr. 1957. Biologic and hydrographic adjustment in a disturbed Gulf coast estuary. Limnology and Oceanography 2:198-212.

Scheiner, S.M., A.J. Hudson, and M.A. VanderMeulen. 1993. An epistemology for ecology. Bull. Ecol. Soc. Amer. 74(1):17-21.

Schomer, N.S., R.D. Drew, and P. Johnson. 1990. Vegetation communities (habitats). p.134-215 *in* An ecological characterization of the Tampa Bay watershed (S.H. Wolfe and R.D. Drew, eds.) U.S. Fish Wildl. Serv. Biol. Rep. 90(20).

Sears, N.E. 1981. Studies on the production and decomposition of *Spartina alterniflora* Loisel in a Galveston salt marsh. MS Thesis, Texas A&M University, College Station.

Sheridan, P.F. 1983. Adundance and distribution of fishes in the Galveston Bay system, 1963-1964. Contrib. Mar. Sci. 26:143-163.

Sheridan, P.F., R.D. Slack, S.M. Ray, L.W. McKinney, E.F. Klima, and T.R. Calnan. 1989. Biological components of Galveston Bay. p. 23-51 *in* Galveston Bay: Issues, Resources, Status, and Management. U.S. Dept. Commerce, NOAA Estuarine Programs Office.

Shipley, F.S. 1991. Characterizing Galveston Bay: connecting science and management at the ecosystem level. Proceedings, Galveston Bay Characterization Workshop, February 21-23, 1991. GBNEP-6.

Stanley, D.W. 1989. Historical trends in water quality and fisheries in Galveston Bay, Texas. Inst. Coastal and Marine Resources, East Carolina Univ.

Stout, J.P., 1984. The ecology of irregularly flooded salt marshes of the northeastern Gulf of Mexico: a community profile. U.S. Fish andd Wild. Serv. Div. of Biological Services. Biological Report 85(7.1) 98 pp.

Taylor, P.J., and A.S. Blum. 1991. Ecosystems as circuits: diagrams and the limits of physical analogies. Biology and Philosophy 6:275-294.

Texas Dept. Water Resources. 1981. Trinity-San Jacinto Estuary: A study of the influence of freshwater inflows. LP-113.

Texas General Land Office, 1976. Texas Coastal Management Program, Report to the Governor and the 65th Legislature, Appendix 2.

Texas Water Commission. 1990. The State of Texas Water Quality Inventory. LP 90-06.652pp.

Turner, R.E., and M.S. Brody. 1983. Habitat suitability index models: northern Gulf of Mexico brown shrimp and white shrimp. U.S. Dept. Int. Fish and Wildl. Serv. FWS/OBS-82/10.54 24 pp.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell, and C.E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130-137.

Ward, G. 1993. Dredge and fill activities in Galveston Bay. GBNEP-28, 286pp.

Ward, G.H., J.M. Wiersema, and N.E. Armstrong. 1982. Matagorda Bay: A Management Plan. National Coastal Ecosystems Team, Fish and Wildlife Service FWS/OB-82/73. 99pp.

Wharton, C.M., W.M. Kitchens, E.C. Pendleton, and T.W. Sipe, 1982. The ecology of bottomland hardwood swamps of the Southeast: a community profile. U.S. Fish and Wildl. Serv. Wash. D.C. FWS/OBS-81/37. 133 pp.

White, W.A., T.R. Calnan, R.A. Morton, R.S. Kimble, T.G. Littleton, J.H. McGowen, H.S. Nance, and K.E. Schmedes. 1985. Submerged lands of Texas, Galveston-Houston area: sediments, geochemistry, benthic macroinvertebrates, and associated wetlands. Bur. Econ. Geol., Univ. Texas.

White, W.A., and J.G. Paine. 1992. Wetland Plant Communities, Galveston Bay System. GBNEP-16, 124pp.

White, W.A., T.A. Tremblay, E.G. Wermund, and L.R. Handley. 1993. Status and trends of wetlands and aquatic habitats, Galveston Bay system, Texas. p.201-205 *in* Proceedings, Second State of the Bay Symposium (R.W. Jensen, R.W. Kiesling, and F.S. Shipley, eds.). GBNEP-23.

Wiegert, R.G. and B.J. Freeman. 1990. Tidal salt marshes of the southeast Atlantic coast: a community profile. U.S. Fish and Wildlife Service Biol. Rep. 85(7.29). 70pp.

Zimmerman, R. 1992a. Marsh Benthos. p.376-412 *in* Status and Trends of Selected Living Resources in the Galveston Bay System (C. Loefller and A. Walton, eds.). GBNEP-19.

Zimmerman, R.J. 1992b. Evaluation of sites for marsh creation in Galveston Bay. unpublished report.

Zimmerman, R., T. Minello, T. Baumer, and M. Castiglione. 1989. Oyster reef as habitat for estuarine macrofauna. NOAA Tech, Mem. NMFS-SEFC-249. 16pp.

Zimmerman, R.J., T.J. Minello, M.C. Castiglione, and D.L. Smith. 1990. Utilization of marsh and associated habitats along a salinity gradient in Galveston Bay. NOAA Tech. Mem. NMFS-SEFC-250, 68pp.

GLOSSARY

abiotic - non-living or physical component.
agroecosystem - an agricultural ecosystem, typically receiving energy and nutrient subsidies from humans.
algae - a diverse group of plants ranging in size from microscopic single cells to large seaweeds.
amphipod - very small crustacean, flattened from side-to-side.
anaerobic - without oxygen.
annelid - segmented worms (as distinguished from nonsegmented roundworms and flatworms).
anthropogenic factor - created by, or the result of, human activity.
assimilative capacity - the limit of a water body to incorporate nutrients or pollutants without degradation of the receiving waters.
autotroph, autotrophic - an organism requiring only simple inorganic molecules to sustain life, or a community containing sufficient photosynthetic organisms to support a food web.
bacteria - single-celled microorganisms which may be autotrophic, saprophytic, or parasitic.
benthic - associated with the bottom of a water body.
benthic algae - algae attached to the bottom, sometimes permanently.
benthos - the community of organisms associated with submerged substrates.
biodeposition - the addition of feces and pseudofeces from suspension feeders to sediments.
biomass - the total mass of living organisms.
biota, biotic - living plants, animals, and microscopic organisms.
bioturbation - the displacement and movement of sediment due to living organisms.
bivalve mollusk - mollusks with a two-piece shell, such as oysters and clams.
blue-green algae - primitive algae whose cells resemble bacteria, lacking a nucleus and other cell structures; they manufacture photosynthetic pigments but lack the specialized organelles, chloroplasts; cyanobacteria.
chaetognath - planktonic marine worm.
chironomid - aquatic larval stage of midge insect.
commensal - a relationship between two organisms where one obtains food, shelter or other benefits from another organism within harming or benefitting the other.
community - the intermingled populations of plants and animals which share a given space, compete for local resources, and consume one another to establish food webs.
congener - closely related members of the same taxonomic genus.
constraint, constraint mechanism - a factor which inhibits or controls some action.
contaminant - a substance released by man's activities (see pollutant).
copepod - small aquatic crustacean prominent in planktonic and benthic communities.
corridor - a narrow strip of land that differs from the matrix on either side.
CPOM - coarse particulate organic matter.

crustacean - joint-legged arthropod with a hard external skeleton; for example, crabs and shrimp.
ctenophore - gelatinous planktonic animal; for example, comb jellies.
culm - the stem of a grass plant.
cyanobacteria - see blue-green algae.
decomposer - an organism which consumes dead biomass.
decomposition - the breakdown of organic matter.
demersal - animals living in the water column but feeding on the bottom; for example, croaker.
deposit feeder - organism which ingests bottom sediments and digests microorganisms and organic matter contained therein.
detrital food web - consumption which begins with dead plant material and its associated decomposing organisms.
detritivore - an organism that derives nutrients and energy by consuming detritus.
detritus - decomposing organic material.
developed site - fuel-powered system, such as urban and industrial sites fabricated by humans.
diatom - nucleated, photosynthetic algal cell with walls of silica; major component of both planktonic and benthic communities.
dissolved material - substance that chemically dissolves into an aquatic medium.
disturbance - an event that causes a significant change from a normal pattern.
diversity - the wide variety of plants and animals in a community.
DOM - dissolved organic matter.
domesticated site - solar-powered system subsidized by human-controlled work energy, such as fossil-fuel-powered machinery, human and animal labor, imported fertilizers, etc.; includes agricultural land, managed woodlands and forests, and artificial lakes and ponds.
ecological niche - the functional role of a species in a community and its specific habitat requirements.
ecosystem - all of the organisms of a given place interacting with the physical environment.
ecotone - a gradient in species distributions along an edge between two distinct habitats.
edaphic factor - related to the soil.
edge - the juncture between two distinct entities.
edge effect - the result of certain species prospering along an edge, as opposed to the interior, of a habitat patch.
edge species - a plant or animal limited or attracted to edges between distinct habitats.
egested material - remnant material returned to the environment following digestion by an organism.
emergent - rooted, aquatic vegetation which stands erect and partially above the water level.
emergent property - one that results from the functional interaction of the component parts.
energy transfer - the interchange of energy-containing molecules between organisms.

environs - that which surrounds.
epifauna - animals living on the surface of the bottom.
epiphytic - growing on, and supported by, a plant.
estuary - a semi-enclosed coastal body of water with salinity intermediate between salt and fresh water.
euhaline - salinities greater than 30 parts per thousand.
euphotic zone - that portion of the water column which receives suffient sunlight to support photosynthesis.
euryhaline - tolerant of a broad range of salinity.
evapotranspiration - the movement of a water molecule from soil to a root, then within the plant to a leaf, where it evaporates to enter the atmosphere.
exotic species - an organism which is not native to an area.
fecal coliform - rod-shaped bacteria which inhabit the colon and are associated with fecal wastes of warm-blooded animals.
feedback loop - linked components of a system, where one affects another, which then either stimulates or inhibits the first.
finfish - vertebrate fish with cartilaginous or bony skeleton and single median or paired lateral fins.
fishable - waters where fewer than 10 percent of dissolved oxygen measurements are less than 3.0 miiligrams per liter, thus capable of supporting fishes.
flocculant - an aggregation of fine suspended particles.
floodplain - the land parallel to a stream or river which is subject to intermittent flooding.
food chain, food web - a biotic pathway for matter and energy transport from primary producer to primary consumer to secondary consumer to top carnivore to decomposer within a community.
FPOM - fine particulate organic matter.
fungus, fungi (pl.) - saprophytic or parasitic lower plants or microorganisms.
gastropod mollusk - mollusk with a one-piece shell, as a snail.
gillraker - a structure on the bony arch of a fish gill that diverts solid substances from the gills; sometimes modified to filter food particles.
grazing food web - consumption which begins with living plants or phytoplankton.
green algae - algal cells with nuclei, and photosynthetic pigments organized in special organelles, the chloroplasts.
groundwater - water flowing in spaces between soil particles.
guild - a group of organisms exploiting a common resource in a similar way.
habitat - a chosen environment of an organism which provides its life requisites.
halophytic - a salt-tolerant plant.
hectare - a metric measure of area, encompassing 10,000 square meters (e.g., a square 100 meters by 100 meters), eguivalent to 2.47 acres.
herbivore - an animal which primarily consumes vegetation or phytoplankton.
heterotroph, heterotrophic - an animal that consumes chemical energy stored in organic molecules made by other organisms; a community which requires the importation of organic matter from elsewhere to support its food web.
hierarchy, hierarchical - a graded series of compartments, each level of which influences activities within adjacent levels.
holoplankton - permanent (all life stages) members of the plankton.

hydrologic cycle - the cycling of water molecules evaporated from the ocean, precipitated on land, and flowing as surface streams or groundwater back to the ocean.
hypersaline - saltier than seawater (35 parts per thousand), the result of evaporation exceeding precipitation and freshwater inflow.
hyphae - extensions of a fungal cellular membrane.
indicator species - a species with wide distribution, sensitivity to changes in the system, and an appropriate life cycle that permits observation of changes in organism density and productivity in association with environmental change.
individual - a single organism.
infauna - animals living immediately beneath the bottom surface.
intertidal - found between the high tide and low tide demarkations, and thus intermittently exposed to the subaerial environment.
invertebrate - animals which lack a spinal column (vertebrae).
isopod - a small crustacean with flattened body.
juvenile - immature individuals of similar appearance as adults.
key species - species important as a conduit of materials and energy throughout the food web; for example, brown and white shrimp, gulf menhaden, bay anchovy.
keystone species - (1) species important as creators of habitat; for example, oysters, seagrasses, smooth cordgrass, etc.; or (2) species which regulate community structure to the extent that disappearance of the keystone species will lead to significant changes in the community or habitat.
laity - the mass of the people as distinguished from those of a particular profession or those specially skilled.
landscape - a heterogeneous land area composed of clustered, interacting ecosystems.
larva, larvae (pl.) - an early life stage of an organism, which may bear little resemblance to the adult stage.
layperson - a person who does not belong to a particular profession or who is not expert in some field.
lentic ecosystem - a system of slow-moving water; for example, a lake.
life cycle - a series of stages in form and functional activity through which an organism passes during its lifetime.
lotic ecosystem - a system of fast-moving water; for example, a stream or river.
macroflora - plants visible to the unaided eye.
macrophyte - a large plant, visible to the unaided eye.
macroplankton - plankton 200 to 2000 micrometers (= 2 millimeters) in size (or greater than 2 millimeters by some authors).
marine - related to the sea.
matrix - the dominant landscape element.
megaplankton - plankton larger than 2 millimeters in size.
meiofauna - animals from 62 to 500 micrometers in size.
meroplankton - temporary member of the plankton, especially (but not restricted to) a larval stage.
mesoplankton - plankton 200 micrometers to 2 millimeters in size.
meter - a metric measure of length, equivalent to 3.28 feet or 39.37 inches.
microbe - a microscopic-size organism.
microfauna - nonphotosynthetic animals smaller than 62 micrometers.
microflora - microbes or plants invisible to the unaided eye.

microplankton - various plankters in the size range 20 to 200 micrometers.
mineralization - the conversion of dead organic matter to inorganic molecules.
mysid - a type of shrimp; crustacean.
nano- or nannoplankton - ultra-small (2 to 20 micrometers) planktonic organisms such as phytoplankton, heterotrophic bacteria and protozoans.
natural site - a solar-powered system dependent on sunlight and indirect forms of solar energy such as wind and rainfall.
nauplius, nauplii (pl.) - a larval stage of many crustaceans.
nearshore gulf - adjacent to the continental shoreline.
nekton - aquatic organism living within the water column and capable of self-directed feeding activity and swimming against a current.
neritic - inhabiting shallow coastal waters.
nonpoint-source contaminant - a contaminant that cannot be traced readily to a specific source, such as fertilizers or pesticides transported as surface runoff from farmlands and developed urban areas.
nursery - a place where young finfishes and shellfishes grow up.
nutrient cycle - the biogeochemical movement and transformation of nutrients from the abiotic environment into the biota, through the food web, and return to the physical environment.
oligohaline - salinities of 0.5 to 5 parts per thousand.
omnivore, omnivorous - an animal that consumes both plant and animal matter.
organic matter - carbon compounds, especially those created by the biota.
organism - an individual plant, animal or microbe.
osmotic stress - stress resulting from a large difference in solute concentration within an organism and its environment.
ostracod - a small crustacean.
oxygen sag - the depletion of oxygen caused by the introduction of oxygen-demanding chemicals or microorganisms into a stream.
oyster reef - the physical structure resulting from aggregated oyster shells adhering to one another.
parasite - an organism living in or on another organism, deriving its nourishment from the host.
patch - a surface area differing in appearance from its surroundings.
pathogen - a microorganism or virus which causes a disease.
pelagic - organisms which live in open waters; not associated with the bottom or the shoreline.
perturbation - a condition or factor which disturbs a system.
pheromone - a chemical substance produced by an animal which stimulates another individual of the same species.
photosynthesis - the creation of chemical compounds with the aid of sunlight.
phytoplankton - photosynthetic members of the plankton.
phytoplanktivore, phytoplanktivorous - animals which consume phytoplankton.
plankter - a single planktonic organism.
plankton - living organisms passively suspended in, and transported by, the water column.
point source contaminant - a contaminant traceable to a specific source, such as a discharge pipe from a factory or sewage treatment plant.
pollutant - a substance that occurs in the environment at least in part as a result of man's activities, and has a deleterious effect on living organisms.

polychaete - segmented worm common in marine benthos.
polyhaline - salinities of 18 to 30 parts per thousand.
POM - particulate organic matter.
population - all of the individuals of a given species within a specified area.
postlarvae - an intermediate life stage in some organisms, between the larval and adult stages.
predator - an animal which consumes other animals as food.
primary consumer - organism that consumes primary producers (green plants, phytoplankton) directly; the second stage of a food chain.
primary producer - an organism capable of capturing the physical energy of sunlight and storing this energy as chemical bonds in organic molecules constructed from carbon dioxide gas; the first stage of a food chain or web.
primary productivity - the creation of organic matter by autotrophic organisms.
productivity - the creation of organic matter by organisms.
propagule - the reproductive product (seed, egg, etc.) of a plant or animal.
protozoan, protozoa (pl.) - small (2 micrometers to 1 millimeter), single-celled, nucleated organisms that lack cell walls; some are photosynthetic.
pseudofeces - material which has been filtered from the mantle cavity of bivalve mollusks but not ingested.
riparian - related to or located on the bank of a watercourse.
river continuum - the concept that river characteristics and biota change in a predictable manner from headwater to terminus.
salinity - the amount of various salts in solution in water.
salinity gradient - a change in salinity, in either a horizontal or vertical direction.
salt pan - an unvegetated or poorly vegetated shoreline zone with high soil salt content due to evaporation of salt water.
SAV - submerged aquatic vegetation.
scavenger - an animal that consumes dead animals.
secondary consumer - an organism that eats primary consumers, rather than primary producers directly.
sediment - matter transported and deposited by water.
sergistid - a type of shrimp (decapod crustacean).
sessile - attached to a hard surface; non-motile.
shellfish - invertebrate organism with hard outer skeleton or shell; for example, crab, shrimp, oyster, clam, snail.
spatial scale - measurements which may differ in various localities.
spawning - the release of eggs and sperm during reproduction.
species (sing. & pl.) - organisms sharing common attributes, potentially capable of interbreeding, and designated by a common name.
standing crop - the total amount of biomass per unit area at a given time.
subaerial - surrounded by air; for example, terrestrial plants and animals.
subaqueous - surrounded by water; for example, aquatic plants and animals.
submerged, submergent - living in and beneath the water.
subtidal - below the low tide demarkation, and thus submerged virtually all of the time.
surface microlayer - the air-water interface, inhabited by a distinct biotic community, the neuston.
surface runoff - the movement of water over a soil surface.

suspended material - substances which do not dissolve in an aquatic medium but are physically suspended within and transported by motion of the water.
suspension feeder - organism which filters suspended particles and plankton from the water column.
sympatric - occupying the same habitat.
temporal scale - measurements which may differ at different points in time.
toxicant - a pollutant that is toxic to living organisms, as distinguished from those that alter the environment without being toxic. Toxic effects depend on exposure and dose.
trophic level - a position in a food chain or web, such as primary producer, primary consumer, secondary consumer, top carnivore.
urban-industrial ecosystem - a fuel-powered system fabricated by humans.
virus - a submicroscopic, nonliving, infective agent.
water column - a mass of water of unspecified dimension extending from the bottom to the surface.
watershed - the area drained by a river or stream and its tributaries.
wetland - land where saturation with water is the dominant factor determining the nature of soil development and the types of plant and animal communities living in the soil and on its surface.
zooplankton - animal members of the plankton.